

The anti-predator function of ‘eyespot’ on camouflaged and conspicuous prey

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Abstract Animals utilise various strategies to reduce the risk of predation, including camouflage, warning colours and mimicry, and many of these protective signals promote avoidance behaviour in predators. For example, various species possess paired circular ‘eyespot’, which startle or intimidate predators, preventing or halting an attack. However, little is known of how the efficacy of such signals relates to the context in which they are found, and no studies have tested the relative effectiveness of anti-predator signals when on otherwise camouflaged and conspicuous prey. We find that the protective value of conspicuous wing spots, placed on artificial moth-like targets presented to wild birds in the field, is strongly affected by the attributes of the prey ‘animal’ on which they are found. Wing spots reduced predation when on conspicuous prey but were rendered ineffective when on otherwise camouflaged targets, indeed they increased the risk of predation compared to non-marked camouflaged controls. These results demonstrate how different anti-predator strategies may interact, and that protective signals can switch from being beneficial to costly under different contexts.

Keywords Eyespot · Camouflage · Conspicuousness · Predation · Protective coloration

Introduction

To reduce the risk of predation, animals utilise a variety of protective markings, including camouflage, warning colours and mimicry (Cott 1940; Ruxton et al. 2004; Stevens 2007). In addition, many species possess paired circular ‘eyespot’, which can startle or intimidate predators, preventing or halting an attack (reviewed by Stevens 2005). The role of eyespots as anti-predator deterrents, most frequently found on butterflies, moths and many tropical fish, has attracted considerable scientific and popular attention for almost 200 years (Kirby and Spence 1818). However, whilst some studies have illustrated that lepidopteran wing spots can reduce the risk of predation from birds (e.g. Blest 1957; Vallin et al. 2005), only two studies to date have tested the specific attributes that make them effective. By using artificial stimuli, printed with grey-scale spots of varying contrast and complexity, Stevens et al. (2007a) showed that continuously visible wing spots reduce the risk of predation from avian predators in the field. In contrast to popular belief, which has long assumed that wing spots work because they mimic the eyes of the predator’s own enemies (hence ‘eye’ spots) (Blest 1957; Rota and Wagner 2006), the features which made the spots most effective were high contrast and complexity, and not eye mimicry, demonstrating the need to consider predator perception and cognition in interpreting such results (Stevens 2007; Stevens et al. 2007a). In addition, Stevens et al. (2008) showed that wing spots were more effective in intimidating predators when they were larger and found in higher numbers, rather than when occurring in pairs, and circles were no more effective than other geometric shapes such as bars. As such, we generally use the term ‘wing spot’ to describe the markings in this experiment (Stevens et al. 2008).

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However, whilst some studies have tested the influence of prey contrast against different backgrounds on warning signal effectiveness and predator avoidance learning (see Lindström 1999; Gamberale-Stille 2001; Ruxton et al. 2004; Prudic et al. 2007), few studies have investigated how the function of specific features on an animal may be influenced by the overall prey coloration, its relationship with the surroundings and whether the interaction between different protective strategies can be costly. For example, the previous work of Stevens et al. (2007a, 2008) used spots only on conspicuous targets, and no studies have tested the protective value of equivalent wing spots on prey that are either concealed or conspicuous against the background environment. This is important as anti-predator markings are found on many animals, often possessing very different overall body patterns. Furthermore, whilst some species of lepidopteran display continuously visible wing spots (e.g. the emperor moth *Saturnia pavonia*), many others hide their spots beneath camouflaged forewings (e.g. the eyed hawk moth *Smerinthus ocellatus*), indicating that there may be a cost to possessing potentially conspicuous spots in terms of reduced camouflage (Edmunds 1974; Brakefield and Larsen 1984; Lyytinen et al. 2004; Stevens 2005). Conversely, there is some comparative evidence that simple spots in mammals may aid concealment, particularly when found on forest dwelling species (Stoner et al. 2003), and it is possible that, in lepidopterans that hide their spots beneath wings, that this may sometimes be to increase the element of surprise, if and when they are involved in a startle display. Finally, in proposing his theory of ‘dazzle’ (distractive) markings, Thayer (1909) argued that a range of high contrast markings may actually promote concealment, by drawing the ‘attention’ of the predator away from the outline of the body, preventing detection (see Stevens 2007). As such, some simple spots may facilitate camouflage. It is therefore important to consider if, and when, different protective strategies may effectively coexist on an animal, and to what extent (Stevens 2007). Here, we used grey-scale artificial ‘moth’ targets, calibrated with respect to avian luminance perception, to test the protective value of simple wing spots on ‘prey’ that were either camouflaged or conspicuous against the tree backgrounds to which they were pinned.

