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A Quantitative Test of the Predicted Relationship between Countershading and Lighting Environment

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abstract: Countershading, a vertical luminance gradient from a dark back to a light belly, is perhaps the most common coloration phenotype in the animal kingdom. Why? We investigated whether countershading functions as self-shadow concealment (SSC) in ruminants. We calculated "optimal" countershading for SSC by measuring illumination falling onto a model ruminant as a function of time of day and lighting environment. Calibrated images of 114 species of ruminant were compared to the countershading model, and phylogenetic analyses were used to find the best predictors of coats' countershading characteristics. In many species, countershading was close to the model's prediction of "optimal" countershading for SSC. Stronger countershading was associated with increased use of open lighting environments, living closer to the equator, and small body size. Abrupt transitions from dark to light tones were more common in open lighting environments but unassociated with group size or antipredator behavior. Though the SSC hypothesis prediction for stronger countershading in diurnal species was not supported and noncountershaded or reverse-countershaded species were unexpectedly common, this basic pattern of associations is explained only by the SSC hypothesis. Despite extreme variation in lighting conditions, many terrestrial animals still find protection from predation by compensating for their own shadows.

Keywords: countershading, ruminantia, artiodactyla, self-shadow concealment, camouflage, mammal coloration.

Introduction

Countershading is a common feature of animal coloration whereby dorsal surfaces are more darkly pigmented than ventral surfaces. The predominant explanation for this arrangement since its apparently independent derivation by Poulton (1890) and Thayer (1896), is that, following the terminology of Kiltie (1988) and Ruxton et al. (2004), it provides self-shadow concealment (SSC). Because sunlight normally comes from above, a shadow often falls on the underside of an animal: on a uniformly colored animal this illumination pattern creates a conspicuous brightness contrast, which could diminish the degree of crypsis by reducing the level of background matching and providing cues to three-dimensional (3D) form. However, an appropriate inverse gradation of dark to light pigmentation from the dorsal to ventral surface would result in a more uniform radiance distribution, which should improve background matching and diminish 3D cues to form. This theory has subsequently been long accepted as the most likely explanation for the widespread occurrence of countershading (Cott 1940), but more recently the paucity of empirical support has been noted, and other candidate explanations have been advanced as also being plausible (Kiltie 1988; Ruxton et al. 2004; Rowland 2009).

Several studies have examined countershading for concealment (e.g., de Ruiter 1956; Turner 1961; Kiltie 1989; Edmunds and Dewhurst 1994; Speed et al. 2005; Rowland et al. 2007), but methodological problems (reviewed in Edmunds and Dewhurst 1994; Ruxton et al. 2004; Rowland 2009) meant that strong evidence that countershading could improve survival by enhancing crypsis was demonstrated only recently. Rowland et al. (2008) placed cylindrical pieces of pastry resembling lepidopteran larvae on beech tree branches in woodland, exposed them to wild avian predators, and measured their survival. In all experiments the countershaded prey survived significantly better than other treatments. Furthermore, when prey were placed on the underside of branches, reverse-countershaded prey survived best.

However, demonstration that countershading can aid concealment does not mean that animals are necessarily countershaded for concealment. The most convincing examples of countershading for camouflage are found in aquatic environments (Korner and Pawelek 1982; Claes et al. 2010; Kekäläinen et al. 2010), where diffuse downwelling light comes from all points of the surface, creating a relatively stable visual environment.

In terrestrial environments, the evidence that countershading is generally an adaptation for concealment is more limited. Because of the variability of terrestrial environments due to weather conditions, daily and annual movement of the sun, movement of the animal, and the influence of environmental structures such as foliage, the effectiveness of a fixed countershaded pattern may seem doubtful (Kiltie 1988; Ruxton et al. 2004). Yet experiments such as those by Rowland et al. (2007, 2008) performed in (variable) field conditions show that countershading does reduce predation. However, it is dangerous to generalize from a single experimental context and infer adaptive explanations for biological phenotype, so replication with other species/systems, and the use of other approaches, is desirable.

This study takes a comparative approach in order to examine coevolution of coloration and ecological traits and evaluate functional hypotheses. Previously, comparative studies investigating countershading have shown some marginal evidence that countershaded artiodactyls (Stoner et al. 2003b) and lagomorphs (Stoner et al. 2003a) are associated with certain open environments and diurnal activity and that smaller primates and those that spent more time in horizontal postural positions had stronger countershading (Kamilar 2009; Kamilar and Bradley 2011a). Although all these results are consistent with a camouflage role of countershading through SSC, the results can also be explained by noncamouflage hypotheses.

There are several noncamouflage explanations for countershading. The simplest is that unexposed surfaces do not experience selective pressures that favor the evolution of costly pigmentation. Countershading thus becomes an epiphenomenon resulting from selection acting on only one surface (Ruxton et al. 2004). Functional noncamouflage hypotheses include protection from the damaging effects of ultraviolet (UV) light (Burtt 1981), thermoregulation (Hamilton 1975), and abrasion protection (Bonser 1995). The predictions each camouflage and noncamouflage hypothesis make are outlined in table 1.

Thus, as dark melanic pigment absorbs more UV light, the presence of countershading on diurnally active artiodactyls and lagomorphs in open environments could also be explained as evidence of an adaptation to reduce dangerous exposure of skin to UV light (Burtt 1981), and because smaller primates may find it harder or more energetically costly to control body temperature (Wheeler 1992), thermoregulatory requirements could plausibly explain variation in primate countershading.

Evaluating competing (though not necessarily mutually exclusive) hypotheses that make overlapping predictions has previously been difficult partly because of how countershading has been measured. Subjective categorical measurement of whether countershading is present or absent in a species (Stoner et al. 2003a, 2003b) obviously masks potentially important variation in the countershading phenotype required to discriminate between hypotheses. Gomez and Théry (2007) improved on this by calculating the contrast between dorsal and ventral brightness from spectrophotometer measurements of museum specimens, as did Kamilar (2009) and Kamilar and Bradley (2011) using digital photography.

