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Improvement of individual camouflage through background choice in ground-nesting birds

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Abstract

Animal camouflage is a longstanding example of adaptation. Much research has tested how camouflage prevents detection and recognition, largely focusing on changes to an animal's own appearance over evolution. However, animals could also substantially alter their camouflage by behaviourally choosing appropriate substrates. Recent studies suggest that individuals from several animal taxa could select backgrounds or positions to improve concealment. Here, we test whether individual wild animals choose backgrounds in complex environments, and whether this improves camouflage against predator vision. We studied nest site selection by nine species of ground-nesting birds (nightjars, plovers and coursers) in Zambia, and used image analysis and vision modeling to quantify egg and plumage camouflage to predator vision. Individual birds chose backgrounds that enhanced their camouflage, being better matched to their chosen backgrounds than to other potential backgrounds with respect to multiple aspects of camouflage. This occurred at all three spatial scales tested (a few cm and five meters from the nest, and compared to other sites chosen by conspecifics), and was the case for the eggs of all bird groups studied, and for adult nightjar plumage. Thus, individual wild animals improve their camouflage through active background choice, with choices highly refined across multiple spatial scales.

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Data availability

All data generated or analysed during this study are included in this published article (and its supplementary information).

Author Contributions

All authors designed and conceived the study. Fieldwork was conducted by J.T., J.K.W-A., and C.N.S. at a study site set up by C.N.S.. Image analysis and vision modelling by J.T., J.K.W-A., and M.S., and the statistical analysis primarily by J.T. M.S. wrote the initial manuscript, which was reviewed and approved by all authors prior to submission.

Competing interests

The authors declare no competing interests.

Keywords

camouflage; animal behaviour; anti-predator; predation; animal coloration; birds

Animal camouflage has played an important role in studies of natural selection and adaptation^{1–7}. Recently, considerable interdisciplinary research has tested the mechanistic basis of how different types of visual camouflage work^{5, 8}. This has included field studies using artificial (human-made) prey, laboratory work and computer experiments with birds and human observers, and theoretical models testing how different types of camouflage function to prevent detection or recognition, and testing optimal camouflage strategies^{9–17}. In addition, other research has investigated camouflage with regards to colour change and the molecular mechanisms of genetic adaptation^{18–20}, demonstrating how camouflaged appearance can be tuned to different visual backgrounds.

Individuals could also substantially alter the effectiveness of their camouflage through choosing appropriate substrates. Such specialized behaviour has long been suspected: Wallace noted that leaf-mimicking *Kallima* butterflies rested in places that facilitated their camouflage²¹. Selection of specific background types may be one way of dealing with visually variable environments, and differs from strategies that strike a compromise between camouflage to two or more background types while matching none closely^{12, 22}. Early work by Kettlewell, alongside his famous peppered moth (*Biston betularia*) selection experiments, tested whether melanic and typical morphs choose appropriate resting backgrounds based on their coloration, showing that melanic individuals came to rest on black stripes, and typical morphs on white stripes²³. Further work confirmed and extended these findings, demonstrating that different morphs of several species of moth select backgrounds that are consistent with their coloration^{24–26}.

The above studies show that individuals of a species, or of a discrete morph, can select appropriate backgrounds that match their species- or morph-specific appearance. In contrast, many animals show considerable, seemingly continuous, within-species variation in coloration. In such cases, we may expect to find individual-level substrate choice in accordance with individual phenotype. Consistent with this, laboratory studies have shown that Japanese quail (*Coturnix japonica*) chose to lay their eggs on background substrates which provide improved camouflage for their own individual egg appearance²⁷. Furthermore, a study of wall lizards (*Podarcis erhardii*) across a range of Greek islands showed that lizards were more likely to be found resting on backgrounds that improved their own individual camouflage compared to resting sites chosen by other lizards on the same island²⁸. This effect was stronger for female lizards (whose coloration is more tuned for camouflage than that of males²⁹), and on islands where the risk of predation is higher. There is also evidence that substrate choice for appropriate backgrounds may occur in individuals of species that can change colour for camouflage, such as fish and prawns^{30,31}.

