Escape distance in ground-nesting birds differs with individual level of camouflage

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Abstract

Camouflage is one of the most widespread anti-predator strategies in the animal kingdom, yet no animal can match its background perfectly in a complex environment. Therefore, selection should favour individuals that use information on how effective their camouflage is in their immediate habitat when responding to an approaching threat. In a field study of African ground-nesting birds (plovers, coursers, and nightjars), we tested the hypothesis that individuals adaptively modulate their escape behaviour in relation to their degree of background matching. We used digital imaging and models of predator vision to quantify differences in color, luminance, and pattern between eggs and their background, as well as the plumage of incubating adult nightjars. We found that plovers and coursers showed greater escape distances when their eggs were a poorer pattern match to the background. Nightjars sit on their eggs until a potential threat is nearby, and correspondingly they showed greater escape distances when the pattern and color match of the incubating adult's plumage, rather than its eggs, was a poorer match to the background. Finally, escape distances were shorter in the middle of the day, suggesting that escape behaviour is mediated by both camouflage and thermoregulation.

Introduction

Camouflage is a classic example of evolution through natural selection, and the selective advantage of cryptic phenotypes in avoiding predation has received considerable attention in recent years (Vignieri et al. 2010; Chiao et al. 2011; Zylinski and Johnsen 2011; Troscianko et al. 2013). A widespread camouflage strategy is background matching, whereby an animal closely resembles its surroundings in color, brightness, and pattern (Stevens and Merilaita 2009*a*). However, in a heterogeneous habitat an animal's ability to match the background can vary (Merilaita 1999), and it should be adaptive for individuals to monitor their own degree of camouflage and use this information to adjust protective behaviour appropriately. For cryptic animals, the degree of individual background matching should influence the decision of when to sit tight or to flee from an approaching predator. Movement has been shown to break the effects of camouflage (Stevens et al. 2011; Hall et al. 2013), presenting a cost to fleeing by revealing the animal's presence and location, and suggesting that camouflage and escape behaviour are likely to be linked. In situations where animals are caring for vulnerable offspring, the movement of a fleeing parent may betray the location of eggs or immobile young, such that escape decisions might also be influenced by the camouflage of offspring.

In this study, we test the hypothesis that individual animals vary their escape behaviour in relation to their degree of background matching and that of their offspring. If escape reveals the location of adults and young, then we should expect adults to escape at greater distances from an approaching predator when either they or their young are poorly camouflaged, since the nest will be under heightened risk of discovery at close range. We tested this prediction across individuals in the wild using a number of African ground-nesting bird species (plovers, coursers, and nightjars). These are an ideal system to test whether camouflage influences escape decisions, because nests are typically in open habitats where they are susceptible to visually hunting predators (Martin 1993) and because in the absence of any nest structure to conceal the eggs, crypsis is the primary defence against predation (Kilner 2006; Šálek and Cepáková 2006). Furthermore, previous work on this study system found that the camouflage of adult birds and their offspring is a strong predictor of nest survival (Troscianko et al. 2016).

Our aim is not to test whether escape distance and camouflage strategies differ between species with different ecological traits, but rather whether individual differences in camouflage are associated with behavioural variation across our focal species. We thus control for each species' shared ecological traits, such as life-history and morphology, which might also influence escape behaviour.

We also consider a second cost that parental escape behaviour can impose on offspring, whereby reduced attendance to other fitness-related activities can complicate decisions of whether or when to flee (Ydenberg and Dill 1986). In nesting birds, the act of fleeing trades off against the maintenance of optimal developmental temperatures (Webb 1987; Conway and Martin 2000). For the eggs of ground-nesting birds, the risk of overheating has been shown to be higher for eggs at a tropical site (where solar radiation is more intense) than at a temperate site, and when egg colouration is darker or more maculated (Gómez et al. 2015). Our study species breed in Zambia (16° south of the equator) during the dry season when air temperatures commonly exceed 35°C (Harris et al. 2014). Fleeing the nest exposes eggs to potentially harmful ambient temperatures and solar radiation, which are more intense at midday (Mougeot et al. 2014). We therefore predicted that the risk of thermal stress to offspring should exacerbate the costs of fleeing, such that birds should be more reluctant to leave their nests at times of day when thermal costs are highest.

In our study system, escape distances corresponded to two different ecological settings: nightjars (Caprimulgiformes) are reported to initiate escape at distances under ten metres (Langley 1984; Jackson 2002), whereas some plover species initiate escape at over forty meters (Charadriiformes) (Blumstein 2006). Although these differences in natural history are likely to be partly phylogenetically determined, they stimulate different predictions about the relationship between camouflage and escape behaviour according to the relative risks to adult and eggs (Lack 1968). For species with long escape distances such as plovers and coursers, predation risk to adults is low, whereas eggs are exposed to potentially harmful solar radiation as well as visually hunting predators. In this ecological context, we expect strong selection for cryptic egg coloration, and for egg rather than adult appearance to be most relevant in

modulating escape behaviour (Lack 1968). For species that do not readily flee the nest, such as nightjars, predation risk to adults is high if they are detected, since predators reach close proximity before the adult initiates escape. In these species, we expect that the camouflage of the adult's own plumage will be more important than that of their eggs in modulating escape decisions (Lack 1968). These predictions are summarised in Figure 1.

