3D animal camouflage

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Abstract

Camouflage is a fundamental way for animals to avoid detection and recognition. While depth information is critical for object detection and recognition, little is known about how camouflage patterns might interfere with the mechanisms of depth perception. We reveal how many common camouflage strategies could exploit 3D visual processing mechanisms.

Main text

Animals live in a 3D world

Animals exist in a 3D world, and **depth** (see Glossary) information is essential for judging the location, shape and orientation of objects. As a result, visual systems have evolved multiple ways to recover depth information. In the 3D arms race between predators and their prey, depth perception is thought to have evolved for camouflage breaking, so animal patterning must have evolved to conceal valid depth cues. Recent studies have revealed some remarkable ways in which non-human animals perceive depth [1, 2]. However, the role of depth information in prey camouflage strategies remains poorly understood. Here we examine how common types of camouflaging colouration may function to manipulate the viewer's mechanisms of depth perception.

Animals can perceive depth using **absolute depth** cues such as **binocular disparity and accommodative** (focus) **effort**, but most 3D information is obtained from **relative depth** cues. Pictorial depth cues such as object shading and **occlusion** could readily defeat the viewer's mechanisms of depth perception, because they exploit the laws of physics and/or use prior knowledge of visual scenes. Human observers, for example, judge distance based on an object's brightness (close objects are often brighter, and brighter, otherwise equivalent, objects are perceived as closer). Visual systems also assume that light comes from above (because sunlight is generally from overhead), and that, consequently, 3D objects produce a **self-shadow**. This correspondence between the direction of illumination and an object's self-shadows provides important information about object depth, location, distance and shape.

Countershading colouration is thought to reduce or eliminate self-shadows to enhance camouflage (**Fig. 1**). Countershading increases prey survival when the shading is optimised for the lighting conditions [3]. However, there is scant evidence that countershading interferes with 3D shape recovery in non-humans. A simpler explanation is that because visual systems detect objects on the basis of contrast, countershading may reduce detectability by reducing contrast across the body, or by reducing contrast at the body edges [4]. This could be particularly relevant when prey are viewed from a distance, where subtle depth cues are less critical than reduced visibility owing to contrast.

Non-human animals can use self-shadows for shape perception. European cuttlefish (*Sepia officinalis*) may exploit this when resting upon backgrounds with depth cues, by creating camouflage colouration that mimics self-shadows present on 3D objects in the background [5]. Cuttlefish are not simply adjusting their colouration in response to background luminance; when placed on 3D backgrounds they displayed a unique colour pattern which is never expressed in response to the equivalent 2D visual cues [6]. Intriguingly, this body pattern produces the illusion of depth to the human visual system [6], suggesting that cuttlefish may deceive their predators using patterning that resembles the 3D geometry of the background.

Animal patterning could produce **pictorial depth cues** in the same way that artists use shading to generate perceived depth on a 2D canvas. This could interfere with the viewer's mechanisms of depth perception in four (non-mutually exclusive) ways. Firstly, pictorial depth cues may mimic the visual information in a natural scene so that the luminance properties of the body surface correspond with the luminance profile produced by the 3D background (Fig. 2a). Secondly, pictorial depth cues could generate a percept of three-dimensionality (**illusory depth)** allowing the patterning to resemble 3D objects in the background (Fig. 2b) [6]. Thirdly, animal body patterning could produce **visual texture** that mimics the surfaces of inedible objects for **masquerade** (Fig. 2c). Fourthly, pictorial depth cues may disrupt the continuity of the body surface to prevent the recognition of an object as a whole (Fig. 2d). For example, surface-specific changes in luminance could produce the illusion of a sloped surface, while sharp transitions in contrast could produce strong edges that segment the body into apparent discontinous surfaces [7]. Edges can also cause illusory effects such as the Cornsweet illusion, which in primates and honeybees, causes strong differences in perceived brightness between adjoining regions, even if those regions are identical in luminance [8].

There are a number of visual processing mechanisms that pictorial depth cues could potentially exploit. **Enhanced edges** excite the visual system's edge detectors, stimulating a stronger signal than the body boundary, leading to incorrect **image segregation** [7]. However, it is also possible that such patterns may create new contours that form closed shapes, that would not normally signal the shape of the animal. Markings that disrupt surface continuity by producing illusory depth are likely to reduce **perceptual grouping** of the whole animal shape, that may be stronger than when considering the 2D effects of **disruptive colouration** (i.e. **false edges**) alone. In human vision, shading gradients and edges (among other cues) are a powerful cue for depth perception, and edges that are closer in luminance to the object tend to be grouped with the object rather than the background [9].

