Three-Dimensional Camouflage: Exploiting Photons to Conceal Form

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abstract: Many animals have a gradation of body color, termed "countershading," where the areas that are typically exposed to more light are darker. One hypothesis is that this patterning enhances visual camouflage by making the retinal image of the animal match that of the background, a fundamentally two-dimensional theory. More controversially, countershading may also obliterate cues to three-dimensional (3D) shape delivered by shading. Despite relying on distinct cognitive mechanisms, these two potential functions hitherto have been amalgamated in the literature. It has previously not been possible to validate either hypothesis empirically, because there has been no general theory of optimal countershading that allows quantitative predictions to be made about the many environmental parameters involved. Here we unpack the logical distinction between using countershading for background matching and using it to obliterate 3D shape. We use computational modeling to determine the optimal coloration for the camouflage of 3D shape. Our model of 3D concealment is derived from the physics of light and informed by perceptual psychology: we simulate a 3D world that incorporates naturalistic lighting environments. The model allows us to predict countershading coloration for terrestrial environments, for any body shape and a wide range of ecologically relevant parameters. The approach can be generalized to any light distribution, including those underwater.

Keywords: countershading, background matching, obliterative shading, camouflage, shape-from-shading.

Introduction

Visual camouflage is the use of color and/or pattern to conceal an object, rendering it more difficult to detect or recognize. Most of the theory and research on camouflage concerns concealment of objects in a two-dimensional (2D) plane

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(reviewed by Stevens and Merilaita 2011). In general, however, camouflage must conceal three-dimensional (3D) objects within a 3D world.

The basic camouflage strategies of background matching and disruptive coloration interfere with object detection through contrast and outline coherence (Stevens and Merilaita 2011). However, 3D objects provide many additional cues that aid in their detection and recognition via shape. Some species use binocular vision for this, but its utility falls off with distance (e.g., Harris 2004); for humans, it is useful only up to a distance of ca. 6 m (Cutting and Vishton 1995). For animals with smaller eye separation but similar resolution, the distance will be even smaller. There are, however, many monocular cues to shape and depth, the strongest coming from surface shading (Gibson 1979; Lovell et al. 2012). For example, even though the reflectance of the cylinder in figure 1a is uniform, because of the directionality of the lighting the upper part is noticeably brighter than the lower (referred to as "self-shadow"). Thus, matching the color of the background does not effectively conceal the object. However, if the animal's pattern is the inverse of the self-shadow, then the two cancel, resulting in constant luminance and perfect self-shadow concealment. This is the basis for the long-influential, but controversial, theory that countershading functions to obliterate shape-from-shading cues, rendering a prey animal perceptually flat to a viewer (Poulton 1890; Thayer 1896; Cott 1940).

There are also other hypotheses specific to concealment of 3D objects, but these remain largely untested. This article anchors theories of 3D concealment in what can be predicted from optical physics and human perceptual psychology. We present a computational modeling framework that allows us to test logically whether theories are mutually exclusive. This is based on a simulated 3D world that allows for naturalistic lighting environments and delivers realistic
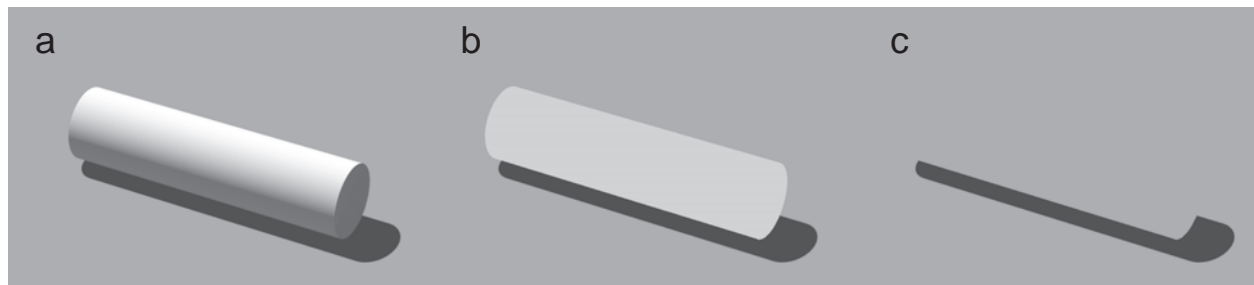
Figure 1: *a*, A uniform cylinder exhibits shading when lit from above. *b*, When the cylinder's reflectance is the inverse of that shading, the two cancel, but the cylinder is still visible. *c*, The reflectance may additionally be chosen so that the radiance from the body also matches that of the background, resulting in both perfect obliterative shading and background matching.

effects that take account of the complex interplay between 3D object, light direction, and environment. Using this, we make predictions about what data we need to test hypotheses around countershading as effective camouflage.

Recovering Shape and Depth Information from 2D Retinal Images

Shape-from-shading is inherently ambiguous because the pattern of stimulation at the retina is the product of shape, reflectance, and lighting, all of which can vary, and different combinations of these can lead to the same image on the retina (e.g., Curran and Johnston 1996). Nevertheless, humans are highly sensitive to it, although our perceptions can be biased by variations in the light direction (e.g., Nefs et al. 2005). There is some evidence for the use of shading cues in other animals (e.g., pigeons; Cook et al. 2012). Any animal using shape-from-shading as a cue to shape should be fooled by countershading, acting to reduce the shape cue (Tankus and Yeshurun 2001). The inverse also follows: if countershading disguises 3D form, then the viewer is likely to have developed perceptual mechanisms that derive shape from shading.

