

Interspecific Variation in Primate Countershading: Effects of Activity Pattern, Body Mass, and Phylogeny

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Abstract Countershading is defined as an animal displaying a dark dorsal and light ventral surface. This color pattern is found in numerous species, yet there are relatively few quantitative tests that examine its potential adaptive nature. The most frequently employed explanation for countershading is its ability to increase crypsis. I used a comparative approach to test 2 predictions of this hypothesis in primates. First, diurnal species should exhibit stronger countershading versus nocturnal species because light levels are low at night, reducing the benefit of countershading. Second, the degree of countershading should decrease as body mass increases because large animals should have a lower predation risk. I collected data from 171 museum specimens representing 63 primate species. Using digital photography, I quantified the average luminance values on the ventral and dorsal surfaces of each specimen and defined the degree of countershading as the ratio of these values. Nocturnal primates displayed similar levels of countershading compared to diurnal species. Previous studies have shown that some nocturnal primates are more active when moonlight levels are high, suggesting that countershaded pelages may act as an antipredator adaptation. I also found support for a negative relationship between body mass and the degree of countershading using both species values and phylogenetically independent contrasts. There were some exceptions to this pattern, including low levels of countershading for most callitrichine species, which may be due to the vertical positional behavior of many callitrichines, thereby reducing any benefit gained from countershading. In sum, variation in primate countershading is related to body mass and phylogeny, but not to activity pattern.

Keywords color · crypsis · mammal · pelage · positional behavior · predation

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Introduction

Numerous animals from a wide variety of lineages exhibit bodies that have a dark dorsal and a light ventral surface (Bortolotti 2006; Bradley and Mundy 2008; Caro 2005; Kiltie 1988; Miller and Treves 2007; Stoner *et al.* 2003b; Thayer 1909). Although these countershaded color patterns are common, they are far from ubiquitous. There is substantial variation in the degree of countershading across species, even among relatively closely related taxa. Several adaptive explanations have been proposed to account for this variation, including crypsis, protection from ultraviolet radiation, and assisting in thermoregulation (Burt 1981; Hamilton 1973; Rowland 2009; Ruxton *et al.* 2004; Thayer 1896), but rigorous tests of these hypotheses are relatively rare.

Most commonly, countershading is thought to be an adaptive trait that increases crypsis, thereby reducing predation risk from visual predators (Kiltie 1989; Rowland 2009; Rowland *et al.* 2008; Thayer 1909). Two main mechanisms are posited for the increased crypsis resulting from countershading; both rely on the idea that the animal is exposed to a light source, e.g., the sun, from above. First, countershading may make an animal appear 2-dimensional from the side by counteracting the normal shading patterns created when an animal is exposed to light from above, with a shadow cast below it (Kiltie 1989). If an animal has a dark dorsal surface, this surface would lighten under bright conditions. In addition, the light colored ventral surface would darken because of a self-cast shadow. The 2 surfaces would converge on a similar degree of luminance, making the animal's color appear more uniform. Because 3-dimensional objects have a strong gradient of shading from top to bottom, increasing shade from top to bottom (Behrens 2009), the reduction or loss of this gradient due to countershading would make the animal appear 2-dimensional when viewed from the side and therefore more difficult to detect by visual predators. The second means by which countershading may act as an antipredator strategy is related to background matching (Rowland *et al.* 2008). Arboreal primates with a bright ventral surface would appear to blend into a bright sky or canopy when viewed by predators from below. Predators from above would observe the dark dorsal surface of the primate against a relatively dark ground below.

Although Thayer (1896) hypothesized that countershading evolved as an antipredator trait more than 100 years ago, there have been relatively few systematic tests supporting this view. In an experimental study, Kiltie (1989) found that horizontally positioned gray squirrel skins with countershaded pelages displayed a reduced shade gradient when exposed to sunlight. This would reduce the 3-dimensional appearance of the squirrel compared to an animal without countershading. In a broad comparative study of artiodactyls, Stoner *et al.* (2003b) found that countershaded bovids were diurnal and lived in desert habitats where bright skies and good visibility are common. In contrast, a companion paper investigating a wide range of lagomorph species found little support for countershading as an adaptation for crypsis (Stoner *et al.* 2003a). More recently, an elegant experiment found that artificial prey resembling larvae varied in the susceptibility to predation in relation to their color patterns (Rowland *et al.* 2008). Countershaded prey avoided predation more effectively than prey that were uniformly shaded or those that displayed a dark ventral surface.