However, two problems with the ratio measure of countershading remain. First, the ratio between dorsal and ventral surfaces does not capture the properties of the transition from light to dark. Some species show a gradual transition from light to dark tones over a wide spatial area whereas others show an abrupt, high-contrast transition. For example, pronghorn *Antilocapra americana* appear to have a similar ratio between dorsal and ventral reflectance as pampas deer *Ozotocereos bezoarticus*, but the transition between them is much more abrupt. The abruptness of the light-dark transition is important because while the UV protection, thermoregulation, and abrasion resistance hypotheses make predictions that overlap with the SSC hypothesis regarding countershading strength, the SSC hypothesis makes unique predictions about the abruptness of the countershading transition (table 1). Second is the assumption that stronger countershading (a larger difference between the tone of dorsal and ventral surfaces) equates to better crypsis, when for SSC to be effective there should be an optimal contrast that minimizes the gradient across the dorso-ventral axis to result in an overall uniform tone (Kiltie 1989; Rowland et al. 2007). For example, very strong countershading with an abrupt transition would be likely to reduce crypsis in dimly lit environments.

Optimal countershading for SSC will be assessed in this study by taking the negative of photographs of a uniform gray animal model taken in a variety of lighting conditions. Comparison of the model of optimal countershading for SSC to observed countershading patterns taken from images of museum specimens and use of comparative tests to establish the factors that explain variation in countershading will enable evaluation of competing hypotheses for countershading.

We chose to study countershading in ruminants (deer, sheep, and cow-like animals). Countershading is widespread in this group of approximately 209 living species (Stoner et al. 2003b), and there is considerable variation in appearance. The taxa should be an ideal candidate for application of countershading for SSC. In general, ruminants are heavily preyed on and rely on camouflage as a first line of defense against predation. Their bauplan should also lend itself to SSC being effective, as long legs and approximately tubular bodies mean that the underside is visible when viewed laterally. As large animals, many ruminants may find it hard to hide completely, so they

Table 1: Predictions made by different functional hypotheses for countershading for associations between aspects of countershading and the eco-behavioral variables that might drive variation

Countershading measure	Lighting environment	Latitude	Activity time	Group size	Stotting/ leaping	Body size
Camouflage hypotheses:						
A. Self-shadow concealment (SSC):						
Strength	+	−	+			
Abruptness	+		+			
Transition point		−	+			
Overall tone						
B. Background matching from side:						
Strength	+					
Abruptness						
Transition point						
Overall tone	+					
Noncamouflage hypotheses:						
C. Conspicuous coloration:						
Strength				+	+	
Abruptness				+	+	
Transition point						
Overall tone						
D. Thermoregulation:						
Strength	+	+				−
Abruptness						
Transition point						
Overall tone		+				
E. UV protection:						
Strength	+	−	+			
Abruptness						
Transition point						
Overall tone	−					
F. Abrasion resistance:						
Strength	−					
Abruptness						
Transition point						
Overall tone	+					
G. Horsefly protection:						
Strength						
Abruptness						
Transition point						
Overall tone	+		+	+		

Note: A plus sign indicates the hypothesis predicts a positive association, for example, between more abrupt countershading transition and brighter lighting environment; a minus sign indicates a negative association is predicted, for example, between stronger countershading and use of lower latitudes. Higher transition points refer to more dorsal locations. Higher activity time means more diurnal activity. Predictions of hypotheses: A, Variation in countershading is dependent on lighting environment (Kiltie 1989; Stoner et al. 2003; Kamilar 2009). B, Countershading by background matching without SSC is likely if backgrounds behind dorsal and ventral surfaces are generally different tones with respect to viewing position. C: Flank markings may amplify leaping and stotting pursuit-deterrence signals (Caro and Stankowich 2009); possible role in disruptive camouflage or intraspecific communication (Stoner et al. 2003). D, Stronger countershading on small species that have difficulty controlling temperature in environments with more fluctuating temperature and cold environments; having a dark and light surface may allow temperature control (Chester 2001; Rowland 2009). E, Variation in skin pigmentation in response to UV light (Burtt 1981; Chedekel and Zeise 1988; Lowe and Goodman-Lowe 1996) predicts stronger countershading in bright environments close to the equator and for diurnally active species. F, Abrasion resistance (Bonser 1995) would predict countershading dependent on differential abrasion on upper and lower surfaces, so possibly stronger in closed lighting environments with dense understory vegetation. G, Light colors and striped patterns are less attractive to horseflies (Horváth et al. 2010; Egri et al. 2012).

are also generally potentially visible (Caro and Stankowich 2009).

Methods

Taxon Sampling and Phylogenetic Analyses

Candidate study species were selected on the basis of membership of the Ruminantia group (order Artiodactyla, suborder Cetruminantia), currently estimated as containing 209 species of the families Tragulidae (10 species), Moschidae (7), Cervidae (55), Girrafidae (2), Antilocapridae (1), and Bovidae (134). Availability of molecular sequence data in January 2010 reduced the sample to 167 species and availability of suitable museum specimens further reduced it to a final sample of 114 species.

As no published tree covered all the species of interest (Hassanin and Douzery 1999, 2003; Fernández and Vrba 2005; Price et al. 2005; Gilbert et al. 2006; Marcot 2007; Agnarsson and May-Collado 2008; Spaulding et al. 2009; Rezaei et al. 2010), we compiled cytochrome *b* records from GenBank and used BEAST v.1.6.1 (Drummond and Rambaut 2007) to infer species' relatedness. Full details on tree construction and the reconstructed phylogeny can be found in the appendix, available online. At the time of conducting the analysis we were unaware of the Cetartiodactyla trees available for download on the 10kTrees website (Arnold et al. 2010) based on 17 genes. The consensus trees of both analyses are very similar.

Imaging of Museum Specimens. We obtained measurements of countershading in the study species by photographing prepared skin specimens held at the Natural History Museum, London, under controlled conditions. Suitable skins were selected on the basis of positive species identification using museum records and the condition of the skin; we rejected specimens that showed signs of experiencing significant insect damage such as holes or hair loss; ultraviolet damage in the form of obvious bleaching; those that were stiff or brittle, preventing them from being laid out flat; and those that had been dyed. All skins had been cut along the approximate ventral line. Because of the time available to utilize museum resources, a maximum of five specimens were photographed for each species. When more than five suitable specimens for a species were available, examples from a range of geographical areas and collection dates were selected. Only adult specimens were selected, and in species that undergo seasonal molting, only summer coats were assessed. When there was clear sexual dimorphism within a species (Caro 2011), only female specimens were selected. Otherwise no attempt was made to either sample the breadth of countershading variation within a species or control for it. Date of entry to

the museum collection was recorded, as was the location, date of death, and sex of the specimen when available. In total, we obtained 366 samples from the 114 study species.

Some variation in color and pattern between individuals unrelated to sex or seasonal differences was observed in most species. In fallow deer (*Dama dama*), red deer (*Cervus elaphus*), bushbuck (*Tragelaphus scriptus*), and wild goat (*Capra aegagrus*), there was evidently clear color polymorphism in our sample. The question of whether or not our countershading measures represent average population coloration is particularly relevant to polymorphic species. However, as we are not aware of any specific sampling biases other than utilization of a single museum's collection and the selection criteria, we felt justified in our approach to sampling.