The way in which texture and pattern distort in the 2D retinal projection of a 3D object is also a useful source of information on depth and shape (Gibson 1979; Knill 2001). Camouflage for countershading and camouflage for texture matching need not be mutually exclusive and can operate in concert (e.g., the countershaded and textured pattern of a leopard pelt). We demonstrate that countershading is effective from most viewing directions but that texture matching is very much dependent on a consistent viewer location for its success (see app. A; apps. A and B available online).

How to Disguise 3D Form

Rowland (2009) highlighted two mechanisms by which countershading might aid concealment: (1) self-shadow concealment and (2) matching different backgrounds when

viewed from different angles. Previous studies have often not clearly delineated between these potential mechanisms, and, to our knowledge, no previous work has made specific predictions that could distinguish between the hypotheses.

Possible Mechanisms by Which Countershading Can Act as Camouflage

Matching Multiple Backgrounds. Countershading might occur as a "side effect" of matching backgrounds that are different according to the angle of viewing (Wallace 1889). For example, if the background when viewed from above is dark (e.g., ground) and that viewed from below is light (e.g., sky), then this predicts a dark dorsum and a light ventrum. On this account, countershading is not a mechanism to defeat cues from 3D form but conforms to the general principles of background matching. Countershading would then be common simply because there are many examples where backgrounds are sky and ground and so have these properties of lighter-background-from-below/darker-background-from-above, with a consistent body side being viewed against each (e.g., pelagic fish, seabirds).

However, there is a logical counterargument to this proposal. No matter how light the animal, it cannot be light enough to match the bright sky. The radiance from the sky is orders of magnitude higher than the radiance reflected from the underside of an animal, because, even if colored white to reflect light maximally, an animal's underside is illuminated only by the (far weaker) indirect light that has itself been scattered and reflected by the ground. Only in certain marine animals can a match to such downwelling light be achieved, via bioluminescence as counterillumination (Johnsen 2014).

Matching One Background but Only One Side of the Body Is Ever Visible. If the background is dark and pigment is costly, then a countershading-type pattern is predicted because it is economic to invest in background-matching pigmentation only on the side of the animal that is viewed

against the ground. By itself, this theory predicts a sharp transition between dark and light regions. This theory does not predict countershading in tree-, sky-, or mid-water-dwellers.

3D Background Matching. If an object is perfectly flat, to match the reflected light from the substrate below it must match the reflectance of the background. However, if an object has volume, it must match the background plane's spatial radiance distribution as projected onto the retina of the viewer. Consider a homogeneous grey cylinder on a grey background. Its shading due to its shape will make it visible (see fig. 1*a*). Here, self-shadowing is revealing because of the creation of discontinuities at the body edge. This view was first promoted by Cott (1940). Predators have been shown to use edge properties of prey in detection (Cuthill et al. 2005; Stevens and Cuthill 2006).

Obliterative Shading to Avoid Identification Using Shape. Consider an environment with an equal number of hemispheres and flat disks. A hemispherical prey could match the background equally well by being a hemisphere or a disk, but it is better to look like a disk because other prey are likely to be three-dimensional. Thus, obliterative shading (also sometimes called optical flattening) allows one to appear flatter, where the benefit is appearing 2D when the prey is in fact 3D. Similar reasoning was mentioned in Thayer (1896). In principle, one could be optically flat without matching the background (fig. 1*b*), detection being impeded because the predator's recognition system expects a 3D prey.

Obliterative Shading to Avoid Detection Using Depth. Depth information is not important only for determining object shape per se; if something is identified as lying in a depth plane different from that of the substrate, then that is a potential cue to its presence. Here, the optical mechanism is obliteration of cues from three-dimensionality, as in "Obliterative Shading to Avoid Identification Using Shape," but it is the detection of a "nonbackground" object that is interfered with rather than cues to shape.

Thus, there are two different benefits of being obliteratively shaded. Unlike background matching, which is essentially 2D, obliterative shading is inherently about canceling 3D cues. A caveat is that if the background is textured, then that texture must be matched/mimicked regardless of the viewer's cognitive mechanisms (app. A). This is something that octopuses are adept at, deforming their skin with specialized muscles in order to mimic the surface texture of the substrate on which they are resting (Hanlon 2007; Allen et al. 2014).

How can we discriminate between the above theories of countershading? Is there a logical distinction between any

of them? Is camouflage being used to not be detected or to not be recognized? The sections below tease apart these subtle distinctions.

The Computational Model

In this section, we briefly outline the form and structure of our computational model of countershading. Specific details and assumptions are described in appendix B.

We start by defining an animal to be camouflaged and its background. Here, we choose an idealized cylindrical body, consistent with an idealized caterpillar or snake, resting on a uniform (gray) horizontal background plane. Figure 2 shows how we define the orientation of the cylinder in terms of yaw, pitch, and roll. For example, a cylinder lying horizontally and facing toward the north has coordinates yaw $= 0°$, pitch $= 0°$, and roll $= 0°$. If it lies vertically with its head looking at the zenith and its back facing toward the south, its coordinates are yaw $= 0°$, pitch $= 90°$, and roll $= 0°$.

Our artificial world is built with the open-source software Radiance (Ward 1994; http://www.radiance-online.org). This software uses the standard description of spatial distribution of daylight provided by the International Commission on Illumination (CIE 2003). This allows the simulation of complex scenes under realistic illumination conditions (e.g., we can vary latitude, time of year, and time of day). We consider only achromatic (noncolored) aspects of countershading in our model because in nature its dominant feature is a dorsoventral difference in pigment intensity rather than in hue.

