Countershading is related to positional behavior in primates

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Abstract

Countershading is often thought to be an adaptation for increasing crypsis, yet few quantitative studies have examined this assumption. A recent study showed that large primates display weaker countershading compared with small species, possibly due to a reduced predation risk. In addition to body mass, other factors likely affect countershading intensity. We predicted that if countershading is related to crypsis, then countershading intensity should be negatively related to the frequency of being in a vertical postural position because dorsoventral countershading is most effective when an animal adopts a horizontal position. In addition, countershading intensity may be positively related to group size if individuals are more conspicuous living in large groups or negatively related to group size if countershading further enhances a cryptic life style. We used color-corrected digital photographs of museum skins to quantify the luminance values of the ventral and dorsal surfaces of 113 primate species. We analyzed these data in a multiple regression using phylogenetically independent contrasts. While accounting for body mass, we found a significant negative relationship between the degree of countershading and the frequency of being in a vertical postural position. In contrast, we did not find a strong effect of group size on countershading. Our results suggest that countershading is weak or absent in species of any size that often adopt vertical postural positions because a crypsis benefit is only gained when being horizontal. Finally, the increased conspicuousness of species in large groups does not have a major effect on countershading intensity.

Introduction

Many animals are known to exhibit countershaded bodies (i.e. typically a light ventral and dark dorsal surface); yet, there is substantial variation in the degree of countershading across species (Caro, 2005; Bradley & Mundy, 2008). Countershading is often thought to be an adaptive trait that reduces predation risk from visual predators by increasing crypsis (Thayer, 1896, 1909; Ruxton, Speed & Kelly, 2004; Bortolotti, 2006; Rowland, 2009), although relatively few quantitative studies have tested this hypothesis.

Increasing crypsis by exhibiting a countershaded body may operate in two ways. First, an animal exposed to the sun from above would exhibit a lighter dorsal surface and also produce a self-cast shadow. If an animal exhibits a countershaded body, then the dark dorsal surface would become lighter from the sun, and the lightly colored ventral surface would become darker from the self-cast shadow. The light gradient across the animal's body would be reduced, thereby appearing more two-dimensional when viewed from the side (Kiltie, 1989; Behrens, 2009). This in turn would make the animal more difficult to detect by a visual predator. The other mechanism related to a crypsis benefit of countershading is related to background matching. An arboreal prey animal with a light ventral surface would blend into a bright sky from the perspective of a terrestrial predator below. Alternatively, an animal with a dark dorsal surface would appear less conspicuous to a predator from above because its body would match the dark color of the ground (Ruxton et al., 2004; Rowland, 2009).

Previous research examining the adaptive function of countershading is sparse (Ruxton et al., 2004), with most studies using an experimental approach. For example, Kiltie (1989) demonstrated that countershaded squirrel skins appeared most cryptic when they were exposed to sunlight in a horizontal position. More recently, Rowland et al. (2007, 2008) tested the predation rate of artificial lepidopteran larvae with and without countershading. They found that prey displaying countershaded bodies were less likely to be attacked by birds compared with prey that were uniformly colored. A comparative approach was used by Kamilar (2009) to explain countershading diversity in primates. He found that small primates have more pronounced countershading compared with large ones, and argued that this may be due to small species needing additional anti-predatory adaptations because of increased predation (Cheney & Wrangham, 1987; Cowlishaw, 1997). Interestingly, most marmosets and tamarins (Subfamily: Callitrichinae)

exhibited weak or no countershading. This was unexpected because they are the smallest living monkeys, with most species weighing <1 kg (Fleagle, 1999). Kamilar (2009) hypothesized that their lack of countershading may be due to their frequent adoption of vertical postural positions (Garber, 1992), which would render countershading less effective (Bradley & Mundy, 2008).

Social group size may be an additional factor explaining variation in the degree of countershading across species. The relationship between group size and countershading may operate in two directions. First, species living in large social groups may be more conspicuous to predators (Ebensperger & Blumstein, 2006). This increased predation risk would generate greater selection for the presence of a strongly countershaded body. Alternatively, species living in small groups may require strong countershading because there are fewer individuals available to detect potential predators (van Schaik et al., 1983; Janson, 1992).