Finally, we expect that for all birds, this trade-off between sitting tight and fleeing should be influenced by circadian patterns of solar radiation and ambient temperature. We predict that adults will have shorter escape distances when these environmental risks are most intense (i.e. at midday) and therefore when prolonged exposure is most likely to threaten embryonic viability. The characteristics of the eggs may also influence their thermal properties, with eggs expected to be more sensitive to ambient temperatures when darker (Kilner 2006; Gómez et al. 2015) and smaller (Turner 1985). We therefore expect that adults will have shorter escape distances when their eggs are less bright and are smaller in size, as these qualities should be coupled with a greater risk of overheating. Finally, shorter escape distances may also be expected when backgrounds are darker, since this may cause the surrounding ground to reach greater temperatures faster and present a greater risk that eggs will overheat.

Following previous studies (e.g. Blumstein 2006; Møller 2010), we assessed escape behaviour by using an approaching human as a proxy for a predatory threat, and measured the distance at which the bird fled its nest. In nesting birds, escape distances are known to be related to degree of concealment through vegetation cover (Klvan et al. 2004; Miller et al. 2013), as well as stage of egg development (Osiejuk and Mickiewicz 2007), and colonial versus solitary breeding (Šálek and Cepáková 2006). However, to our knowledge the present study is the first to investigate escape behaviour in relation to directly quantified camouflage, as seen by the visual systems of relevant predators.

Methods

Study System

We studied ground-nesting birds within an area of c. 3,100 ha around Musumanene and Semahwa Farms (centred on 16˚46'S, 26˚54'E) and c. 400 ha on Muckleneuk farm (centred on 16˚39'S, 27˚00'E) in the Choma District of southern Zambia. The study was conducted during September–November 2012–2013, corresponding to the late dry season. Monthly averages of daily minimum air temperatures for the Choma region during this period were 13.5–18.0°C, and monthly averages of daily maxima were 30.5–32.1°C (Harris et al. 2014). The habitat is a mixture of deciduous miombo woodland, grassland and fallow and active agricultural fields. Nests were principally located by local farm labourers when flushing the birds while walking around farm fields or herding livestock. We studied three plover and two courser species (Charadriidae: crowned plover *Vanellus coronatus* (25 nests), wattled plover *Vanellus senegallus* (3 nests) and three-banded plover *Charadrius tricollaris* (4 nests); Glareolidae: bronze-winged courser *Rhinoptilus chalcopterus* (13 nests) and Temminck's courser *Cursorius temminckii* (8 nests)) and three nightjar species (Caprimulgidae: fiery-necked nightjar *Caprimulgus pectoralis* (50 nests, 45 incubating adults), Mozambique nightjar *Caprimulgus fossii* (46 nests, 46 adults) and pennant-winged nightjar *Macrodipteryx vexillaria* (13 nests, 11 adults)). Despite belonging to two different orders of birds, these species all have small clutches (Table 1) and lengthy maximum recorded longevities (8–22 years for the two plover and two nightjar species with available data; Hockey et al. 2005). These shared life-history traits suggest that they all are likely to prioritise their own survival over that of their offspring.

Data Collection

Methods followed Troscianko et al. (2016); in brief, once a nest was shown to us by its finder, it was photographed and its coordinates were recorded with a Garmin eTrex 20 GPS. Camouflage was quantified from digital photographs taken with a Nikon D7000 camera converted to full spectrum sensitivity (Advanced Camera Services Limited, Norfolk, UK), and fitted with a 105 mm Micro-Nikkor lens. Human-visible spectrum photographs were taken through a Baader UV-IR blocking filter (Baader Planetarium, Mammendorf, Germany) and UV photographs were taken with a Baader UV pass filter. Consistency between UV and visible images was maintained by using a custom-made filter holder that facilitated a smooth transition between filters

without the need to move the camera. Ambient lighting conditions were controlled for by photographing a 40% Spectralon (Labsphere) grey standard (Stevens et al. 2007, Troscianko et al. 2016) beside nests from 2 m using identical camera settings (a sequential calibration method; Stevens et al. 2009). Photographs were not taken within 2 hours of sunrise or 2 hours before sunset, and were only taken in direct sunlight with a fixed aperture of f8 (ISO 400) in RAW format. These lighting conditions are representative of the dry season's weather, and ensured consistency in lighting between photographing the grey standard and target (adult or eggs). Consequently, photographs were not always taken on the first visit to the nest. Photographs of adult nightjars were taken from 5 m, with the camera angled towards the most visible flank of the adult. A few nightjar individuals and all adult plovers and coursers fled at distances greater than 5 m, such that it was not possible to photograph them. Eggs were photographed under natural lighting conditions from 1.25 m directly above, and again in controlled lighting conditions: shaded on a uniform white background, alongside a scale bar and grey standard.