Binocular overlap is common among vertebrates, and depth perception using **stereopsis** allows predators to judge the distance of prey to increase their strike accuracy. Praying mantises (*Sphodromantis lineola*) were fitted with minature glasses permitting 3D displays (with a different coloured filter over each eye) and presented with coloured images (anaglyphs) that generate a **percept** of prey distance [2]. Mantises altered their striking behaviour according to perceived depth, but this was not based on luminance correlations in the two images, as in vertebrates, but on the relationship between two areas defined by common motion relative to the background, overcoming uncorrelated luminance textures which defeat stereopsis in humans [2]. Cuttlefish also use binocular stereopsis, placing themselves in an optimal position prior to attacking prey [1], but the mechanisms are different to those in mantises, which are only able to obtain stereoscopic depth information when prey targets are in motion [2].

Stereopsis has been argued to assist with image segregation, because recognition of intrinsic borders aids segmentation of image regions, while recognition of extrinsic borders faciliates grouping [10]. Camouflage strategies that defeat image segregation, such as disruptive colouration, are therefore excellent candidates for defeating stereopsis. Binocular disparity facilitates detection of prey with disruptive patterning by aiding the discrimination of false edges from the real object boundaries [11]. Human participants asked to locate snake images of targets as if viewed separately for each eye (monoscopic trials) or by both eyes simultaneously (stereoscopic trials), found targets with enhanced edges harder to detect, but only when viewed by one eye, confirming that stereoscopic vision may facilitate detection of camouflaged prey [11].

Pictorial depth cues such as enhanced edges take advantage of the viewer's ability to resolve depth using monocular cues (e.g. shading, texture). In experiments with human observers, targets with enhanced edges were deemed to have more depth than the background, and were particularly hard to detect when the background contained **cast shadows** [12]. These findings suggest that in the context of human vision, enhanced edges impede object detection by interfering with perceptual grouping [12]. Importantly, work with human observers suggests that multiple sources of depth information (i.e. binocular and monocular) can be integrated during visual search [11].

Our understanding of how predators perceive depth cues, and how prey colouration exploits these mechanisms of visual processing to enhance camouflage, has only just begun. Most animals use multiple cues to perceive depth, but it is unclear how this information is combined into a single depth estimate. Many fundamental questions about 3D camouflage remain. Can pictorial depth cues improve **background matching**, and over what viewing distances is this strategy successful? Addressing these questions requires novel approaches for measuring depth perception in non-human animals, but would greatly enhance our understanding of animal camouflage.

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Glossary

Absolute depth: A measure of the actual distance between the observer and the object, based on cues such as binocular convergence and accommodation.

Accommodative effort: Use of the intra-ocular muscles to change the plane of focus of the eye's lens.

Background matching: Body colouration that generally matches the colour, luminance and pattern of the background.

Binocular disparity: Differences in the position of the retinal images of objects in the left and right eyes, due to the separation of the eyes.

Cast shadows: Shadow produced by an object and projected onto another surface (e.g. another object, the substrate).

Countershading colouration: Describes the ubiquitous phenomenon whereby animals tend to be most darkly coloured on the surface (usually the dorsal) that receives the most light.

Depth: The measurement or perception of the relative distances between an observer and the objects in a scene. This includes information on the distance, spatial arrangement and distance to parts (shape or depth variation) of an object as viewed by the observer.

Disruptive colouration: A set of markings that create the appearance of false edges and boundaries, hindering detection or recognition of the body outline.

Enhanced edges: Type of colour pattern where the borders of colour patches are accentuated, so that light patches have lighter edges, and dark patches have even darker edges.

False edges: Patterns that create the appearance of false boundaries, making the real outline of the body harder to detect and recognise.

Illusory depth: The perception of distance, spatial arrangement or shape, that does not correspond to the physical dimensions arising from the actual visual scene.

Image segregation: A high-level feature integration used to determine which parts of an object form a whole by separating regions according to perceived contours or boundaries.