We expand on previous studies using a comparative approach to test the idea that positional behavior and group size affect the degree of countershading in primates, independent of body mass. Primates make an excellent system to examine these questions considering their high level of diversity in these characteristics. With particular reference to positional behavior, the majority of primates are arboreal quadrupeds that are usually oriented in a horizontal position, yet several species more commonly adopt vertical postures. This is most often accomplished by either suspending from their appendages below branches or by clinging vertically to tree trunks (Fleagle, 1999).

We predict that the degree of dorsoventral countershading should be (1) negatively related to the degree of vertical postural behavior because countershading is most effective when a mammal is horizontal (e.g. while moving quadrupedally); (2) either positively or negatively related to group size if it makes the prey more conspicuous to predators or reduces predator detection ability, respectively. In addition, we expect to confirm the results of Kamilar (2009), by finding a negative relationship between body mass and countershading intensity using our larger dataset.

Methods

We measured the degree of countershading for 226 female museum skins representing 113 primate species. Only females were used to reduce the possible confounding effects of sexual selection that commonly affects male color patterns (Bradley & Mundy, 2008). We only examined adult specimens that appeared in good condition and were not used in museum exhibits, which would expose the specimen to light for long periods of time.

We used a Canon Rebel XTI camera (Canon Inc., Tokyo, Japan) to obtain photographs. We used established methods to obtain objective color measurements from these photos (Gerald et al., 2001; Stevens et al., 2007; Kamilar, 2009). The camera's color mode was set to 'faithful' (i.e. true color), with the white balance calibrated with an 18% gray card. An X-rite (formerly Greytag-Macbeth) colorchecker card

(X-rite Grand Rapids, MI, USA) 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 a linearized 16-bit TIFF file from the RAW file. The Pictocolor plugin for ADOBE PHOTOSHOP and the colorchecker card were used to color-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 (Fig. 1). We calculated countershading as the difference between the mean luminance values of the ventral and dorsal surfaces. Higher countershading scores indicated stronger countershading.

We obtained data from the published literature for the three independent variables: (1) female body mass; (2) frequency of adopting a vertical posture (low, medium,
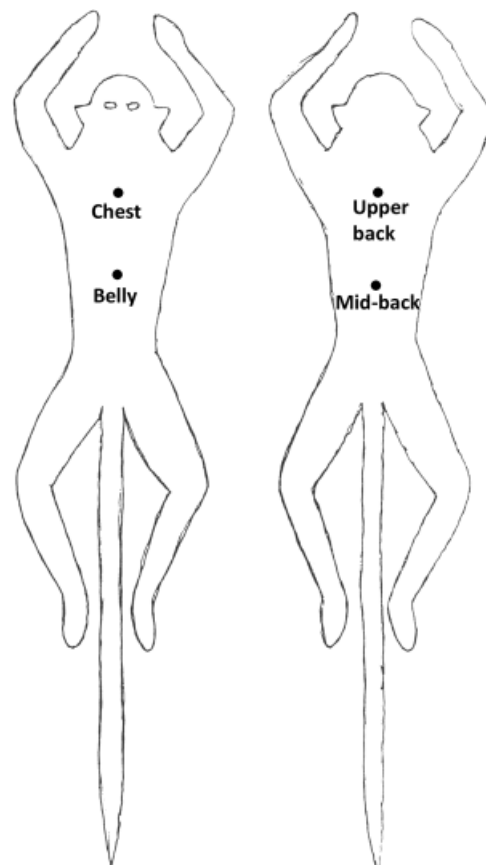

Figure 1 Sampling locations on primate specimens used to calculate countershading values.

high); (3) group size. Body mass data were obtained from Smith & Jungers (1997) and supplemented with additional sources (see supporting information for details). Positional behavior data were derived from descriptions of species behavior (Fleagle, 1999; Campbell *et al.*, 2007). Most primates are quadrupedal, spending most of their time in a relatively horizontal position. Yet, there is inter-specific variation in the positional behavior within the order. Our quantification of positional behavior was defined by the following scheme: generally, species that are rarely found in vertical positions, such as baboons (*Papio*) were scored a zero; species that are known to spend some time in a vertical postural position, such as spider monkeys (*Ateles*) or capuchin monkeys (*Cebus*) were scored a one; and species that are reported to commonly adopt a vertical position to feed or move, such as marmosets (*Callithrix*), gibbons (*Hylobates*) and bushbabies (*Galago*) were scored a two. We did not distinguish between the different types of vertical positional behavior, for example bipedal hopping, brachiating and vertical clinging and leaping. Using this rough measure of positional behavior is not ideal and may decrease our explained variance, yet is necessary because long-term quantitative data are unavailable for most species. All data and data sources may be found in the supporting information .

