Habitat geometry rather than visual acuity limits the visibility of a ground-nesting bird's clutch to terrestrial predators.

George Hancock[1], Lizzie Grayshon[2], Ryan Burrell[3], Andrew Hoodless[4], Innes Cuthill[5], and Jolyon Troscianko[6]

[1]University of Exeter College of Life and Environmental Sciences
[2]Game and Wildlife Conservation Trust
[3]Bournemouth University
[4]The Game & Wildlife Conservation Trust
[5]University of Bristol
[6]University of Exeter

July 19, 2023

Abstract

The nests of ground-nesting birds rely heavily on camouflage for their survival, and predation pressures, often linked to human activity, are a major source of mortality. Numerous ground-nesting bird populations are in decline, so understanding the effects of camouflage on their nesting behaviour is of relevance to their conservation concern. Habitat three-dimensional (3D) geometry together with predator visual abilities, viewing distance, and viewing angle determine whether a nest is either visible, occluded or too far away to detect. While this link is intuitive, few studies have investigated how fine-scale geometry is likely to help defend nests from different predator guilds. We quantified nest visibility based on 3D occlusion, camouflage, and predator visual modelling in northern lapwing, Vanellus Vanellus, on different land management regimes. Lapwings selected local backgrounds that had a higher 3D complexity at a spatial scale greater than their entire clutches compared to nearby control sites. Importantly, our findings show that habitat geometry – rather than predator visual acuity restricts nest visibility to terrestrial predators, and that an open field would actually be perceived as a closed habitat to a terrestrial predator searching for nests on the ground. Taken together with lapwings' careful nest site selection, our findings highlight the importance of considering habitat geometry for understanding the evolutionary ecology and management of conservation sites for ground-nesting birds.

Habitat geometry rather than visual acuity limits the visibility of a ground-nesting bird's clutch to terrestrial predators.

Authors: George R.A. Hancock*[1], Lizzie Grayshon[2], Ryan Burrell[3], Innes Cuthill[4], Andrew Hoodless[2], Jolyon Troscianko[1]

*Corresponding author: ghancockzoology@gmail.com

1. Centre for Ecology & Conservation, University of Exeter, Penryn, TR10 9FE, UK
2. Game & Wildlife Conservation Trust, Fordingbridge, SP6 1EF, UK
3. Faculty of Science and Technology, Bournemouth University, Fern Barrow, Poole, Dorset, BH12 5BB, UK
4. School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

Key Words

Camouflage, 3D Scanning, Occlusion, Ground-nesting Birds, Lapwing

Abstract

The nests of ground-nesting birds rely heavily on camouflage for their survival, and predation pressures, often linked to human activity, are a major source of mortality. Numerous ground-nesting bird populations are in decline, so understanding the effects of camouflage on their nesting behaviour is of relevance to their conservation concern. Habitat three-dimensional (3D) geometry together with predator visual abilities, viewing distance, and viewing angle determine whether a nest is either visible, occluded or too far away to detect. While this link is intuitive, few studies have investigated how fine-scale geometry is likely to help defend nests from different predator guilds. We quantified nest visibility based on 3D occlusion, camouflage, and predator visual modelling in northern lapwing, Vanellus Vanellus, on different land management regimes. Lapwings selected local backgrounds that had a higher 3D complexity at a spatial scale greater than their entire clutches compared to nearby control sites. Importantly, our findings show that habitat geometry – rather than predator visual acuity restricts nest visibility to terrestrial predators, and that an open field would actually be perceived as a closed habitat to a terrestrial predator searching for nests on the ground. Taken together with lapwings' careful nest site selection, our findings highlight the importance of considering habitat geometry for understanding the evolutionary ecology and management of conservation sites for ground-nesting birds.

1 INTRODUCTION

Camouflage is one of the most common anti-predator strategies exhibited by animals, as reducing the ability of predators to detect or distinguish a target from its background reduces the risk of predation (Cott, 1940; Cuthill, 2019; Endler, 1981). Ground-nesting birds are no exception to this, with many of their species exhibiting camouflage at various phases in their life history (Stevens et al., 2017, 2017; Stoddard et al., 2016). One notable phase where camouflage has evolved is that of the egg (Kilner, 2006; Westmoreland, 2008). The comparative openness and accessibility of ground-nesting wader nests, such as coursers (Cursoriinae) and plovers (Charadriinae), renders them particularly vulnerable to predation. When predators approach, adults abandon their nests (Blumstein, 2003; Wilson-Aggarwal et al., 2016), relying on the patterns of their eggs to camouflage them while the parent(s) harass or distract the predator (Armstrong, 1954; Simmons, 1951). The nests of species that rely more on the parents' plumage for camouflage have been shown to have less camouflaged eggs. Whereas in other ground-nesting species the eggs can be occluded by either burying them, or by relying on vegetation from surrounding hedgerows, scrub or forest understory (Bravo et al., 2022; Masero et al., 2012; Stevens et al., 2017; Stoddard et al., 2011; Troscianko et al., 2016a). Occlusion by natural structures is arguably one of the most effective forms of camouflage (Troscianko et al., 2016a). Partial occlusion can mask important visual cues for detection and recognition such as an object's outline, size and identifiable morphological features (limbs, eyes, etc) (DiPietro et al., 2002; Sharman et al., 2018; Sovrano and Bisazza, 2008; Tvardíková and Fuchs, 2010). While total occlusion forces observers to rely on other sensory cues to detect the occluded object, providing that the source of occlusion isn't also recognisable e.g., nesting material or incubating parent (Bailey et al., 2015; Broughton and Parry, 2019; Stevens et al., 2017).

Occlusion isn't without costs. The openness of the nests of ground-nesting birds is thought to be a balance between multiple trade-offs. Nest predation, parent predation, thermoregulation and both habitat and nesting material availability all contribute to the appearance of ground-nesting bird nests (Gillis et al., 2012; Kubelka et al., 2019; Mainwaring et al., 2014; Stevens et al., 2017; Swaisgood et al., 2018). Local vegetation height has been shown to influence nest site selection and predation risk of ground-nesting birds; taller vegetation results in shorter flushing distances, higher nest survival and greater parent predation risk (Bertholdt et al., 2017; Gómez-Serrano & López-López, 2014). A study using periscopes to assess the visibility of dogs and humans from the perspective of nesting Kentish plovers (*Charadrius alexandrines)* showed that sites selected by parents offered greater predator visibility at the cost of increased nest predation risk (Gómez-Serrano and López-López, 2014).

When measuring nest camouflage, the visual ecology of the observing parents and predators should be considered. Visual modelling using colour-calibrated images has increasingly been used to assess animal camouflage from different visual systems, accounting for differences in observer colour reception and spatial acuity (Caves et al., 2018; Maia et al., 2013; van den Berg et al., 2020). These measures have been used to show that camouflage from local background pattern match can predict nest survival in ground-nesting birds (Troscianko et al., 2016b). However, an aspect of visual ecology rarely considered is predator height in combination with distance and habitat structure. The height of an animal's eye relative to its object of interest changes the angles and distances required for the object to be occluded by surrounding structures (Martin, 2011). A nest that appears exposed from a human height may be undetectable to a smaller mammalian predator even at closer distances, while an avian predator excluded to the edge of a field by harassing parents may be at too great a distance to detect a clutch of eggs (Gómez-Serrano and López-López, 2014). Microhabitat selection likely helps balance the trade-offs between predator and nest visibility (Gómez-Serrano and López-López, 2014; Lovell et al., 2013; Stoddard et al., 2016). By selecting areas of surrounding local elevation ground-nesting birds should be able to increase visibility of predators. Combined with the depression of the scrape, local elevation should paradoxically decrease nest visibility; requiring a greater viewing angle to be seen unobstructed by approaching predators.