Here I build on previous investigations by utilizing a comparative approach to examine the possible function of countershading as an adaptation for decreasing predation risk in primates. I tested the following predictions: 1) Countershading should be weak in nocturnal primates because light levels are low when they are most active; consequently there would be little benefit gained from having a countershaded pelage (Bradley and Mundy 2008). 2) The degree of countershading should decrease as body mass increases because large-bodied individuals should experience lower levels of predation risk versus small ones (Cheney and Wrangham 1987; Cowlshaw 1997; Stanford 2002; *cf.* Zuberbuhler and Jenny 2002). Primates make an excellent study system to examine the potential antipredator function of countershading because they exhibit substantial interspecific variation in their degree of pelage countershading, body mass, and activity period (Bradley and Mundy 2008; Fleagle 1999).

Methods

Data Collection

I collected data on 171 adult female museum specimens representing 63 species. This included 21 strepsirrhines and tarsiers, 20 platyrrhines, and 22 catarrhines (Table 1). I included ≥ 2 specimens for each species. I included only female specimens in the study because female pelage coloration is less likely to be influenced by sexual selection than males (Bradley and Mundy 2008). I did not include specimens that displayed significant damage and/or wear. Similarly, I did not include specimens that were stuffed and posed in naturalistic positions and had obviously been on display in the past. All specimens were housed at the Field Museum and the American Museum of Natural History. It is important to note that I did not systematically account for differences in pelage preservation method. This would likely add some degree of error to the data set, thereby increasing type II error rates in the analyses.

I quantified color patterns using digital photography and digital imaging software. I photographed all specimens from several perspectives, e.g., dorsal, ventral, lateral, via a Canon Rebel XTI digital camera with the following settings: 1) no flash, 2) images stored in RAW format, 3) faithful color setting, and 4) custom white balance. I subsequently set the camera's white balance using an 18% gray card. I employed these settings to reduce the amount of color processing from the camera. In addition, I placed an Xrite Colorchecker card near each specimen so both appear in each image. I subsequently converted RAW files to 16-bit TIFF files with the Canon Digital Professional Photo software package. I then used the Pictocolor plugin for Adobe Photoshop to standardize each image based on the known color values contained in the Colorchecker card. I resaved the color standardized images as TIFF files and used these images for measuring luminance, i.e., brightness, values.

I used Adobe Photoshop to obtain luminance values for 2 locations on both the ventral and dorsal surface of the specimen's torso. On the dorsal surface, I 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.