We conducted a multiple regression to find the best predictors of countershading using phylogenetically independent contrasts (Felsenstein, 1985). Independent contrasts were generated using the primate phylogeny presented in Bininda-Emonds *et al.* (2007) and the PDAP module (Midford, Garland & Maddison, 2007) for Mesquite (Maddison & Maddison, 2007). We used the tree typology from Ossi & Kamilar (2006) for the species in the genus *Eulemur* because several were absent from the Bininda-Emonds *et al.* (2007) primate tree. All branch lengths were set to one, as this best met an important assumption of independent contrasts, the lack of relationship between the absolute values of the contrasts and their branch lengths (Garland Jr, Harvey & Ives, 1992). We scored positional behavior on a scale from zero to two, indicating low, moderate and high frequency of being in vertical postural positions. We treated this measure as a continuous variable in the analyses, following previous comparative studies working with variables that are measured on an interval scale (e.g. extinction risk level) (Purvis *et al.*, 2000; Kamilar & Paciulli, 2008). All variables, except for the frequency of vertical positional behavior, were log transformed before analysis. We examined the residuals of each regression for outliers, which were defined by samples with a studentized residual greater than an absolute value of three and/or a Cook's distance of one or near one (Quinn & Keough, 2002).

Results

We found that the degree of vertical postural position and body mass were independent and significant predictors of the degree of countershading across primates. Small species and species spending more time in a horizontal postural position displayed stronger countershading compared with large species and species that commonly moved and fed in a vertical position (Table 1 and Figs 2 and 3). We did not find outliers in any analysis.

Examples of species that spend a significant amount of time in vertical postural positions and exhibit little countershading include numerous *Saguinus* and *Hylobates* species, and strepsirrhines from the family Indridae such as *Indri indri* and *Propithecus verreauxi* (see supporting information for details). Although most primates without countershading exhibit a relatively dark coat on both the dorsal and ventral surface, some species are brightly colored across their entire torso, for example *P. verreauxi*, *Leontopithecus rosalia* and *Callithrix argenta*.

Small species with strongly countershaded pelages are found in all major primate lineages. These include platyrrhines, such as *Saimiri boliviensis* and *Aotus miconax*, catarrhines like *Cercopithecus wolfi* and *Cercopithecus mona* and strepsirrhines such as *Lemur catta* and *Eulemur rubriventer*. In contrast, relatively large bodied species such as *Alouatta seniculus*, *Cercopithecus neglectus*, *Macaca nigra* and *Trachypithecus francoisi* display weak or no countershading.

We did not find a significant effect of group size on the degree of countershading, yet the direction of the relationship was positive and approached statistical significance at the $P = 0.07$ level (Table 1).

Discussion

To our knowledge, this is the first broad comparative study examining the potential relationship between positional behavior and countershading. We found that countershading intensity is significantly related to positional behavior across primates. In particular, species that spend more time in vertical postural positions, such as vertical clingers (e.g. *Callithrix*, *Saguinus*, *Indri*), brachiators (e.g. *Hylobates*) and suspensory species (e.g. *Ateles*, *Chiropotes*), exhibit weak or no dorsoventral countershading, independent of their body mass and group size.

It is worth noting that countershading was reduced for vertical postures that concealed the ventral surface (clingers) as well as vertical postures that exposed the ventral surface (suspension, brachiating). For example, marmosets and tamarins (as well as some lemuriformes) spend a significant amount of time in vertical postural positions clinging to tree trunks, with their ventral surface not readily observable by potential predators, while gibbons suspend from tree limbs,

Table 1 Results of multiple regression predicting the degree of countershading using phylogenetically independent contrasts

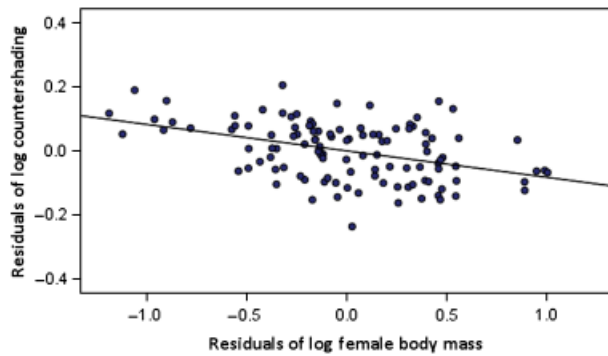| Predictor variable	Standardized β	P value
Female body mass	−0.266	0.004
Degree of vertical positional behavior	−0.283	0.002
Group size	0.162	0.072
Full model results	$r^2 = 0.141$, $P = 0.001$, d.f. $= 3,109$	

