



What, if anything, is the adaptive function of countershading?

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Countershading, the gradation of colour from dark on the dorsum to light on the ventrum, is generally considered to have the effect of making organisms difficult to detect. The mechanism that facilitates this form of crypsis is often considered to be concealment of shadows cast on the body of the animal. We review the current empirical evidence for the cryptic function of countershading and for the mechanism underlying it. We argue that there is no conclusive evidence that countershading per se provides any selective advantage in terrestrial or aerial environments. However, the highly refined adaptations of some marine organisms to match the different background light conditions against which they are set when viewed from different aspects strongly suggest an adaptive advantage to countershading in these environments. In none of the cases discussed in this review was the conventional explanation of self-shadow concealment a more plausible explanation for countershading than the alternative explanation that the dorsum and ventrum experience different selection pressures (often associated with background matching).

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Writing in another age A. H. Thayer (1896, pp. 124–125), painter and naturalist, proposed a ‘beautiful law of nature’ which he described ‘as the law of gradation in the coloring of animals [that] is responsible for most of the phenomena of protective colouration except those properly called mimicry’. Thayer (1896, page 125) noted that ‘animals are painted by nature, darkest on those parts which tend to be most lighted by the sky’s light, and vice versa’; and according to Thayer (1896, page 125), this pattern of shading (now called countershading) ‘makes [an animal] appear not to exist at all’. Thayer (1896) used painted animals and models to demonstrate this vanishing trick (see Fig. 1). Reporting a demonstration by Thayer to the Oxford University Museum, Poulton (1902, page 596) wrote that ‘In fact, the model which is the same shade of

colour all over appears to be a different shade everywhere because of the difference in illumination: while the model which is a different shade at every level appears to be the same shade all over because the differences of shade exactly counterbalance differences in illumination’. (Reprinted by permission from *Nature*, 1902, **65**, 596, Macmillan Publishers Ltd.)

This mechanism of self-shadow concealment (Kiltie 1988), as it is now called (also described by Poulton himself, e.g. Poulton 1888), is supposed to reduce the capacity of a predator to recognize the animal as a three-dimensional, solid object, and hence its chance of detecting it. Thayer (1902, page 597) was sufficiently confident that this mechanism of self-shadow defensive concealment is robust that he wrote: ‘All who believe in Natural Selection will, of course, feel that this colour law is at work, and since it is so almost universally in use, and accounts, apparently so almost exhaustively, for all the attributes of graded animal coloring, I believe it will ultimately be recognised as the most wonderful form of Darwin’s great Law’. (Reprinted by permission from *Nature*, 1902, **65**, 597, Macmillan Publishers Ltd.)

Thayer was certainly correct that countershading is a common trait in many animal species, and this view has