Table 1 Data used in this study

Genus	Species	Taxonomic group	Activity pattern	Female body mass (kg)	Countershading value	No. of specimens
<i>Cercocebus</i>	<i>torquatus</i>	Catarrhine	Diurnal	5.50	1.22	2
<i>Cercopithecus</i>	<i>Ascanius</i>	Catarrhine	Diurnal	2.92	2.87	3
<i>Cercopithecus</i>	<i>mitis</i>	Catarrhine	Diurnal	3.93	1.69	5
<i>Cercopithecus</i>	<i>neglectus</i>	Catarrhine	Diurnal	3.55	0.95	2
<i>Cercopithecus</i>	<i>pogonias</i>	Catarrhine	Diurnal	2.90	1.85	2
<i>Cercopithecus</i>	<i>preussi</i>	Catarrhine	Diurnal	4.50	1.09	2
<i>Cercopithecus</i>	<i>wolffi</i>	Catarrhine	Diurnal	2.87	3.64	4
<i>Chlorocebus</i>	<i>aethiops</i>	Catarrhine	Diurnal	2.98	2.09	6
<i>Colobus</i>	<i>angolensis</i>	Catarrhine	Diurnal	7.57	0.97	2
<i>Colobus</i>	<i>guereza</i>	Catarrhine	Diurnal	9.20	1.04	2
<i>Hylobates</i>	<i>concolor</i>	Catarrhine	Diurnal	7.62	1.02	2
<i>Hylobates</i>	<i>klossi</i>	Catarrhine	Diurnal	5.92	0.98	2
<i>Hylobates</i>	<i>lar</i>	Catarrhine	Diurnal	5.34	0.86	2
<i>Hylobates</i>	<i>muelleri</i>	Catarrhine	Diurnal	5.35	0.85	2
<i>Lophocebus</i>	<i>albigena</i>	Catarrhine	Diurnal	6.02	1.28	3
<i>Macaca</i>	<i>assamensis</i>	Catarrhine	Diurnal	6.90	1.69	3
<i>Macaca</i>	<i>fascicularis</i>	Catarrhine	Diurnal	3.59	2.13	2
<i>Papio</i>	<i>anubis</i>	Catarrhine	Diurnal	13.3	1.09	2
<i>Procolobus</i>	<i>badius</i>	Catarrhine	Diurnal	7.21	2.18	2
<i>Semnopithecus</i>	<i>entellus</i>	Catarrhine	Diurnal	6.91	1.73	2
<i>Trachypithecus</i>	<i>cristata</i>	Catarrhine	Diurnal	7.35	1.61	3
<i>Trachypithecus</i>	<i>phayrei</i>	Catarrhine	Diurnal	6.30	1.08	3
<i>Alouatta</i>	<i>palliata</i>	Platyrrhine	Diurnal	5.35	1.31	2
<i>Alouatta</i>	<i>seniculus</i>	Platyrrhine	Diurnal	5.21	0.97	3
<i>Aotus</i>	<i>infulatus</i>	Platyrrhine	Nocturnal	1.24	2.31	2
<i>Aotus</i>	<i>lemurinus</i>	Platyrrhine	Nocturnal	0.87	2.65	3
<i>Callicebus</i>	<i>cupreus</i>	Platyrrhine	Diurnal	1.12	1.40	3
<i>Callithrix</i>	<i>argentata</i>	Platyrrhine	Diurnal	0.36	0.99	2
<i>Callithrix</i>	<i>humeralifer</i>	Platyrrhine	Diurnal	0.38	1.92	2
<i>Callithrix</i>	<i>jacchus</i>	Platyrrhine	Diurnal	0.38	1.01	4
<i>Cebus</i>	<i>albifrons</i>	Platyrrhine	Diurnal	2.29	1.66	2
<i>Cebus</i>	<i>apella</i>	Platyrrhine	Diurnal	2.52	1.90	3
<i>Chiropotes</i>	<i>satanas</i>	Platyrrhine	Diurnal	2.58	0.67	2
<i>Lagothrix</i>	<i>lagotricha</i>	Platyrrhine	Diurnal	7.16	1.02	3
<i>Pithecia</i>	<i>pithecia</i>	Platyrrhine	Diurnal	1.58	1.28	2
<i>Saguinus</i>	<i>fuscicollis</i>	Platyrrhine	Diurnal	0.36	1.15	4
<i>Saguinus</i>	<i>midas</i>	Platyrrhine	Diurnal	0.58	0.82	3
<i>Saguinus</i>	<i>mystax</i>	Platyrrhine	Diurnal	0.54	0.90	4
<i>Saguinus</i>	<i>nigricollis</i>	Platyrrhine	Diurnal	0.48	1.03	3
<i>Saguinus</i>	<i>oedipus</i>	Platyrrhine	Diurnal	0.40	2.06	6
<i>Saimiri</i>	<i>boliviensis</i>	Platyrrhine	Diurnal	0.71	3.79	2

Table 1 (continued)

Genus	Species	Taxonomic group	Activity pattern	Female body mass (kg)	Countershading value	No. of specimens
<i>Saimiri</i>	<i>sciureus</i>	Platyrrhine	Diurnal	0.66	2.40	4
<i>Avahi</i>	<i>laniger</i>	Strep + tarsier	Nocturnal	1.32	1.50	2
<i>Cheirogaleus</i>	<i>major</i>	Strep + tarsier	Nocturnal	0.36	1.70	2
<i>Cheirogaleus</i>	<i>medius</i>	Strep + tarsier	Nocturnal	0.23	2.52	2
<i>Eulemur</i>	<i>coronatus</i>	Strep + tarsier	Cathemeral	1.35	2.04	2
<i>Eulemur</i>	<i>fulvus</i>	Strep + tarsier	Cathemeral	2.15	1.73	2
<i>Eulemur</i>	<i>rufus</i>	Strep + tarsier	Cathemeral	2.25	1.63	3
<i>Eulemur</i>	<i>sanfordi</i>	Strep + tarsier	Cathemeral	1.83	1.99	3
<i>Eulemur</i>	<i>macacao</i>	Strep + tarsier	Cathemeral	2.13	1.74	2
<i>Eulemur</i>	<i>rubriventer</i>	Strep + tarsier	Cathemeral	1.94	2.48	2
<i>Euoticus</i>	<i>elegantulus</i>	Strep + tarsier	Nocturnal	0.26	1.66	2
<i>Galago</i>	<i>alleni</i>	Strep + tarsier	Nocturnal	0.27	1.79	2
<i>Galago</i>	<i>moholi</i>	Strep + tarsier	Nocturnal	0.17	1.79	4
<i>Galago</i>	<i>senegalensis</i>	Strep + tarsier	Nocturnal	0.20	1.69	5
<i>Galagoides</i>	<i>demidovii</i>	Strep + tarsier	Nocturnal	0.06	1.85	2
<i>Lepilemur</i>	<i>mustelinus</i>	Strep + tarsier	Nocturnal	0.78	1.83	2
<i>Microcebus</i>	<i>murinus</i>	Strep + tarsier	Nocturnal	0.09	1.87	2
<i>Nycticebus</i>	<i>coucang</i>	Strep + tarsier	Nocturnal	0.63	1.89	4
<i>Otolemur</i>	<i>crassicaudatus</i>	Strep + tarsier	Nocturnal	1.11	1.49	4
<i>Perodicticus</i>	<i>potto</i>	Strep + tarsier	Nocturnal	1.21	1.61	3
<i>Tarsius</i>	<i>syrichta</i>	Strep + tarsier	Nocturnal	0.12	1.25	2
<i>Varecia</i>	<i>variegata</i>	Strep + tarsier	Diurnal	3.52	0.32	2

I 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. I also recorded the luminance values at analogous locations from the ventral surface.