Methods

The experiment and stimuli calibration followed the same general procedure as Stevens et al. (2006, 2007a). We created artificial ‘moth-like’ ‘prey’, 70-mm wide and 35-mm high, from triangular pieces of waterproof paper (HP LaserJet Tough Paper; Hewlett Packard, Palo Alto, CA, USA). These were printed with specific patterns on a

Hewlett Packard LaserJet 2200dn printer. We used grey-scale targets because these have been effective in previous work (Stevens et al. 2006, 2007a, 2008) and the calibration of a printer for luminance perception is easier than that for colour. In addition, using grey-scale targets rendered all manipulations of target luminance virtually identical regardless of the assumptions about predator species or retinal mechanism, as these may vary between species (Hart 2001; see Stevens et al. 2007a and below).

We had six treatments, three of which consisted of targets where the wing background matched the average luminance (perceived lightness) of the trees on which they were placed (‘camouflaged’/matching) and three treatments where the target background was significantly lighter (‘conspicuous’/non-matching) than the tree backgrounds (Fig. 1). Four of the treatments (two camouflaged and two conspicuous) comprised targets that were marked with a pair of simple spots, which were either lighter than the target background (treatments ML and NL) or darker than the target background (treatments MD and ND); for simplicity, we call these ‘light’ and ‘dark’ spots, respectively. Two control treatments consisted of matching (camouflaged) or non-matching (conspicuous) grey targets without any spots (treatments M and N, respectively), giving six treatments in total (Fig. 1). The contrast of both the light and the dark spots on both the camouflaged and the conspicuous prey was calculated to be identical to a foraging bird (see below). The stimuli were not intended to mimic any real species of animal, and so the experiment is best regarded as a form of field psychophysics (Cuthill et al. 2005). Whilst it would have been interesting to also have conspicuous prey that were darker than the background, this was not possible with the present study because, as Fig. 2 shows, the tree backgrounds were themselves quite dark, with various individual trees having very dark patches. This meant it was not possible to print a target that was sufficiently darker than the tree backgrounds to be conspicuous and further marked with dark spots.

Target calibration followed Stevens et al. (2006, 2007a). The targets needed calibrating before printing because a

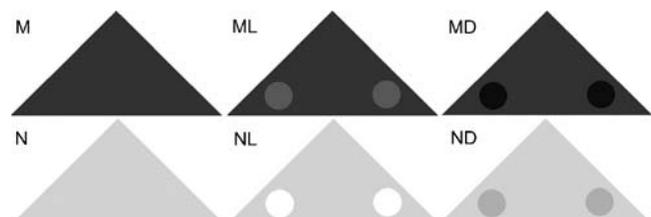


Fig. 1 Treatments used in the experiment. *Top row*: treatments where the target background matched the average luminance of trees on which the stimuli were placed (*M* camouflaged control, *ML* camouflaged with light spots, *MD* camouflaged with dark spots). *Bottom row*: treatments where the target background was lighter than the trees on which the stimuli were placed (*N* conspicuous control, *NL* conspicuous with light spots, *ND* conspicuous with dark spots)