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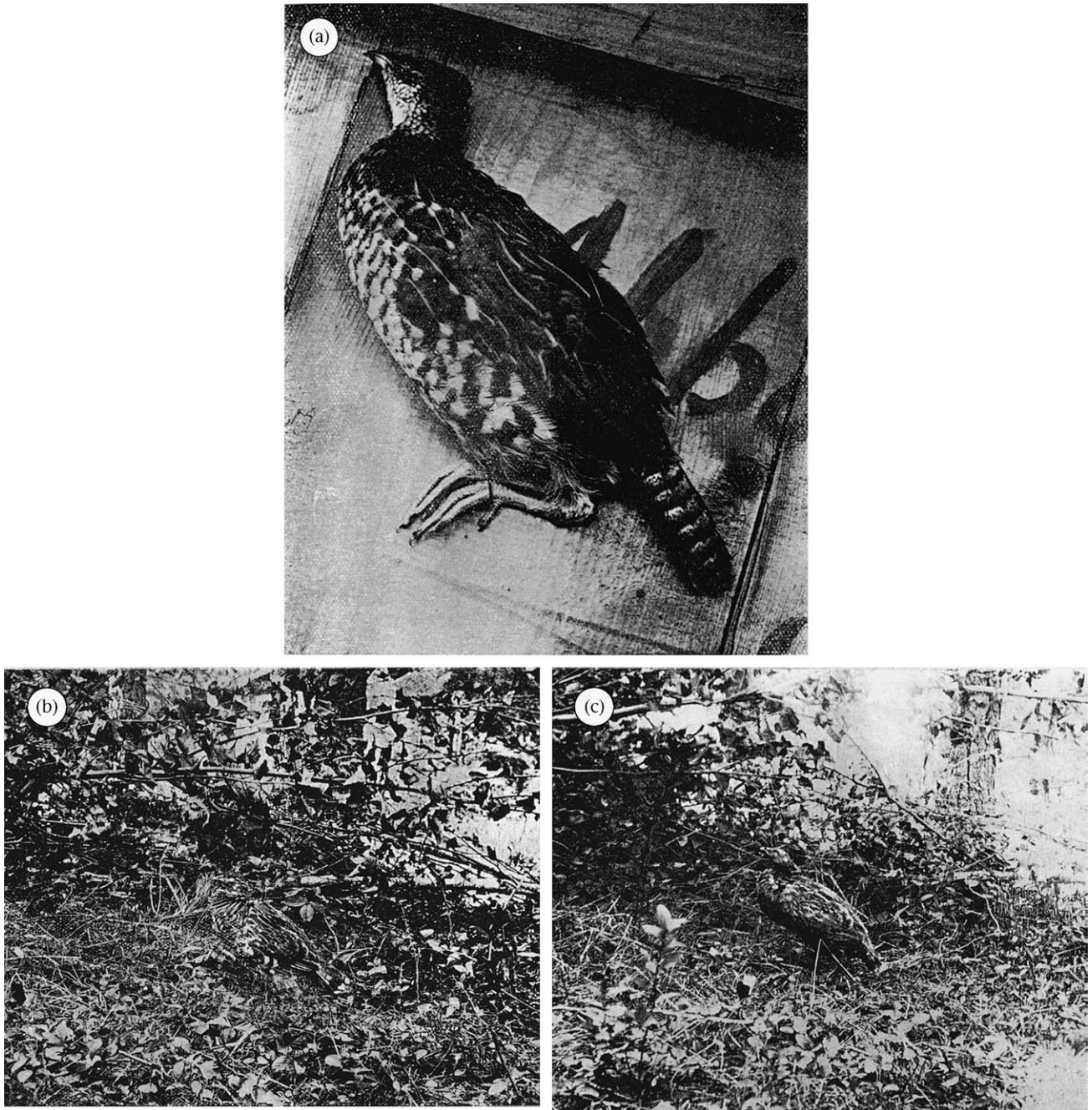


Figure 1. (a) Example of countershading in a dead grouse used by Thayer (1896). (b) Grouse positioned by Thayer as 'in life'. (c) Grouse positioned by Thayer as 'in life' but here the countershading has been removed by tinting the underside of the animal with dye. Reprinted from Thayer (1896) with kind permission from *The Auk*.

been shared over the decades by a number of authors (notably S. J. Gould 1991, page 213, mirroring Thayer, wrote that 'light bellies [are] perhaps the most universal feature of animal coloration'). In addition, the presence of shading is indeed known to make solid objects stand out from their backgrounds, at least to the human eye (Ramachandran 1988). In theory at least, an animal could be coloured in such a manner that visually informative shading would be obliterated, thereby reducing the chance of predators recognizing it as prey. Gould (1991,

page 213) agreed at least that shadow self-concealment is real and important, writing that: 'Thayer correctly identified the primary method of concealment—a device that makes creatures look flat'. Authorities such as E. B. Ford (e.g. Ford 1957) used the idea to explain paler undersides in larvae of the purple emperor, *Apatura iris*, and brimstone, *Gonepteryx rhamni*, butterflies (and see discussion in Cott 1940; Edmunds 1974, 1990; Sheppard 1975). However, the evidence for this mechanism is at best questionable and, as Kiltie (1988) argued, the

frequency of the phenomenon does not prove the existence of a particular cause; countershading may be common, but for a plurality of reasons of which self-shadow concealment may, or indeed may not, be one.

To distinguish the trait in question from Thayer's causal explanation for it, we refer to a pattern of dark/light dorsoventral patterning as countershading, and Thayer's mechanism as self-shadow concealment (Kiltie 1988). Note that this is a very general definition of countershading that does not specify whether the transition from dark to light coloration is abrupt or gradual, a point to which we return in the discussion. It is important to discriminate self-shadow concealment from background matching, another likely (perhaps more likely) mechanism driving countershading, especially in aquatic organisms (Kiltie 1988). In a situation where light comes from above, an aquatic individual viewed from below must try to match the bright downwelling light to reduce the ease with which it can be detected. Conversely, when viewed from above, it should match the backdrop of the dark deeper waters. This too should generate countershading and relies only on the well-understood mechanism of background matching.