I defined countershading as the mean luminance value of the ventral surface divided by the mean luminance value of the dorsal surface. Countershading values approaching 1 indicate that the luminance scores of the ventral and dorsal surfaces are similar, and therefore countershading is weak or absent. High countershading values indicate a greater difference in the luminance scores of the ventral and dorsal surfaces, with the ventral surface being brighter than the dorsal surface.

For each species, I obtained body mass data from Smith and Jungers (1997) and activity pattern data from the literature (Campbell *et al.* 2007; Fleage 1999). I categorized activity pattern as diurnal or nocturnal. I did not include cathemeral species ($n=6$) in analyses focused on activity pattern and countershading.

Data Analyses

I conducted all analyses using both species values and phylogenetically independent contrasts (PIC; Felsenstein 1985). Interspecific analyses have benefitted from

modern comparative methods, which account for the non-independence of data, due to shared evolutionary history (Felsenstein 1985; Harvey and Pagel 1991; Nunn and Barton 2001). I conducted independent contrast analyses with the PDAP module for Mesquite (Maddison and Maddison 2007; Midford *et al.* 2007). For these analyses, I obtained a recent primate phylogeny that was published as part of the mammal supertree in Bininda-Emonds *et al.* (2007). Some *Eulemur* spp. were not included in the Bininda-Emonds *et al.* (2007) phylogeny, therefore, I used the tree typology presented in Ossi and Kamilar (2006) for the species in this genus. I set all branch lengths equal to 1, as this method best met the assumptions of PIC analyses (Garland *et al.* 1992; Nunn and Barton 2001).

I used a Mann-Whitney *U* test with species values to examine the difference in countershading between nocturnal and diurnal primates. To examine activity pattern and countershading using PIC, I used a linear regression treating activity pattern as an ordinal, independent variable. I coded nocturnal primates as 0 and diurnal primates as 1. Treating activity pattern this way is analogous to using IUCN category, e.g., 5 categories of progressively greater extinction risk, as an ordinal variable in broad comparative studies of extinction risk (Cardillo *et al.* 2008; Kamilar and Paciulli 2008; Purvis *et al.* 2000).

I employed linear regressions to investigate the relationship between body mass and countershading using both species values and PIC. I examined this relationship using 1) all primates, 2) strepsirrhines and tarsiers only, 3) platyrrhines only, and 4) catarrhines only. This may provide important insights considering the ecological and evolutionary differences among major primate groups. I examined strepsirrhines and tarsiers together because although tarsiers have a closer phylogenetic affinity with monkeys and apes than they do with the strepsirrhines (Ross 2000), they share many biological traits with lemurs and lorises that are particularly relevant for their risk of predation: they are small, nocturnal, and live in dispersed social networks (Gursky 2002). Using this taxonomic arrangement did not produce qualitatively different results compared to analyses grouping tarsiers with monkeys and apes.

Following previous studies, I included a 0-intercept in regressions using PIC (Nunn and Barton 2001). I examined all analyses for outliers, defined as samples with a studentized residual >3.0 or <-3.0 , and/or a Cook's distance value near or 1.0 (Quinn and Keough 2002). If outliers were present, I reanalyzed the data without the outlier. In addition, I \log_{10} transformed all body mass and countershading values before analysis. I conducted the Mann-Whitney and regression analyses using Statistica 6.0.

Results

As predicted, I found that primates vary widely in their degree of countershading. Several species exhibit little or no countershading, with countershading values of *ca.* 1.0 (Table 1). These taxa include all the gibbon species, several callitrichids including silvery marmosets (*Callithrix argentata*), common marmosets (*Callithrix jacchus*), black-mantled tamarins (*Saguinus nigricollis*), and moustached tamarins (*Saguinus mystax*), as well as both *Colobus* species, olive baboons (*Papio hamadryas anubis*) and red howlers (*Alouatta seniculus*). The majority of species display some degree of countershading, with their ventral surface $\geq 20\%$ brighter

than their dorsal. In addition, 13 of the 63 species displayed high levels of countershading with their ventral surface more than twice the brightness of their dorsal surface. Species with some of the highest levels of countershading include Wolf's guenons (*Cercopithecus wolfi*), redbtail monkeys (*Cercopithecus ascanius*), Bolivian squirrel monkeys (*Saimiri boliviensis*), gray-bellied night monkeys (*Aotus lemurinus*), and lesser dwarf lemurs (*Cheirogaleus medius*). Finally, a single species, ruffed lemurs (*Varecia variegata*), displayed a pelage with a much darker ventral surface versus the dorsal surface.