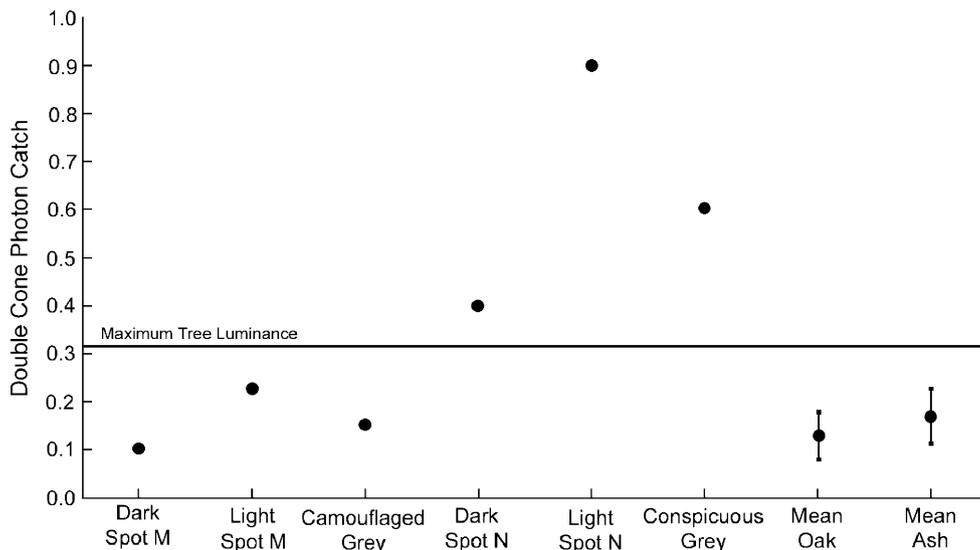


Fig. 2 Blue tit *Parus caeruleus* double cone photon catch values for the experimental stimuli and the tree backgrounds used in the experiment. Values *left to right* correspond to: the dark spots on the camouflaged targets, the light spots on the camouflaged targets, the camouflaged grey target background, the dark spots on the conspicuous targets, the light

spots on the conspicuous targets, the conspicuous grey target background, mean oak bark (plus standard deviation) and mean ash bark (plus standard deviation). The figure also shows the maximum double cone value measured for any tree (an ash; 0.31). See “Methods” for the calibration details

printer’s grey scale (here 0–255) is not linearly related to perceived luminance (Westland and Ripamonti 2004; Stevens and Cuthill 2005). Evidence from previous work indicates that luminance-based tasks stem from the double cones in birds (Osorio et al. 1999a, b; Jones and Osorio 2004; Osorio and Vorobyev 2005). We therefore calibrated our stimuli according to the calculated photon catch of a blue tit’s (*Parus caeruleus*) double cones (Hart et al. 2000), when viewing the printed patterns in an illuminant measured in our study site typical of woodland shade (Endler 1993). To calibrate the stimuli, ramp images (21-cm long) were created with grey values increasing from left to right from 0 to 255 in unit increments, and printed out from the same printer and on the same paper type as used for the experimental stimuli. Reflectance values from the grey-scale ramp were measured at 1-cm intervals, normal to the image plane, using an Ocean Optics (Dunedin, FL, USA) USB2000 spectrometer held at 45° to normal, with illumination by a PX-2 pulsed xenon lamp. Five replicate measurements were taken from each region of the image, recorded in 1-nm intervals from 300 to 700 nm, expressed relative to a Spectralon™ 99% white reflectance standard (Labsphere, Congleton, UK). This procedure was followed by modelling of avian double cone photon catches using irradiance spectra from woodland shade under overcast skies, collected at the field site using the spectrometer fitted with a cosine corrector (Maddocks et al. 2001; Endler and Mielke 2005). As with Stevens et al. (2007a), we generated a calibration curve by quadratic regression of calculated photon catch against grey-scale value ($R^2 > 99\%$). Stimulus grey values were then scaled to correspond to the required

luminance values when printed and were double-checked via spectrophotometry and photon catch modelling before use. The calibration calculations were repeated for the double cones of a starling (Hart et al. 1998), and with different daylight illuminants (cloudy and blue sky), to assess the robustness of our estimates. As with previous work (Stevens et al. 2006, 2007a), and as one may expect for grey-scale patterns, this made negligible difference (less than 1 point on the 256-point grey scale), indicating that our calibrations were highly robust to changes in the illumination.

Wing spots were created in Image J (Rasband 1997–2008; Abràmoff et al. 2004), and Photoshop Elements 2.0 (Adobe Systems Inc., San Jose, USA). On each non-control target was a pair of eyespots, 10 mm in diameter and 15 mm from the target midline. As with previous work, our stimuli lacked an ultraviolet (UV) component as it is not possible to print stimuli with UV reflectance using conventional printers and paper. However, whilst diurnal birds are sensitive to UV (Cuthill et al. 2000; Cuthill 2006), this is not a problem with the experimental design because double cones have limited UV sensitivity (Hart 2001), and the lichen-absent tree backgrounds to which the targets were pinned also lack UV reflectance (Majerus et al. 2000; Cuthill et al. 2006a), resulting in minimal internal and external UV contrast for all treatments.