Nests were revisited every other day until hatching or depredation, using binoculars and a GPS to relocate the nest from a distance. On every visit time of day was recorded in addition to escape distance (when possible). An approaching human (either JT or JWA) was used as a model predator, a method widely used in studies of escape behaviour (e.g. Frid and Dill 2002; Stankowich and Blumstein 2005). On some nests camera traps were set up to identify the main nest predators (see below and Troscianko et al. 2016 for details). One such predation event involved human predators, further supporting the use of humans as a model predator. Nest visits were not constrained by lighting conditions and so were conducted throughout the day. Nests were checked by one observer, except for the first visit when the nest finder was present and when the nest was photographed. Escape distance was measured from when the incubating adult was seen fleeing the nest; for plovers and coursers escape distance was measured using GPS, and for nightjars escape distance was paced out, with distances less than 1.5 paces measured in foot-lengths to the nearest 10 cm (approximating distance in meters, since GPS was not reliable within ~5 m). Nests were always approached from the same direction at normal walking pace. We did not directly measure egg temperature, since

accurately doing so would involve inserting a temperature probe directly into the egg, preventing its development. Other ecological variables affecting egg temperature (such as air temperature, radiance, wind, convection and conduction) have complex interactions and are difficult to measure *in situ* without disturbing the nest. Instead, we used time of day as a proxy for thermal risk, since at midday solar radiation is at its most intense due to the sun's elevation.

Image processing

Camera traps revealed a broad range of diurnal predators, including dichromats (banded mongoose *Mungos mungo*), trichromats (vervet monkey *Chlorocebus pygerythrus* and human) and tetrachromats (grey-headed bushshrike *Malaconotus blanchoti*), all of which consumed the entire clutch (Troscianko et al. 2016). In the absence of data on the visual systems of these particular species, we modelled images to the most phylogenetically relevant predator visual systems; ferret *Mustela putorius furo* vision (representing banded mongoose), human vision (representing primates), and common peafowl *Pavo cristatus* vision (representing the violet-sensitive grey-headed bushshrike). A companion paper found that this approach to quantifying camouflage is biologically realistic, since clutch survival was predicted in this suite of ground-nesting birds (Troscianko et al. 2016).

Before converting images to predator vision, both visible and UV images were linearized, scaled and aligned (Stevens et al. 2007; Troscianko and Stevens 2015). Predicted cone catch values for each predator visual system were modelled from digital images after a transformation from camera to animal color space following a widely used mapping technique (Párraga et al. 2002; Stevens et al. 2007; Pike 2010; Troscianko and Stevens 2015). Cone catch images (32-bits/channel) were used for all image processing, for each predatory visual system. Target selections were made for adult nightjars, 'cutting' them out using a free-hand selection tool. Target metrics were then compared to the surrounds (excluding the *in situ* eggs) in the same photograph. Egg targets in photographs with controlled lighting conditions were 'cut out' using an egg selection tool (Troscianko 2014) and down-sized using bilinear interpolation to match the pixels/mm of the nest surrounds.

Luminance (lightness as perceived by a visual system (Osorio and Vorobyev 2005)) distribution differences (Luminance$_{diff}$) were calculated by comparing absolute differences in counts of the numbers of pixels in each target (egg or adult nightjar plumage) to its background (Troscianko and Stevens 2015). Luminance$_{diff}$ values describe the difference between the target's and background's overall reflectance values in terms of predator vision. In addition we measured the intrinsic mean luminance of both the target and the background, as well as their intrinsic contrast (by calculating the standard deviation of luminance pixel values following a square-root transformation to generate a normal distribution of luminance values). Similar to Luminance$_{diff}$, spatial frequency differences (Pattern$_{diff}$) were calculated by summing the absolute differences in energy between target and background at different spatial scales (Troscianko and Stevens 2015). Fast Fourier Transform bandpass was used with filters at 17 levels and the 'energy' determined by the standard deviation of luminance values at each spatial scale. This allowed us to calculate how similar birds/eggs were in terms of marking sizes to those of the substrate, providing a measure of background matching camouflage. Color analysis was based on a widely used model of noise determined color discrimination (Vorobyev and Osorio 1998), using visual system-specific cone ratios (supplementary materials) and a Weber fraction of 0.05 for generating "just noticeable differences" (JNDs), whereby a JND of less than one means that two colors should be indiscriminable to an observer. A script was used to determine the dominant colors in an image (up to 32 different colors). Color difference (Color$_{diff}$) for targets was the mean difference (in JNDs) between the most abundant color of the target and all the colors found in its surrounds, weighted by coverage (Troscianko and Stevens 2015); see supplementary materials and Troscianko et al. (2016) for more information on how camouflage metrics were calculated.