Masquerade: Resemblance of an organism to an object of no inherent interest to the observer, such as an inedible object.

Occlusion: Where the edges of one object are partially obscured by another, giving information on relative distance and order (e.g. whole objects are in front of/closer than obscured objects).

Perceptual grouping: Determination of which component parts belong to a 'whole'.

Percept: Representation of the external world created by the sensory system, which is then interpreted using rules or knowledge about the world.

Pictorial depth cues: Patterns such as surface shading, enhanced edges and texture gradients, which mimic the properties of visual scenes to produce apparent changes in depth where none exist.

Relative depth: Perception of the relative spatial relationships among different objects (e.g. order, separation), or between parts of the same object (e.g. object shape) without knowing the actual distance from the observer.

Self-shadow: A shadow that is produced on the occluding object itself.

Stereopsis: The experience of depth that is obtained as a result of combining the visual information received from two eyes.

Surface relief: The physical geometry of a surface.

Visual texture: An ensemble of image elements that conveys the properties of a much larger collection of images, allowing recognition of a material (e.g. glass, wood, plastic).

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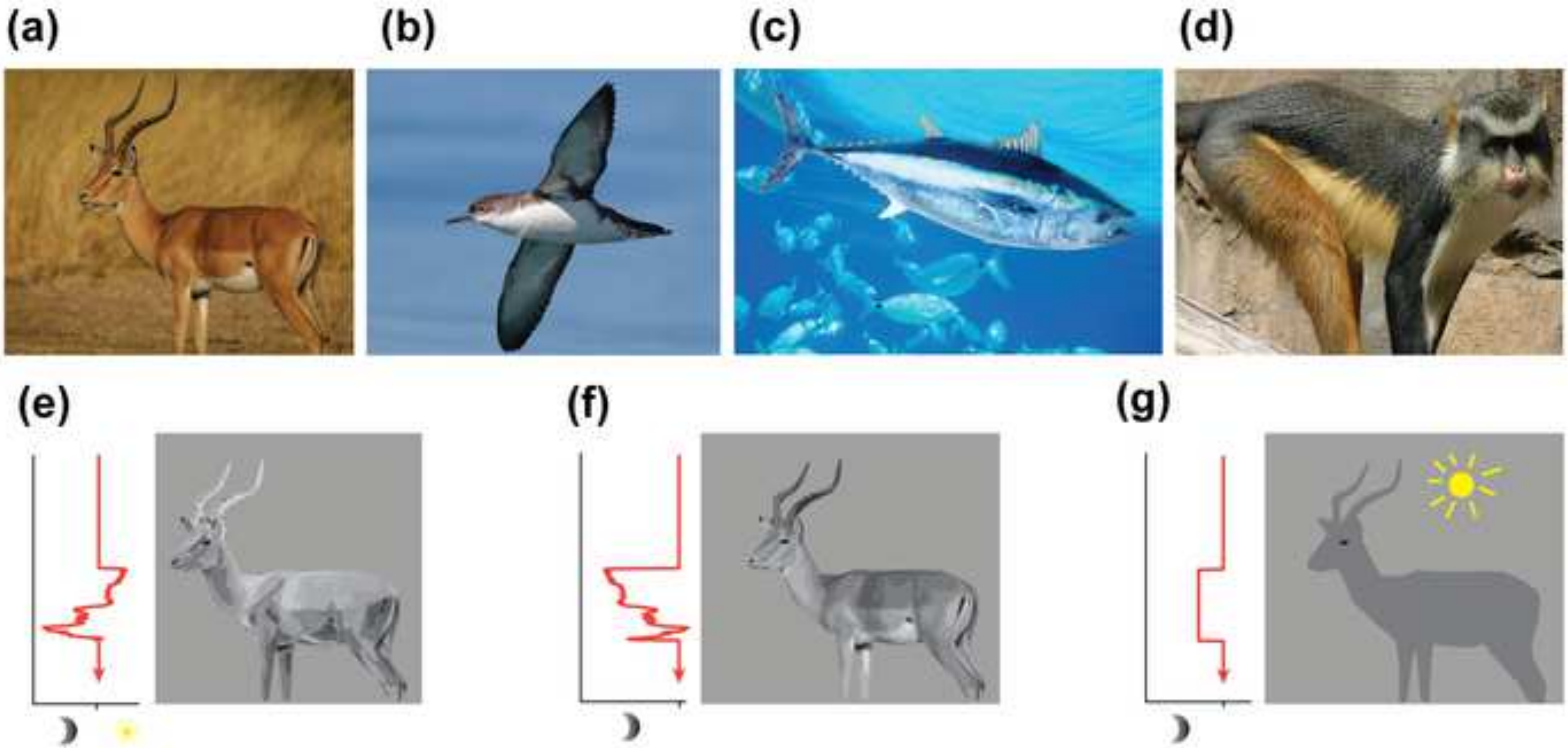
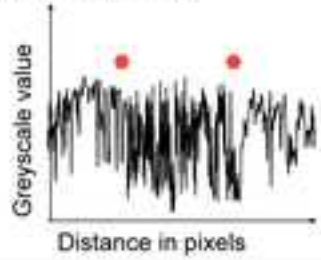
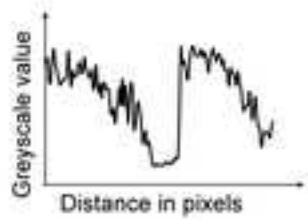
Figure captions