Animals may also adjust their own alignment to improve camouflage. Sargent suggested that moths could modify their resting positions to coincide with the texture of the background³². This idea has been confirmed in recent studies showing that moths released onto trees adjusted their body position and orientation from their original landing site and alignment,

which increased their camouflage^{33,34}. Moreover, individual moths were more likely to adjust their resting position when their initial level of camouflage (judged by human observers) was lower³⁵. The potential for changes in body posture for camouflage exists widely in nature, from stick insects to cuttlefish; the latter, for example can use visual cues to adjust the posture of their arms to improve their camouflage³⁶.

Although the above studies clearly demonstrate the potential for individual animals to select appropriate backgrounds, a number of limitations and questions remain. First, most studies of background choice have judged camouflage based on human observation or metrics of coloration relevant to human vision (but see^{28, 34}). Second, current evidence for individual background selection is limited to relatively few species and taxa, with the most comprehensive work based on one laboratory study using simple artificial backgrounds, one species of wild lizard, and on controlled releases of moths by humans onto natural backgrounds. Third, past work has not investigated substrate choice at different spatial scales within a habitat. To date, only one study (on lizards) has tested the hypothesis that wild, free-ranging individuals in natural habitats select appropriate backgrounds for concealment. While this study considered predator vision, it only focused on one species that moves around an area actively, and whose appearance is also complicated by the need for socio-sexual signals^{28, 29}. Generally, we still know comparatively little about how animals achieve successful camouflage in complex real environments.

Here, we studied nine species of ground-nesting birds (nightjars, plovers and coursers) in Zambia (Fig 1), and used image analysis and modelling of predator vision to test whether individual appearance (the eggs from all nine species, and the plumage of adult nightjars that sit tightly on their eggs) better matched their chosen backgrounds than other potential backgrounds. The different species all nest in the hot Zambian dry season, sitting on their eggs and fleeing when a predator approaches (see below). They utilise different visual backgrounds, ranging from dry leaf litter to scorched bare ground, with little to no nest structure built.

We studied background (nest site) selection at three spatial scales corresponding to adjacent backgrounds approximately 5 m from the nest and 5 cm from the nest, and the backgrounds of nest sites chosen by conspecific individuals (Fig 2). The first (m) and second (cm) spatial scales allow us to test whether individuals refine their nest site selection towards a given substrate area or patch, and then choose a specific fine-scale point within that patch. The third spatial scale allows us to determine whether individuals choose nest sites that improve their own individual camouflage compared to other potential nest sites chosen by other individuals.

Our past work has shown that the degree of camouflage in these birds directly influences the likelihood of nest survival against wild predators³⁷. Specifically, nest survival in nightjars is predicted by adult camouflage (since adults sit tightly on the nest until a threat is very close), whereas nest survival in plovers and coursers (which flee early when a threat arises) depends on egg camouflage. Furthermore, we have also recently shown that the birds modify their escape distance based on their individual level of camouflage: plovers and coursers show greater escape distances when their eggs are a poorer match to the background (with good

camouflage, adults can flee late because the eggs are still well hidden), and nightjars show greater escape distances when their own adult plumage matches the background less effectively³⁸. This suggests that, as with quail²⁷, individual birds seem to be able to assess their eggs' level of camouflage (or that of their own plumage), and use this in their decision-making. Coupled with this evidence, our study system is ideal for investigating camouflage and microhabitat choice because the background environment where the birds nest is unambiguous, and because each species nests in areas that differ with respect to the range of substrates encountered and the type of visual background.