Statistical Methods

R v3.1.0 (Team R Core 2013) was used to conduct all statistical tests. Potential predictors of variation in escape distance were simultaneously tested using linear mixed-effect models implemented using the lme4 package v1-6 (Baayen et al. 2008), fitted with restricted maximum likelihood and a Gaussian error structure. Model simplification was done through backwards

fitting the fixed effects with AIC and log-likelihood, facilitated by the function fitLMER from LMERConvenienceFunctions v2.5. Data on ferret vision and peafowl vision were not put through the model simplification process and instead interrogated using the simplified model for human vision, since humans were the relevant approaching threat. The pamer function was used to obtain p-values, and the most conservative values were reported. Prior to model simplification, variables were transformed to meet assumptions of homogeneity of variance and a normal error structure. Time of day was converted to decimal hour and treated as a polynomial since it was used as a proxy for temperature. We analysed the two orders of birds (Charadriiformes and Caprimulgiformes) in separate models owing to different predictions based on their different ecology (Lack 1968). To confirm the differences in escape distances between the different species groups (nightjars, plovers and coursers), we ran an additional model with data on escape distances from all species; the mcposthoc function was used for testing planned contrasts between variables. For all models, nest ID and visit number were included as random effects; the latter controlled for any habituation effect across multiple visits to the same nest. Species was retained in all models, meaning any remaining effects found were detected across all species. Covariance between model variables was tested for using a combination of the vcov and cor2cov functions.

Results

Here we report only the results for data from the trichromatic primate vision model. All results for data from ferret and peafowl vision models did not alter the conclusions, and are reported in the supplementary material. All data, including that for the different predator visual systems are deposited in the Dryad Digital Repository: doi:10.5061/dryad.3h6r1. We found that escape distances did not differ between plover and courser species (t_{385} = 1.256; p = 0.210), but nightjar escape distances were significantly shorter than both plover (t_{385} = 19.590; $p < 0.001$) and courser (t_{385} = 16.663; $p < 0.001$) escape distances.

Plovers and coursers

The distance at which incubating adults initiated escape was shorter when egg background matching was better with respect to pattern (i.e. $pattern_{diff}$ was lower), and this effect differed with time of day: it declined as midday approached and increased thereafter, with this effect more pronounced when egg $pattern_{diff}$ values were lower (Figure 2: $Pattern_{diff}$*Time of day: $F_{2,61}= 4.509$; $p=0.014$). $Color_{diff}$ was not retained in the model after simplification, indicating that escape distance was not influenced by degree of color match. $Luminance_{diff}$ was retained in the simplified model, but was not found to be significant ($F_{1,61}= 3.594$; $p = 0.063$). Mean egg luminance was not retained in the simplified model; however, it was found to positively co-correlate with egg contrast ($R^2 = 0.760$). Escape distances were greater for higher contrast eggs and this effect was stronger when eggs were larger (Egg Contrast* Logged Mean Egg Volume: $F_{1,61}= 16.634$; $p < 0.001$). Due to the collinearity between mean egg luminance and egg contrast, it is not clear which variable is driving this relationship. Lastly, birds initiated escape at greater distances when background contrast was higher (i.e. when backgrounds had a greater variance in luminance: $F_{1,61}= 14.551$; $p<0.001$).

Nightjars

No aspect of egg camouflage predicted escape distance, with no model better than the null. However, there were complex relationships between adult camouflage and escape distance. When adult $pattern_{diff}$ values were low (good pattern match), escape distances did not differ with varying degrees of $color_{diff}$. However, when $pattern_{diff}$ was high (poor pattern match), escape distances were greater when adult $color_{diff}$ values were higher ($Color_{diff}$* $Pattern_{diff}$: $F_{1,270}= 14.441$, $p<0.001$). After simplification the model did not retain $luminance_{diff}$, adult mean luminance, adult contrast or background mean luminance. The distance at which escape was initiated varied according to time of day, depending on background contrast: escape distances were shortest at midday and when background contrasts were high (Background Contrast*Time of day: $F_{2,270}= 5.682$, $p=0.004$).

Discussion

We investigated whether components of background matching camouflage predicted escape behaviour in ground-nesting birds. We found that plovers and coursers initiated escape at greater distances when their eggs were less well-camouflaged in terms of pattern, as expected if escape behaviour at close quarters would exacerbate the costs of poor camouflage by revealing nest location. This implies that ground-nesting birds are able to assess the camouflage of their eggs against their nesting background, and respond appropriately. We found that this effect was most pronounced at midday (Figure 2). The strong relationship between escape behaviour and time of day is consistent with previous studies demonstrating that birds adjust their incubation behaviour according to seasonal and daily variations in environmental temperature (Brown and Downs 2003; Yasué and Dearden 2006; Tieleman et al. 2014). While the circadian correlation we observed could potentially be explained by another factor that co-varies with time of day (e.g. predator activity), temperature seems the most likely given its strong circadian pattern, and the extremes it reaches at ground level in our study area during our focal species' breeding season. Conditions at another tropical site have recently been shown to impose greater thermal stress on experimentally placed eggs in ground-nesting species' natural nest sites, than those at a temperate site (Gómez et al. 2015). Some of our study species in particular are known to engage in thermoregulatory behaviour when incubating (including gular fluttering and wetting their eggs using soaked belly feathers (Hockey et al. 2005)). Taken together, our results suggest that camouflage is able to mitigate not only predation risk but also thermal risks from predator-induced disturbance, by permitting adults to shade their eggs for longer when the risk of overheating is highest.