Ground-nesting waders are in decline across their range due to habitat loss, agricultural intensification, reduced prey availability and elevated predation risk from mesopredators, such as foxes, mustelids, corvids and raptors (Evans, 2004; Galbraith, 1988; Roos et al., 2018; Vickery et al., 2004). Consequently, mechanisms of further understanding the habitat features that both encourage nesting and minimise predation are of increasing conservation interest, as predation is typically the leading cause of nest mortality (Baines, 1990; Ricklefs, 1969; Teunissen et al., 2008). Just as camera quality has advanced colour analyses of visual scenes, increasing accessibility of terrestrial and aerial 3D scanners allow for the measurement of topography and vegetation structure at different spatial scales (de Vries et al., 2021; Hill et al., 2014; Li et al., 2022). Terrestrial scanners have even been used to compare the volume and shape of bowl nesting birds, though these were taken *in vitro* (Simonov and Matantseva, 2020). 3D scanning allows for a more complete measure of local 3D composition than more traditional chart and ruler based measurements of vegetation height and cover (Gómez-Serrano and López-López, 2014; Gregg, 1991; Pendleton and Nickerson, 1951).

In this study, we used hand-held 3D scanners and colour-calibrated images to measure the shape and appearance of northern lapwing (*Vanellus vanellus*) nests in pastoral, arable and wet grassland sites. The goal was to investigate how the 3D and colour environment influences lapwing nesting decisions. The methods of habitat management and local variation should also influence the colour and 3D composition of the habitat, changing the occlusion of nests, the number of distractive structures with similar 3D shape to the nests and the colour match of the nests. We hypothesised that lapwing should favour backgrounds of higher local elevation, greater surrounding 3D variation at scales relative to the size of their nests, and which are more obstructed from the perspectives of their predators. We also compared the distances where modelled occlusion and acuity influence detectability by predators and investigated whether background match and occlusion predict predation in lapwing. A full breakdown of the 3D scanning methods and scripts required is provided within our supplementary material, including methods for using photogrammetry generated point clouds in place of 3D scanners.

2 MATERIALS AND METHODS

Study System:

The northern lapwing (*Vanellus vanellus*) is a ground-nesting wader that commonly breeds in lowland wet grassland and arable sites across temperate Eurasia (Cramp and Brooks, 1992). The species is of conservation concern in the UK and mainland Europe as their populations have been in decline since the 1970s (Wilson et al., 2001). Unsustainable nest predation is cited as a barrier to population recovery (Evans, 2004; Laidlaw et al., 2021; Roos et al., 2018).Northern lapwing nests comprise shallow scrapes in bare ground or short mixed vegetation, lined with varying amounts of dead plant matter (Kubelka et al., 2019). Their nests are defended from predators by using a combination of mobbing, distractive displays, behavioural crypsis and egg camouflage (Salek and Cepáková, 2006). While positioning away from trees and around waterbodies also protects nests (Eglington et al., 2009; Kaasiku et al., 2022).

We sampled lapwing nests from sites in two separate locations monitored by the Game and Wildlife Conservation Trust (GWCT); the Avon Valley in Hampshire and Burpham in Sussex. The Avon Valley sites included a variety of habitats, predominantly under UK agri-environment schemes, such as wet grassland, marshland, pasture, and a restored ex-gravel quarry. Conversely, the Sussex sites consisted of arable fields in various stages of rotation between plough, spring cereal, and fallow. Predation was monitored at the sites using iButton (Thermochron iButton, Maxim Integrated Products, Inc., Sunnyvale, CA) nest temperature loggers and weekly nest checks (Hartman and Oring, 2006). Nest outcomes (hatched, abandoned, flooded, trampled and predated) were determined by both interpretation of nest temperature logger plots and accepted in-field techniques (Hartman & Oring, 2006; Sheldon et al., 2010). All sites utilised some form of predator control or management to protect wading birds. These varied in intensity and included deterrents such as electric fences and crow scarers and removal methods such as Larsen traps, tunnel traps, and shooting (Fletcher et al., 2010; Laidlaw et al., 2021; Malpas et al., 2013).

Ethics Statement:

Corresponding permissions were granted as part of a collaboration with the GWCT and were approved by the University of Exeter Ethics Committee.

3D Scanning & Calibrated Photography:

From March to Mid-June of 2021 and 2022, we photographed, and 3D scanned 83 lapwing nests. Each nest was scanned with an ASUS Zenfone AR using the Matterport Scenes app from a height of 1.2m (Shults et al., 2019). Phone 3D scanners provides a cheap and relatively easy method for capturing 3D point clouds using triangulation from an structured light time-of-flight sensor (Froehlich et al., 2017). Scans were taken from a height of 1.2 metres at a flat 90° polar (vertical) angle from the ground. Each scan taking 7 seconds to complete. For each nest, an additional nest-less photo and scan were taken at a distance of 1-2 metres (4 paces) from the nest, by backtracking in the direction of the approach to avoid further trampling the surrounding area. These additional photos and scans were used as a paired null for each nest.

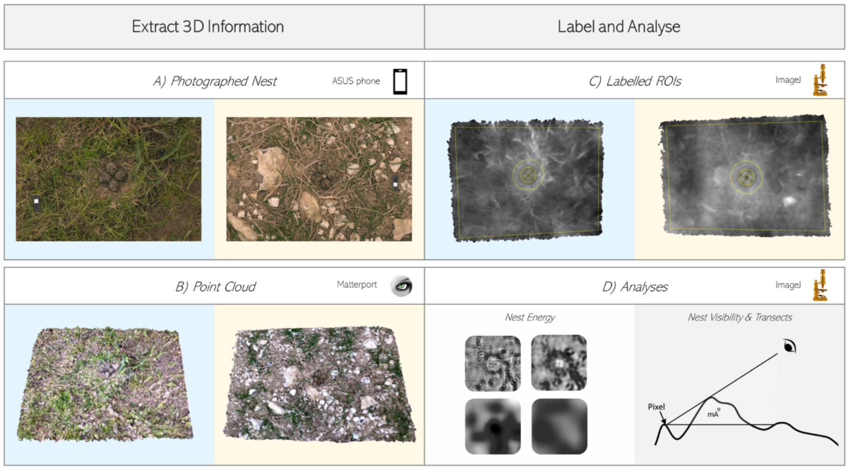


Figure 1. Framework for 3D analyses of ground-nesting bird nests. Example images are from an agri-environment scheme site (left-blue) and spring-cereal arable site (right-yellow). A) Photograph of nest taken with colour calibrated Sony camera. B) 3D scan nests with ASUS phone and upload the point cloud into Matterport scenes for standardisation of formatting. C) Import and label point clouds in ImageJ. D) Run nest 3D energy and visibility transect analysis scripts.

Photographs of the nests and nulls were taken using a MICA colour-calibrated Sony A6000 with a baader venus-u 52mm UV filter and the camera's own visible light filter (Moher Alsady et al., 2016). A 7% and 93% uniform (λ 200-700nm) reflectance standard was placed in situ for each photograph (Troscianko et al., 2016b). Standards were created using Zenith Polymer sintered PTFE sheets. As the lighting environment was highly variable with weather conditions, all photos were taken with a 1m^2 pop-out NEEWER diffuser sheet at times greater than 2 hours from dawn and dusk (Duarte et al., 2018; Troscianko et al., 2016b). Photographs were calibrated and converted to multispectral images using the MICA toolbox v2.2.2 for ImageJ (Schneider et al., 2012; Troscianko and Stevens, 2015; van den Berg et al., 2020).

Constructing Height Maps:

The 3D scans were processed using the open-source program MeshLab v.2022.02 (Visual Computing Lab – ISTI – CNR, http://meshlab.sourceforge.net/), to extract only the height data and export the scans as .ply files (Simonov and Matantseva, 2020). These files were then imported into ImageJ, using a custom script, to create images containing each nest's X, Y, and Z (height) coordinates, with 1 pixel representing 1mm (Schneider et al., 2012). Missing Z values (0.07% of pixel values) were filled with the mean background value. Finally, ImageJ was used to label the different parts of each scan, including the clutch (area around all the eggs), the nest (area around the scrape), the background (non-blank parts of the scan), and the individual eggs (group of regions of interest around each egg), see Figure 1. Instructions can be found within our supplementary material and on our GitHub.