Results

Based on camera-trap recordings of predation events at our monitored nests, we modelled camouflage with respect to the visual systems of the main predator groups, specifically tetrachromatic birds, trichromatic primates, and dichromatic mammals. We chose these predator visual systems based on recordings of egg predation by diurnal predators including grey-headed bush-shrikes (*Malaconotus blanchoti*), vervet monkeys (*Chlorocebus pygerythrus*), and banded mongooses (*Mungos mungo*)³⁷. Modelling of predator vision and image analysis allowed us to quantify several metrics of camouflage, including colour, luminance (perceived lightness), and pattern^{39–41}. We used a range of metrics that have previously been shown to predict survival of nests in the field and escape behaviour by adults, as well as predicting human detection times of camouflaged artificial targets (see Methods). Data for plovers and coursers were analysed separately from data for nightjars because plovers and coursers (Charadriiformes) flee the nest early in response to a potential threat, exposing the eggs to potential detection for long periods. In contrast, adult nightjars (Caprimulgiformes) sit tight on their nest until a predator is close, such that adult plumage camouflage is also crucial for egg survival³⁷. First, since there is variation in egg and plumage appearance among individuals, the hypothesis that nesting birds choose microhabitats that improve their camouflage predicts that birds should choose nest sites that improved their own specific camouflage compared to sites selected by conspecific individuals. Second, the hypothesis predicts that background selection for camouflage should occur at two further spatial scales: over several metres (5 m away, and representing nest site selection within a given area of a habitat) and within a few cm of the chosen nest area (photographed from directly above the clutch) representing the specific substrate patch chosen within a site; see Methods and Fig 2). Furthermore, based on past work^{37, 38} the hypothesis predicts that microhabitat choice would be based on egg camouflage in plovers and coursers, and on both egg coloration and adult plumage camouflage in nightjars.

As predicted, individuals of a given species chose nest sites that were a better match to their own eggs than to the nest sites of other individuals of the same species (all results summarized in Table 1; Fig 3). Egg pattern match in plovers and coursers ($n = 92$ nests) showed an interaction between nest site and species (in linear mixed-effect models; see Methods): three-banded courser, crowned plover, and Temminck's courser eggs matched the pattern of their chosen nest site better than the nest sites of conspecifics, whereas three-banded plovers, bronze-winged coursers and wattled plover eggs did not (Table 1, Fig 3). Plover and courser egg luminance and colour matches did not significantly differ between their own versus conspecific nest sites. For nightjars ($n = 105$ nests), egg patterns matched

their own nest site better than the nest sites of conspecifics. For egg luminance, an interaction showed that Mozambique and pennant-winged nightjars matched their own nest site luminance better than the nest sites of conspecifics, whereas fiery-necked nightjars instead matched the luminance of conspecifics' nest sites better than their own. Nightjar egg colour matches did not differ between their own and conspecific nest sites.

Next, we tested whether individual egg camouflage was a better match to *i*) the chosen background versus comparable areas 5 m away, and *ii*) the chosen background within *ca.* 5 cm of the clutch versus a comparable area immediately surrounding the nest. This resulted in four zones, with two comparisons planned between these zones (i.e. the few cm scale and 5 m scale, Fig 4). For plover and courser eggs ($n = 92$ nests), pattern and luminance matching varied significantly between background zones ($F_{3,1277} = 67.50$, $P < 0.001$ and $F_{3,1277} = 14.89$, $P < 0.001$ respectively). In all cases bar one, eggs were better matched to the chosen background than to non-chosen backgrounds a few cm away and 5 m away (Fig 4; see statistical results in Table 1). However, eggs matched the luminance of their chosen background less closely than the background a few cm away. This suggests a potential trade-off resulting in pattern-matching being selected over luminance-matching. Further modelling demonstrated a significant negative correlation between pattern-matching and luminance-matching in the zones nearest the egg ("immediate" and "near" surrounds in Fig. 2), but this correlation flattened out in zones further from the nest centre ("distant" surrounds, model interaction between zone and luminance-matching level: $F_{2,1278} = 16.74$, $P < 0.001$; comparison between 'immediate' and 'distant' zones: $t = 6.823$, $P < 0.001$). This finding shows that pattern and luminance matching are independent of each other in randomly selected patches of habitat. However, the areas chosen as nest sites matched the patterns of the eggs better than expected, and matched luminance worse than expected. This finding is consistent with the hypothesis that plovers and coursers select nest sites that match the patterns of their eggs at the expense of matching the luminance. Egg colour match did not differ between chosen and nearby non-chosen backgrounds at either spatial scale.