Escape behaviour of plovers and coursers also differed according to egg contrast (intrinsic variation in egg luminance) and egg size. However, egg contrast was positively correlated with mean egg luminance, with darker eggs having lower variation in luminance values (i.e. less pronounced patterns), and it is therefore unclear which variable is the driver of this relationship. As expected if darker (Kilner 2006; Gómez et al. 2015) and smaller (Turner 1985) eggs absorb more solar radiation, parents escaped at greater distances when egg

contrast/luminance was higher, and this effect was greater for larger eggs. More research is needed to confirm whether egg contrast/luminance and egg size reflect risk of overheating, since the evidence for the relationship between egg color and heat transfer has been disputed and still requires appropriate quantitative evidence (Ruxton 2012).

For birds such as nightjars that initiate escape only at very close range, we expected to find an association between escape distance and the camouflage of adult plumage, rather than that of the eggs (Lack 1968). As predicted, nightjar escape distance showed no association with egg camouflage. Instead, escape distance was associated with the degree of both color and pattern matching between adult plumage and the background. Irrespective of their color match, adults initiated escape at shorter distances when their pattern was a good match to the background. However, when their pattern match was poor, adults with less effective color match initiated escape at greater distances. This suggests that pattern may be the more important cue in determining escape behaviour for nightjars, but that these birds may also be sensitive to color when making the decision to flee.

Background contrast was found to be an important predictor of escape decisions of all species, with escape distances shorter when background contrast was high, and for nightjars this effect was most prominent at midday. It is possible that high contrast backgrounds reduce detection risk. This is plausible given that higher contrast backgrounds are typically more heterogenous, and predator search times can be longer in these complex habitats (Merilaita 2003; Dimitrova and Merilaita 2009). Longer search times would reflect a lower detection risk from the prey's perspective, and background contrast may therefore be a reliable indicator of when best to flee. These results imply that nesting birds may use absolute properties of their surrounding habitat to modulate escape behaviour, in addition to using their degree of background match.

A strength of this study is that it was conducted on a community of wild, free-ranging animals under natural conditions with clear fitness consequences. However, our results are inevitably correlative and experimental manipulations are needed to confirm the mechanisms underlying the patterns we have uncovered. Ideally, background matching and thermal costs

should be experimentally manipulated, but doing so in a biologically realistic way is very challenging and potentially destructive. Such a manipulation would also shed light on how adult birds assess their degree of camouflage. We might speculate that egg camouflage could be directly assessed visually, predicting that escape behaviour should respond to experimentally manipulated background matching. Alternatively, camouflage might be indirectly assessed through experience: individuals with poor camouflage may experience more predation attempts and therefore associate those circumstances with the need to initiate escape at greater distances when subsequent breeding attempts are in similar habitats. Such self-assessment of camouflage may also be relevant to other behavioural decisions, such as when to initiate an attack from an ambush predator's perspective.

To our knowledge, this study is the first to show empirically that animals modulate risk-taking behaviour according to their direct degree of camouflage as perceived by relevant visual systems. We also found strong circadian patterns in escape distance, consistent with the hypothesis that ambient temperatures and solar radiation influence escape decisions, and suggesting for the first time that this trade-off is modulated by camouflage. Similarly, we found that escape distances were correlated with habitat and egg characteristics that could influence risk of overheating. Future studies should monitor egg temperatures in addition to quantifying camouflage, in order to directly measure the thermal costs of escape behaviour and how they vary in a circadian manner. Although our work has focused on background matching camouflage with regards to color, luminance, and pattern, it would be valuable in future studies to consider other potential types of camouflage which are important to concealment, such as disruptive coloration (Cuthill et al. 2005). However, this will be challenging because defining and quantifying disruptive markings on three-dimensional objects is problematic (Stevens and Merilaita 2009*b*). Overall, our results suggest that animals are able to assess their degree of camouflage against the background, and use this information to fine-tune behavioural decisions in response to predation risk.

Acknowledgements

Online Appendix A: Supplementary Material

Materials and Methods

Image processing

Between taking visible and UV photographs there was the possibility of camera movement and the need to refocus the lens. To ensure accurate alignment of images, a script was used to align and scale the visible and UV images (Troscianko and Stevens 2015). This produced a 16-bit TIFF image with visible red, green and blue channels, and the red and blue channels from the UV pass filter (the green channel was discarded). Most cameras have a non-linear relationship between light intensity and image pixel values (Stevens et al. 2007). We corrected for this by modelling linearisation curves from eight calibrated Spectralon reflectance standards from 99 to 2% reflectance (Labsphere). Linearisation models for all channels had R^2 values ≥0.999 (Troscianko and Stevens 2015). Conversion of images to reflectance often discards (saturates) values above 100% relative to the reflectance standard; to avoid this, the 16-bit reflectance pixel values were scaled down to preserve the whole dynamic range of the image, and then scaled back to reflectance prior to processing in 32-bit floating point.