To determine the value of the grey target ‘wing’ backgrounds, 35 digital photographs of ash *Fraxinus excelsior* and oak *Quercus robur* tree trunks in the study site were taken with a Fuji Finepix S7000 digital camera. Because digital cameras often show a non-linear relation-

ship between the image value recorded and changes in light intensity, the images were first calibrated to linearise them (Stevens et al. 2007b). This was followed by a mathematical transformation to convert the images to data corresponding to the relative photon catch of a blue tit (Stevens and Cuthill 2006; Stevens et al. 2007b). This is highly accurate and shows a maximum of 2% error compared to modelling of photon catches with reflectance and irradiance data (Stevens and Cuthill 2006). For the camouflaged prey, the grey wing background was chosen to match the average photon catch value of the tree trunks. For the conspicuous prey, the grey wing was chosen to be significantly lighter than the lightest trees measured, whilst still allowing the creation of wing spots lighter than the target background (Fig. 2). Our subjective assessment supported this; the camouflaged prey were hard to spot in the field, whereas the conspicuous targets were highly visible from greater than 70 m. As with Stevens et al. (2007a), the contrasts between the stimuli were designed on a ratio scale because the visual contrast between two stimuli is liable to be a function of their ratio rather than their absolute difference (Kelber et al. 2003). Wing spots were therefore set on either a conspicuous or a camouflaged grey background, corresponding to a calculated grey-scale value such that the photon catch for the grey lay halfway between that for the light and dark spots, on a ratio scale (Fig. 2). The visual contrast between light spots and grey target was therefore set equal to that between grey and dark spots for both the conspicuous and camouflaged prey, and the contrast between all spots and their wing backgrounds was identical (all contrasts between spots and target backgrounds equalled 1.5). The calibration procedure was repeated each time a new set of stimuli was printed, as the level of print toner affects the printed grey values (Stevens et al. 2007a).

Targets were pinned to ash and oak trees at a height of between 1 and 2 m in the mixed deciduous University of Cambridge Maddingley Woods, Cambridgeshire, UK (0°3.2' E, 52°12.9' N) and checked at approximately 3, 24 and 48 h. Attached to each target was a dead mealworm (*Tenebrio molitor* larvae) to provide an edible component. Unlike previous work (Stevens et al. 2007a), the mealworm was attached to the underside of the targets, partially projecting out (as Schaefer and Stobbe 2006), because placing the mealworm on top in this instance may have affected target camouflage. Predation was determined by the disappearance of all or most of the mealworm from the target. As with studies undertaken in similar woodland elsewhere (Cuthill et al. 2006a, b), the main avian predators in the area were blue tits, great tits (*Parus major*), European robins (*Erithacus rubecula*), chaffinches (*Fringilla coelebs*), blackbirds (*Turdus merula*) and house sparrows (*Passer domesticus*). Other forms of predation left obvious signs: slugs left slime trails, ants were seen swarming on the target and spiders left hollow

exoskeletons. The latter two occurrences, complete target disappearance, or the 'survival' of the target to 48 h, were treated as censored values in the survival analysis (Cuthill et al. 2005).

The experiment was a randomised block design, consisting of 10 blocks each with 10 replicates of each treatment (100 total per treatment), randomly pinned to trees in June and July 2007. Each block comprised a non-linear transect 1–3-km long and 30-m wide, using under 5% of the available trees, each in a different woodland region on a different date. Treatments were randomly allocated to suitable trees, defined as having little or no lichen cover and a trunk circumference of greater than 0.9 m. The low density of targets within each block and the use of different parts of the wood minimised the chance that any one bird would encounter multiple targets.