Figure 2 The relationship between female body mass and the degree of countershading, independent of positional behavioral and group size. Samples are species values.
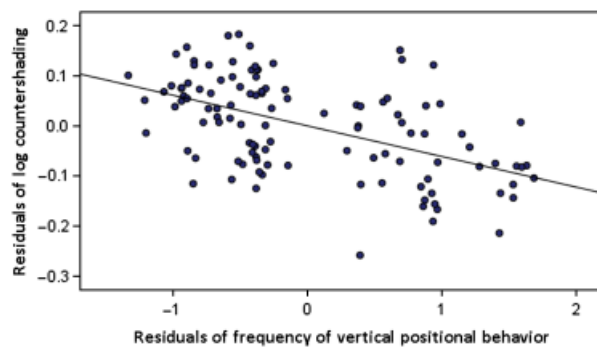

Figure 3 The relationship between positional behavioral and the degree of countershading, independent of female body mass and group size. Samples are species values.

exposing both their dorsal and ventral surfaces to predators. If countershading is due to different selective forces acting on exposed and unexposed body surfaces (Ruxton *et al.*, 2004), we would expect vertical clingers to exhibit levels of countershading similar to arboreal quadrepeds. Thus, our results do not support the proposition that countershading is simply due to different selection pressures acting on the exposed dorsum and unexposed ventrum (Ruxton *et al.*, 2004).

The evolutionary relationship between positional behavior and countershading is emphasized by the fact that primate species showing this pattern are found in distantly related clades, which strongly suggests the independent evolution of these traits. In addition, these primates vary substantially in body size, from the smallest living monkeys, such as the marmosets and tamarins (weighing <0.75 kg) to the largest strepsirrhines, the indri (weighing >6 kg) (Smith & Jungers, 1997). Although small species may gain anti-predator benefits from exhibiting a countershaded pelage, their derived positional behavior renders dorsal–ventral countershading ineffective. Alternatively, one may expect that species commonly in vertical positions may evolve a countershaded pelage that is cranio-caudal in nature, as opposed to the more commonly observed dorso-ventral orientation. Although we did not specifically measure differences in the luminance patterns of the upper

versus lower torso, we did not observe any detectable amount of countershading in a cranio-caudal orientation, except for *Saguinus bicolor*.

Our finding provides further support for the experimental work by Kiltie (1989), showing that dorsoventral light gradients are not reduced when an animal is in a vertical position. Interestingly, Kiltie (1989) noted that the shadow gradient of his squirrel skins was not fully broken when in a horizontal position. While this may be true, we suggest that animals commonly in horizontal postural positions still gain enough of a crypsis benefit to drive the evolution of counter-shading, especially when compared with species that are often in vertical positions.

Predation risk has been theorized to be a strong selective force shaping various biological characteristics in primates, including living in gregarious social groups (Crook & Gartlan, 1966), group structure (Hill & Lee, 1998) and the frequency of vigilance behavior (Cords, 1990; Cowlishaw, 1998). In addition, primates are well-known prey for both terrestrial and arboreal predators (Isbell, 1990; Struhsaker & Leakey, 1990; Wiens & Zitzmann, 1999). Predation risk may also affect pelage color, with primates that are under strong predation risk gaining a crypsis benefit from counter-shading by appearing more two dimensional or by increased background matching from the perspective of both terrestrial and arboreal predators.

Our finding that large primates display less countershad-ing compared with small species confirms Kamilar (2009), yet our current dataset includes nearly twice the sample size. Similar to the previous study, we suggest that this result is likely related to increased levels of predation risk for small species (Cheney & Wrangham, 1987; Cowlishaw, 1997), where displaying more pronounced countershading patterns is an adaptation for increased crypsis (Thayer, 1909; Row-land, 2009).