Pattern, luminance and contrast metrics were based on the luminance channel (as with past work, e.g. (Stevens et al. 2007)) because pattern is widely thought to be encoded by achromatic vision (Stoddard and Stevens 2010). Ferret luminance was taken as the L cone sensitivity (L-cones outnumber S-cones 14:1 (Calderone and Jacobs 2003)), human luminance was taken as (L+M)/2 (Lovell et al. 2005), and peafowl luminance was taken as double cone

sensitivity (Hart 2002). Luminance distribution differences (Luminance$_{diff}$) were calculated by comparing absolute differences in counts of the numbers of pixels in each target (plover egg or adult nightjar plumage) to its background at 32 linear levels of luminance (*lum*) from 0% to 100%:

$$Luminance_{diff} = \sum_{lum=100\%}^{lum=0\%} \left| Target_{lum} - Background_{lum} \right|$$

Luminance$_{diff}$ values describe to what extent the egg or nightjar reflectance values as perceived by a given predator matched the values of their surrounds. Similar to other studies, pattern differences were generated using Fast Fourier Transform with bandpass filtering via a 'granularity' approach (Godfrey et al. 1987; Chiao et al. 2009; Stoddard and Stevens 2010). We ran 17 isotropic filters (increasing exponentially from 2 to 512 pixels) and, at each filter, calculated the standard deviation of luminance values to represent the 'energy'. Spatial frequency differences (Pattern$_{diff}$) were calculated in a similar manner to Luminance$_{diff}$, by summing the absolute differences in energy between target and background at each spatial scale measured (*s*):

$$Pattern_{diff} = \sum_{s=max}^{s=min} \left| Target_{s} - Background_{s} \right|$$

Any differences in pattern energy between the corresponding target and background spatial scales, increases the Pattern$_{diff}$ value (Troscianko and Stevens 2015). Thus Pattern$_{diff}$ describes the degree to which egg and plumage patterns match their size and spacing to the patterns in their surrounds, and the degree of difference in contrast between their patterns. Pattern$_{diff}$ is used to specifically test a background-matching hypothesis, and does not take into account the phase information of a Fourier spectrum. The latter is problematic to analyse and is more relevant for identifying different classes and shapes of objects (i.e. object recognition), which would be better suited for investigations into masquerade (object mimicry). Previous methodologies for investigating background matching separate out the energy spectra into multiple descriptive statistics (Chiao et al. 2009; Stoddard and Stevens 2010), only analysing

one peak frequency or peak energy and discarding potentially important pattern information at other scales. This method accounts for multi-modal spectra, combining pattern similarity into a single measure, making statistical analysis more straightforward.

Color analysis was based on the widely used Vorobyev & Osorio (1998) noise model of color discrimination, which is frequently used to compare how discriminable two colors are likely to be to an observer. In most previous studies, researchers have compared two distinct color patches to one another with the model. However, the substrate (visual background) and eggs/birds in our study show continuous variation in color spatially, meaning that it is not possible (or accurate) to simply pick pairs of color patches to compare. Instead, we extended the model technique to find patches of color in the eggs/birds and background that were indiscriminable to the model, and therefore of the same color 'type', to compare camouflage between eggs/birds and substrate. Thus, while the analysis includes information on the colors across the visual scene, the aim was not to calculate spatial pattern information (our granularity approach does this), but rather to compare the principal colors of the eggs/birds with the background to obtain a measure of color camouflage. We used visual system-specific cone ratios (shortest to longest wavelength; ferret 1 : 14 (Calderone and Jacobs 2003); human 1 : 5.49 : 10.99 (Hofer et al. 2005); peafowl 1 : 1.9 : 2.2 : 2.1 (Hart 2002)) and a Weber fraction of 0.05 for generating "just noticeable differences" (JNDs). A script was used to determine the most common colors in a scene at both the local and global levels for each visual system (Troscianko and Stevens 2015). The script searched for adjacent pixels that were within a 0.05 JND (local) threshold and again for those within a 1 JND (global) threshold. Once identified, these pixels were classed as a single color area, and clumped together to form smooth color gradients before moving to the next common color. The script ran until 99% of the image was accounted for, or the 32 most abundant colors were found. Color difference was calculated as the mean difference (in JNDs) between the most abundant color in the target and all the colors found in the background, weighted by coverage.

Additional Results

As seen in table A1, the output from models with data on ferret and peafowl vision are qualitatively very close to those of human vision. For plover escape distances, there was one additional significant result for ferret vision: escape distances were shortest when both pattern and luminance match was good. All predictors of nightjar escape distance for data on egg camouflage in ferret and peafowl vision were dropped from the model during model simplification. For nightjar escape distances and adult plumage metrics in peafowl vision, there was one less significant result: the interaction between adult color$_{diff}$ and adult logged pattern$_{diff}$ was not significant.

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Tables

Table 1: Summary statistics for escape distances and clutch sizes from our study

Species	n (nests)	Escape distance (m)	Clutch size
Plovers & Coursers:			
Three-banded plover	4	35.1 ± 21.4	2.0 ± 0.0
Crowned plover	25	82.1 ± 40.5	2.6 ± 0.6
Wattled plover	3	88.7 ± 45.3	3.0 ± 1.0
Bronze-winged courser	13	43.8 ± 15.9	2.7 ± 0.4
Temminck's courser	8	55.4 ± 13.4	2.0 ± 0.0
All	53	66.0 ± 36.8	-
Nightjars:			
Fiery-necked nightjar	54	1.88 ± 1.5	1.9 ± 0.3
Mozambique nightjar	51	1.86 ± 0.9	2.0 ± 0.1
Pennant-winged nightjar	13	2.15 ± 1.2	2.0 ± 0.0
All	118	1.90 ± 1.3	-

Notes. - Values are means $\pm$ 1 standard deviation. Since we recorded multiple escape distances for each nest, species means were calculated from nest means.