In a dark corner of the museum archives, each selected specimen was in turn laid flat on a protective foam sheet and oriented centrally along the dorsal line. When necessary, glass weights were used to hold the specimen flat. Images were taken from 119 cm directly overhead with a Canon EOS 400D mounted on a tripod with a boom stand extension. Controlled lighting was provided by an Elinchrom FreeLite ringflash powered by an Elinchrom Ranger RX battery system (Elinchrom, Geneva) set to power level 5.0. This bright illuminant and a short exposure (1/200 s) meant the influence of ambient light on images was negligible. Aperture was fixed at *f*16 and the focal length at 28 mm to enable large specimens to be photographed and remain in focus across the image. Camera sensitivity was set to ISO 100, and a remote trigger was used to minimize camera shake. Camera and flash settings were chosen through trial and error to avoid clipping of any of the colors in the sample, from those of dark species (e.g., *Ovibos moschatus*) to light (e.g., *Addax nasomaculatus*). A square of 18% uniform gray card was placed in the corner of each image. Images were taken in RAW format. The RAW files were converted to TIFFs using DCRAW v.9.06 (Coffin 2011), with a fixed custom white balance selected using the gray card in one of the images.

Image Processing. Images were linearized using a modification of the procedure described in Stevens et al. (2007), resulting in pixel values with a linear relationship with surface reflectance. We analyzed only the green channel as it has a spectral sensitivity that approximates the response of mammalian longwave cone receptors. To compensate for uneven illumination across the images, we photographed the uniform gray protective foam sheet under the same lighting conditions and, after smoothing the image to remove the texture of the sheet, calculated the percentage difference in response for each pixel from a reference pixel. The images of the specimens were then corrected using these percentage differences to give all pixels

A

B   C   D
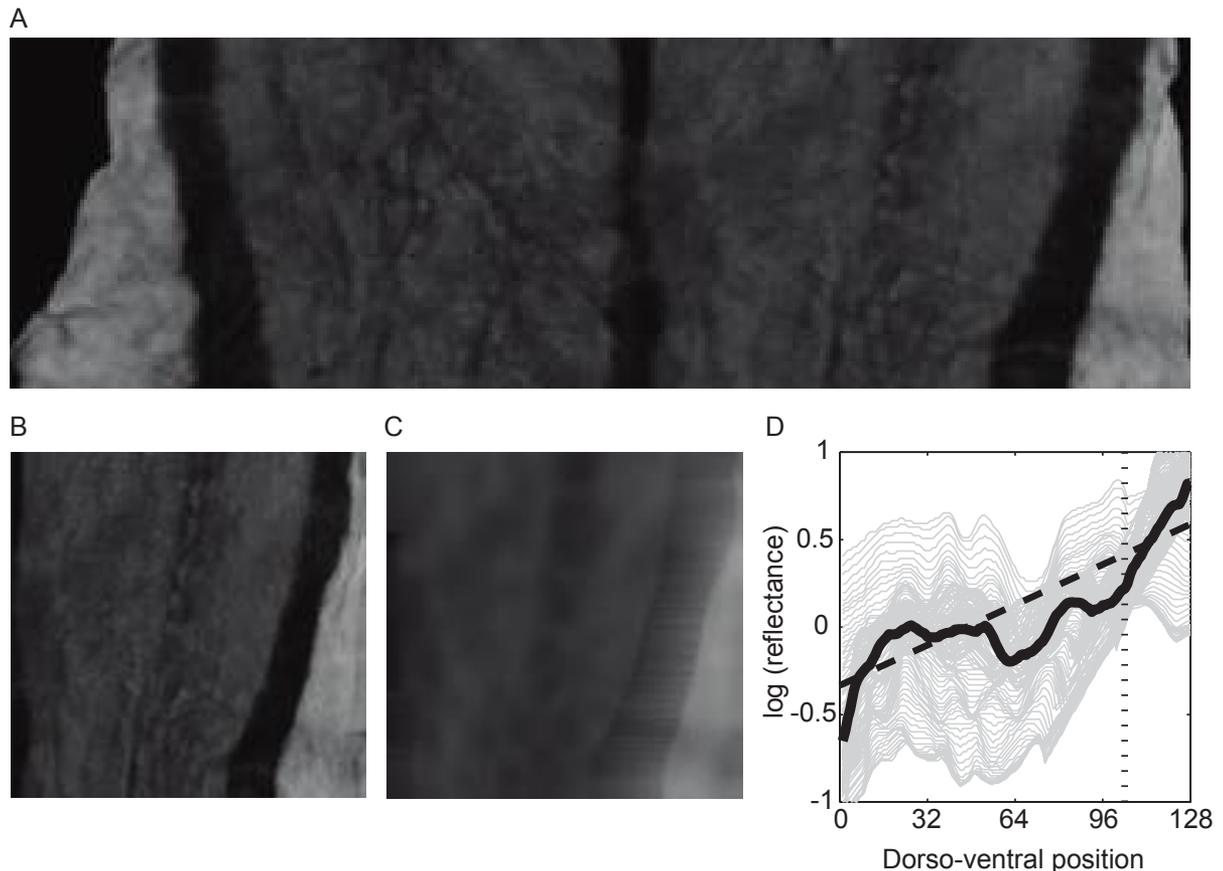
Figure 1: After adjusting, linearizing, and cropping photographs of the museum specimens (*A*), each transect was split along the dorsal line and stretched or shrunk to 128 pixels length (*B*). Images were smoothed, and features such as dorsal stripes and side-stripes were removed (*C*). Smoothed images were then logged, and mean log reflectance was subtracted from each transect. Gray lines in *D* show log reflectance for each transect in *C*, the solid black line shows median log reflectance for all transects at each pixel, the dashed line is the median best linear fit of all transects, indicating countershading strength, and the vertical dashed line is the median dark-light transition point for all transects.

the value they would have had under the same illumination intensity as the reference pixel, assuming that the spectral power of the flash was approximately equal at all relevant wavelengths.