Since the idea of self-shadow concealment as the mechanism driving countershading is now more than a century old, is still generally accepted as a plausible and important explanation (e.g. Edmunds & Dewhirst 1994; Braude et al. 2001; Encyclopaedia Britannica 2001) and has not been reviewed for some time (Kiltie 1988), we intend here to review the literature that claims to support cryptic benefits from countershading. In particular, we focus on (1) whether the results of direct experiments and other analyses enable the general conclusion that crypsis is indeed enhanced through countershading and (2) whether any demonstrable advantage is gained through either the 'classical' mechanism of self-shadow concealment, the alternative background-matching mechanism or indeed some other mechanism(s).

DIRECT EMPIRICAL TESTS

One way to examine the hypothesis of defensive countershading by self-shadow concealment is to test the prediction that, when illuminated from above, a countershaded animal does indeed appear to be uniformly shaded when viewed from the side. Thus Kiltie (1989) took photographs of taxidermic mounts of grey squirrels, *Sciurus carolinensis* (a species identified by Thayer as an example of countershading). The mounts were illuminated from above and photographs were taken when placed horizontally (as if running along a branch parallel to the ground) and vertically (as if running up the trunk of a tree, perpendicular to the ground). In both cases the specimen was placed in a natural position (with its feet in contact with the substrate) and a photograph taken of the animal's flank. The specimens were also laid on their side, so that a photograph of the dorsum could be taken. The pictures were then analysed by taking transects and looking for a correlation between pixel brightness and position on the axis of illumination.

A strong, positive correlation was assumed to indicate a pronounced shadow and therefore high visibility. When placed horizontally, the flank views showed lower correlations than the dorsal views, consistent with the hypothesis that countershading enhances crypsis of animals viewed from the side. However, the opposite was true in the case of vertically oriented specimens and this suggested to Kiltie that countershading may work when squirrels are horizontally but not vertically oriented. However, interpretation of these results relies on assuming that a strong correlation is directly indicative of high visibility, something that the study does not explore. In addition, Kiltie (1989, page 543) noted that on horizontal substrates, 'the degree of shadow obliteration is imperfect and hence of questionable value in deterring predators'.

More direct empirical approaches have examined the behaviours of predators presented with real or artificial prey. In an attempt to test whether countershading enhanced crypsis, de Ruiter (1956) used freshly killed reverse-countershaded caterpillars (i.e. with a light dorsum and dark ventrum) as prey and three captive jays, *Garrulus glandarius*, as predators. Some caterpillars were tied in their naturally occurring position beneath twigs (such that their dark side was uppermost) and others in the reverse position above twigs (such that their light side was uppermost). Consistent with the prediction that countershading enhances crypsis, de Ruiter found that normally positioned prey were taken less frequently than those put in reverse positions. However, since it can equally be argued that the jays simply preferred prey positioned above rather than below the twigs, the results of this experiment do not represent definitive evidence that countershading enhanced crypsis.

A second, direct test was reported by Turner (1961), who used a now much copied experimental set-up in which garden birds were predators and dyed pastry baits were presented as artificial prey. Turner (1961) found that wild birds took uniform green, artificial pastry prey more than simultaneously presented countershaded prey. However, Edmunds & Dewhirst (1994) pointed out that since the countershaded prey were a slightly brighter hue than the uniform green controls, an aversion to this brighter hue might explain the results, rather than the results demonstrating any cryptic effects of countershading itself. In a subsequent experiment, Edmunds & Dewhirst (1994) rectified this problem by making two types of pastry: light and dark green. From these they fashioned four types of prey: uniform dark, uniform light, countershaded (dark on the top half, light on the bottom) and reverse shaded (countershaded prey turned upside down).

Equal quantities of these four types were presented to wild garden birds. Uniform light prey and reverse-shaded prey were taken approximately equally (96 and 82 items taken, respectively, a nonsignificant difference; Wilcoxon test); light prey were taken significantly more often than uniform dark prey (96 versus 41 items, respectively); countershaded prey were taken significantly less often than reverse-shaded prey (18 versus 82, respectively) and, crucially, countershaded prey were taken significantly less than dark prey (18 versus 41, respectively). This is, in our view, one of the best and most important direct

experimental attempts to demonstrate that countershading, by whatever mechanism, can enhance crypsis in terrestrial habitats. Indeed, Edmunds & Dewhirst's study is now cited as evidence for the effects of countershading on camouflage (e.g. Braude et al. 2001) and their results are highly suggestive of such an effect.