Fig. 1. Colouration that is proposed to remove depth information. Countershading colouration is one of the commonest forms of colouration, observed in animals such as mountain gazelle (**a:** *Gazella gazelle*), Manx shearwater (**b:** *Puffinus puffinus*), bluefin tuna (**c:** *Thunnus thynnus*) and Wolf's Mona monkey (**d**: *Cerophithecus wolfi).* Countershading is thought to enhance camouflage by reducing or eliminating self-shadows. When lit from overhead, objects such as a mountain gazelle produce a self-shadow on the underside of the body (**e**). Countershaded patterns (**f**) reverse this effect, increasing camouflage by reducing contrast and/or removing 3D shape cues (**g**). The plots (red lines in e-g) show changes in luminance across the body (dorsal to ventral direction); the x-axis indicates whether the body's luminance is darker (moon image) or brighter (sun image) than the background. Image sources: a: www.pexels.com (Harvey Sapir); b: www.hubpages.com; c: www.stock.adobe.com; d: www.wikipedia.org.

Fig. 2. Other camouflage strategies that may interfere with depth perception. a) The wing patterns of the geometrid moth *Alcis repandata* **(a)** produce a similar luminance profile to the background (plot shows changes in greyscale value across a transect (red dotted line in image), the red asterisks denote the wing edges). The wing patterning resembles the changes in luminance produced by the background relief, preventing prey detection by defeating the edge detectors and preventing image segregation. The cuttlefish *Sepia officinalis* (**b**) dislays a unique disruptive pattern when placed on a 3D background, which may produce a percept of depth. Cuttlefish may therefore exploit predators' ability to recover depth from pictorial cues to prevent image segregation. The flat wings of the moth *Uropyia meticulodina* (**c**) have patterns that produce changes in luminance that are associated with sloped surfaces and edges (plot shows changes in greyscale across the transect marked by the red dashed line in the image). This patterning exploits depth cues such as shading and texture to facilitate misidentification. Geometrid moth (Mottled Umber, *Erannis defolaria*; **d**) with patterns that may alter the perceived depth of parts of the wing surface. These false edges mimic the changes in luminance that are associated with an object's boundaries and/or may generate illusory depth, causing incorrect boundary resolution and incorrect segregation. Image sources: a & d: www.stock.adobe.com; b: kindly provided by Sarah Zylinski; c: Shipher Wu (CC-BY-SA 2.0).

Figure 1



Camouflage strategy	Visual signal/percept	Mechanisms exploited	Outcome
(a) Background matching (luminance profile)			
		Edge detectors defeated	Luminance profile matches background relief
(b) Background matching (3D percept)			
		Pictorial depth cues generate false surface contours and shading correspondences	Illusory depth on body surface Incorrect boundary resolution and image segregation
(c) Masquerade			
		False edges stimulate edge detectors Pictorial depth cues used to generate false texture and relief	Incorrect boundary resolution promotes object mis-identification Luminance gradient resembles surface of object being mimicked
(d) Surface disruption			
		Enhanced edges stimulate edge detectors Enhanced edges simulate changes in surface depth	Incorrect boundary resolution Breaks up body surfaces into additional depth planes, causing incorrect segregation