Nightjar eggs ($n = 105$ nests) were better matched with respect to both pattern ($F_{3,1460} = 57.47$, $P < 0.001$) and luminance ($F_{3,1444} = 11.47$, $P < 0.001$) to their chosen backgrounds than to backgrounds a few cm away and 5 m away (Table 1; Fig 4). An exception was nightjar egg luminance, which was better matched to non-chosen backgrounds 5 m away than to their chosen nest site. As above, we tested whether this represents a trade-off between pattern-matching and luminance-matching across the zones, but there was no significant interaction between zone and luminance-difference ($F_{2,1442} = 1.72$, $P = 0.161$). Nightjar egg colour match was predicted by a significant interaction between predator visual system and zone ($F_{4,1434} = 41.59$, $P < 0.001$): egg colours were better matched to the chosen nest site than to backgrounds a few cm away for all visual systems, but the effect was most pronounced for the dichromatic mammalian visual system. However, nightjar eggs were less well matched to the chosen background under trichromatic and dichromatic mammalian vision, whereas they were better matched under avian tetrachromatic vision. Zone remained a significant predictor in the model on its own ($F_{3,1434} = 6.97$, $P < 0.001$), showing overall that eggs were a better match to their chosen background than to the adjacent background a few cm away, but there was no significant difference in match to the chosen background versus other potential backgrounds 5 m away.

Finally, since nightjars flee from the nest only when a predator is nearby (our data show a mean flush distance across all three nightjar species of $1.9 \text{ m} \pm 1.3$ standard deviation³⁸), we expected nest survival to be more strongly affected by parental camouflage than egg camouflage³⁷. As predicted, nightjar plumage ($n = 98$ adults) matched the pattern, luminance and colours of the individuals' chosen backgrounds better than those of their conspecifics' backgrounds (Table 1). When comparing camouflage at a scale of cm and m ($n = 98$ nests), the pattern model retained an interaction between zone and species (zone \times species: $F_{6,1358} = 3.41$, $P = 0.002$; zone $F_{3,1358} = 15.22$, $P < 0.001$; luminance: $F_{3,1364} = 10.15$, $P < 0.001$; colour: $F_{3,1360} = 11.05$, $P < 0.001$; Fig 4; Table 1). The plumage pattern of Mozambique and pennant-winged nightjars matched their chosen nest backgrounds better than the adjacent background a few cm away, whereas fiery-necked nightjars did not; individuals of all nightjar species matched their chosen background for pattern better than other potential backgrounds 5 m away. For luminance, nightjars were better matched to chosen backgrounds than to adjacent backgrounds both a few cm away and 5 m away. Plumage colour was a better match to chosen nest sites at the metre scale, but not the cm scale.

Discussion

Our study demonstrates that individual camouflage in multiple species of free-ranging wild animals can be improved not just by changes in an animal's own appearance, but also by behavioural selection of appropriate resting backgrounds as viewed through their predators' eyes. Nine species of ground-nesting bird (based on over 90 individual plover/courser nests and over 100 nightjar nests) were capable of highly nuanced nest site selection that improved their egg and plumage camouflage at several spatial scales. First, they were able to choose a suitable nesting patch in the general habitat at a scale of approximately five metres, and second, they refined their nest site selection within that patch at a very fine scale (within a few cm). Moreover, because females selected sites that matched their own eggs and plumage better than those of their conspecifics, decisions were made with reference to their own individual phenotype rather than following a general species-wide strategy.

Our findings are consistent with those of a recent laboratory study on substrate selection in nesting quail²⁷, and also tie in with our recent study of escape distances in the present study system. The latter showed that individuals modulate escape behaviour based on their level of camouflage, providing further evidence that nesting birds can modify their behaviour in response to perceived levels of concealment³⁸. These findings also concur with a study of island populations of wall lizards, which found that individuals were more likely to be found sitting on backgrounds that provide better camouflage than on other potential sites²⁸. Our work here shows that the benefits of microhabitat choice and behavioural changes based on assessment of individual camouflage extend across a wide range of avian species, several spatial scales, and two life history stages (adults and eggs).

The above results demonstrate that behavioural choice of substrates and backgrounds may offer a major route to enhancing camouflage, and suggest that studies that simply compare the camouflage of individuals against random background samples may sometimes yield inaccurate findings if individuals vary both in appearance and substrate preference. Many

camouflaged species show either discrete polymorphisms or high levels of continuous phenotypic variation^{3, 9, 19, 42, 43}. In such cases it may be particularly beneficial for individuals to have corresponding substrate preferences, both to improve their level of camouflage and perhaps to increase the range of microhabitats exploited. Microhabitat choice may also have important broader evolutionary consequences. For example, some insect species comprise several morphs that occur on different host plants, and disruptive selection against intermediates may potentially drive speciation through reproductive isolation of populations in sympatry⁴².