There is a statistically significant difference in the degree of countershading between nocturnal and diurnal primates using species values, but in the opposite direction predicted: nocturnal primates exhibited higher levels of countershading (Fig. 1, Mann-Whitney U test: $Z=2.63$, $p=0.009$, $n=41$ diurnal species and $n=16$ nocturnal species). After examining the boxplots, 1 species, *Varecia variegata*, appeared to be an outlier. After removing it from the analysis, the results were nearly identical (Mann-Whitney U test: $Z=2.54$, $p=0.011$, $n=40$ diurnal species and $n=16$ nocturnal species). The initial regression between activity pattern and countershading using PIC generated similar results, with diurnal species exhibiting lower levels of countershading versus nocturnal taxa ($r^2=0.109$, $\beta=-0.330$, $p=0.012$, $df=55$). However, removing the outlier contrast (*Cercopithecus neglectus* vs. *C. pogonias* + *C. wolfi* vs. *C. mitis* + *C. ascanius*) from the data set yielded a nonsignificant relationship.

The predicted negative relationship between body mass and the degree of countershading was supported, especially when phylogeny was taken into account and outliers were removed (Tables II and III; Fig. 2a–e). Using species values and the total primate data set, the degree of countershading declined as body mass increased (with and without the outlier species *Varecia variegata*). Accounting for phylogeny revealed a stronger relationship ($p=0.014$ and $p=0.005$ with the outlier contrasts *Eulemur coronatus* vs. *E. fulvus* + *E. rufus* and *Tarsius syrichta* vs. Catarrhini + Platyrrhini removed).

There is some variation in the results when I examined the major primate lineages separately. There was no relationship between body mass and countershading when using species values for strepsirrhines and tarsiers, particularly when the outlier

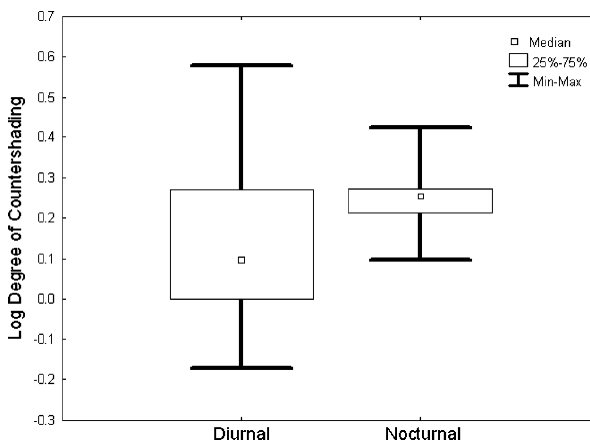


Fig. 1 Boxplots of log countershading values without the outlier species, *Varecia variegata*.

Table II Results of regression analyses examining the relationship between body mass and the degree of countershading in primates using species values

Data set	r^2	β	df	p
All primates	0.065	-0.254	61	0.045
All primates*	0.060	-0.247	60	0.054
All primates ^a	0.143	-0.379	53	0.004
All primates ^{a,*}	0.161	-0.401	52	0.002
Strepsirrhines and tarsiers	0.077	-0.277	19	0.224
Strepsirrhines and tarsiers*	0.007	0.086	18	0.718
Platyrrhines	0.020	-0.142	18	0.552
Platyrrhines ^a	0.546	-0.739	10	0.006
Catarrhines	0.282	-0.531	20	0.011

*Asterisk indicates regression results with outliers removed.

^aData set without species from the Callitrichinae subfamily.

Bold font highlights $p < 0.05$.

Varecia variegata was removed from the analysis. Phylogenetic analyses of strepsirrhines and tarsiers produced somewhat different results. Using independent contrasts, p values were substantially lower. The p value was 0.079 when I used all data and 0.041 when I removed the outlier contrast *Varecia variegata* vs. *Eulemur*.