Each image was then cropped by hand using GIMP v.2.6.11 (GIMP Development Team 2011) to select all complete dorso-ventral transects (image rows) from the body region between the fore and rear legs. The image column of the dorsal midline was recorded. This could be estimated from the position of the head and the tail and features of coloration such as countershading and the contrasting dorsal stripe found down the spine of several species studied such as the common eland (*Taurotragus oryx*). Background pixels were set as a transparent layer. To standardize each transect and control for different-sized animals and varying body circumference between the fore and rear legs, we performed a number of operations using

Matlab v2009a (Mathworks 2009). First, each image was divided along the dorsal midline. The two halves were then joined along the ventral line. The region around where the two halves joined featured irregularities, so to heal these we removed the first 5 pixels from either side and replaced them with a random sample of the previous 5. Each transect was shrunk to 128 pixels wide using bilinear interpolation, divided in half, and the second half was flipped, resulting in a series of equal-length transects for each sample of each species from the dorsal midline to the ventral midline for both halves of the body (fig. 1).

Calculating Optimal SSC

We chose to base our description of optimal SSC on the European roe deer (*Capreoulus capreolus*) as it is of average size and has a body shape typical of the majority of our

Figure 2: Example image of the model deer. Image taken at dusk in an open lighting environment, with the illumination coming from behind and to the left of the deer. In this case the cast shadow would require an intermediate level of countershading to conceal (countershading strength = 0.098, transition point = 94, probability of light step edge = 0).

study species. We were unable to procure a life-sized model so we constructed our own 1 : 1 scale model by building onto a wooden "skeleton" using wireframe and papier-mâché techniques (fig. 2). We used the average species measurements for an adult female found in Danilkin (1996): total length = 117 cm, shoulder height = 75 cm, body girth = 70 cm, body length = 67 cm, and hind foot length = 38 cm.

The model was spray-painted a uniform midgray using multiple coats of "Fortress Grey" matte model spray paint (Games Workshop, Nottingham, UK). Two red circular stickers (6 mm diameter) were placed on the side and rear of the model to facilitate photograph alignment.

We photographed the model in countryside surrounding Bristol, UK, in a range of conditions. To determine how optimal SSC changes at midday and dusk, each photography session began either approximately 20 minutes before solar noon or at sunset according to times provided by www.timeanddate.com for Cardiff, Wales, UK (26.7 miles/43 km from Bristol). In total there were 6 midday sessions and 6 dusk sessions. To examine how optimal SSC changes in different lighting environments, each session we selected an open and a closed location. Open locations were fields with no overhead cover or obstructions between the model and point of illumination. Closed locations were areas of mainly deciduous woodland with overhead cover provided by foliage.

Photography took place in all seasons. To avoid damaging the model we avoided rain and snow but otherwise photographed year-round in a range of weather conditions. Images were taken with the same camera and setup as for the museum specimens with the exception of se-

lecting aperture priority mode so well-exposed photographs were produced across the range of conditions. We randomly selected at the start of each session whether to photograph in an open or closed environment first, which compass point to orient the model to in the first image, and whether to rotate the model clockwise or anticlockwise for subsequent images. Images were taken at each of 8 compass points (every 45 degrees from north), and at each compass point the model was shot in profile. Each shot was aligned using a jig placed on a fixed point on the middle of the model's back and taken from a distance of 234 cm. The camera was mounted on a tripod at a height of 64 cm and the center of the image was aligned with the red circle on the flank or rear as appropriate using the camera viewfinder. The camera was allowed to automatically focus on the model except in low-light conditions when manual focus had to be used.

Images were prepared for analysis in the same way as those of the museum specimens, with the exception that the exposure value ($EV = \log 2(N^2/t) + \log 2(S/100)$, where N is the aperture f number, t is integration time, and S is ISO sensitivity) was used to adjust images to the same reflectance scale as the images of museum specimens. Optimal countershading was established by taking the inverse of the model reflectance (i.e., a negative).

Measures Taken from Transects. We took an image-processing approach to analyzing both the specimen and model images. First, we blurred the images to reduce noise and local features (such as a hair texture, areas where the hair ran in different directions, areas where the skin could not be completely flattened and areas of damage) by convolving the image with a 10 × 10-pixel Gaussian filter with a standard deviation of 3 and mirroring the image at borders to prevent edge effects. To identify high-contrast features such as stripes and sharp tonal steps, we used Sobel edge detection with a threshold of 3.75 to find the edges in each crop. The threshold was chosen through trial and error to detect (for human perception) contrasting features across the data set while minimizing detection of local irregularities in the image object. Calculating the second derivative at edge pixels gave the direction of the edge (light to dark or dark to light), and by using simple heuristic rules we were able to classify each transect as containing light side-stripes (or spots) on the flank, dark side-stripes (or spots), darkening step edges, and lightening step edges and record the positions of these features. We considered side-stripes and spots to be coloration features overlaid on a background, so we removed these pixels and replaced them with a linear interpolation between pixels either side of the feature before measuring the strength of underlying countershading.

The strength of countershading in each transect was

determined by finding the least squares fit to a simple linear regression model of log reflectance at each of the 128 pixels against position (pixel number) for each transect. The abruptness of the transition between light and dark tones was measured by the probability of finding a light step edge in all image transects. To record the point where the transition from dark to light tones is most abrupt we took the maximum of a 3-point moving average of the second derivative of pixel values (fig. 1). The species summary for all these measures was the median score for all transects of each species.

Assessment of Fading in Museum Specimens. Although museum specimens are stored in the dark, to account for potential fading of specimens over time (Armenta et al. 2008; Doucet and Hill 2009), we normalized the average strength of countershading and average reflection of all species with respect to an exemplar. The standardized difference of individual specimens' normalized average reflection and countershading strength to the exemplar was regressed with the standardized age of the specimen, measured in years, using SPSS. The age of the specimen did not predict either strength of countershading ($\beta =$ 0.006, SE $= 0.055$, $t = 0.118$, $P = .906$) or average tone ($\beta = -0.58$, SE $= 0.055$, $t = 1.057$, $P = .291$), so no correction for age was applied to measures.

Ecological Measures. Information on the ecological measures taken was gathered from several sources (Estes 1992; Kingdon 1997; Nowak and Paradiso 1999; Schaller et al. 2000; Caro et al. 2004; Wilson and Reeder 2005; Prothero and Foss 2007; Caro and Stankowich 2009; Wikipedia species accounts; International Union for Conservation of Nature and Natural Resources (IUCN) Red List species accounts).

We assessed the impact of activity time on countershading by scoring species on a 3-point scale (yes = 1, occasional = 0.5, and no = 0) on each of three traits; nocturnal, crepuscular, and diurnal activity. From these scores we then formed a composite 9-point activity time score with purely nocturnal species scoring 1; nocturnal and occasionally crepuscular species scoring 1.5; nocturnal and crepuscular species scoring 2; nocturnal, crepuscular, and occasionally diurnal or crepuscular and occasionally nocturnal species scoring 2.5; purely crepuscular species or species active equally at all times scoring 3; and so on.