Definitions and Assumptions. We first captured the irradiance falling on a surface patch of our cylinder. Irradiance is a measure of the power, or the number of photons per sec-
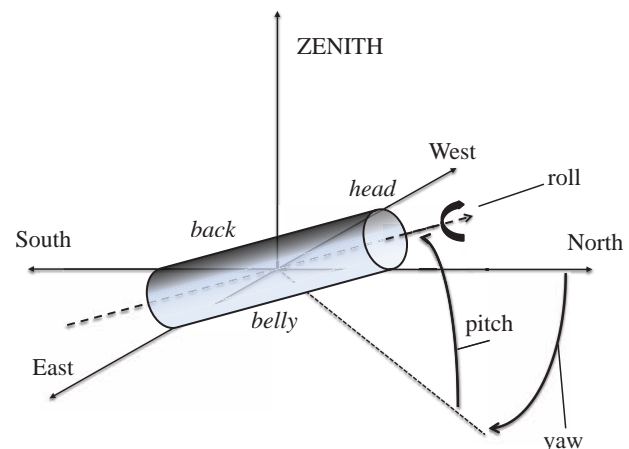
Figure 2: Cylinder orientation in terms of yaw, pitch, and roll. The represented cylinder rests back uppermost and has coordinates yaw $= 45°$, pitch $= 30°$, and roll $= 0°$.

ond, impinging on a surface per unit area. Irradiance thus describes the amount of incident light falling on an object per unit time, whatever the direction of the rays. The next step is to characterize the appearance of a particular location on an object, and to do this, the viewing direction must be taken into account. Radiance describes the power, or the number of photons per unit time, emitted or reflected from a particular location in a given direction per unit angular size. Reflectance is the proportion of incident light reflected from a surface patch, and we use the term "coloration" to refer to the overall pattern of reflectance across the body, even though our simulations are achromatic. We make the simplifying and commonly used assumption (Johnsen 2002; Fleishman et al. 2006) that the animal's surface has a Lambertian reflectance (reflects the impinging light equally in every direction, as opposed to a specular surface that acts as a mirror). In a Lambertian world, once a description of the irradiance is available, the radiance outgoing from a surface is easily computed as the product of the incoming irradiance and the skin reflectance (Johnsen 2002; Bohren and Clothiaux 2006; Fleishman et al. 2006) and is independent of viewer direction. This simplifies the description of optimal coloration for camouflage.

We computed the optimal pattern of reflectance for different forms of potential crypsis from countershading (details in app. B). The aim is to find the pattern of reflectance that provides the radiance that best agrees with the crypsis function under consideration. The forms of concealment we considered were background matching (BM) and obliterative shading (OS). We also considered a more demanding version of obliterative shading (OS+) that also fulfills BM constraints (see fig. 1c).

Modeling Background Matching. In our simple environment, we used the difference in radiance between the rendered animal and the rendered background as a measure of BM. For this difference to be 0, the reflectance of the body should be chosen in such a way that its product with irradiance matches the (constant) radiance of the background. However, this solution is not always feasible. Notably, physical reflectance cannot be greater than 1. Thus, the best achievable BM may be partial only for strong gradients of illumination. For example, because the reflectance saturates at 1, it may not be possible to fully compensate for regions of the animal body that receive little light. In that case, only the part of the body that receives a greater light intensity can match the radiance of the background; BM is only partially fulfilled. The rest of the body will have a white coloration, but its outgoing radiance will be lower than that of the background (see app. B for details).

Modeling Obliterative Shading. In OS, the pattern of coloration conceals 3D form. This means that the typical gradient of radiance, the shading, is counterbalanced by the countershading coloration. One way to fulfill this property is to aim for a flat appearance, that is, no gradation at all. Computationally, we determined the patterns of reflectance that minimize radiance variations. To implement OS, we chose a pattern of reflectance so that its product with the irradiance was constant. Unlike for BM, it is always possible to choose a pattern that fits this rule. However, when the gradient of irradiance is very strong, OS may result in a very dark pattern of coloration.

Modeling OS That Also Achieves BM: OS+. For OS+, we require the outgoing radiance both to be flat and to match the radiance of the background. As appendix B shows, for our simple environment, the mathematical definitions of BM and OS+ coincide. As noted for BM, in some lighting environments and for some values of the background reflectance, OS+ is feasible for only part of the body.

Figure 1 illustrates the logical link between OS and BM. In figure 1b, a cylinder is given a pattern proportional to the inverse of the pattern of irradiance (for a given light distribution). The resulting outgoing radiance is constant, and thus OS is obtained. However, the outgoing radiance does not match that of the background; although shape information has been removed, the object is still potentially conspicuous. Figure 1c shows a cylinder with a reflectance obtained by multiplying the reflectance of the cylinder in figure 1b such that the outgoing radiance matches that of the background. This coloration delivers BM, OS+, and, of course, OS, showing that in such a simple environment BM is an instance of OS (see app. B, fig. B2 for details of the principle underlying the computation). The method directly generalizes to objects with nonuniform spectral reflection (i.e., chromatic; see app. B).

Discoveries from Modeling the Physics/Optics of Optimal Countershading

We next demonstrate how optimal countershading varies with primary and secondary illumination, body orientation, and the reflectance of the background.

Primary Illumination. By primary illumination, we refer to the variation in lighting conditions, where the scene might be sunny or cloudy, light might be filtered through vegetation, and so on. The total radiance given off by a surface patch depends on its reflectance, its orientation with respect to the light source, and the distribution of the light source. In open environments, two extreme cases of light distribution are generally present (e.g., Endler 1993): a sunny sky, where the irradiance shows a strong peak in the direction of the sun, and a cloudy sky, where the irradiance distribution is nearly isotropic in the hemispherical sky.

The sun directly illuminates only a hemisphere of patches directed toward it. Skylight, on the other hand, has a radiance that is orders of magnitude less than that of the sun, but its angular area is huge, making its contribution to the total irradiance substantial.