We found a statistically non-significant but positive group size effect on the degree of countershading across primate species. We hypothesized that group size may be positively or negatively related to the degree of counter-shading, depending on the conspicuousness of species living in large social groups or the reduced predator detection ability of species in small groups. Considering the biological diversity within primates, it is possible that both scenarios are true and these opposing factors essentially render the results of a broad comparative analysis non-significant. More detailed studies at the species level may produce more definitive results.

Another commonly proposed explanation for the presence of countershading is thermoregulation (Hamilton, 1973). Animals may gain thermoregulatory benefits from evolving a dark color on the surface that is most often orientated toward the sun, in the case of most mammals, the dorsal surface. This is unlikely to be a major factor influencing countershading intensity in primates. Kamilar (2009) showed that there was no difference in the countershading intensity of diurnal versus nocturnal primates. In fact, numerous nocturnal strepsirrhines displayed moderate to strongly countershaded pelages. These findings are not

consistent with the thermoregulation hypothesis, considering these species are not exposed to a significant amount of sunlight.

Although our model is statistically significant, the combined effect of our predictor variables did not explain a majority of variation in countershading. The unexplained variation is likely due to several factors. First, we do not explicitly account for within-species variation in any of the traits we examined. Intra-specific variation in body mass (Smith & Jungers, 1997), pelage color (Bradley & Mundy, 2008) and ecology (Kamilar, 2006; Kamilar & Muldoon, 2010) is well documented for many primate species. Not explicitly accounting for this variation likely increases inter-specific unexplained variation, but should not bias our results in any one direction. With regard to color patterns in particular, it is also important to consider that prey coloration is probably related to predator behavior and visual system characteristics (Stevens, Stoddard & Higham, 2009; Tankus & Yeshurun, 2009). For instance, Speed *et al.* (2004) showed that blackbirds attacked countershaded baits less frequently than light, dark or reverse countershaded items. In contrast, blue tits and robins were less discriminating between different colored baits. This may be due to visual system differences between species or inter-specific behavioral variation related to the time spent visually inspecting the bait. Moreover, there are numerous other factors that influence animal coloration, and therefore may affect patterns of countershading, including sexual selection, species recognition and intra-specific communication (Fitze & Richner, 2002; Gerald, 2003; Caro, 2005; Bortolotti, 2006; Setchell, Wickings & Knapp, 2006; Bradley & Mundy, 2008). Finally, the evolutionary history of genetic modifications might influence the extent to which dorsal–ventral countershading is physiologically possible, whether it would be adaptive or not. For example, gibbons have lost the gene coding for agouti signaling protein (Nakayama & Ishida, 2006), which likely plays a key role in this aspect of mammalian pigmentation (Vrieling *et al.*, 1994).

Our finding that both body mass and positional behavior are independently related to countershading diversity does not inform us about the mechanism of countershading at work. Most primates spend the majority of their time moving quadrupedally in trees, with potential predators from below and above. In this case, countershaded pelages may improve background matching with light bellies blending into a bright sky from the perspective of terrestrial predators and a dark dorsum matching a dark ground from the perspective of an arboreal predator. It is also possible that a countershaded pelage produces an optically flat appearance through obliterating the primate's self-cast shadow (Rowland, 2009). This two-dimensional appearance would make an animal more difficult to detect by a visual predator. In this latter scenario, dorsoventral gradation in luminance may also be an important factor to consider. Thayer (1896) and others (e.g. Ruxton *et al.*, 2004) have intimated that the pelage's degree of gradation from dark to light should be similar to the shading produced from the sun. We did not quantify the luminance values on the lateral surface of the pelages. Therefore, we cannot evaluate the degree to which the transition from dark to light is abrupt or gradual. In addition, it is important to note that the relationship between countershading effectiveness and the degree of transition from dark to light color on an animal's body (e.g. being abrupt or gradual) has not been well tested.

Conclusion

Our study supports the idea that inter-specific variation in the degree of countershading is related to positional behavior and to body size, which the latter may be a proxy for predation risk. Our findings suggest that countershading is an important anti-predator adaptation for small species and species that are typically found moving and feeding in a horizontal position. In contrast, species that are adapted for vertical locomotion do not exhibit countershaded coats. This pattern emphasizes the importance of the relationship between the direction of the light source and the animal's body for gaining anti-predator benefits from countershading. Finally, our finding that aspects of coloration can be predicted from positional behavior and body size will aid attempts to reconstruct color and pigment patterns for extinct species. Such species are generally known only from fossilized bones, which leave no indication of coloration but often include anatomical signatures of size and positional or locomotor behavior.