Nest 3D Measures:

Cross-section maps of each nest were constructed by creating a circle selection (radius=300mm) centred on the clutch ROI. At each integer distance (radius = 0-300mm), the mean Z-value was measured and translated either to the minimum of the clutch (nest-normalised) or the surrounding background (radius-normalised) (see supplemental material). These cross-sections allowed for comparisons of the scans' peak nest, peak clutch and trough heights and calculation of the nest's slope.

To quantify how rough or smooth the terrain at nest locations was at different spatial scales, we used methods similar to those used for 2D pattern analysis. We measured the 'energy' (SD) of the Z value at different spatial scales relative to the mean wavelength of the clutches ($\sqrt{\text{clutch}\ area} = 86mm$), in the following octaves (1/8, 1/4, 1/2, 1, 2, 4) (Lindeberg, 2015; Michalis et al., 2017). Energy maps for each spatial scale were made using difference of Gaussians (DoG); subtracting each octave by 1.6x the same scale (Figure 2).

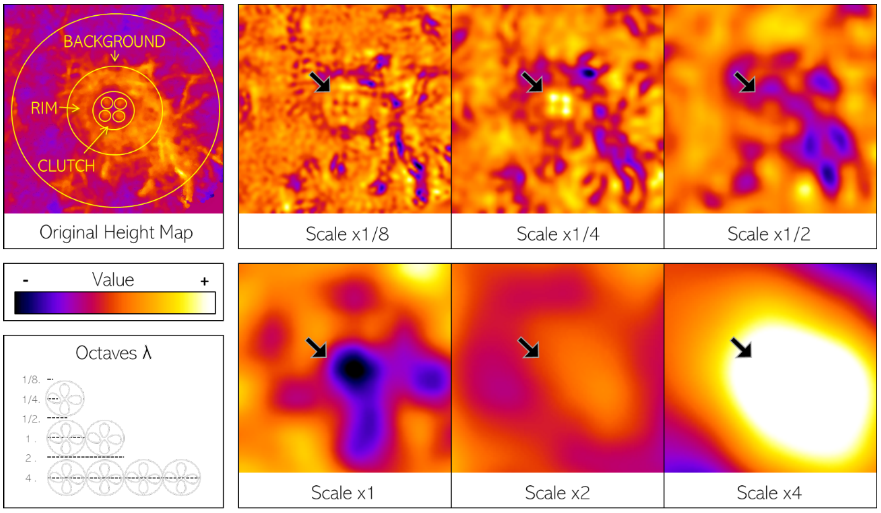


Figure 2. 3D scan energy at different spatial scales relative to clutch size: x1/8, x1/4, x1/2, x1, x2, x4. The left-hand side shows the original height map and associated ROIs: eggs, clutch, rim and background. More elevated (positive) regions are shown as lighter, while less elevated regions are shown as darker. The right-hand images show the separated spatial scales with the position of the clutch marked by a black arrow. The eggs are most visible at x1/4 scale, the scrape at x1 scale and the nest elevation at x4 scale.

Clutch Occlusion & Visibility:

For each depth map, occlusion maps were created for 16 different observer orientations around the azimuth of the nest, from 0°-337.5°, in 22.5° intervals. To calculate occlusion, for each pixel in the clutch, the shallowest/minimum elevation angle (mA) that allowed it to be un-occluded was calculated from each of the 16 bearings, given the 3D depth profile, see Figure 1. Elevation angles above a pixel's mA allow that pixel to be visible. For observer elevation angles between 0.5^0 - 60^0we measured the visibility. The visibility at a given polar angle was equal to the mean percentage of pixels un-occluded across the 16 bearings. The distance required to achieve viewing angles was calculated at fox height [0.4m] and a matrix of corvid flight heights [1.6m, 3.2m, 6.4m, 12.8m, 25.6m].

Colour Metrics:

Luminance ΔS and colour ΔS (JND) from the local (nest) and distal (background) surrounding each clutch was modelled for corvid vision and fox vision as a metric of camouflage, using the mica toolbox (Jacobs et al., 1993; Martin, 2017; Moher Alsady et al., 2016; Vorobyev and Osorio, 1998). Where higher ΔS values correspond with a poorer match. The Siddiqi method was used for ΔS luminance (Weber fraction 0.2) and RNL model for ΔS colour (Weber fraction of most abundant cone of 0.05) (Lind et al., 2013; Moher Alsady et al., 2016; Pretterer et al., 2004; Siddiqi et al., 2004; Vorobyev and Osorio, 1998). For each observer, we used the most phylogenetically relevant systems known. These were the common peafowl *Pavo cristatus,* for the corvid vision, and the red fox *Vulpes vulpes* , for the fox vision (Jacobs et al., 1993; Malkemper, 2014; Malkemper and Peichl, 2018; Ödeen and Håstad, 2013).

ΔS values were measured for images acuity corrected for the hypotenuse distance required for a given series of polar viewing angles [1.875°, 2.5°, 3.75°, 5°, 7.5°, 10°, 15°, 20°, 30° and 40°], when at the height of the model observers (fox 0.4m, corvid 3.2m) (van den Berg et al., 2020). The polar viewing angles for corvid vision were adjusted post-hoc to the matrix of values used for clutch occlusion [1.6, 3.2, 6.4, 12.8 and 25.6 m], by calculating the polar angle and horizontal distance required to produce the same observer distance. Acuity correction was carried out using the known peak resolving power, magpie *Pica pica* 33.33 cp/d and red fox *Vulpes vulpes* 8 cp/d (Malkemper, 2014; Martin, 2017).

Statistical Analyses:

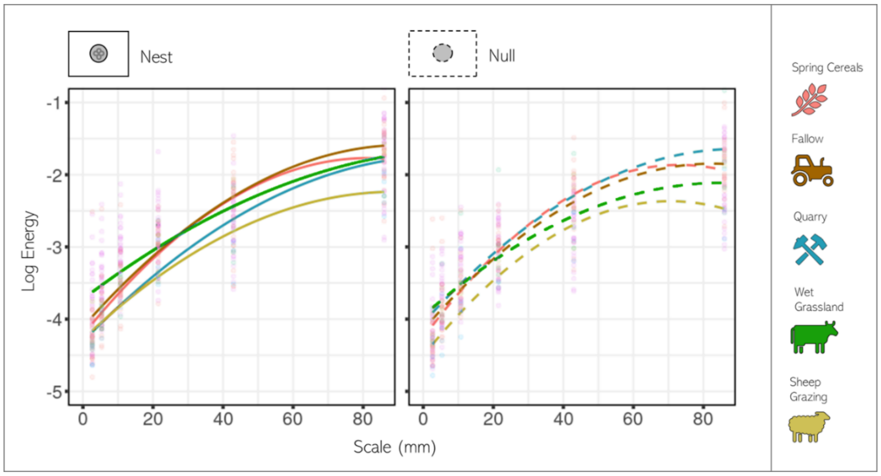
Statistical analyses were performed using R, version 3.6.3 (Team, 2013). The 3D energy metrics were treated as continuous variables and were log-transformed so that residuals fitted a normal distribution. The energy of the nest and null sites were compared at each spatial scale with the lme4 package using linear mixed models derived from the following formula:

*lmer (log (Energy) ~ poly(Scale,2)*ROI+(1|Site)+(1|ScanID) +(1|NestID)) , where ROI specifies nest vs null measurement, ScanID specifies the label for the individuals can and NestID is the shared ID for the nest and its corresponding null.*

The influence of 3D energy and habitat type on visibility was also assessed using linear mixed models, while visibility's effect on predation was analysed using generalised mixed models with predation as a binary (yes/no) variable. We also compared the effect of broad scale (agri-environment and arable)) and fine-scale (wet grassland, gravel, crop, fallow, cattle-grazed and sheep-grazed) on 3D energy using Tukey's post-hoc tests.