Figure 3 illustrates the total radiance emitted by surface patches of different pitch (see fig. 2) illuminated by a point light source "sun" at the geographical zenith (dotted curve) and by a perfectly hemispherical "sky" (solid curve). A noticeable feature is that the sun contributes to direct irradiance only for patches whose pitch is between 0° and 90°. This, together with the fact that the irradiance of the sun is far more than that of skylight, explains why sunny weather causes a strong gradient of irradiance on objects. Similarly, sky conditions strongly affect the spatial distribution and intensity of illumination. The distribution of irradiance of a thickly cloudy sky is similar to that of a uniform hemispherical light source. For a sunny sky, the distribution of irradiance is a weighted combination of the irradiance coming from skylight and the irradiance coming from the sun.

To illustrate the effects of lighting conditions, we have chosen standard skies implemented in Radiance (cloudy and sunny) and different elevations of the sun. Figure 4 shows the influence of the lighting conditions on the optimal coloration of a model deer for BM and OS+, for a specific location and date (St. Andrews, Scotland, 56°20′ 25.44″N, 2°47′43.8″W, June 21, noon). The radiance of the background is illustrated by the rectangular box at the bottom left.
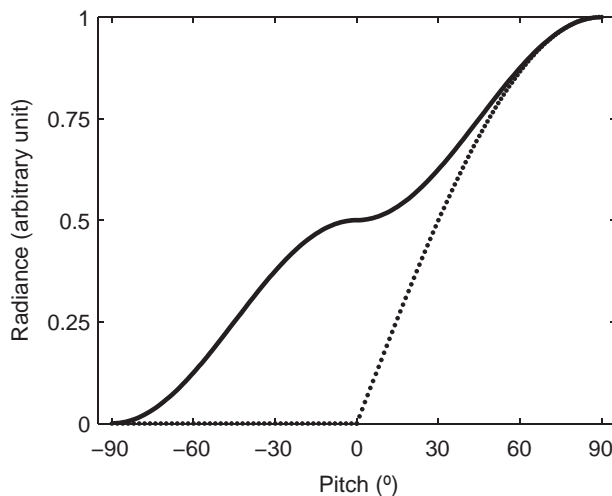

Figure 3: Total radiance given off by a surface patch as a function of pitch when the patch is illuminated by a point light source at the geographical zenith (elevation 90°, dotted curve) or a hemispheric sky (solid curve). Radiances are normalized separately, so their maximum value is 1.

For a cloudy sky (fig. 4*a*, *left*), the gradient of irradiance on the body is shallow. Therefore, the gradient of reflectance to compensate for the gradient of irradiance is also shallow. BM and OS+ are fulfilled across the whole body, as shown by the match between the radiance of the body (fig. 4*b*, *left*) and that of the rectangular box; thus, no information about shape can be extracted from the shading or outline. In contrast, the gradient of irradiance is steep for a sunny sky (fig. 4*a*, *middle and right*), and so is the resulting gradient of reflectance. In the middle panel, for a sunny morning, BM and OS+ are fulfilled across a great part of the body, but some areas of the belly and under the jaw have a lower outgoing radiance; the corresponding shading provides some cues about the shape of the body. This occurs because, by definition, reflectance cannot be greater than 1. Thus, when the gradient of irradiance is steep, parts of the body that receive less irradiance (including the bottom of the belly) have reflectance of 1 (maximally light). This can be observed to an even greater extent in the right-hand panel for a sunny midday. Here, part of the body has a radiance lower than that of the background, and BM and OS+ can be only partially achieved. In these cases, the shading provides some clues about the shape of the body.

To summarize, when a body is in an open environment, its optimal reflectance for crypsis through OS and BM shows a transition between a dark coloration on the back and a light coloration on the belly. The optimal coloration is not constant but depends on weather. When the body receives direct light from the sun, a sharp transition is predicted, and complete BM for the whole body may not be achieved (fig. 4, *middle and right*). On a cloudy day, the distribution of illumination is more homogeneous, and the transition between the darker and lighter parts of the body is smoother, but a gradient is still present (fig. 4, *left*).

Altitude of the Sun: Time of Day, Time of Year. In addition to illumination conditions, optimal coloration for crypsis varies with time of day and time of year. The deer pictured in the middle and right-hand columns of figure 4 have an optimal coloration for sunny weather and different sun elevations. On the right, the sun is at its maximum elevation, whereas in the middle it is lower in the sky. The coloration most cryptic at noon shows stronger gradients from back to belly than the corresponding coloration at 7:00 a.m. A description of how the spatial distribution of such downwelling irradiance (light coming from above) changes with time of day and time of the year can be found in figures B4, B5.