Acknowledgments

References

Behrens, R.R. (2009). Revisiting Abbott Thayer: non-scientific reflections about camouflage in art, war and zoology. *Philos. Trans. Roy. Soc. B* **364**, 497–501.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007). The delayed rise of present-day mammals. *Nature* **446**, 507–512.

Bortolotti, G.R. (2006). Natural selection and avian coloration: protection, concealment, advertisement or deception? In *Bird coloration: Volume 2: Function and evolution*: 3–35.

Hill, G.E. & McGraw, K.J. (Eds). Cambridge: Harvard University Press.

Bradley, B.J. & Mundy, N.I. (2008). The primate palette: the evolution of primate coloration. *Evol. Anthropol.* **17**, 97–111.

Campbell, C., Fuentes, A., MacKinnon, K., Panger, M. & Bearder, S. (Eds). (2007). *Primates in perspective*. Oxford: Oxford University Press.

Caro, T. (2005). The adaptive significance of coloration in mammals. *BioScience* **55**, 125–136.

Cheney, D.L. & Wrangham, R.W. (1987). Predation. In *Primate societies*: 227–239. Smuts, B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T. (Eds). Chicago: University of Chicago Press.

Cords, M. (1990). Vigilance and mixed-species association of some East African forest monkeys. *Behav. Ecol. Sociobiol.* **26**, 297–300.

Cowlishaw, G. (1997). Refuge use and predation risk in a desert baboon population. *Anim. Behav.* **54**, 241–253.

Cowlishaw, G. (1998). The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour* **135**, 431–452.

Crook, J.H. & Gartlan, J. (1966). Evolution of primate societies. *Nature* **210**, 1200–1203.

Ebensperger, L.A. & Blumstein, D.T. (2006). Sociality in New World hystricognath rodents is linked to predators and burrow digging. *Behav. Ecol.* **17**, 410–418.

Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Fitze, P.S. & Richner, H. (2002). Differential effects of a parasite on ornamental structures based on melanins and carotenoids. *Behav. Ecol.* **13**, 401–407.

Fleagle, J.G. (1999). *Primate adaptation and evolution*, 2nd edn. San Diego: Academic Press.

Garber, P.A. (1992). Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichinae. *Am. J. Phys. Anthropol.* **88**, 469–482.

Garland, T. Jr, Harvey, P.H. & Ives, A.R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.

Gerald, M.S. (2003). How color may guide the primate world: possible relationships between sexual selection and sexual dichromatism. In *Sexual selection and reproductive competition in primates: new perspectives and directions*: 141–171. Jones, C.B. (Ed.). Norman: American Society of Primatologists.

Gerald, M.S., Bernstein, J., Hinkson, R. & Fosbury, R.A.E. (2001). Formal method for objective assessment of primate color. *Am. J. Primatol.* **53**, 79–85.

Hamilton, W.J. (1973). *Life's colour code*. London: McGraw-Hill.

Hill, R.A. & Lee, P.C. (1998). Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *J. Zool. (Lond.)* **245**, 447–456.

Isbell, L.A. (1990). Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *Am. J. Primatol.* **21**, 41–52.

Janson, C.H. (1992). Evolutionary ecology of primate social structure. In *Evolutionary ecology and human behavior*: 95–130. Smith, E.A. & Winterhalder, B. (Eds). New York: Aldine de Gruyter.

Kamilar, J.M. (2006). Geographic variation in savanna baboon (*Papio*) ecology and its taxonomic and evolutionary implications. In *Primate biogeography*: 169–200. Lehman, S.M. & Fleagle, J.G. (Eds). New York: Springer Press.

Kamilar, J.M. (2009). Interspecific variation in primate countershading: effects of activity pattern, body mass, and phylogeny. *Int. J. Primatol.* **30**, 877–891.

Kamilar, J.M. & Muldoon, K.M. (2010). The climatic niche diversity of Malagasy primates: a phylogenetic approach. *PLoS One* **5**, e11073, doi:10.1371/journal.pone.0011073.

Kamilar, J.M. & Paciulli, L.M. (2008). Examining the extinction risk of specialized folivores: a comparative study of colobine monkeys. *Am. J. Primatol.* **70**, 1–12.