3 RESULTS

Nest Site 3D Background Selection



As spatial scale increases, z energy increases following a quadratic (scale^{2}, β = -13.96, SE= 0.16, p <0.0001 | scale, β= 24.12, SE= 1.15, p<0.0001); see Figure 3. Compared to the null scans, lapwing nest surrounds possessed higher 3D variation across all spatial scales (nest, β = 2.90, SE=0.12, p=0.00379) and variation increased with spatial scale at a faster rate for nest sites at the smaller spatial scales (nest:scale^{2}, β = 2.621, SE=0.04, p= 0.0089 | nest:scale, β = -2.029, SE=0.13, p= 0.042). Post hoc comparison of site management strategies showed the nests of sheep grazed fields had significantly lower 3D variation compared to other sites, while wet grassland sites had significantly higher 3D variation (see supplemental material) For scales below the size of the clutch, 3D energy originates from deviation in height between small vegetation (grasses) or from the substrate (large stones, gravel). The 3D energy of pastoral nest sites at higher spatial scales was more similar to those of the arable sites than their null sites, except for at sheep grazed sites. At scales above the size of the nest, high energy results from large clumps/mounds of weedy vegetation, trampling and sloping terrain (hills). On average, clutches were elevated 4.5cm above their local surroundings. There was no significant difference between management type and nest elevation; nest elevation was instead predicted by 3D energy of the surroundings (energy : elevation, β = 2.894, SE= 53.816, p = 0.00493).

Nest Predation

Over the 2 years, we sampled the Avon Valley and Sussex Sites we photographed 115 lapwing nests, 86 of which were scanned. Of the nests found, 13 (8 in 2021, 5 in 2022) were predated. The proportion of nests predated varied widely between county and site, with no predation events of scanned nests recorded in the Sussex sites. Though nest predation of unscanned nests did occur. Predation was the most common cause of nest failure, followed by abandonment. On average, predated nests had poorer colour matches and lower surrounding luminance complexity (SD). However, no significant result was observed and none of the camouflage metrics used were able to predict nest failure from predation (see supplementary material).

Clutch Occlusion & Camouflage:

The percentage visibility (un-occluded) of the clutch (eggs only) increases with the observer viewing angle in a sigmoid fashion. On average, a viewing angle of 15^{o} elevation (equivalent Horizontal Distance: Fox 1.5m, corvid [6.0m, 11.9m, 23.9m, 47.8m, 95.5m]) is required for 25% visibility and an angle of 27^{o} (Horizontal Distance: Fox 0.8m, corvid [3.14m, 6.2m, 12.6m, 25.1m, 50.2m]) to see 50% (Figure 4). Increased 3D energy across spatial scales increases nest occlusion at low viewing angles (10 ^{o} -30 ^{o}), particularly at spatial scales below the clutch size, with the lower scales to the clutch having the largest effect (scale of grasses) on occlusion (See Supplemental Material).

The JND colour and luminance difference of the clutches from the local surround are in line with those of highly camouflaged animals (fox, lum ΔS μ 1.10 ± 0.02 SE | col ΔS μ 0.85 ± 0.02 SE) (Corvid, Lum ΔS, μ 0.9 ± 0.02SE | Col ΔS μ 1.58 ± 0.02 SE). Clutches were of a better colour match to bare crop and fallow sites as opposed to vegetated wet grassland sites for both visual systems (Sussex-Hampshire : corvid colour ΔS β= -6.33, SE= 0.87, $p < 0.0001$) (Sussex-Hampshire : fox colour ΔS, β= -7.43, SE= 0.80, $p < 0.0001$). ΔS colour and ΔS luminance follow a negative exponential with increasing viewing angle (Figure 4). For a decrease in viewing angle to drop ΔS colour and/or ΔS luminance by just 0.1 JND, the clutch would already be 75% occluded from most viewing heights. The exceptions were for corvid vision from a height of 12.8m (22.5 ^{o} for -0.1 JND) and 25.6m (32.5 ^{o} for -0.1 JND).

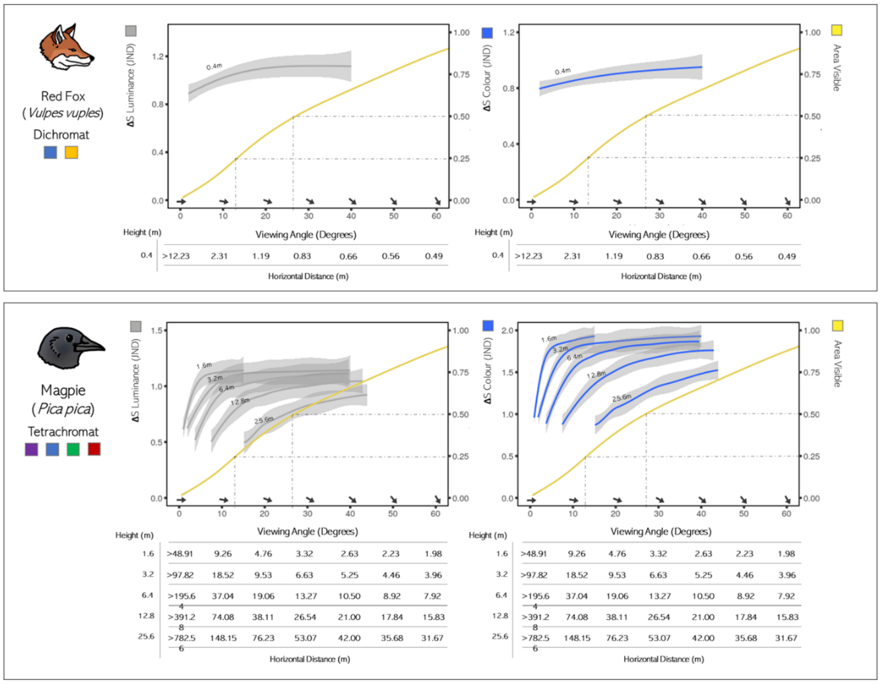


Figure 4 The effect of viewing angle on both the percentage of the clutch un-occluded by surrounding structures (yellow curve, right hand axis) and the ΔS luminance (grey) / ΔS colour (blue) (left hand axes) from the perspectives of a red fox (height = 0.4 m) and magpie (height = [1.6, 3.2, 6.4, 12.8, 14.6] m). The X axis shows both the viewing angle and the hypotenuse distance required to be at that viewing angle for the different heights. The dashed lines show the angle required for 25% and 50% of the nest to not be occluded.

4 DISCUSSION

Here we provide one of the first empirical measures of animal occlusion from different predator viewing angles and the first use of observer height as a factor for acuity modelling. Measurements of camouflage from arrays of different distances are increasingly being used in publications on the functions of animal colour patterns (Caves et al., 2018; Nokelainen et al., 2021). However, studies frequently fail to account for occlusion in determining whether or not the viewing distances used for visual models are biologically relevant. Our results show that 'openness' at a human scale does not reflect openness at scales relative to the nests (Allen et al., 2011), with nest occlusion being more likely to limit detection distance than visual acuity. Especially when viewed at the height of terrestrial predators, where the scales of the clutches and observers render the 3D scene more akin to a closed habitat, the bowl shape of the nest occluding the clutches at low angles. The ability to obtain a broader array of unobscured viewing angles, independent of physical height and topography, is a likely driver of the increased acuity of aerial predators. Short terrestrial predators should not be under selection for visual acuities capable of segmenting objects from further than they are capable of observing. Previous work investigating the search behaviour of foxes and domestic dogs trained to find nests have found them to possess a short localisation distance, less than 2m, for nests. Previous work investigating the search behaviour of foxes and domestic dogs trained to find nests has found them to have a short localisation distance of <2 metres (Seymour et al., 2003; Storaas et al., 1999). Both our ΔS measurements and occlusion measures support this observation. Discrimination of the clutch outline at short distances is likely to be the mechanism of egg detection for all, barring the few poorly background-matching background matching clutches. Nests with greater visibility (less vegetated) were also found to have better colour match in the corvid visual model. Whether the increased differences were due to higher selection intensity when less occluded or limitations in the avian egg colour palette's ability to match live vegetation is difficult to disentangle with our current dataset (Hanley et al., 2015).