Variations in the altitude of the sun during the day and the year are also governed by latitude. The range of altitudes of the sun between dawn and noon is always large in the tropics (from [0°, 67°] at the solstices to the full range
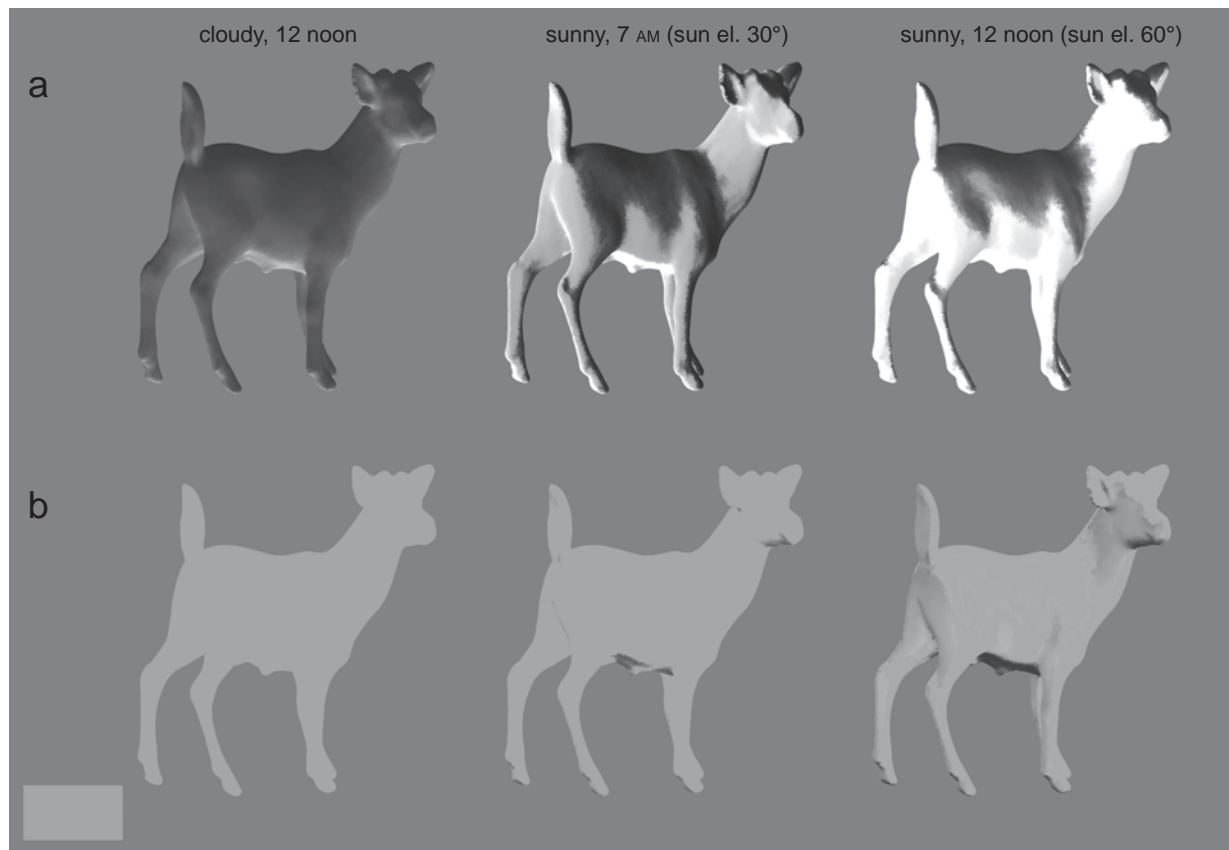
Figure 4: *a*, Optimal coloration, for background matching (BM) and obliterative shading that also fulfills BM (OS+), of a model deer for different lighting conditions. In all cases, the body is oriented toward the sun, and background reflectance is 0.15. *b*, Radiance outgoing from the deer body and that outgoing from the background (rectangular box at bottom left; BM is optimal when this patch matches animal coloration). The distribution of irradiance corresponding to these three different conditions (and other examples) is available in the appendix (fig. B5). The data and model underlying this figure and figures 5–7 are deposited in the Dryad Digital Repository: http://datadryad.org/resource/doi:10.5061 /dryad.pt532 (Penacchio et al. 2015).

at the equinoxes). The range lowers with latitude, for example, at 56°N, from [0°, 60°] at the summer solstice to [0°, 11°] at the winter solstice. Accordingly, optimal colorations for camouflage will vary more across the day at lower than at higher latitudes.

Importantly, the altitude of the sun, not the mean solar intensity, is a driving factor in determining optimal reflectance patterns. Indeed, given a type of illumination (sunny, cloudy), the relative sky luminance distribution depends only on the elevation of the sun (CIE 2003).

Angle of Viewer. By definition, a Lambertian surface has the same outgoing radiance for any viewing direction. Thus, optimal patterns of reflectance to implement OS and BM for a Lambertian body do not depend on the viewer position, as long as the background remains the same as the viewer changes position. If the viewer is sufficiently low that the target is viewed against the sky, then no coloration can conceal it; it will be silhouetted because the radiance of the sky will

always be greater in magnitude than the reflected light from the animal (see "Matching Multiple Backgrounds"). This is not to say that it will be conspicuous—if the sun is behind the target then the viewer may be blinded—but no surface coloration can match the sky's radiance.