A similar approach was taken to scoring species' lighting environments. Whether a species was found in direct light, dappled light or shade was scored on the same 3-point scale, and a 9-point lighting environment score was formed the same way as the activity time score.

Maximum group size was mainly based on estimates reported by Nowak and Paradiso (1999). Species' rank position on maximum group size was used in the analysis.

The minimum and maximum latitude either north or south of the equator of each species' range was estimated to the nearest half degree using the range maps provided on the IUCN Red List website and Google Earth, and the midpoint was calculated as the mean of northerly and southerly extent. Rank score on latitude midpoint was used in the analysis.

Species body size was recorded as the midpoint of the body mass ranges provided by Nowak and Paradiso (1999), and rank body size was used as a predictor. The stotting measure used in the analysis was taken from Caro and Stankowich (2009).

Comparative Analyses. We conducted the comparative analyses using the CAPER package (Orme 2011) for R (R Development Core Team 2011) to implement the method described by Freckleton et al. (2002), which constructs a phylogenetic variance-covariance matrix to control for expected similarity due to shared evolutionary history within a standard linear model. Minimal adequate linear regression models for each of the response measures (strength of countershading, transition point, probability of a light step edge, probability of a dark stripe, average reflectance, and reverse countershading) were constructed using backward elimination.

Results

In total we analyzed 68,934 transects from museum specimens and 22,400 transects from the model. We had to exclude 498 of the specimen transects as the edges identified were in an arrangement that our heuristic rules were unable to classify. These were mainly from samples with glossy coats where the specimen did not lay completely flat, causing specular reflections unrelated to any feature in the specimen's coloration. A dark stripe was identified in over half the transects of eight species, and one or more light step edges were identified in over half the transects of 32 species. In contrast, light stripes were present in only one species (*Axis axis*), and no species had dark step edges. Light or dark dorsal stripes were identified in three species. Because of the rarity of dorsal stripes, light stripes, and dark step edges, these features were not analyzed further. Eight species had median countershading slopes that were negative; that is, they had reverse countershading. We repeated comparative tests both with and without these species included, as well as with and without species with light step edges, and found that removal of these groups made no qualitative difference to the pattern of associations, so we report only results of the full data set.

Examination of the strength of countershading distri-

butions (fig. 3) shows that in general there is good correspondence between what optimal countershading for SSC would predict and what was observed on museum specimens. Figure 4 shows how countershading is distributed over the Cervidae family and its association with species' lighting score.

We built models for each of the countershading measures listed in table 2 using backward elimination of terms from the full model (table A2, available online) containing all predictors listed in table 2 using the CAPER package (Orme 2011) for R (R Development Core Team 2011), as described in "Methods." The best supported model of countershading strength showed that species with stronger countershading have higher lighting environment scores (see table 3 for statistical tests). They are also smaller and found at lower latitudes (closer to the equator). The activity time of species was not a significant component of the final model. We did not observe particularly strong countershading in diurnal species using open habitats, as predicted by our model of optimal SSC.

The model of optimal SSC suggested that diurnal species and those that use open environments should have higher transition points, but the point where a countershaded animal makes the most rapid transition from dark to light was unrelated to any of the predictors.

Dark average tone was associated with living in closed environments that had low lighting scores. This is consistent with a background matching function for general coloration.

There was a strong relationship between the probability of an animal having a lightening step edge and lighting score, with species found in open environments being more likely to have a step edge.

The best model for predicting whether a species had a dark stripe included only its rank group size. This is consistent with hypotheses suggested in the literature such as an interspecific signaling function, or disruptive/confusion camouflage in large herds (Stoner et al. 2003).

We had no specific hypotheses for why species have reverse countershading. Because we observed that eight species had negative countershading slopes the ecological correlates were investigated, suggesting that reverse countershading was more common on larger species.

A full table of phylogenetically controlled correlations between predictor and response variables is found in table A3, available online. In summary, species with light step edges have both stronger countershading slopes and lower transition points. Species with dark stripes also have stronger countershading. Among predictors, lighting environment had a strong positive correlation with activity time, latitude, body size, and group size.

To check whether model selection had been affected by colinearity of predictors, we constructed regression models using forward elimination. For all response variables except the probability of dark stripes, the best-supported models were identical to those built using backward elimination. Using forward elimination, stotting/leaping behavior as well as increasing group size was a significant predictor of dark stripes ($n = 114$, $\lambda = 0$; group size: $r^2 = 0.001$, $\beta = 0.0005$, $t = 3.09$, $P = .003$; stotting: $r^2 = 0.075$, $\beta = 0.032$, $t = 2.31$, $P = .022$), a relationship that was also predicted by the hypothesis that this feature has a signaling function.

Discussion

Of the multiple potential explanations for the occurrence and diversity of countershading in ruminants (table 1), both our model data and comparative analysis highly favor the concealment of shadows as the major determinant of these stereotyped motifs.

The first and most obvious evidence for this conclusion is that, in general, the strength of countershading observed empirically was well matched to that expected from a system that was attempting to nullify its own shadow (fig. 3). We found this surprising given intuitions based on photographs or videos of animals. Based on these it might be expected that animals are usually countershaded too strongly, since many photographs show clear white bellies and dark backs, not the more uniform coloration that would be expected if SSC was operating effectively. This, we propose, is mainly an artifact of good photographic practice. When taking a (good) photograph, it is usually best to have the light source behind you (and often the best photographs are taken at dawn and dusk). In this situation, ruminants would indeed be over-countershaded, but in the natural world, with lighting direction relative to viewer and subject being highly variable, our analysis shows that the strength of countershading for the majority of specimens in both open and closed environments fell within the range predicted by our model of optimal countershading (fig. 3).

One feature of transects of both the museum specimens and model is just how variable they are. The variability of lighting environments is perhaps the primary objection to a SSC function of countershading in terrestrial environments (Kiltie 1988). Despite all images of the model being taken in a small geographical area of northern Europe, in either fields or mixed woodland, and on just 24 separate occasions, there was considerable variety in the reflectance profile of shadows across dorso-ventral transects. This was especially true for open habitats, and the observed variability would only increase if measured in a wider range of conditions. This means that a given countershading profile will only rarely ever achieve perfect or near-perfect SSC.