Previous research on landscape effects on lapwing nest success has shown that increased proximity to taller ground vegetation, being at a greater distance from the tree line and having surrounding bodies of water decrease the risk of nest predations. The lapwings within our study system were shown to nest preferentially in local habitats with higher 3D variation at scales above the size of the clutch. Habitats that feature depressions and topography (plough, cattle and horse grazing) with similar scales to their nests should decrease lapwing predation by increasing the amount of noise at the scales relative to nests (Swaisgood et al., 2018). Existing guidelines for creating suitable lapwing nesting sites, promoted by the UK conservation organisations (e.g., RSPB, BTO and GWCT), recommend fields with short patchy vegetation in pastoral sites (Ausden and Hirons, 2002; Smart et al., 2013). Analysis of lapwing habitat structure with our 3D scans supports this preference for patchy local sites with 3D variation above the scale of their nests. These results also emphasise previous work advising the avoidance of grazing species that create homogenous and flat vegetation, such as sheep (Winter et al., 2005). The null scans of the arable sites were more similar to those of the nests than the pastoral sites. Chalk arable sites offer both better colour match and local 3D variation match to the lapwings' nests. While not significant, these sites had the lowest proportion of predations, 0, but were also under intense predator control. Northern lapwing populations have long been associated with spring cropland throughout Eurasia (Galbraith, 1988; Salek and Cepáková, 2006). Selection of these habitats has been thought to be and is likely, driven by the large-scale match to the locally preferred background 3D and colour features found naturally within wet grassland. Nesting preference at these sites may be sub-optimal for survival at later stages of their life history, acting as a sensory/ecological trap, with higher chick predation and lower food availability present within these sites (Baines, 1990; Schekkerman et al., 2009).

Modelling occlusion with handheld 3D scanners can be a useful tool for estimating an object's visibility; however, it does not account for taller features at greater distances. The nests of the sampled lapwing were found in fields without much obstruction except at the boundaries (hedgerows & forests) (MacDonald & Bolton, 2008). Other UK ground-nesting waders, e.g., Eurasian curlew *Numenius arquata* and redshank *Tringa totanus* , and populations of lapwing in more forested areas are more likely to have visibility influenced by structures further from the nest than in our 3D scans. Using large-scale LIDAR scans in conjunction with fine scale scans could provide a broader map of visibility and cover of nests (Lone et al., 2014). It is also worth reminding that observing from lower visual angles will in of itself influence the match to the surrounding background. Partial and self-occlusion will reduce the visible area of the clutch and nesting material and mask recognisable features such as the clutch's shadow and edge (Lovell et al., 2013; Webster, 2015). Future work should consider measuring camouflage in the presence of obstruction and/or from different visual angles. In particular, experiments measuring the survival of sedentary objects, such as eggs or model animal targets, where object motion and changes in the local 3D environment are less prevalent an issue. Using of 3D multispectral models or colour-calibrated video cameras may also provide potential alternate technological solutions to the challenges of measuring visibility from multiple viewing angles (Miller et al., 2022; Vasas et al., 2022). However, these methods are slower and more computationally expensive than our 3D phone scans. Finally, our study serves as a reminder of how occlusion is integral to understanding the distances with which visual systems can interact with natural objects and the adaptations required to break camouflage from biologically relevant distances.

Author Contributions

The initial camouflage and 3D structure approach was conceived by JT and AH and carried out by GRAH. Colour-calibrated photographs and 3D scans were collected by GRAH, with nests located and monitored by LG and RB. The code for converting .ply files to depth maps and for measuring the difference of Gaussian energy was created by JT and modified by GRAH. GRAH created the code for measuring occlusion. Manuscript and supplementary guides were first written by GRAH, with subsequent edits by all authors. GRAH performed data analyses with guidance from JT and IC.

Acknowledgements.

NERC GW4+ NE/S007504/1 funded GRAH in a CASE partnership with the GWCT. JT was funded by a NERC Independent Research Fellowship NE/P018084/1. We thank the GWCT, and the landowners, gamekeepers and farmers involved associated farming bodies for allowing us to carry out our research at their field sites.

Conflict of Interest

The authors declare no conflict of interest.

Data Accessibility

[Data will be accessible from Dryad on publication, see attached supplementary R folder, temporary link via dropbox https://www.dropbox.com/s/e9kuk9g3x60si2r/R_Code_EE.zip?dl=0], ImageJ scripts for running RNL and 3D analyses with the MICA toolbox can be downloaded from our GitHub, https://github.com/GeorgeHancock471/3D_RNL_Tools.

References

Allen, W.L., Cuthill, I.C., Scott-Samuel, N.E., Baddeley, R., 2011. Why the leopard got its spots: relating pattern development to ecology in felids. Proc. R. Soc. B Biol. Sci. 278, 1373–1380.

Armstrong, E.A., 1954. The ecology of distraction display. Br. J. Anim. Behav. 2, 121–135. https://doi.org/10.1016/S0950-5601(54)80001-3

Ausden, M., Hirons, G.J.M., 2002. Grassland nature reserves for breeding wading birds in England and the implications for the ESA agri-environment scheme. Biol. Conserv. 106, 279–291.

Bailey, I.E., Muth, F., Morgan, K., Meddle, S.L., Healy, S.D., 2015. Birds build camouflaged nests. Auk Ornithol. Adv. 132, 11–15.

Baines, D., 1990. The roles of predation, food and agricultural practice in determining the breeding success of the lapwing (Vanellus vanellus) on upland grasslands. J. Anim. Ecol. 915–929.

Bertholdt, N.P., Gill, J.A., Laidlaw, R.A., Smart, J., 2017. Landscape effects on nest site selection and nest success of Northern Lapwing Vanellus vanellus in lowland wet grasslands. Bird Study 64, 30–36.

Blumstein, D.T., 2003. Flight-initiation distance in birds is dependent on intruder starting distance. J. Wildl. Manag. 852–857.

Bravo, C., Sarasa, M., Bretagnolle, V., Pays, O., 2022. Detectability and predator strategy affect egg depredation rates: Implications for mitigating nest depredation in farmlands. Sci. Total Environ. 829, 154558.

Broughton, R.K., Parry, W., 2019. A Long-tailed Tit Aegithalos caudatus nest constructed from plastic fibres supports the theory of concealment by light reflectance. Ringing Migr. 34, 120–123.

Caves, E.M., Brandley, N.C., Johnsen, S., 2018. Visual Acuity and the Evolution of Signals. Trends Ecol. Evol. 33, 358–372. https://doi.org/10.1016/j.tree.2018.03.001

Cott, H.B., 1940. Adaptive coloration in animals.

Cramp, S., Brooks, D.J., 1992. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic, vol. VI. Warblers. Oxford: Oxford university press.

Cuthill, I.C., 2019. Camouflage. J. Zool. 308, 75–92.

de Vries, J.P.R., Koma, Z., WallisDeVries, M.F., Kissling, W.D., 2021. Identifying fine-scale habitat preferences of threatened butterflies using airborne laser scanning. Divers. Distrib. 27, 1251–1264.

DiPietro, N.T., Wasserman, E.A., Young, M.E., 2002. Effects of occlusion on pigeons' visual object recognition. Perception 31, 1299–1312.