However, a demonstration that countershaded prey were attacked less often than the other prey forms is necessary, but is not in itself sufficient to confirm an effect of countershading in enhancing crypsis. We need, in addition, to be able to rule out the possibility that all four prey types were equally easy to detect, but the birds showed postdetection biases in prey choice. Thus, the birds might have been particularly averse to countershaded prey or simply preferred the other three prey types. Eliminating these alternatives could be achieved by presenting the four prey types on a contrasting, white background as well as on one such as a lawn against which the colours match.

In acknowledging that the birds may have shown an aversion to countershaded prey, Edmunds & Dewhirst proposed two lines of refutation. First, they suggested that an aversion by predators to edible prey with horizontal stripes would not benefit a predator and hence would not be stable over an evolutionary timescale. An inhibition of attacks on the two-toned prey would then soon be wiped out. Second, they argued that an aversion to two-toned prey per se is an unlikely explanation given that the predators attacked reverse-shaded prey at a high rate not significantly different to that with light prey.

Although they obviously have merit, neither of these refutations, in our view, entirely and conclusively removes the problem that postdetection preferences may explain the results. One reason for this view is that neither of Edmunds & Dewhirst's refutations rules out the possibility that the avian predators showed a special aversion to countershaded but not to reverse-shaded prey. This reservation could be merely devil's advocacy, since we know of no evidence for an association between countershading and noxiousness in prey.

However, a more challenging interpretation is that the birds were unfamiliar with countershaded, two-toned food items and preferred uniformly light and dark items because these were generally more familiar (cf. Raymond & Allen 1990). The fact that the birds took reverse-shaded prey at a rate not significantly different to that with light prey may indicate that the birds could not discriminate a uniformly light prey from a prey that is light on top and dark on the bottom. One reason for an absence of discrimination might be that if shadows were cast on the ventral areas of the baits, then the direction of the light/dark gradient would be the same in both light and reverse-shaded prey (i.e. lighter on top than the bottom), making them appear similar to predators (field observations indicate that reverse-shaded baits are to human observers visually very similar to light prey when presented on lawns: M. Speed, unpublished data). If this explanation were true, then simple unfamiliarity, rather than enhanced crypsis, could explain Edmunds & Dewhirst's results. Hence, without diminishing the importance of Edmunds & Dewhirst's study, further replication

with prey on a colour-matching and a contrasting background is, in our view, essential for a conclusive demonstration that countershading enhances crypsis.

The experiments of Kiltie, Ruiter, Turner and Edmunds & Dewhirst represent, to our knowledge, the sum total of published manipulative experimental tests of the adaptive value of countershading. None provides clear and unambiguous evidence that countershading reduces detectability; only Kiltie's experiment probes the specific mechanism that might lead to such a reduction and even here there is no test of alternative hypotheses such as background matching. In the absence of clear direct tests, we next turn to indirect evidence from nonmanipulative studies to evaluate evidence that countershading contributes to crypsis.

INDIRECT EVIDENCE

The role of countershading in naked mole-rats, *Heterocephalus glaber*, has recently been evaluated by Braude et al. (2001). Most naked mole-rats are countershaded, with a purple-grey dorsum and pale-pink ventrum. The exceptions (newborn pups, most queens, breeding males and animals older than 7 years) are uniform pink. Braude et al. (2001) considered the case that countershading in these animals has one or more reasons for existence, suggesting that countershading: (1) is a vestige of adaptive countershading in surface-dwelling ancestors; (2) provides protection from ultraviolet light; (3) facilitates thermoregulation; (4) provides protection from abrasion; and (5) facilitates camouflage for those individuals (typically younger than 7 years) that disperse above ground. Crucially, Braude et al. were open minded about the precise mechanism by which countershading can enhance or generate crypsis; thus self-shadow concealment and background matching were both entertained as equally plausible explanations.

After weighing the evidence, Braude et al. concluded that their data were most consistent with the camouflage hypothesis. Dark dorsa may help camouflage the animals, especially if, Braude et al. suggest, dispersal happens only at night, when visually oriented birds of prey that use moonlight illumination are the most likely predators. However, rather than providing a self-concealing shadow mechanism, countershading may simply, as Braude et al. suggested, be a by-product of the ventral side remaining pink because it is not visible to predators, especially with the short legs of the mole-rat. In addition, there may be nontrivial costs associated with the production of melanin or other dark pigments in this and other animals (either in energetic terms or because it reduces the availability of tyrosine for other important functions; see examples & discussions in Nappi & Vass 1993; Wilson et al. 2001; Thompson et al. 2002). Hence countershading may well be a product of the optimization of the use of costly pigmentation. Braude et al.'s study is important, therefore, not least because the authors bring an open mind to the phenomenon of countershading, rather than relying unquestioningly on traditional explanations.