Body Orientation. The optimal pattern of reflectance varies with body orientation. We illustrate this point by using our idealized cylindrical animal. Figure 5 demonstrates that there is variation in the optimal coloration for a cylinder that lies in four different positions. When the cylinder lies horizontally, back uppermost, and oriented south-north (sun-facing at noon), the ratio of the irradiance falling on the back of the body to that falling on its belly is very high. The optimal reflectance for this orientation shows a strong gradient to compensate for this high ratio (fig. 5*a*). Under the same lighting conditions, the gradient of reflectance is even stronger when the pitch of the cylinder is 30° (fig. 5*b*), since the back of the cylinder more directly faces the sun. In contrast,
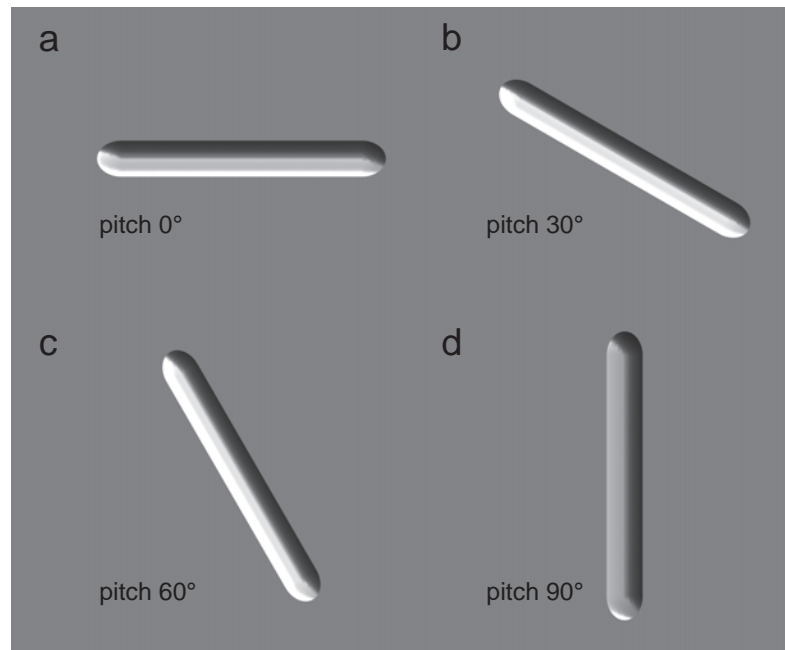
Figure 5: Optimal reflectance varies with body position (yaw, pitch, and roll). The panels display the optimal coloration for a cylinder with yaw = 0° (i.e., head directed toward the north), roll = 0°, and pitch = 0° (*a*), 30° (*b*), 60° (*c*), or 90° (*d*). Irradiance corresponds to June 21 at noon in St. Andrews, Scotland (sun elevation 60°), with a standard CIE (Commission Internationale de l'Eclairage) sunny sky.

the optimal reflectance shows a smaller gradient when the cylinder lies vertically (fig. 5*d*), because the belly is now illuminated by half the hemisphere of the sky. In this example, the vertical orientation is the only orientation that enables BM and OS+ to be fulfilled.

In all the examples so far, we have assumed that the long axis of the body is oriented toward the sun. Since the spatial distribution of irradiance is symmetric with respect to the azimuth of the sun, this assumption delivers symmetrical optimal patterns, as observed in the vast majority of species. However, body orientation can have an influence for low sun angles (fig. 6). In all the plots, the coloration has been optimized so that the right part of the body achieves BM and OS+ (fig. 6*a*(*i*), body coloration matches background; rectangular patch in figure). Coloration for the left side of the body is set to be the same as that for the right (we impose symmetry). In figure 6*a*, the body is orthogonal to the sun direction. The radiance given off by the left side of the body is much lower than that from the right side. When viewed from the left (fig. 6*a*(*ii*)), the body pops out from the background; BM is not achieved. In figure 6*b*, the angle between the body and the azimuth of the sun is small (15°), so both faces are exposed to more similar distributions of light. Nevertheless, BM is not achieved for the left side of the body (fig. 6*b*(*ii*)), and strong cues about the shape are provided by the shading; both 2D and 3D camouflage are broken.

Influence of the Reflectance of the Background. Photons come from the sky and from objects that reflect light. The Radiance software allows the incorporation of indirect illumination through multiple bounces; thus, we can explore how objects in the environment contribute to the irradiance of the body. We measured how optimal reflectance for BM varies with the reflectance of the background, ranging from 0.05 for a dark wet soil to 0.85, typical of fresh snow (McEvoy et al. 2012). Figure 7 shows the optimal reflectance pattern for sunny (fig. 7*a*) and cloudy (fig. 7*b*) conditions. The higher the reflectance of the background, the earlier the saturation point (where reflectance reaches its maximum value of 1) of the cylinder's optimal reflectance. These variations predict that, for animals that spend most of the time on light backgrounds, the dorsoventral gradient in shading is less steep (with the animal on average lighter), and the transition to lighter shading occurs nearer the spine.