Duarte, R.C., Stevens, M., Flores, A.A.V., 2018. The adaptive value of camouflage and colour change in a polymorphic prawn. Sci. Rep. 8, 1–10.

Eglington, S.M., Gill, J.A., Smart, M.A., Sutherland, W.J., Watkinson, A.R., Bolton, M., 2009. Habitat management and patterns of predation of Northern Lapwings on wet grasslands: the influence of linear habitat structures at different spatial scales. Biol. Conserv. 142, 314–324.

Endler, J.A., 1981. An overview of the relationships between mimicry and crypsis. Biol. J. Linn. Soc. 16, 25–31.

Evans, K., 2004. The potential for interactions between predation and habitat change to cause population declines of farmland birds. Ibis 146, 1–13.

Fletcher, K., Aebischer, N.J., Baines, D., Foster, R., Hoodless, A.N., 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. J. Appl. Ecol. 47, 263–272.

Froehlich, M., Azhar, S., Vanture, M., 2017. An investigation of Google Tango(r) tablet for low cost 3D scanning. Presented at the ISARC. Proceedings of the International Symposium on Automation and Robotics in Construction, IAARC Publications.

Galbraith, H., 1988. Effects of agriculture on the breeding ecology of lapwings Vanellus vanellus. J. Appl. Ecol. 487–503.

Gillis, H., Gauffre, B., Huot, R., Bretagnolle, V., 2012. Vegetation height and egg coloration differentially affect predation rate and overheating risk: an experimental test mimicking a ground-nesting bird. Can. J. Zool. 90, 694–703. https://doi.org/10.1139/z2012-035

Gomez-Serrano, M.A., Lopez-Lopez, P., 2014. Nest site selection by Kentish plover suggests a trade-off between nest-crypsis and predator detection strategies. PloS One 9, e107121. https://doi.org/10.1371/journal.pone.0107121

Gregg, M.A., 1991. Use and selection of nesting habitat by sage grouse in Oregon.

Hanley, D., Grim, T., Cassey, P., Hauber, M.E., 2015. Not so colourful after all: eggshell pigments constrain avian eggshell colour space. Biol. Lett. 11, 20150087.

Hartman, C.A., Oring, L.W., 2006. An inexpensive method for remotely monitoring nest activity. J. Field Ornithol. 77, 418–424.

Hill, R.A., Hinsley, S.A., Broughton, R.K., 2014. Assessing habitats and organism-habitat relationships by airborne laser scanning. For. Appl. Airborne Laser Scanning Concepts Case Stud. 335–356.

Jacobs, G.H., Deegan, J.F., Crognale, M.A., Fenwick, J.A., 1993. Photopigments of dogs and foxes and their implications for canid vision. Vis. Neurosci. 10, 173–180.

Kaasiku, T., Rannap, R., Mannil, P., 2022. Predation-mediated edge effects reduce survival of wader nests at a wet grassland-forest edge. Anim. Conserv. 25, 692–703.

Kilner, R.M., 2006. The evolution of egg colour and patterning in birds. Biol. Rev. 81, 383–406.

Kubelka, V., Sladeček, M., Šálek, M., 2019. Great variability in nest lining size: support for thermoregulation but not for anti-predatory adaptation hypothesis. J. Ornithol. 160, 993–1002.

Laidlaw, R., Smart, J., Ewing, H., Franks, S., Belting, H., Donaldson, L., Hilton, G., Hiscock, N., Hoodless, A., Hughes, B., 2021. Predator management for breeding waders: a review of current evidence and priority knowledge gaps. Wader Study 128, 44–55.

Li, S., Hou, Z., Ge, J., Wang, T., 2022. Assessing the effects of large herbivores on the three-dimensional structure of temperate forests using terrestrial laser scanning. For. Ecol. Manag. 507, 119985.

Lind, O., Karlsson, S., Kelber, A., 2013. Brightness discrimination in budgerigars (Melopsittacus undulatus). PLoS One 8, e54650.

Lindeberg, T., 2015. Image Matching Using Generalized Scale-Space Interest Points. J. Math. Imaging Vis. 52, 3–36. https://doi.org/10.1007/s10851-014-0541-0

Lone, K., Loe, L.E., Gobakken, T., Linnell, J.D., Odden, J., Remmen, J., Mysterud, A., 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. Oikos 123, 641–651.

Lovell, P.G., Ruxton, G.D., Langridge, K.V., Spencer, K.A., 2013. Individual quail select egg-laying substrate providing optimal camouflage for their egg phenotype. Curr Biol 23, 260–264.

Maia, R., Eliason, C.M., Bitton, P.-P., Doucet, S.M., Shawkey, M.D., 2013. pavo: an R package for the analysis, visualization and organization of spectral data. Methods Ecol. Evol. 4, 906–913. https://doi.org/10.1111/2041-210X.12069

Mainwaring, M.C., Hartley, I.R., Lambrechts, M.M., Deeming, D.C., 2014. The design and function of birds' nests. Ecol. Evol. 4, 3909–3928.

Malkemper, E.P., 2014. The Sensory Biology of the Red Fox-Hearing, Vision, Magnetoreception.

Malkemper, E.P., Peichl, L., 2018. Retinal photoreceptor and ganglion cell types and topographies in the red fox (Vulpes vulpes) and Arctic fox (Vulpes lagopus). J. Comp. Neurol. 526, 2078–2098.

Malpas, L.R., Kennerley, R.J., Hirons, G.J., Sheldon, R.D., Ausden, M., Gilbert, J.C., Smart, J., 2013. The use of predator-exclusion fencing as a management tool improves the breeding success of waders on lowland wet grassland. J. Nat. Conserv. 21, 37–47.

Martin, G.R., 2017. The sensory ecology of birds. Oxford University Press.

Martin, G.R., 2011. Understanding bird collisions with man-made objects: a sensory ecology approach. Ibis 153, 239–254.

Masero, J.A., Monsa, R., Amat, J.A., 2012. Dual function of egg-covering in the Kentish plover Charadrius alexandrinus. Behaviour 149, 881–895.

Michalis, C., Scott-Samuel, N.E., Gibson, D.P., Cuthill, I.C., 2017. Optimal background matching camouflage. Proc. R. Soc. B Biol. Sci. 284, 20170709.

Miller, A.E., Hogan, B.G., Stoddard, M.C., 2022. Color in motion: Generating 3-dimensional multispectral models to study dynamic visual signals in animals. Front. Ecol. Evol. 10.

Moher Alsady, T., Blessing, E.M., Beissner, F., 2016. MICA—A toolbox for masked independent component analysis of fMRI data. Wiley Online Library.

Nokelainen, O., Scott-Samuel, N.E., Nie, Y., Wei, F., Caro, T., 2021. The giant panda is cryptic. Sci. Rep. 11, 1–10.

Odeen, A., Hastad, O., 2013. The phylogenetic distribution of ultraviolet sensitivity in birds. BMC Evol. Biol. 13, 36. https://doi.org/10.1186/1471-2148-13-36

Pendleton, R.L., Nickerson, D., 1951. Soil colors and special Munsell soil color charts. Soil Sci. 71, 35–44.

Pretterer, G., Bubna-Littitz, H., Windischbauer, G., Gabler, C., Griebel, U., 2004. Brightness discrimination in the dog. J. Vis. 4, 10–10.

Ricklefs, R., 1969. An analysis of nesting mortality in birds. m Smithsonian Contrib.

Roos, S., Smart, J., Gibbons, D.W., Wilson, J.D., 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. Biol. Rev. 93, 1915–1937.

Salek, M., Cepáková, E., 2006. Do northern lapwings Vanellus vanellus and little ringed plovers Charadrius dubius rely on egg crypsis during incubation? FOLIA Zool.-PRAHA- 55, 43.