Is this a problem? The associations presented here show
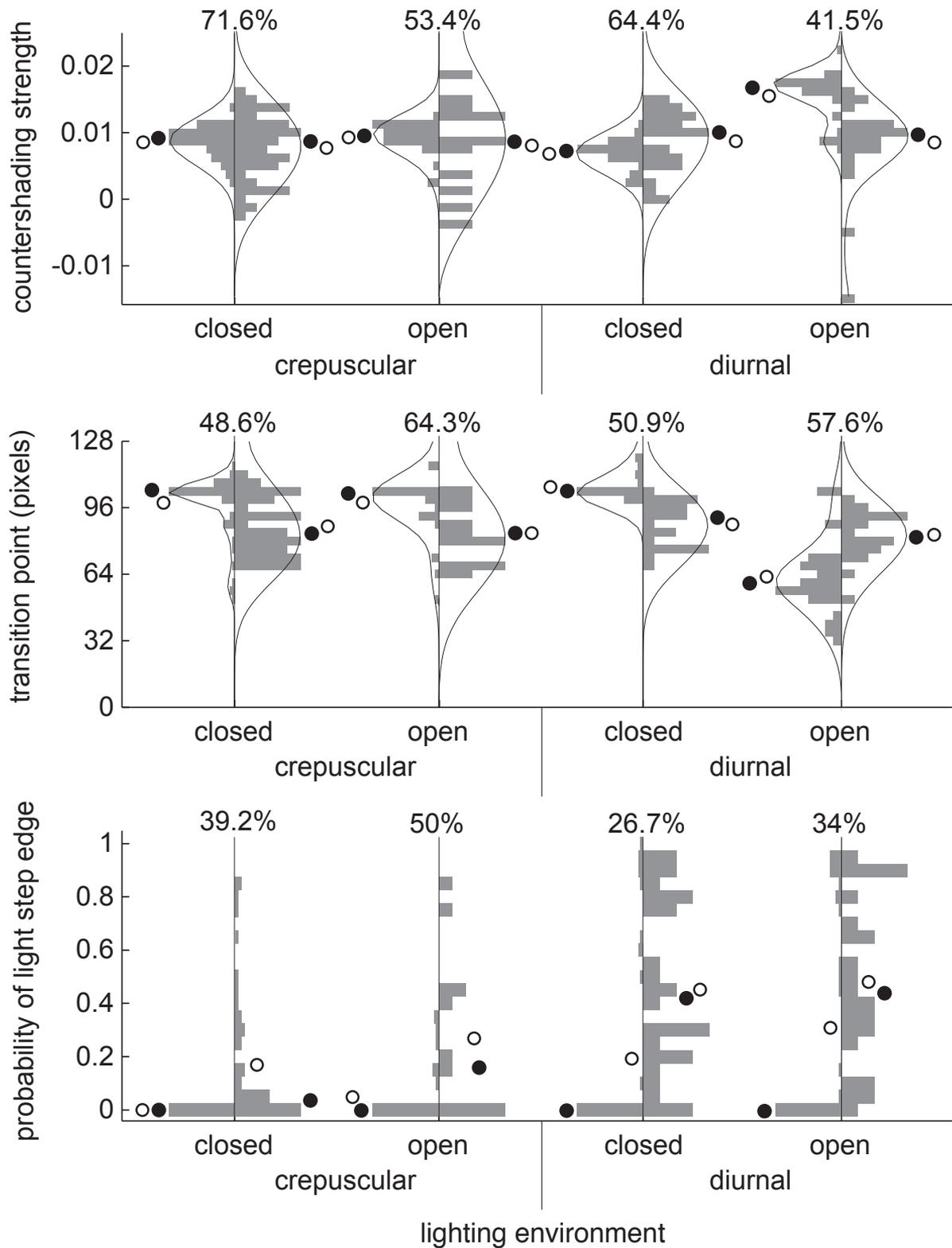
that variation in countershading on ruminants is explained by the predictions the SSC hypothesis makes, supported by the empirical model of optimal countershading (fig. 3), for a given lighting environment, latitude, and body mass (table 1). This suggests that many species find that suboptimal solutions still give worthwhile protection, an idea supported by psychophysical experiments that used countershaded stimuli that were unlikely to achieve perfect SSC and yet still found a survival advantage for countershaded models (e.g., Rowland et al. 2008).

Higher lighting environment scores represent utilization of more open habitats such as grasslands and deserts. In these environments, both brighter diffuse lighting and direct lighting are more common than in more closed habitats. This creates stronger shadow contrast, which animals would need to oppose to achieve SSC through countershading. This also makes lightening step edges more likely. These effects were observed in the analysis of the photos of the model (fig. 3). This pattern was mirrored in the analysis of museum specimens. The comparative analyses showed good support for species' lighting environment scores explaining variation in countershading strength: countershading was stronger and step edges more common in species with higher lighting scores.

The association between lighting environment and step edges is particularly important because, of the explanations for countershading considered, only SSC predicts this finding (table 1). The UV protection hypothesis also predicts stronger countershading on species with higher lighting scores but not an abrupt transition from dark to light tones. Other explanations for an abrupt transition from light to dark tones, including enhancement of leaping or stotting predator deterrence signals or involvement in intraspecific communication (Caro and Stankowich 2009), were not supported: step edges were not associated with either the stotting measure or group size.

Further supporting evidence for the SSC hypothesis included the finding that species closer to the equator generally had stronger countershading. The sun is more often more overhead closer to the equator, and it rises and falls rapidly. Images of the model showed that overhead illumination creates the strongest self-shadows. However, this association is also consistent with a UV protection explanation of countershading, as distance to the equator explains much, though not all, variation in UV radiation levels (Herman et al. 1999).

Small body size was also associated with stronger countershading. Kamilar (2009) reported the same association in their study of primate countershading and interpreted it in relation to greater predation on smaller species increasing the importance of effective protective coloration, leading to stronger countershading. Although we cannot confirm that smaller species had more optimal countershading for SSC than large species, small ruminants, like primates, are predated on at a higher frequency than large ruminants (Hopcraft et al. 2011), so we agree with Kamilar (2009) that this association suggests a camouflage function of countershading.