Discussion

To date, the only quantitative test of optimal countershading with a real environment involved the empirical determination of cast shadows on a physical model organism (Allen et al. 2012). While a gold standard for prediction, that study was specific to one shape of organism and, necessarily, sampled a limited range of environments and conditions. The approach we present here allows modeling
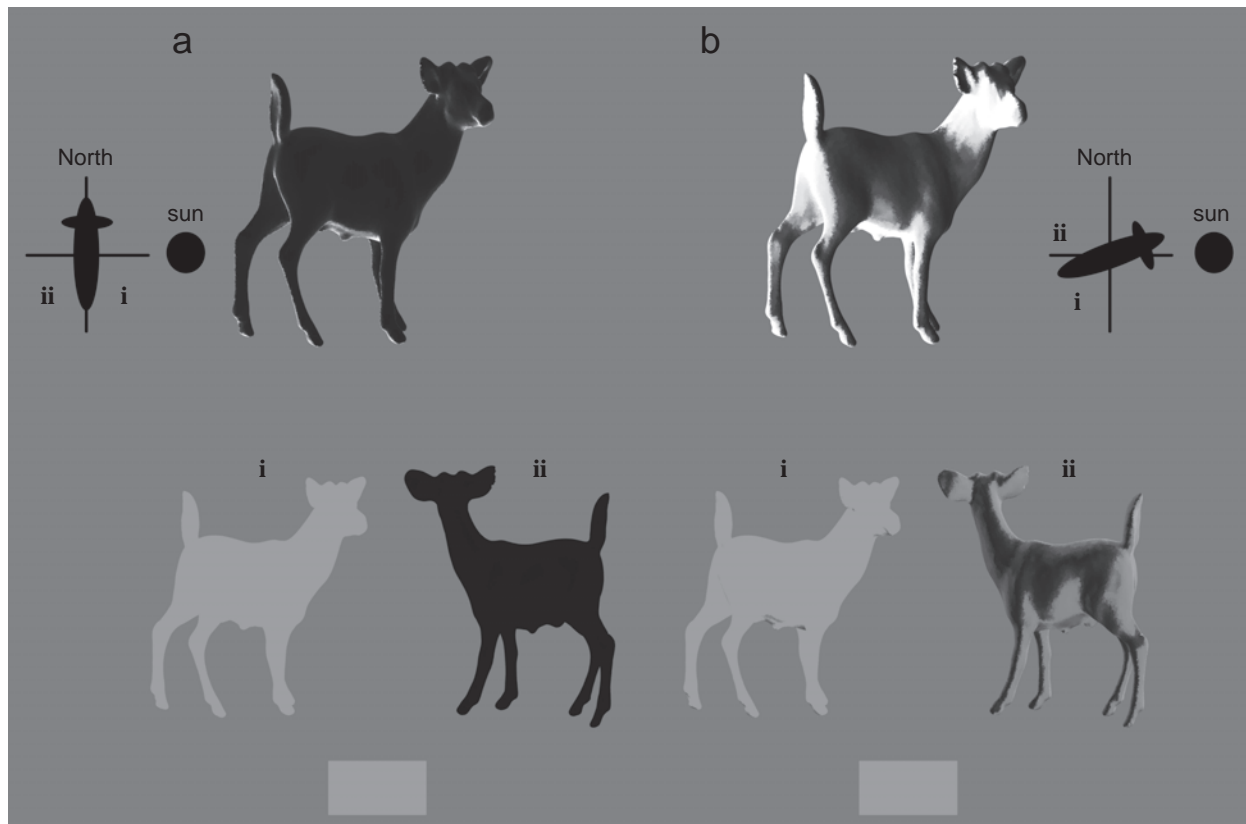
Figure 6: Conditions are 7:00 a.m., June 21, in St. Andrews, Scotland, with a sunny sky. Sun elevation = 30°, azimuth = 90°, (sun is in the east). *Top*, symmetrical coloration of a model deer optimized so the right side of the body achieves background matching (BM) and obliterative shading that also fulfills BM (OS+). *Bottom*, radiance outgoing from the right (*i*) and left (*ii*) parts of the deer body and radiance outgoing from the background (rectangular patch). *a*, 90° between the body and the sun azimuth; BM and OS+ are fulfilled for the right side of the body (*i*) but not the left (*ii*). *b*, 15° between body and sun azimuth; BM and OS+ are also fulfilled for the right side of the body (*i*) but not the left (*ii*).

of any shape and derivation of predictions (summarized below) for a very wide range of light environments, at any place and at any time. We encourage empirical testing of our predictions about the effects of direct versus indirect sunlight, orientation, time of day, year, latitude, and background reflectance. Our model is available in the Dryad Digital Repository (http://datadryad.org/resource/doi:10.5061/dryad.pt532; Penacchio et al. 2015) and can be run to generate predictions to test any of these effects. The approach can also be generalized to underwater light environments by using, instead of Radiance, software such as HydroLight (Sequoia Scientific, Bellevue WA) to generate irradiance distributions. Our modeling has allowed us to make several specific and novel discoveries.

Logical Distinction between OS and BM

We drew a logical distinction between the optimal countershading required to obliterate 3D cues from shading (OS) and that to achieve background matching (BM or OS+). In the early accounts of countershading, these dis-

tinct benefits were conflated (Poulton 1890; Thayer 1896, 1909; Cott 1940). We have shown that countershading is not conclusive evidence for BM or OS. Countershading that achieves BM implies only that the viewer from which the animal is concealed can detect a 2D difference in intensity, a rather minimal visual capacity. In addition, even finding animals with coloration that achieves OS but not BM (fig. 1*b*) would not be proof that the coloration is an adaptation to defeat shape-from-shading mechanisms in the viewer; it may simply not be camouflage.

Conclusion. The analysis of animal color patterns can never differentiate between these hypotheses; the only way of testing whether nonhuman animals use shape-from-shading cues is a behavioral test to show that they are deriving depth information from that shading.

Should Animals Face the Sun?

We have found that by far the largest potential influence on achieving crypsis through countershading is orientation with respect to the sun. Orientation interacts with lat-
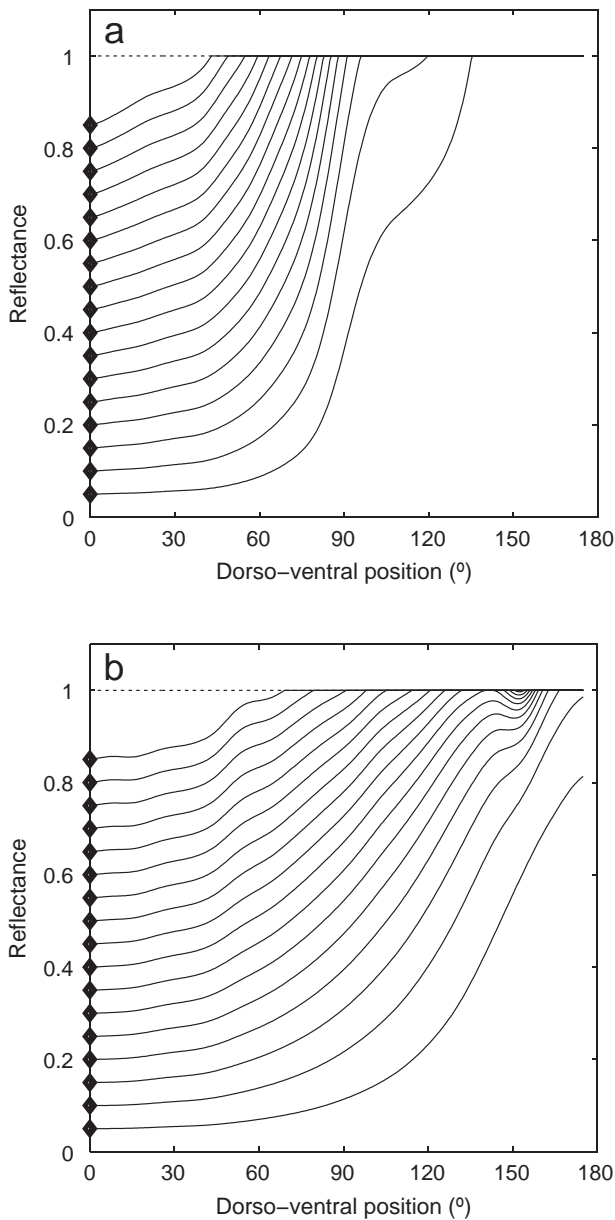
Figure 7: Reflectance versus position on vertical transect of the body for a sunny sky (*a*) and a cloudy sky (*b*) on June 21 at noon in St. Andrews, Scotland, for background reflectance from 0.05 to 0.85. Background reflectance reads as the *Y*-intercept for each curve, because the top of the back of the cylinder has the same orientation as the background, hence receiving the same light per unit area.