Schekkerman, H., Teunissen, W., Oosterveld, E., 2009. Mortality of Black-tailed Godwit Limosa limosa and Northern Lapwing Vanellus vanellus chicks in wet grasslands: influence of predation and agriculture. J. Ornithol. 150, 133–145.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675.

Seymour, A.S., Harris, S., Ralston, C., White, P.C., 2003. Factors influencing the nesting success of Lapwings Vanellus vanellus and behaviour of Red Fox Vulpes vulpes in Lapwing nesting sites. Bird Study 50, 39–46.

Sharman, R.J., Moncrieff, S.J., Lovell, P.G., 2018. Dissociating the effect of disruptive colouration on localisation and identification of camouflaged targets. Sci. Rep. 8, 6599.

Shults, R., Levin, E., Habibi, R., Shenoy, S., Honcheruk, O., Hart, T., An, Z., 2019. Capability of matterport 3d camera for industrial archaeology sites inventory.

Siddiqi, A., Cronin, T.W., Loew, E.R., Vorobyev, M., Summers, K., 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog Dendrobates pumilio. J. Exp. Biol. 207, 2471–2485.

Simmons, K.E.L., 1951. The Nature of the Predator-Reactions of Breeding Birds 1). Behaviour 4, 161–171. https://doi.org/10.1163/156853951X00115

Simonov, S., Matantseva, M., 2020. 3D scanning as a powerful tool for the analysis of bird nests. Avian Biol. Res. 13, 57–62.

Smart, J., Bolton, M., Hunter, F., Quayle, H., Thomas, G., Gregory, R.D., 2013. Managing uplands for biodiversity: Do agri-environment schemes deliver benefits for breeding lapwing V anellus vanellus? J. Appl. Ecol. 50, 794–804.

Sovrano, V.A., Bisazza, A., 2008. Recognition of partly occluded objects by fish. Anim. Cogn. 11, 161–166.

Stevens, M., Troscianko, J., Wilson-Aggarwal, J.K., Spottiswoode, C.N., 2017. Improvement of individual camouflage through background choice in ground-nesting birds. Nat. Ecol. Evol. 1, 1325–1333. https://doi.org/10.1038/s41559-017-0256-x

Stoddard, M.C., Kupan, K., Eyster, H.N., Rojas-Abreu, W., Cruz-Lopez, M., Serrano-Meneses, M.A., Kupper, C., 2016. Camouflage and Clutch Survival in Plovers and Terns. Sci. Rep. 6, 32059. https://doi.org/10.1038/srep32059

Stoddard, M.C., Marshall, K.L., Kilner, R.M., 2011. Imperfectly camouflaged avian eggs: artefact or adaptation? Avian Biol. Res. 4, 196–213.

Storaas, T., Kastdalen, L., Wegge, P., 1999. Detection of forest grouse by mammalian predators: A possible explanation for high brood losses in fragmented landscapes. Wildl. Biol. 5, 187–192.

Swaisgood, R.R., Nordstrom, L.A., Schuetz, J.G., Boylan, J.T., Fournier, J.J., Shemai, B., 2018. A management experiment evaluating nest-site selection by beach-nesting birds. J. Wildl. Manag. 82, 192–201.

Teunissen, W., Schekkerman, H., Willems, F., Majoor, F., 2008. Identifying predators of eggs and chicks of Lapwing Vanellus vanellus and Black-tailed Godwit Limosa limosa in the Netherlands and the importance of predation on wader reproductive output. Ibis 150, 74–85.

Troscianko, J., Stevens, M., 2015. Image calibration and analysis toolbox–a free software suite for objectively measuring reflectance, colour and pattern. Methods Ecol. Evol. 6, 1320–1331.

Troscianko, J., Wilson-Aggarwal, J., Spottiswoode, C.N., Stevens, M., 2016a. Nest covering in plovers: How modifying the visual environment influences egg camouflage. Ecol. Evol. 6, 7536–7545.

Troscianko, J., Wilson-Aggarwal, J., Stevens, M., Spottiswoode, C.N., 2016b. Camouflage predicts survival in ground-nesting birds. Sci. Rep. 6, 19966. https://doi.org/10.1038/srep19966

Tvardikova, K., Fuchs, R., 2010. Tits use amodal completion in predator recognition: a field experiment. Anim. Cogn. 13, 609–615.

van den Berg, C.P., Troscianko, J., Endler, J.A., Marshall, N.J., Cheney, K.L., 2020. Quantitative Colour Pattern Analysis (QCPA): A comprehensive framework for the analysis of colour patterns in nature. Methods Ecol. Evol. 11, 316–332. https://doi.org/10.1111/2041-210X.13328

Vasas, V., Lowell, M.C., Villa, J., Jamison, Q.D., Siegle, A.G., Katta, P.K.R., Bhagavathula, P., Kevan, P.G., Fulton, D., Losin, N., 2022. Recording animal-view videos of the natural world. bioRxiv 2022–11.

Vickery, J.A., Bradbury, R.B., Henderson, I.G., Eaton, M.A., Grice, P.V., 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biol. Conserv. 119, 19–39.

Vorobyev, M., Osorio, D., 1998. Receptor noise as a determinant of colour thresholds. Proc. R. Soc. Lond. B Biol. Sci. 265, 351–358.

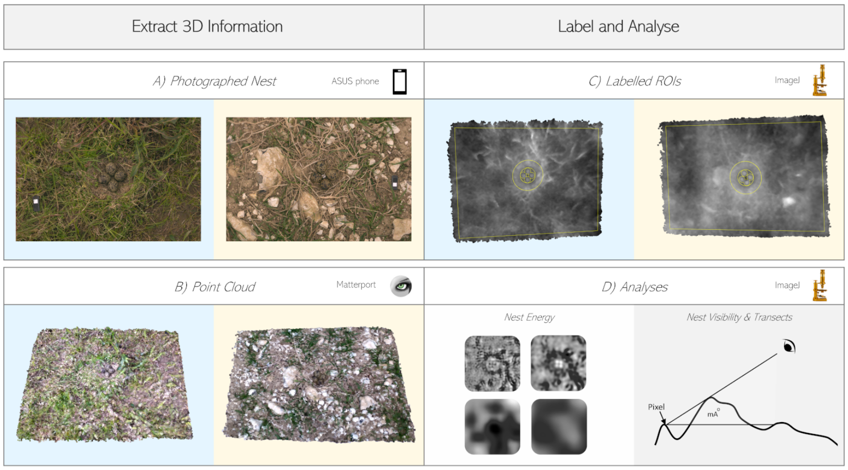
Webster, R.J., 2015. Does disruptive camouflage conceal edges and features? Curr. Zool. 61, 708–717.

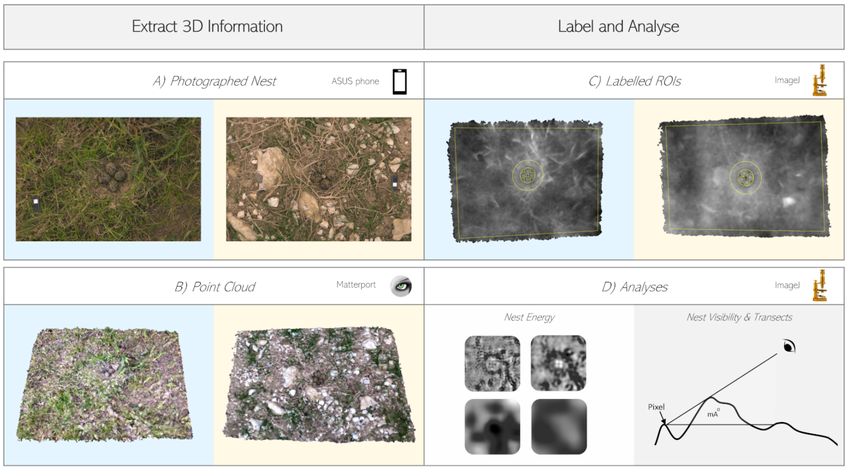
Westmoreland, D., 2008. Evidence of selection for egg crypsis in conspicuous nests. J. Field Ornithol. 79, 263–268.