There is no relationship between body mass and countershading for all platyrrhines using species values (Table II) or independent contrasts (Table III). Species from the Callitrichinae subfamily exhibited unusually low levels of countershading for their body size (Fig. 2b, c). Removing these species from the analyses using the platyrrhine-only data set produced a significant relationship

Table III Results of regression analyses examining the relationship between body mass and the degree of countershading in primates using phylogenetically independent contrasts

Data set	r^2	β	Df	p
All primates	0.095	-0.308	61	0.014
All primates*	0.124	-0.353	59	0.005
All primates ^a	0.127	-0.356	53	0.008
All primates ^{a,*}	0.196	-0.443	51	<0.001
Strepsirrhines and tarsiers	0.154	-0.392	19	0.079
Strepsirrhines and tarsiers*	0.211	-0.460	18	0.041
Platyrrhines	0.093	-0.305	18	0.191
Platyrrhines ^a	0.422	-0.650	10	0.022
Platyrrhines ^{a,*}	0.590	-0.768	9	0.006
Catarrhines	0.148	-0.385	20	0.077

*Asterisk indicates regression results with outliers removed.

^aData set without species from the Callitrichinae subfamily.

Bold font highlights $p < 0.05$.

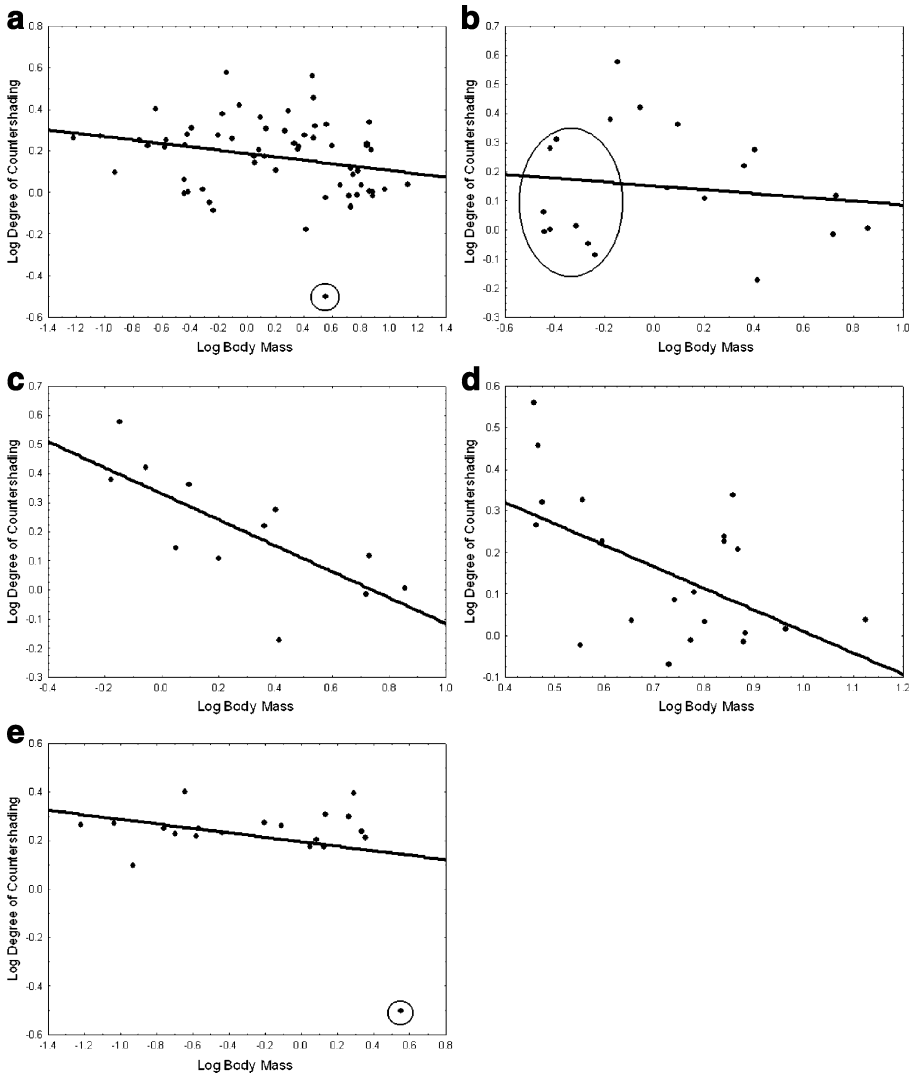


Fig. 2 Plots of the relationship between body mass and the degree of countershading using species values. **(a)** All primates; the highlighted sample is the outlier species, *Varecia variegata*. **(b)** All platyrrhines; the highlighted samples are callitrichine species. **(c)** Platyrrhines without callitrichine species. **(d)** All catarrhines. **(e)** All strepsirrhines and tarsiers; the highlighted sample is the outlier species, *Varecia variegata*.

between body mass and countershading using species values (Table II) and independent contrasts (Table III). Similarly, a reanalysis of the total primate data set produced a better fit when I removed the callitrichines (Tables II and III).