Survival analysis was performed via Cox proportional hazards regression (Cox 1972; Lawless 2002; Klein and Moeschberger 2003; Cuthill et al. 2005), which can accommodate censored data and non-uniform changes in predation risk with respect to time of day. Significance was tested with the Wald statistic (abbreviated W), and five pairwise contrasts were used to compare specific treatments. Only five post hoc comparisons were used because if these are planned a priori, and one does not use more degrees of freedom than in the experiment-wise test (i.e. one is just dividing up the existing degrees of freedom), then p -value correction of post hoc tests is not needed (see Rosenthal et al. 2000). Furthermore, Rosenthal et al. (2000) also make a stronger point for adopting this approach; the original experiment-wise test is often less relevant to the hypotheses being tested than are the pairwise tests, and for many experiments, such as ours, the researcher does not usually wish to know whether at least one treatment differs from at least one other, but rather if one, or sets of, specific treatments differ from a specific other or other(s). Here, we wish to test the cost or benefit of wing spots on specific treatments, and therefore undertake the five pairwise tests that best investigate our hypotheses. A full discussion and guidelines of similar arguments are also presented and discussed at length in Ruxton and Beauchamp (2008). Effect sizes are odds ratios (OR), which are simply the ratio of the probability of predation in one treatment to the probability of predation in another treatment, such that a value of 1.00 occurs when two treatments have the same survival probabilities.

Results

There was a significant effect of treatment ($W=45.473$, $df=5$, $p<0.001$; Fig. 3). Survival of the conspicuous spotted treatments exceeded that of the conspicuous controls

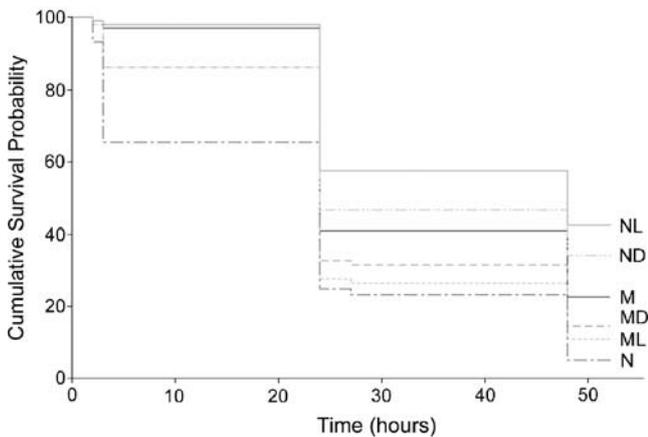


Fig. 3 Survival plot of the experimental treatments, with curves being the probability of surviving bird predation as a function of time (hours). Survival top to bottom: NL, ND, M, MD, ML, N

(treatment ND, which had a lower survival than NL, survived better than N; $W=23.064$, $df=1$, $p<0.001$, $OR=2.220$). In contrast, the treatment with light spots on camouflaged targets survived significantly worse than the camouflaged controls (ML versus M; $W=4.128$, $df=1$, $p=0.042$, $OR=0.722$), and the camouflaged treatment with dark spots survived qualitatively worse than the camouflaged controls (MD versus M; $W=2.264$, $df=1$, $p=0.132$, $OR=0.785$). The camouflaged controls also survived significantly better than the conspicuous controls ($W=14.432$, $df=1$, $p<0.001$, $OR=1.840$). All treatments survived better than the conspicuous controls (the second worst surviving treatment ML survived qualitatively better than N; $W=3.428$, $df=1$, $p=0.064$, $OR=1.328$). There was no significant difference between blocks ($W=14.624$, $df=9$, $p=0.102$), which relates to the differences in average predation rates in different parts of the woods on different dates, and is not relevant to our hypotheses.

Discussion

This experiment first supports the conclusions of Stevens et al. (2007a, 2008) that simple, continuously visible wing spots can reduce the risk of predation from avian predators when on targets which are conspicuous against the background environment. Those treatments with spots placed on conspicuous wings survived better than all the other target types. However, here we show that the protective value of such spots is strongly affected by the overall attributes of the prey. Whilst wing spots were highly effective in reducing predation when on otherwise conspicuous targets (both treatments NL and ND had survival probabilities more than twice that of treatment N), spots were rendered significantly less effective when placed on otherwise camouflaged targets. In fact, on camouflaged prey, wing spots were

actually detrimental and increased the risk of predation compared to the unmarked camouflaged controls (treatment M had survival probabilities of approximately 1.3 times higher than those of ML and MD). Overall, the conspicuous control had the lowest survival rate of all six treatments. There was no difference in survival between those treatments with white and black spots on equivalent target types (either camouflaged or conspicuous; Fig. 3).