In a key example in aquatic organisms, Korner (1982) found three examples of a species of fish louse, *Anilocra*

physodes, that showed countershading. These lice were each attached to the flank of a fish that itself showed countershading. One particular point of interest is that two lice were attached to the right flank of the fish with their head facing forward, but the other was attached in the same position on the left side. Despite this, all the lice showed darkening on their upper side, even though morphologically this was a different half of the louse in the two cases. Korner suggested that the colour pattern emerges after the louse attaches as a more plausible explanation than postulation of the existence of two flank-specialist colour morphs.

Furthermore, Korner proposed two benefits that the louse might receive from countershading: avoiding being detected by cleaner fish, and reducing the risk of being eaten along with its host by a predator. The mechanism of crypsis for the louse was, in Korner's view (1982, page 250), that countershading 'increases the optical illusion of flattening in the attached fish louse' and Kiltie (1988) later agreed with this interpretation. However, while a fascinating piece of natural history, this study provides no evidence for the adaptive value of countershading in this louse. Indeed, countershading could be interpreted more simply as a means to background matching when viewed from above or below (and perhaps when viewed from the side against the countershading of the fish's flank), rather than self-shadow concealment.

Some catfish of the family Mochokidae swim with their ventral side uppermost while feeding from (or breathing at) the water's surface at night (Chapman et al. 1994; Stauffer et al. 1999 and references therein). These fish show reverse countershading with a light dorsum and dark ventrum. Particularly interesting is the report by Nagaishi et al. (1989) that one of these species (*Synodontis nigriventris*) is uniformly coloured by day (when it avoids the surface) but changes to reverse countershading at night. However, we note that there is again no evidence available to differentiate between self-shadow concealment and background matching as potential drivers of this coloration.

Seabirds that feed on fish at medium depths seem to be countershaded with greater frequency than either bottom or surface feeders (Cairns 1986; Bretagnolle 1993). Cairns, in particular, concluded that this coloration provides self-shadow concealment. However, no evidence was presented to support this. Furthermore, it seems to us that such predators would particularly value being hidden from prey beneath them in the water column, rather than to the side. There is good experimental evidence that a white underside confers cryptic benefits to diving seabirds during flight when they are foraging for fish in surface waters (Phillips 1962; Cowan 1972; Götmark 1987). Hence, we have evidence for background matching from below (if not from above), but no evidence for self-shadow concealment.

Several aquatic animals use bioluminescence apparently to produce light that matches the downwelling ambient light so as to make detection from below more difficult; this is often called counterillumination (see Widder 1999 for an overview). Some species alter the intensity and wavelength distribution of the light they produce

appropriately as they change depth, so as to match the changing downwelling light (Young & Roper 1976; Young & Arnold 1982; Young 1983). Some animals also produce light that matches the angular distribution of the ambient light (Latz & Case 1982). When some countershaded cephalopods change from their normal orientation they can often rapidly change their chromatophore use over the body so as to retain countershading in their changed orientation (Ferguson et al. 1994). Although there is no direct evidence, we agree with Kiltie (1988) that only the most cynical would argue that these adaptations are not fine-tuned to reduce the conspicuousness of the animals involved. Also, to the extent that light production is biased to the dorsa of animals, this tends to generate countershading. However, the primary mechanism seems once again to be background matching rather than self-shadow concealment, since in the three-dimensional world of the open ocean, attack can come from any direction, not simply from the side. Indeed prey can generally be detected most easily from below (against the strong downwelling light).

Many mid-water fish are predominantly silver on their lateral and ventral aspects but darker on the dorsum. This is also likely to be an adaptation to provide background matching (Denton 1971) with the dark dorsum matching the dark deep waters below, whereas the reflective ventral/lateral fish scales may match the intensity and wavelength of downwelling background light (so-called 'radiance matching'). Shashar et al. (2000) showed that cuttlefish, *Sepia officinalis*, predators are able to discriminate light reflected from fish scales from background light by using the partial linear polarization that is characteristic of reflected, but not scattering background, light. Shashar et al. (2000) proposed that sensitivity to linearly polarized light in the cuttlefish may therefore function as a means of breaking the background-matching countershading camouflage of light-reflecting silvery fish. None the less, a role for self-shadow concealment cannot be ruled out for this or other aquatic predators. Despite the considerable research that has been devoted to understanding the physiology of reflective surfaces (Herring 1994), the key experiments are lacking.