As the four conditions the model was photographed in are unlikely to have the same lighting as that experienced by each species in each condition, comparison between individual species and model averages does not precisely relate to how effectively each species achieves SSC. In open lighting environments, the distribution of predicted countershading strengths for model transects was clearly bimodal. Whether the shadows were strong or weak depended mainly on whether the model was photographed at midday or sunset but also on the weather (direct sun or cloud cover) and orientation to the illuminant. Transition points were more dorsal at midday in open lighting environments, as strong shadows cast from more overhead are more common, and step edges were more likely in open environments because of stronger directional light. Few species showed countershading strong enough, or

Figure 3: Violin plots showing the distribution of countershading measures from museum specimens and inferred from photographs of a uniform gray model roe deer. Each "violin" shows histograms of the median score for each image of the model in the condition on the left-hand side and the median score for each species in the condition on the right-hand side. The 2 × 2 design results in four lighting conditions; open habitats at noon and dusk, and closed habitats at noon and dusk. Filled circles mark median scores and open circles mark mean scores. Each histogram has been normalized so maximum widths are equal for ease of comparison. A kernel density estimate of the distributions for countershading strength and transition point is shown. The number above each histogram is the percentage of the total area of the density estimates (countershading strength and transition point) or raw histograms (probability of a step edge) that is shared by both the model and the specimen. Countershading strength is the linear regression coefficient between the normalized log reflectance of the 128 pixels in each transect and pixel position. Details of preceding image processing steps are given in the methods section. Transition point is the pixel number at the maximum of the second derivative of the three-point moving average and indicates where on the dorso-ventral axis the transition from light to dark tones is most abrupt. Probability of a light step edge measures whether there is an abrupt or gradual transition from dark to light tones. Species were placed in open/closed and crepuscular/diurnal conditions depending on their lighting environment and activity time scores. Species with lighting scores equal to or greater than 4.5 (corresponding to utilization only of open environments, or open environments and partial utilization of lightly shaded environments) were placed in the open condition ($n = 53/114$), and species with activity time scores equal to or greater than 3.5 (corresponding to a preference for diurnal activity) were placed in the diurnal condition ($n = 36/114$).
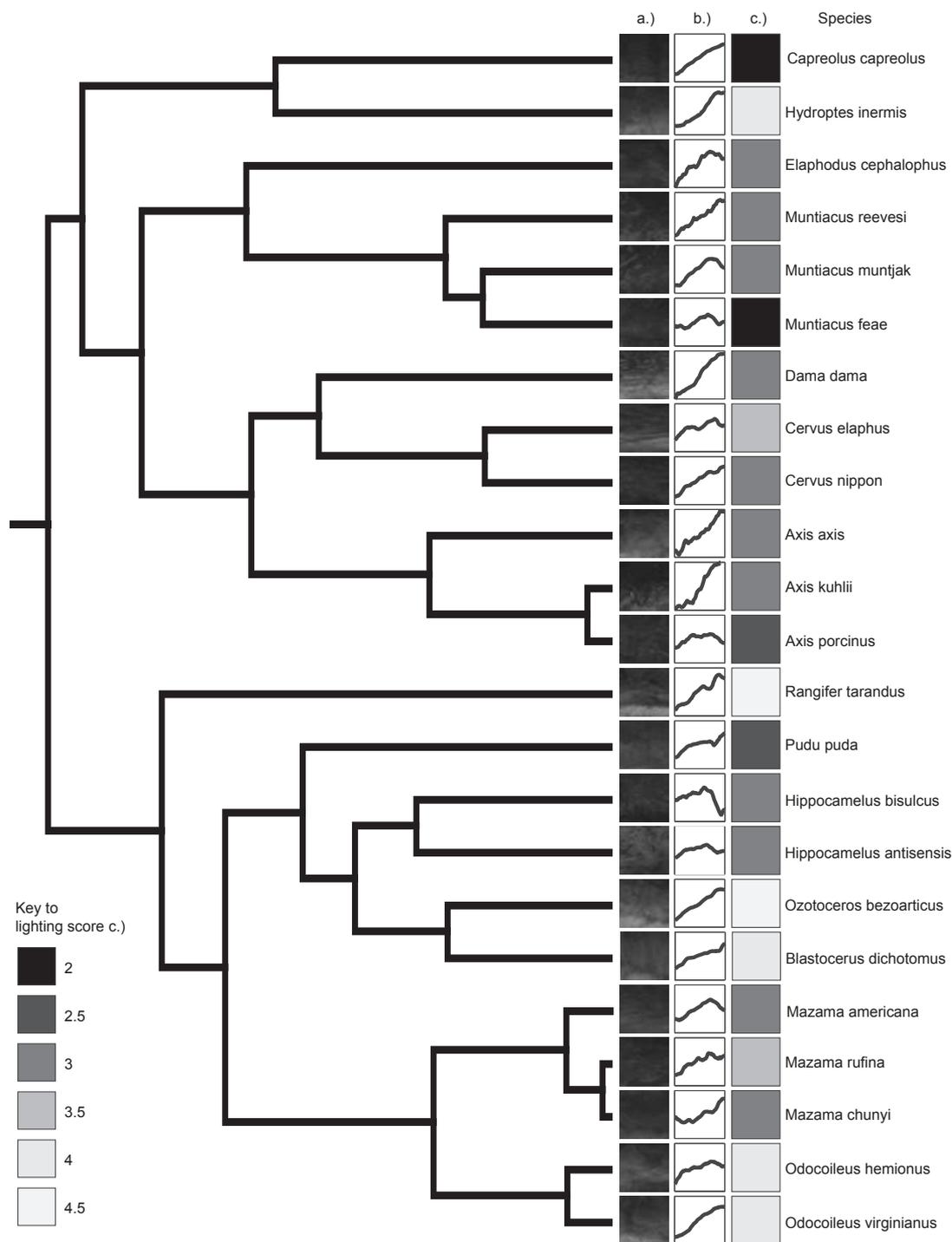
Figure 4: Countershading traced over the phylogeny of the 23 species of Cervidae studied. Branch lengths are proportional to divergence time. Images in column *a* show an example for each species of the change in reflectance across the trunk of the body. Images are those taken of specimens, linearized, and fitted to a standard frame. Column *b* shows on the *Y*-axis the median log reflectance of all transects analyzed from a species, after removing features such as stripes, at each dorsoventral point on the *X*-axis. Column *c* represents the lighting score assigned to the species (see *key*, bottom left).