itude, season, and time of day (they affect the sun's altitude) and with cloud and vegetation cover (they affect the strength of directional illumination). At midday in the tropics, it does not matter which way an animal faces; the optimal countershading will be the same. As soon as the sun is lower and the animal ceases to face toward or away from

it, the pattern of shadow on the two sides of its body will differ. But almost all animals are bilaterally symmetrical. Except in the tropics at midday, this places a major behavioral constraint on the effectiveness of countershading as camouflage: the animal would always need to face toward or away from the sun. As soon as it changed orientation, it would become conspicuous. This constraint is relaxed if the lighting is more diffuse (under cloud or vegetation).

Prediction. Animals will commonly face toward or away from the sun to maximize the crypsis benefits of countershading.

Optimal despite Changes across Day and Season?

How should an animal be countershaded, given that the optimal pattern will differ across the day and time of year? If the animal has a limited range of activity times or seasons, optimization for a narrow range of conditions can be achieved. Similarly, if the environment is one where illumination is diffuse (e.g., predominantly cloudy skies, forest canopy, or microhabitats where vegetation routinely filters direct sunlight), then optimal countershading will vary less with time of day, because the directionality of the illumination varies less. This will also be true if the sun is so low in the sky that skylight dominates (i.e., at high latitudes and during twilight).

Prediction. The "face-the-sun" rule predicted above could be relaxed for animals living in cloudy regions, in dense vegetation, or at high latitudes or if animals typically break cover only at dawn or dusk.

Living on a Light Substrate

If the substrate is light, then the optimal color for BM is also light, and so the optimal dorsoventral gradation in shading will be shallow and less variable with time of day. However, on very light substrates, countershading for background matching may not be achievable because the animal's reflectance cannot be greater than 1. For example, polar bears and other animals that live on snow and ice cannot both match the high background reflectance and obliterate shadow.

Prediction. Animals living on light substrates (sun, snow) should exhibit less countershading than those living on dark ones, because countershading cannot be optimized.

Is There an "Average Optimal" Countershading?

Where illumination can vary between direct and diffuse or animals are active throughout the day, what trade-off should be adopted? The optimum will depend on the relative costs of departing from perceived flatness (OS) or background matching (BM). For example, if we have a range of

intensities and want to be as close to flatness as possible across the range, the best pick is likely to be a middling intensity. If we primarily want to avoid convexity, we should pick the brightest intensity; then, for lower intensity ranges, the object will be "over-countershaded" and could, in principle, appear concave. In particular, if the countershading is very strong, so that the body looks flat for the strongest gradient of radiance across the year, the body will never look convex.

Prediction. Measurements of actual countershading patterns on real animals would determine which, if any, of the two distinct strategies is used: (1) looking as flat as possible at all times or (2) never looking convex.

Heterogeneous Backgrounds

We have modeled an animal viewed against a homogeneous gray background. Real backgrounds are heterogeneous, and an animal can be viewed against backgrounds as different as black volcanic rock and the sky. We have already explained why no surface coloration can match the sky's radiance ("Matching Multiple Backgrounds" and "Angle of Viewer"), so matching this type of background is within the reach of only bioluminescent organisms. A heterogeneous background will certainly demand different coloration for camouflage, but this is an issue separate from countershading. It is straightforward, in principle, to modify our model to incorporate a colored and/or heterogeneous background and generate the predicted coloration that would combine matching of this heterogeneous background with countershading. We have avoided this here because the model would become a habitat-specific prediction for the overall camouflage pattern of a species rather than a general prediction for optimal countershading. We encourage biologists working on particular species in specific habitats to adapt our model to predict the color patterns that would satisfy both background texture matching and obliteration of the gradients caused by illumination.

Summary and Conclusion

We have developed a computational model of countershading for crypsis based on simulating animals in realistic lighting environments. We make this freely available for others to test the hypotheses put forward. Importantly, it allowed us to draw a logical distinction between the previously rather muddled definitions of BM and OS. Our model allowed us to discover important constraints on countershading and has provided predictions for how animals should look, depending on their lifestyle and location. Just how close to the optimal the countershading must be for an animal to avoid detection and identification and whether animals actually use shading cues to recover depth and so

3D shape information are empirical questions that should be addressed in future studies.

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Aglia tau caterpillars (*Tau emperor*) have a darker belly and a lighter back; they usually stand upside down. Photograph by Olivier Penacchio.