In summary, several studies have used indirect evidence from observation of unmanipulated systems to infer the concealment mechanism for observed countershading. However, none of these studies satisfactorily demonstrates that self-shadow concealment is a more plausible candidate explanation than any alternatives. We find that in most cases, background matching as an explanation is at least as plausible as (and often more plausible than) self-shadow concealment. However, these unmanipulated studies, by their very nature, do not allow definitive evaluation of the relative plausibility of different mechanisms.

DISCUSSION

In theory, background matching could act to produce countershading on flying animals as well aquatic ones. However, it is likely to be less important in air than in water. One reason for this is that flying animals will seldom need to hide from eyes both above and below. For

example, owls would benefit from hiding from their mammalian prey beneath them, but have little to fear from above. Most attacks on flying animals are mounted from above, where the attacker can work with gravity rather than against it. At least in terrestrial ecosystems, the background against which flying animals would be seen from above is less uniformly dark than in aquatic habitats. Both these arguments suggest that background matching will be a less potent mechanism for generating countershading in flying animals than in swimming ones.

However, it is also true that the classical explanation of countershading (self-shadow concealment) may also work better in an aquatic environment than in aerial or terrestrial ones. The reason for this is that scattering of light in water tends to lead to an unchanging distribution of light direction, whereas in terrestrial ecosystems the direction of the strongest light source, the sun, changes markedly throughout the day, and is strongly affected by cloud cover, and so the position and intensity of shadowing change throughout the day.

What about terrestrial animals? An alternative explanation for countershading is that the dorsal surface of the animal is pigmented to give some adaptive advantage (crypsis or protection from ultraviolet light or abrasion; see discussion in Kiltie 1988; Braude et al. 2001) and the ventral side is unpigmented because there would be no similar benefit to pigmenting this area and pigmentation is itself costly. This explanation is similar to background matching, in that it argues that the phenomenon of countershading is not a primary adaptation in itself; it is rather an epiphenomenon, the result of different selection pressures operating on the dorsal and ventral surfaces of the animal. Appealing though this general explanation is, we note that melanin (a commonly occurring dark pigment) has complex proximate functions; in addition to those already mentioned, melanin is used to generate intraspecific signals of quality (e.g. Fitze & Richner 2002) and in antiparasite defences (e.g. discussions and data in Mackintosh 2001; Wilson et al. 2001). Hence we should not exclude the possibility that the widespread phenomenon of countershading results from the action of many different proximate and ultimate mechanisms and therefore has no simple general explanation.

To include as many lines of evidence as possible, we have adopted a very general definition of countershading, without specifying how gradually or abruptly dark coloration changes to light. It is clear that there is much variation between countershaded species in this spatial gradient. It does seem that (except for oddly shaped objects) self-shadow concealment requires a gradual change from dark to light. However, we do not consider that an abrupt change should necessarily be predicted if background matching is the mechanism underlying countershading. Such a prediction would hold only if countershaded prey were observed by predators whose orientation towards the prey (in three dimensions) was highly repeatable between encounters. This is unlikely to be the norm in either terrestrial or aquatic ecosystems. Hence the abruptness of change from dark to light is not a perfect discriminator between candidate explanations for the mechanism underlying countershading in a given species.

In summary, there is to our knowledge no utterly conclusive evidence that countershading per se provides any enhancement of crypsis in terrestrial or aerial environments. The highly refined adaptations of some marine organisms to match the different background light conditions against which they are set when viewed from different aspects strongly suggest an adaptive advantage to countershading in these environments. Experimental quantification of the effectiveness of these adaptations would clearly be very welcome.

Despite Thayer's optimism, the establishment of a popular science folklore (which extended even to policy on the coloration of warships e.g. Gould 1991), and the passage of more than a century, there is no experimental evidence that conclusively tests and supports the Thayer/Poulton explanation of self-shadow concealment. The alternative explanation, that the dorsum and ventrum face different selection pressures (often associated with background matching) is often more plausible, and indeed there may be a plurality of explanations for this single phenomenon. Current understanding of the selection pressures that drive countershading is very patchy indeed. If possessing a contrasting dorsum and ventrum is really 'the most universal feature of animal coloration' (Gould 1991) then we must strive to explain why this is so.

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