We cannot entirely rule out the possibility that our results could be partially explained by predation having eliminated poorly-camouflaged nests from our dataset before we could record them. While this would itself be an important finding (given that individual variation in camouflage matching in wild animals has rarely been directly demonstrated to affect predation risk), we feel that this explanation is unlikely to fully explain our results. First, our dataset includes sufficient variation in camouflage among individuals to predict predation risk (shown recently using the same sample of nests³⁷), which demonstrates that we did not exclusively study individuals with ‘good’ camouflage. Second, a proximate mechanism of background selection based on individual egg coloration has already been established in controlled laboratory experiments with ground-nesting birds, implying that this is a more parsimonious explanation for our results²⁷. They do not preclude other factors, beyond the scope of this study, influencing nest site selection in birds; these may include habitat visibility for detecting predator approaches, thermal considerations, and vicinity to other nesting birds. In addition, some of the plover and courser species in our study make modest modifications (‘scrapes’) to their nest area, potentially influencing camouflage match by modifying their environment via an extended phenotype^{44, 45}. This is, however, highly unlikely to have affected the majority of our findings (see Supplementary Information). These factors may add to a rich complexity of factors influencing background selection in birds and other animals.

Beyond the question of how widespread background choice for camouflage might be, there is much to be gained from trying to disentangle the mechanisms involved. In birds, egg coloration appears to be strongly heritable, with relatively little environmental influence⁴⁶. Exactly how birds make appropriate decisions is not yet clear but we suggest it could arise through two (not mutually exclusive) mechanisms. First, if background choice is also heritable, a genetic correlation could allow individuals with a given egg phenotype to also inherit the appropriate substrate preference. Alternatively, behavioural preferences could develop with experience as birds learn what their eggs look like, and so to make appropriate decisions. The latter mechanism seems more likely because inherited behavioural choice would offer little flexibility, and also because there is good evidence that birds learn their egg appearances in other contexts. For example, hosts of brood parasites appear to learn what their own eggs look like in initial breeding attempts, and then reject any subsequent parasitic eggs that deviate from this template of appearance⁴⁷. Our results suggest that other birds likely have mechanisms to ‘know’ not only what their own eggs look like, but also their own plumage, and use this information to make adaptive decisions. A further and related potential mechanism could involve chicks imprinting on specific backgrounds after hatching, and basing nest site choice on this when they later become breeders. Future work

could test these potential mechanisms by addressing whether and how substrate choice differs between naïve first-time breeders and more experienced individuals.

Conclusions

Overall, camouflage can be enhanced not only through genetic or developmental changes in individual appearance, but also through individual behavioural choices. Thus, in many species the value and tuning of animal camouflage may result from a complex mixture of morphology, behaviour, and environment. More broadly, our study underlines that animals possess sensory and potentially cognitive mechanisms that allow them to improve the adaptive value of their own individual phenotype by choosing appropriate backgrounds. We should further look for individual background choice in the many other contexts where signalling success is affected by aspects of the environment, such as conspicuous warning coloration and sexual signals^{48–50}.

Methods

The study system, general methods, and quantification of camouflage closely followed our past work (including that demonstrating how our camouflage metrics predict survival of the nests of the birds we study here) and a range of past and recent methodological approaches^{37, 38, 51}. Our dataset here overlaps with our previous work with respect to the individual birds recorded and measured, and to some of the images of the natural backgrounds used to assess camouflage, with the addition of further comparison background images taken at 5 m scales used only for this study.