Table A1: Linear mixed effects model output for data based on human, ferret and peafowl vision for predictors of plover and courser escape distances and nightjar escape distances.

Predictor of Escape Distance	Human Vision	Ferret Vision	Peafowl Vision
Plover & Courser Eggs:			
Egg Logged Pattern$_{diff}$	$F_{1,61} = 16.31$; $P < 0.001$	$F_{1,61} = 23.832$; $P < 0.001$	$F_{1,61} = 20.671$; $P < 0.001$

Egg Luminance$_{diff}$	$F_{1,61} = 3.59$; $P = 0.062$	$F_{1,61} = 2.887$; $P = 0.094$	$F_{1,61} = 1.956$; $P = 0.167$
Egg Contrast	$F_{1,61} = 20.66$; $P < 0.001$	$F_{1,61} = 38.873$; $P < 0.001$	$F_{1,61} = 43.005$; $P < 0.001$
Background Contrast	$F_{1,61} = 14.55$; $P < 0.001$	$F_{1,61} = 20.941$; $P < 0.001$	$F_{1,61} = 19.963$; $P < 0.001$
Time (poly)	$F_{2,61} = 9.10$; $P < 0.001$	$F_{2,61} = 10.327$; $P < 0.001$	$F_{2,61} = 9.608$; $P < 0.001$
Logged Mean Egg Volume	$F_{1,61} = 22.84$; $P < 0.001$	$F_{1,61} = 30.892$; $P < 0.001$	$F_{1,61} = 37.661$; $P < 0.001$
Species	$F_{4,61} = 11.53$; $P < 0.001$	$F_{4,61} = 13.446$; $P < 0.001$	$F_{4,61} = 12.722$; $P < 0.001$
Egg Logged Pattern$_{diff}$ * Egg Luminance$_{diff}$	$F_{1,61} = 0.90$; $P = 0.347$	$F_{1,61} = 4.299$; $P = 0.042$	$F_{1,61} = 0.525$; $P = 0.472$
Egg Logged Pattern$_{diff}$ * Time (poly)	$F_{2,61} = 4.51$; $P = 0.014$	$F_{2,61} = 4.939$; $P = 0.010$	$F_{2,61} = 5.262$; $P = 0.008$
Egg Contrast* Logged Mean Egg Volume	$F_{1,61} = 16.63$; $P < 0.001$	$F_{1,61} = 24.268$; $P < 0.001$	$F_{1,61} = 25.176$; $P < 0.001$
Nightjar Adult:			
Adult Color$_{diff}$	$F_{1,270} = 3.05$; $P = 0.082$	$F_{1,270} = 1.955$; $P = 0.163$	$F_{1,270} = 2.113$; $P = 0.147$
Adult Logged Pattern$_{diff}$	$F_{1,270} = 2.13$; $P = 0.146$	$F_{1,270} = 1.078$; $P = 0.300$	$F_{1,270} = 0.303$; $P = 0.582$
Background Contrast	$F_{1,270} = 0.44$; $P = 0.508$	$F_{1,270} = 0.058$; $P = 0.810$	$F_{1,270} = 0.461$; $P = 0.498$
Time (poly)	$F_{2,270} = 1.47$; $P = 0.233$	$F_{2,270} = 1.409$; $P = 0.246$	$F_{1,270} = 1.467$; $P = 0.233$
Adult Color$_{diff}$ * Adult Logged Pattern$_{diff}$	$F_{1,270} = 14.44$; $P < 0.001$	$F_{1,270} = 8.013$; $P = 0.005$	$F_{1,270} = 0.279$; $P = 0.598$
Background Contrast * Time (poly)	$F_{2,270} = 5.68$; $P = 0.004$	$F_{2,270} = 5.322$; $P = 0.005$	$F_{1,270} = 7.879$; $P < 0.001$

Notes.- (Poly) indicates a polynomial term. Model output is after model simplification.