Finally, catarrhines exhibited a similar pattern to the other data sets, with the degree of countershading decreasing as body mass increased. However, the analysis using species values produced a better fit ($p=0.011$; Table II) versus using independent contrasts data ($p=0.077$) (Table III).

Discussion

Primates of all sizes and activity patterns are known prey for a wide variety of visual predators, including eagles, hawks, carnivorous mammals, and snakes (Chapman 1986; Fay *et al.* 1995; Karpanty 2003; Miller and Treves 2007; Terborgh 1983; Zuberbuhler and Jenny 2002). Several authors have argued that predation risk is a primary factor driving the evolution of group living in primates and other mammals (Janson 1992; Jarman 1974; van Schaik 1983; van Schaik and van Hooff 1983; Wrangham and Cheney 1985). Based on the comparative analyses presented in this current study, I suggest that predation risk also plays an important role for the evolution of primate color patterns. After examining 63 primate species I found that the degree of countershading declines as body mass increases. Nocturnal species display more extreme countershading compared to diurnal species, though this effect disappears once phylogeny and an outlier are taken into account. Nonetheless, nocturnal primates display at least as much countershading as diurnal species, suggesting that they also gain an antipredator benefit. In addition, these results demonstrate the importance of using quantitative approaches to measure pelage color characteristics, which allow for rigorous statistical analyses. Most traditional studies of pelage color patterns use qualitative descriptions to define countershading as simply present or absent. Quantitatively measuring luminance values allows more accurate descriptions of the degree of countershading across numerous species, capturing detailed interspecific variation.

Unfortunately, it is not possible to examine the independent effects of body mass and activity pattern on countershading using the current data set because of the close relationship between activity pattern and body mass: strepsirrhines and tarsiers are generally small and nocturnal, whereas monkeys and apes are medium, large, and diurnal. This may be remedied in the future by expanding the data set to include a greater number of diurnal lemurs.

Activity Pattern and Countershading

Bradley and Mundy (2008) logically predicted that nocturnal primates would display little countershading due to the fact that they are most active at night, when light levels are low. Under this scenario, primates exhibiting countershaded pelages would gain little benefit from crypsis. My analyses do not support this prediction. Nocturnal primates display similar or greater levels of countershading versus diurnal species. This may be partly due to the overall relationship between body mass and countershading because all nocturnal primates are small bodied. However, the fact that small nocturnal primates exhibit pelage countershading suggests that these species are gaining some antipredator benefit or that some other factor is driving the color pattern.

Although nocturnal primates are most active when light levels are relatively low compared to daytime light levels, many nocturnal primates vary their activity levels according to variation in moonlight (Bearder *et al.* 2006; Nash 2007). In a review of the behavioral responses of primates to moonlight, Nash (2007) found that most primates increase activity levels, e.g., traveling, foraging, feeding, when moonlight levels are high. This is opposite to the pattern that occurs in most mammals, and may

be related to primates being able to detect predators more effectively when nighttime light levels are high (Allman 1977; Bearder *et al.* 2006). In addition, most small nocturnal primates are visual predators themselves, and may be responding to increased activity levels of their insect prey. Nocturnal primates may be able to detect insects more efficiently when moonlight levels are high (Nash 2007). Regardless of the particular cause of the increased activity levels during bright moon phases, small nocturnal primates would be more exposed to visual predators at this time and the presence of countershaded pelages would help to reduce predation risk.

Body Mass, Phylogeny, and Countershading

The prediction that large primates would display less countershading compared to small species was supported when I examined all primates together, as well as within the major primate clades. This finding is most likely related to increased levels of predation risk for small species (Cheney and Wrangham 1987), where displaying more pronounced countershading patterns is an adaptation for increased crypsis. However, some interesting exceptions to the pattern also emerged. In both the complete primate dataset and the strepsirrhine+tarsier analysis, black-and- white ruffed lemurs (*Varecia variegata variegata*) were an outlier, displaying pelage patterns opposite of those expected with countershading, i.e., dark ventral and light dorsal surfaces. Black and white ruffed lemurs have pelages with seemingly randomly distributed patches of black-and- white hair and some additional small areas of brownish red. According to the most recent Malagasy primate field guide (Mittermeier *et al.* 2006), black-and-white ruffed lemurs show noticeable across and within population variation in pelage coloration in terms of the amount of each color, as well as their distribution on the body. Therefore, the reverse pattern of countershading quantified in my study may be partly due to small sample size. Increasing the number of ruffed lemur specimens would likely yield more reliable results.