Study system

The study site comprised *c.* 3100 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 southern Zambia (Choma District), during September–November 2012–2013. Fieldwork was undertaken during the hot dry season, when an open understorey affords nesting habitat for the ground-nesting bird species we studied. The field sites are in an agricultural region, but the cultivated areas (primarily maize and tobacco crops) are comparatively small and occur within a greater area of natural habitat (deciduous miombo woodland and grassland). As such, predator communities should not differ greatly from conditions occurring before than human impact on the region. We studied three nightjar species (fiery-necked nightjar *Caprimulgus pectoralis*, Mozambique nightjar *Caprimulgus fossii* and pennant-winged nightjar *Macrodipteryx vexillaria*), three plover species (crowned plover *Vanellus coronatus*, wattled plover *Vanellus senegallus* and three-banded plover *Charadrius tricollaris*), and three courser species (bronze-winged courser *Rhinoptilus chalcopterus*, Temminck's courser *Cursorius temminckii* and three-banded courser *Rhinoptilus cinctus*). Most nests were found by local farm workers, detected when the birds flushed on approach, or through nocturnal eye-shine from torchlight. Our sample of nests may lack the extremes of camouflage matching if we were unable to find the most camouflaged nests, and if some of the least camouflaged nests were attacked by predators first. However, our resulting sample should remain ecologically representative of the surviving nests, and indeed there was considerable variation in survival and camouflage among them³⁷. All work was approved by the

University of Exeter Animal Ethics Committee (application number 2013/282) and conducted under licence from the Zambia Wildlife Authority. The field locations are private land accessed with the landowners' permission, and no further licenses or permits were needed.

Photography and vision modelling

We took digital images with Nikon D7000 cameras, fitted with 105 mm Micro-Nikkor lenses, which transmit ultraviolet (UV) light. The cameras had undergone a quartz conversion (Advanced Camera Services Limited, Norfolk, UK) to allow sensitivity to both human-visible and ultraviolet wavelengths, involving replacing the UV and IR blocking filter with a quartz sheet to allow visual analysis throughout the avian-visible spectrum^{51, 52}. For photographs in the human-visible part of the spectrum, the lens was fitted with a Baader UV-IR blocking filter (transmitting 420 to 680 nm). UV photographs were taken using a Baader UV pass filter (transmitting 320 to 380 nm). All images were taken at f/8, ISO400, in RAW format, avoiding a time period within two hours of sunrise or sunset, and were only taken in direct sunlight as this corresponded most closely with weather and light conditions during in the Zambian dry season and with the diurnal predation events we recorded. During the brief crepuscular periods at our study site, there would be changes in ambient light spectra, background contrast, and shadows, but we cannot test those effects with our current dataset.

To quantify adult nightjar camouflage, we closely followed past work on the same system^{37, 38}. Images of nightjars sitting on their nests were taken from a standing position from 5 m distance and the flank least obscured by vegetation. If both sides were clearly visible, images were taken so as to avoid directly facing the sun. Acquiring images of adult plovers and coursers was not possible because these birds frequently flush at long distances. After the adult nightjar was flushed from its nest, a 40% Spectralon grey standard (Labsphere, Congleton, UK) was placed beside the eggs and photographed from 2 m using the same camera settings to those for the adults. This enabled us to control for lighting conditions in the adult bird images without the standard needing to be in the same photograph (the sequential method⁵³). Images of plover, courser, and nightjar eggs were acquired *in situ* from 1.25 m directly overhead, as well as under more controlled lighting; shaded from sunlight and against a white background with the eggs next to the grey standard. We chose 5 m as the photography distance for the meter scale because adult nightjars could reliably be photographed at this distance without fleeing their nests, and because control photographs taken 5 m on either side of the nest did not overlap with one another. For the fine cm scale, we photographed from directly above the clutch because this included both the largest clutches and surrounding nest site area.

To calibrate the images, all photos were linearized to control for the non-linear response of the camera to light intensity, and then standardized against the grey standard to remove effects of the light conditions³⁹. For the linearization and mapping to predator vision, we measured the image values of eight Spectralon reflectance standards with values ranging from 2–99% (Labsphere) and produced polynomial linearization curves; all channels having R^2 values > 0.99951 . Visible and UV photographs were aligned and scaled using an