Figure 1: Summary of predictions for each order of birds. Images show a Temminck's courser fleeing its eggs (left, courtesy of Warwick Tarboton) and a fiery-necked nightjar 'sitting tight' on its eggs (right).
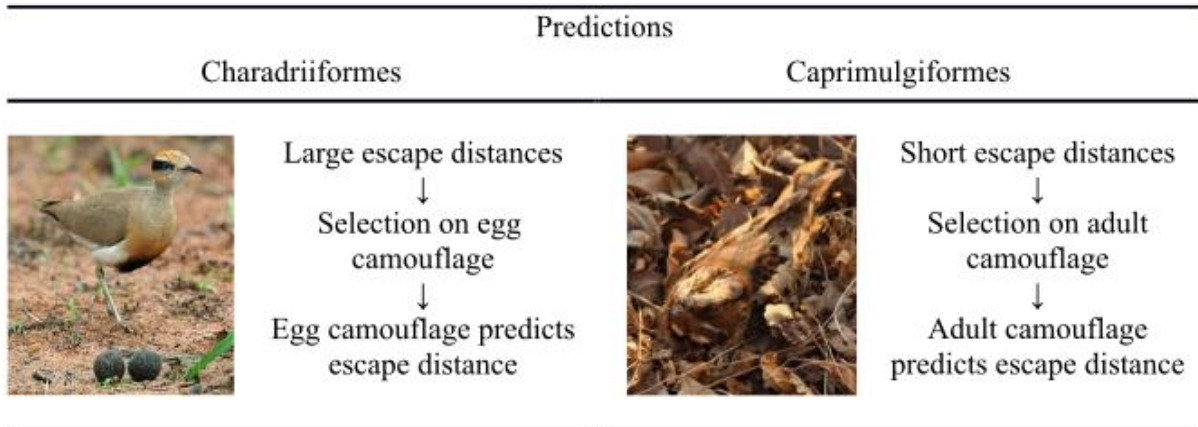
Figure 2: Model predictions for the log-transformed escape distance (meters) of crowned plovers in relation to time of day (decimal hour), when egg pattern match to the background is good (blue; pattern match values at the 0.25 confidence interval with standard errors) and poor (red; pattern match values at the 0.75 confidence interval with standard errors). Plotted points are from the raw data. Both images show crowned plover nests; above, with good pattern match and below, with poor pattern match.
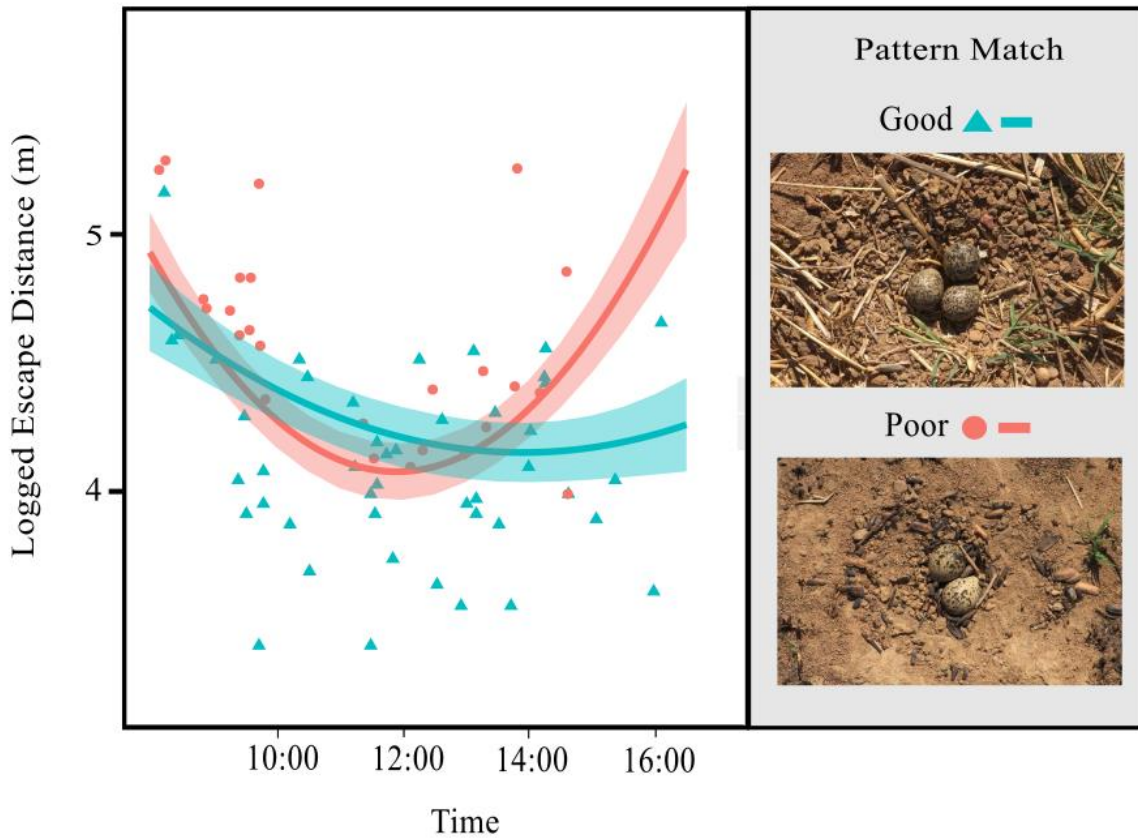
Figure A1: Example photographs. Images A-C are photographs of adult nightjars taken at a distance of 5 m with the nightjar in the centre of the image; in the bottom right of each is a zoomed in image of the nightjar. Examples A and B are of Mozambique nightjars and C is a Fiery-necked nightjar. Images D-I are photographs of nests taken from directly above at a distance of 1.25 m. D and E are clutches from the Mozambique nightjar, F is a Fiery-necked nightjar clutch, G and H are clutches from the Crowned plover and I is a Bronze-winged courser clutch.