These results indicate that the value (if any) of certain types of protective signal can switch from being beneficial to costly under different contexts, such as with different overall prey coloration. The poor survival of the spotted camouflaged treatments was probably because the targets were easier to detect than the equivalent unmarked controls; subjectively, we found the spotted targets easier to locate in the field, and their lower survival indicates that the birds saw the spots but did not avoid them. Whilst the unmarked camouflaged controls survived worse than the conspicuous spotted treatments, we cannot conclude that conspicuous signals are a more effective anti-predator strategy than camouflage because in our experiment the level of concealment was only for avian luminance, and lacked spatial and chromatic information from the environment. As with previous studies, there was no difference in survival between the dark- and light-spotted treatments (on equivalent target backgrounds; Fig. 3), again indicating that contrast and conspicuousness effects, rather than eye mimicry, can explain the survival of the spotted treatments (Stevens 2005, 2007; Stevens et al. 2007a, 2008).

Our study also fails to support Thayer's (1909) hypothesis, that wing spots on camouflaged prey may enhance concealment by means of a dazzling effect, distracting predator attention away from the prey's body outline (Stevens 2007), although this hypothesis merits further systematic study. Additionally, whilst simple spots may increase camouflage in some situations (e.g. in some mammals; Stoner et al. 2003), we feel this is highly unlikely in our study for several reasons. First, all the targets with conspicuous wings, with and without spots, were highly visible to us from a significant distance (>70 m). Second, as Fig. 2 shows, the avian perceived luminance of the light grey (conspicuous) target background was well above that of the trees to which they were pinned (for both the means of oak and ash and the lightest tree measured). Additionally, the treatment with the highest survival was that with the light spots on conspicuous 'wings'; this is not what would be predicted if the spots act to increase camouflage because the dark spots are closer to the background values than the light spots. Finally, if the spots did promote camouflage instead of predator avoidance, we would expect the non-matching ('conspicuous') prey with spots to survive worse than the dark, more concealed targets. Therefore, whilst simple spots may increase concealment in some situations, it seems highly unlikely in this

case and we can be confident that the predators saw but avoided the conspicuous spotted targets.

These results show that the protective value of conspicuous markings is strongly affected by the overall prey coloration and its relationship to the environment. Additionally, rather than simply becoming less effective, a protective signal may actually become costly under some circumstances (perhaps especially on animals found over several background types). The findings also indicate that prominent markings may more easily evolve in prey which are already conspicuous (behaviourally or morphologically) than in camouflaged animals. This corroborates current opinion that wing spots may in some circumstances increase predation risks, leading to a range of life history strategies and adaptations to minimise such costs (Brakefield and Larsen 1984; Stevens 2005). For example, many lepidopterans conceal their wing spots beneath camouflaged or closed wings, and some species even have seasonal variations in phenotype so that wing spots only develop when the cost of possessing them is low (Brakefield and Larsen 1984; Lyytinen et al. 2004). This may enable some species to possess conspicuous markings (e.g. for startle displays or deflection) without reducing camouflage. However, further work is clearly needed to experimentally assess the level of camouflage provided (if any) by simple spots and blotches in real species, such as on animals in dappled environments, and in what forms of camouflage the spots may function (e.g. disruptive coloration, background matching, dazzle markings and so on). Overall, many of these avenues of future work would be greatly strengthened by a firmer understanding of how such spots and colour patterns relate to behaviour.

The spots in our experiment were simple, consisting of one component, and so future work should investigate the function of more complex and potentially more intimidating stimuli of different sizes on a range of target backgrounds, and to incorporate effects of colour. In our study, we investigated the survival of prey items with different markings located on the same habitat background types. As such, an alternative revealing future study could investigate the survival of the same phenotype on multiple and differing background types. This is particularly relevant for animals found against several backgrounds or in multiple habitat types. In addition, it would be intriguing to investigate how the function of other protective signals, such as warning colours, may be affected by prey which are found under various conditions, potentially resulting in different levels of overall conspicuousness against the background. This is especially important as there is currently much discussion as to whether different forms of protective strategies can effectively coexist and how they relate (Stevens 2007). For example, it is possible that certain forms of camouflage such as disruptive coloration

may still be effective even with markings not matching the background (Schaefer and Stobbe 2006; Stevens et al. 2006) and that warning colours and camouflage markings can be present on the same animal, functioning at different distances (Tullberg et al. 2005). These findings indicate that there is much still to understand regarding how visual signals function under different conditions and contexts.

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