automated script, minimizing the absolute spatial difference between pixels. This accounted for focal length changes when re-focusing in UV, and minor shifts in camera position. Aligned images were saved as 16-bit TIFFs for the visible LW ('red'), MW ('green') and SW ('blue') channels, and UV. To model predator vision, we chose appropriate visual systems based on recorded predation events at a subset of nests from custom built motion-triggered cameras³⁷. The diurnal predators we recorded included animals with three different visual systems: dichromats (banded mongoose *Mungos mungo*), trichromats (vervet monkey *Chlorocebus pygerythrus* and human), and tetrachromats (grey-headed bushshrike *Malaconotus blanchoti*). We used the ferret *Mustela putorius* as the closest available visual system for modelling banded mongoose vision. Ferret cone sensitivities (absorbance data) were obtained from electroretinogram flicker photometry-based data⁵⁴ and used to model visual pigment absorbance⁵⁵, corrected for light transmission through the ocular media⁵⁶. Vervet monkey cone sensitivities are very similar to those of humans⁵⁷, and so we used human vision models here⁵⁸. For birds, the grey-headed bushshrike likely has a violet sensitive (VS) visual system⁵⁹, and so we used representative peafowl *Pavo cristatus* sensitivity data for this visual system⁶⁰.

For each vision model, predicted cone catch values were obtained by transforming the images from camera to animal colour space with a widely used mapping technique^{39, 51, 61}. We used a dataset of 3139 natural reflectance spectra to model predicted camera and visual system responses. This comprised 2361 reflectance spectra from the Floral Reflectance Database⁶² and the remainder from spectra of bird eggs, plumage, insects, minerals, tree bark, and vegetation collected by us using an Ocean Optics USB2000+ spectrometer with an Ocean Optics PX2 pulsed xenon lamp⁵¹. All calculations were based on data from 300 to 700 nm in 1 nm increments, under D65 illumination. Models were calculated using custom code in ImageJ⁶³ and R⁶⁴. As has been demonstrated in multiple previous studies, mapping from camera to animal colour space is highly accurate and with very low error rates compared to modelling of photon catch data with spectrometry^{e.g.} 15, 51, 52. In fact, images much more accurately account for illuminating conditions and angles, and measure larger areas of the focal object or scene, than is possible with spectrometry, meaning that using image analysis is likely even more accurate than purely based on its high correspondence with spectrometry data. The R^2 values of the models converting from image values to animal cone catch values were all 0.99. Cone catch images for each visual system were used for all subsequent image processing in 32-bits/channel floating point operations, ensuring that no data were lost due to saturation that can occur at the top of the 16-bit range.

Image processing and analysis

Our aim was to compare how closely the eggs of all species and adult plumage of nightjars matched their chosen nest site compared to other potential sites at different spatial scales. We therefore compared egg/adult camouflage to the nest locations that individuals had chosen themselves, relative to nest locations chosen by other individuals of the same species. The conspecific comparison revealed whether individual birds chose sites based on their own specific egg/adult appearance. In addition, we also compared how closely egg and adult birds matched chosen nest sites and potential other sites in the same area at a very fine (< 5 cm) and larger (5 m) scale.

For the analyses of egg coloration, our overhead photographs were segregated automatically into two zones corresponding to the clutches' immediate surroundings (an area with a radius of 400 pixels, or approximately 4.4 cm, from the edge of the clutch) and neighbouring surroundings occupying the remainder of the image beyond 400 pixels from the target. We chose an area of 400 pixels because this reliably encompassed the nest area (including any potentially modified substrates around the nest) and centre of the image. This comparison of the 'immediate' chosen nest area to that of an adjacent 'near' patch enabled us to test nest site selection at a very fine scale. Next, the amalgamation of these 'immediate' and 'near' zones, called the chosen 'local' zone was analysed and compared to the two 'distant' control photographs 5 m away. We used an amalgamated zone rather than just the 'immediate' nest area so that similarly sized areas could be compared. The second comparison of the chosen 'local' patch with 'distant' patches enabled us to test microhabitat choice at a larger scale within the general nest area. For the conspecific nest comparisons we compared the camouflage of the birds' chosen 'local' zones to those of other individuals.