Table 2: Maximum likelihood estimates of phylogenetic signal (λ) present in characters

Character	Λ	Maximized log-likelihood	Maximized log-likelihood ($\lambda = 0$)	Maximized log-likelihood ($\lambda = 1$)
Pattern measures:				
Countershading strength	.60	444.62	434.64***	407.09***
Probability of a light step edge	.69	−13.74	−29.93***	−34.47***
Transition point	.53	−435.17	−441.30***	−488.08***
Overall tone	.79	−470.78	−492.54***	−497.68***
Probability of a dark stripe	.34	33.87	33.61[a]	2.88***
Reverse countershading	.51	−9.55	−12.39*	−4.29[a]
Ecological predictors:				
Lighting environment	.98	−130.21	−165.20***	−131.63[a]
Activity time	.79	−138.23	−142.17**	−151.64***
Average latitude rank	.75	−542.99	−560.82***	−579.86***
Average mass rank	1	−492.32	−569.28***	−492.29[a]
Maximum group size rank	.85	−544.84	−567.07***	−574.77***
Stotting/leaping	.28	−79.42	−80.96[a]	−132.93***

Note: Characters not significantly different from $\lambda = 0$ have no detectable phylogenetic component to character variation. Characters not significantly different from $\lambda = 1$ fit a Brownian motion model of character evolution.

[a] Not significant.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

with high enough transition points to provide full SSC at midday in direct sun, though as this is when shadows are at their strongest, optimizing to the maximum of the range is not expected under the SSC hypothesis. Instead, the histograms of the distribution of countershading strengths show a peak for the specimens in between the two peaks for the models, suggesting that most species have evolved a compromise solution that works most effectively when the sun is at neither its highest or lowest.

In contrast, light step edges were more common than the model predicted, especially for diurnal species. A possible reason for this may be that the lighting environments of the species may generally have stronger directional light that the lighting environments the model was sampled in. Approximately 65% of images of the model were taken in what would be classified as "overcast" conditions, typical of the United Kingdom, whereas globally, most other regions receive more sunshine.

The smooth form of the model also possibly made step edges less likely than for the specimens. The transverse cross section of the model was based on drawings of roe deer, which have a smooth profile. We did not have precise information on the cross sections of other study species, though clearly there is some important variation relevant to SSC, with some species having broad backs (e.g., takin *Budorcas taxicolor*), others having relatively long and narrow transverse planes (e.g., silver dik-dik *Madoqua piacentinii*), and others bulging bellies (e.g., nilgai *Boselaphus tragocamelus*). Those with wide backs relative to their undersides would be expected, on our measures, to have

lower transition points and those with wide undersides to have higher transition points, as these areas toward or away from the sun take up a greater fraction of the circumference. Abrupt changes of curvature may also be important to the abruptness of countershading transitions and be a determinant of transition point.

Both reasoning about diurnal and crepuscular lighting environments and our model of optimal SSC suggested that if countershading is an adaptation for SSC, diurnal species should have stronger countershading and transition points higher up the body than crepuscular species. However, like Kamilar (2009) but in contrast to Stoner et al. (2003*b*, 2003*a*), we found no associations between the activity time of an animal and either the strength of countershading or the position of the transition point. An assumption underlying this prediction is that camouflage should be optimized to the conditions where predation risk is highest and that this is when an animal is most active (Endler 1978, 1984). Being generally large animals, many ruminants are still potentially conspicuous when inactive, especially those utilizing open lighting environments. This may mean that predation is not highest when most active, and consequently camouflage does not evolve to be most effective at the time of most activity.

The exceptions to conventional countershading included several reverse countershaded species such as musk ox (*Ovibos moschatus*). The only typical lighting conditions that could possibly favor this pattern for self-shadow concealment are those when the substrate is highly reflective, such as over snow or water. Though this phenotype was not

Table 3: Regression results for the best phylogenetically informed generalized least squares models explaining variation in countershading strength, countershading transition point, overall tone, probability of light step edges (measuring transition abruptness), and probability of dark stripes

Response variable	Pagel's λ	P $(\lambda = 0)$	P $(\lambda = 1)$	Fixed effect	Coefficient	SE	t value	P value
Countershading strength (slope)	.674	.076	<.001	(Intercept)	8.61E−03	4.82E−03	1.79	.077
				Lighting score	2.01E−03	5.84E−04	3.44	8.24E−04
				Latitude rank	−3.90E−05	1.54E−05	2.53	.01279
				Body mass rank	7.41E−05	1.78E−05	4.15	7.11E−05
Overall tone	.719	<.001	<.001	(Intercept)	21.4	16.3	1.31	.192
				Lighting score	7.00	1.69	4.14	6.71E−05
Probability of a light step edge	.756	<.001	<.001	(Intercept)	.165	.326	.505	.614
				Lighting score	.074	.032	2.30	.024
Probability of a dark stripe	0	1	<.001	(Intercept)	−.021	.030	.713	.477
				Group size rank	1.5E−03	4.6E−04	3.16	.002
Reverse countershading	0	1	<.001	Lighting score	−.055	.026	−2.10	.038
				Body mass rank	2.7E−03	7.6E−04	3.62	4.41E−04

related to species' proximity to water, that it was unassociated with higher latitude suggests that this phenotype does not have a self-shadow concealment function. The comparative analysis found that it was associated with large body size and dark lighting environments. Reverse countershading is typically discussed in terms of increasing visibility (Hailman 1977), which explains the coloration of birds such as the bobolink (*Dolichonyx oryzivorus*), who adopt reverse countershading in the breeding season. Reverse countershading is more common on large birds as well (Riegner 2008). Though large animals may be able to afford conspicuous signals, this does not seem a likely explanation in ruminantia as the reverse countershading observed is quite subtle. On the musk ox, the species with the strongest reverse countershading, the light dorsal color is the result of the "qiviut" layer of lightly pigmented insulating underhair showing through. For other species, the reverse countershading is either very subtle or one of two of more distinct pattern types in the species (e.g., bushbuck, *Tragelaphus scriptus*). Whether this phenotype has functional significance merits further investigation.

Interestingly, estimates of phylogenetic signal (λ) were generally lower for the countershading measures than the ecological variables (table 2). This supports previous findings that pattern traits are often evolutionarily labile (Allen et al. 2011) and can adapt over relatively short timescales (Endler 1980), suggesting that large changes in pattern appearance can be controlled by relatively minor genetic and developmental alterations (Hoekstra 2006).

In summary, variation in the countershading patterns on ruminants is only satisfactorily explained by the self-shadow concealment hypothesis. The optimal countershading pattern for removing the effects of self-cast shadows in terrestrial environments is highly variable, depending on properties of the illuminant and overhead cover. This means that most of the time the countershaded patterns observed on many ruminants would not completely remove self-cast shadows. Despite this, over the range of lighting conditions in which an animal is predated in, shadow contrast would be overall reduced, perhaps close to optimally, in most of the ruminants observed. We propose that even imperfectly minimizing the effects of self-cast shadows aids survival and that much of the variation in countershading appearance has evolved in response to species SSC requirements under different lighting environments.

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