Kiltie, R.A. (1989). Testing Thayer's countershading hypothesis – an image-processing approach. *Anim. Behav.* **38**, 542–544.

Maddison, W.P. & Maddison, D.R. (2007). Mesquite: a modular system for evolutionary analysis. Version 2.0. Available at http://mesquiteproject.org (accessed 3 March 2010).

Midford, P.E., Garland, T. & Maddison, W.P. (2007). PDAP: PDTREE package for Mesquite, version 1.1. Available at http://mesquiteproject.org/pdap_mesquite/ (accessed 3 March 2010)

Nakayama, K. & Ishida, T. (2006). *Alu*-mediated 100-kb deletion in the primate genome: the loss of the agouti signaling protein gene in the lesser apes. *Genome Res.* **16**, 485–490.

Ossi, K.M. & Kamilar, J.M. (2006). Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates: Lemuridae). *Behav. Ecol. Sociobiol.* **61**, 53–64.

Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000). Predicting extinction risk in declining species. *Proc. Roy. Soc. Lond. Ser. B–Biol. Sci.* **267**, 1947–1952.

Quinn, G. & Keough, M. (2002). *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Rowland, H.M. (2009). From Abbott Thayer to the present day: what have we learned about the function of countershading? *Philos. Trans. Roy. Soc. B* **364**, 519–527.

Rowland, H.M., Cuthill, I.C., Harvey, I.F., Speed, M. & Ruxton, G.D. (2008). Can't tell the caterpillars from the trees: countershading enhances survival in a woodland. *Proc. Roy. Soc. Lond. Ser. B* **275**, 2539–2546.

Rowland, H.M., Speed, M.P., Ruxton, G.D., Edmunds, M., Stevens, M. & Harvey, I.F. (2007). Countershading enhances cryptic protection: an experiment with wild birds and artificial prey. *Anim. Behav.* **74**, 1249–1258.

Ruxton, G.D., Speed, M. & Kelly, D.J. (2004). What, if anything, is the adaptive function of countershading? *Anim. Behav.* **68**, 445–451.

van Schaik, C.P., van Noordwijk, M., Warsono, B. & Sutriono, E. (1983). Party size and early detection of predators in Sumatran forest primates. *Primates* **24**, 211–221.

Setchell, J.M., Wickings, E.J. & Knapp, L.A. (2006). Signal content of red facial coloration in female mandrills (*Mandrillus sphinx*). *Proc. Roy. Soc. B–Biol. Sci.* **273**, 2395–2400.

Smith, R.J. & Jungers, W.L. (1997). Body mass in comparative primatology. *J. Hum. Evol.* **32**, 523–559.

Speed, M.P., Kelly, D.J., Davidson, A.M. & Ruxton, G.D. (2004). Countershading enhances crypsis with some bird species but not others. *Behav. Ecol.* **16**, 327–334.

Stevens, M., Párraga, C.A., Cuthill, I.C., Partridge, J.C. & Troscianko, T.S. (2007). Using digital photography to study animal coloration. *Biol. J. Linn. Soc.* **90**, 211–237.

Stevens, M., Stoddard, M.C. & Higham, J.P. (2009). Studying primate color: towards visual system dependent methods. *Int. J. Primatol.* **30**, 893–917.

Struhsaker, T.T. & Leakey, M. (1990). Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behav. Ecol. Sociobiol.* **26**, 439–443.

Tankus, A. & Yeshurun, Y. (2009). Computer vision, camouflage breaking and countershading. *Philos. Trans. Roy. Soc. B* **364**, 529–536.

Thayer, G.H. (1896). The law which underlies protective coloration. *Auk* **13**, 124–129.

Thayer, G.H. (1909). *Concealing-colouration in the animal kingdom: and exposition of the laws of disguise through colour and pattern: being a summary of Abbot H. Thayer's discoveries*. New York: Macmillan.

Vrieling, H., Duhl, D.M., Millar, S.E., Miller, K.A. & Barsh, G.S. (1994). Differences in dorsal and ventral pigmentation result from regional expression of the mouse agouti gene. *Proc. Natl. Acad. Sci. USA* **91**, 5667–5671.

Wiens, F. & Zitzmann, A. (1999). Predation on a wild slow loris (*Nycticebus coucang*) by a reticulated python (*Python reticulatus*). *Folia Primatol.* **70**, 362–364.

Supporting Information

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

Table S1. Dataset used in the study.

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