The callitrichines also displayed unusual countershading patterns. Nearly all marmoset and tamarin species exhibited low levels of countershading, particularly considering their very small body size. This primate subfamily is well known for their diversity of hair style and color patterns (Fleagle 1999), yet few studies have applied rigorous quantitative techniques to explain across species variation in these traits. One possible explanation for the countershading pattern of callitrichines may at least partly be related to their evolutionary history (Hershkovitz 1968; Hershkovitz 1977; *cf.* Jacobs *et al.* 1995). In one scenario, Hershkovitz argued for the importance of metachromism for influencing the color patterns of extant primates. Hair color would become irreversibly lighter over evolutionary time, eventually resulting in a complete loss of pigment. This may help to explain the light dorsal and ventral hair color of the silver marmoset (*Callithrix argentata*). Yet, most callitrichine species that have low levels of countershading exhibit relatively dark pelage coloration on both the dorsal and ventral surfaces. Another factor influencing coat coloration in callitrichines may be related to their positional behavior. Most callitrichine species feed on tree exudates and insects while in a vertical position, clinging to the tree's trunk (Garber 1992). The increased crypsis that may be obtained from a countershaded pelage would not be gained when the animal is in a vertical position (Bradley and Mundy 2008; Kiltie 1989). Kiltie (1989) demonstrated that countershaded

squirrel skins were effective at reducing natural light gradients when placed in a horizontal position, but not in a vertical one. Interestingly, compared to other non-callitrichine platyrrhines, *Pithecia pithecia* and *Chiropotes satanas* exhibit lower levels of countershading than expected for their body size. Both of these species are known to spend time in vertical positions, either by vertically clinging to tree trunks (*Pithecia*) or by hindlimb suspension from tree branches (*Chiropotes*; Walker 1996). In addition, although not included in this study, *Propithecus* and *Indri* spp. typically do not have countershaded pelages and spend a substantial amount of time in vertical postural positions (Demes *et al.* 1996; Mittermeier *et al.* 2006). The importance of positional behavior for explaining variation in pelage countershading can be tested in the future with an expanded dataset including species exhibiting a variety of postural positions.

When I examined strepsirrhines and tarsiers alone, I found no relationship between body mass and countershading using species values, but a moderately strong relationship when I took phylogeny into account. The difference in the traditional versus phylogenetic analyses is likely due to the differences in body mass and countershading patterns between closely related species. Phylogenetic comparative methods place more weight on differences between closely related species than those between distantly related species. There were 5 contrasts between sister species, and all of them supported the hypothesis that larger species exhibit less countershading. For instance, *Galago senegalensis* is larger than *G. moholi* and exhibits a weaker degree of countershading. The same pattern occurs in *Cheirogaleus major* vs. *C. medius*, and *Perodicticus potto* vs. *Nycticebus coucang* (Table I).

Other Factors Affecting Countershading

I did not account for several factors that may influence countershading patterns. Besides crypsis, the 2 other commonly proposed explanations for the presence of countershading are protection from ultraviolet radiation (Burt 1981) and thermoregulation (Hamilton 1973). Animals exposed to high levels of sunlight may evolve a dark-colored dorsal surface for protection against potentially harmful ultraviolet radiation or for absorbing sunlight to increase body temperature. Based on the current data set, I suggest that there is little support for these explanations for most primate species. Both of these hypotheses stress the importance of sun exposure for driving the evolution of countershaded color patterns. Therefore, nocturnal species should display low levels of countershading, a prediction not supported by my analyses.

The presence of a countershaded pelage relies on a dark dorsal surface. For mammals, dark hair coloration is primarily the result of eumelanin production (Bradley and Mundy 2008; McGraw 2006). Previous work suggests that deficiencies in certain amino acid acids, e.g., tyrosine, reduce melanin production (Anderson *et al.* 2002; Yu *et al.* 2001), thereby producing more lightly colored hair. Consequently, some primates may exhibit weakly countershaded pelages due to diets containing low levels of these amino acids. In addition, intraspecific variation in countershading may be partly related to varying levels of tyrosine in the diet. More work focused on the molecular components of primate diets and intraspecific variation in countershading may help to explain the proximate mechanisms for variation in coun-

tershading and be an important complement to research focused on ultimate explanations.

Conclusions

This study provides evidence that interspecific variation in primate countershading can be explained, at least in part, by the benefits gained from increasing crypsis. The antipredator benefits conferred from countershaded pelages appear to be important for both nocturnal and diurnal species. Small nocturnal primates have similar and possibly greater degrees of countershading versus diurnal species. A countershaded pelage in nocturnal primates is likely an important antipredator strategy associated with their increased activity levels during nights with bright moonlight. In addition, body mass influences the degree of countershading in species, with weak or absent countershading in large primates versus small ones, and is likely due to crypsis being less important for large primates because they have fewer predators.

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