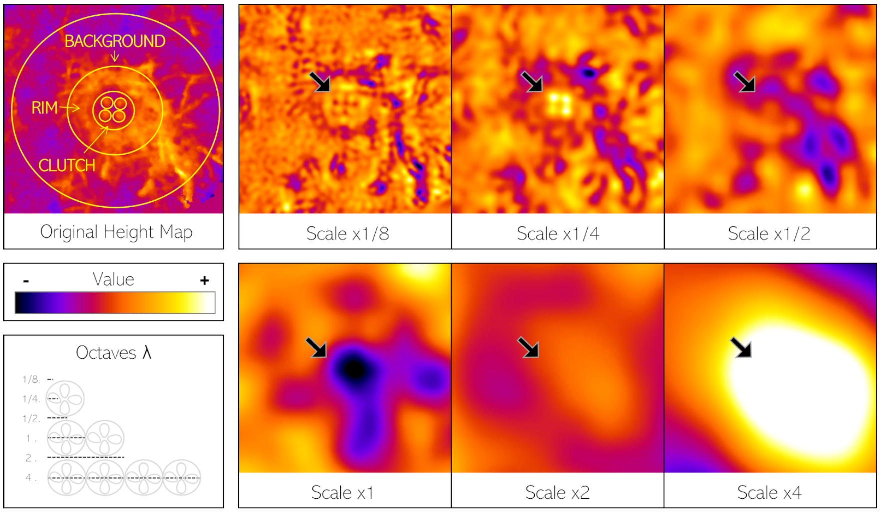
Wilson, A.M., Vickery, J.A., Browne, S.J., 2001. Numbers and distribution of Northern Lapwings Vanellus vanellus breeding in England and Wales in 1998. Bird Study 48, 2–17.

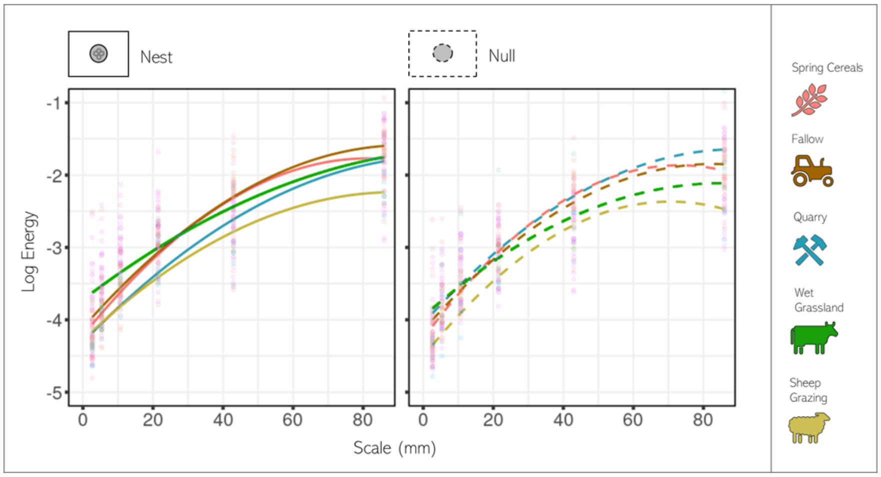
Wilson-Aggarwal, J.K., Troscianko, J.T., Stevens, M., Spottiswoode, C.N., 2016. Escape Distance in Ground-Nesting Birds Differs with Individual Level of Camouflage. Am. Nat. 188, 231–239. https://doi.org/10.1086/687254

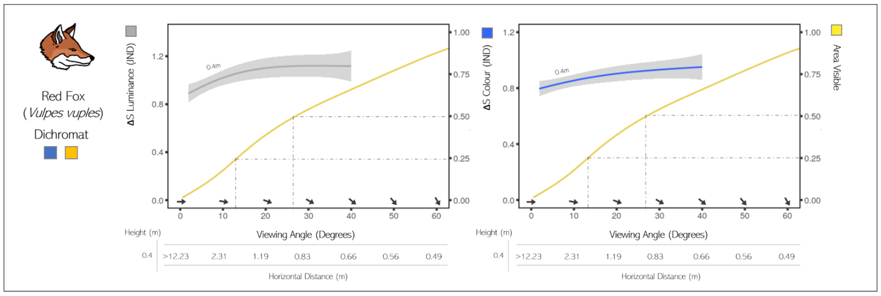
Winter, M., Johnson, D.H., Shaffer, J.A., 2005. Variability in vegetation effects on density and nesting success of grassland birds. J. Wildl. Manag. 69, 185–197.

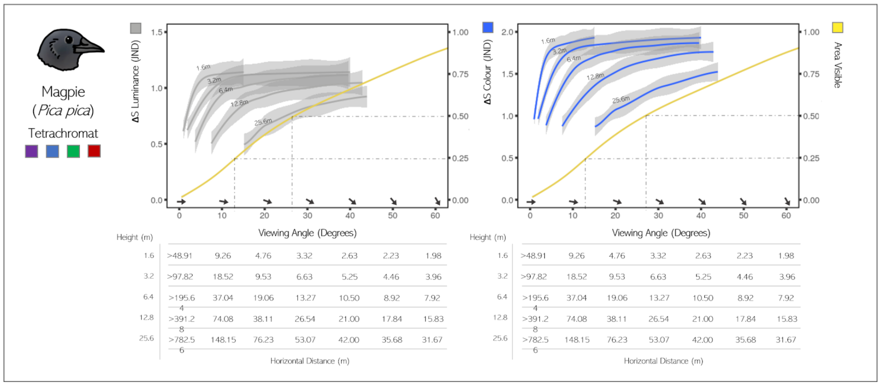

Extract 3D Information
Label and Analyse
A) Photographed Nest
ASUS phone
C) Labelled ROIs
ImageJ
B) Point Cloud
Matterport
D) Analyses
ImageJ
Nest Energy
Nest Visibility & Transects
Pixel
mA°


Extract 3D Information
Label and Analyse
A) Photographed Nest
ASUS phone
C) Labelled ROIs
ImageJ
B) Point Cloud
Matterport
D) Analyses
ImageJ
Nest Energy
Nest Visibility & Transects
Pixel
mA°


BACKGROUND
RIM
CLUTCH
Original Height Map
Scale x1/8
Scale x1/4
Scale x1/2
Value
-
+
Octaves λ
1/8.
1/4.
1/2.
1.
2.
4.
Scale x1
Scale x2
Scale x4


Nest
Null
Log Energy
-1
-2
-3
-4
-5
0
20
40
60
80
Scale (mm)
Spring Cereals
Fallow
Quarry
Wet Grassland
Sheep Grazing


Red Fox
(Vulpes vuples)
Dichromat
ΔS Luminance (JND)
ΔS Colour (JND)
0.4m
Area Visible
Viewing Angle (Degrees)
Height (m)
0.4
>12.23
2.31
1.19
0.83
0.66
0.56
0.49
Horizontal Distance (m)


Magpie
(Pica pica)
Tetrachromat
ΔS Luminance (JND)
ΔS Colour (JND)
1.6m
3.2m
6.4m
12.8m
25.6m
Area Visible
Viewing Angle (Degrees)
Height (m)
1.6 >48.91 9.26 4.76 3.32 2.63 2.23 1.98
3.2 >97.82 18.52 9.53 6.63 5.25 4.46 3.96
6.4 >195.64 37.04 19.06 13.27 10.50 8.92 7.92
12.8 >391.28 74.08 38.11 26.54 21.00 17.84 15.83
25.6 >782.56 148.15 76.23 53.07 42.00 35.68 31.67
Horizontal Distance (m)