Eggs were selected using an egg-shape selection tool⁶⁵. For the adult nightjars, we also followed the above area selections and comparisons, with individuals selected using the freehand selection tool in ImageJ. Egg/bird edges were generally clearly visible, but any obstructing objects were avoided to prevent ambiguous areas of the target or background from being measured (although this process was not undertaken blind to our hypotheses, we minimized any subconscious bias by analysing nest photos separately from the 5 m control photos, precluding any possibility of direct comparison). Adult nightjars could not be caught and photographed under controlled (diffuse) lighting conditions. As such, colour and pattern metrics for adult nightjars were based on *in situ* images, and any local lighting effects (such as dappled shadows) would have been cast on both the adult bird and its surrounds. Although the normalisation would control for overall colour and luminance differences, pattern could have been affected by dappled shadows. This effect should be most pronounced in fiery-necked nightjars, which often nested under dappled light, whereas Mozambique and pennant-winged nightjars tended to nest in open sites. However, in our previous study³⁷, we found that the pattern match between adult nightjars and their surroundings was the best predictor of nest survival, suggesting that our *in situ* measures of pattern were at least ecologically relevant. Eggs were photographed under controlled lighting, selected from these images and re-sized to match the pixels/mm scale of the *in situ* surrounds in the background images (excluding the *in situ* eggs), using bilinear interpolation image reduction.

We calculated three metrics for camouflage matching: the level of colour, luminance (perceived lightness), and pattern match by the bird or egg to the relevant background sample. Our metrics have been used in several past studies and, crucially, they predict both the survival of wild birds/nests by predators in the field³⁷, and the detection times of humans when searching for artificial targets on computer screens⁶⁶. They also relate to other aspects of behaviour linked to camouflage, such as escape behaviour by incubating adults³⁸. Therefore, we can be highly confident that the metrics used here provide ecologically relevant measurements of camouflage. Pattern and luminance metrics used the luminance-channel image (following past work⁴⁰) because pattern is widely thought to be encoded principally by achromatic vision⁶⁷. Ferret luminance was based on the LW cone

sensitivity since these are more abundant than the SW cones by 14:154. Human luminance was derived as $(L+M)/261$, and the double cones were used to calculate peafowl luminance⁶⁰.

Natural backgrounds have luminance levels that are spatially correlated due to a mix of light and dark objects, with a roughly log-normal distribution of intensities. However, while animal patterns also demonstrate this spatial non-independence of intensities, they often have two or more main levels (such as dark spots on a pale background in eggs). Parametric approaches are therefore not suitable for analysing these multi-modal distributions. As with our past work^{37, 38, 66}, luminance distribution differences ($Luminance_{diff}$) were calculated as absolute differences in counts of the numbers of pixels in each target (plover egg or adult nightjar plumage) to the relevant background at 32 linear levels of luminance spanning 0% to 100%^{37, 38}:

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

$Luminance_{diff}$ values quantify to what extent the egg or nightjar luminance values, to each visual system, match the values of their surrounds^{37, 51}. This metric overcomes the problems of relying on mean values in data that are not normally distributed, and significantly predicts human detection times of camouflaged objects⁶⁶.

Pattern differences were generated based on Fourier analysis and bandpass filtering via a 'granularity spectrum', following a wide range of past studies that have used this approach to quantify animal patterns in questions spanning avian brood parasitism and egg mimicry to camouflage in cuttlefish^{e-g-40, 68}, and detection times of humans searching for hidden camouflaged targets⁶⁶. Pattern differences were generated with Fast Fourier Transform bandpass filters at 17 levels (from 2 pixels, increasing exponentially with the square root of 2, up to 512 pixels), using the standard deviation of the luminance values at each spatial scale to derive the 'energy' at that spatial scale. Fourier analysis and bandpass filtering has been used in various previous studies to analyse animal markings in terms of a 'granularity spectrum'^{40, 68}. Next, we calculated overall energy differences across all spatial frequencies ($Pattern_{diff}$) in a similar manner to $Luminance_{diff}$, by summing the absolute differences in energy between the target and the background at each spatial scale ^{s37, 38, 66}:

$$Pattern_{diff} = \sum_{s=max}^{s=min} |Target_s - Background_s|$$

Differences in pattern energy between the samples over the spatial scales results in increased $Pattern_{diff}$ values. As such, $Pattern_{diff}$ quantifies how closely egg and plumage patterns match the size and contrast of those background features^{37, 51}. This metric should provide several advantages over past approaches that derive multiple descriptive statistics from granularity spectra^{40, 68}. For example, granularity spectra are often multi-peaked, such that selecting only the main peak in the spectrum discards potentially important information at other scales. As with luminance intensities (above), the pattern energy in adjacent scale

bands is correlated, resulting in smooth energy spectra. Utilising just one metric of pattern match also simplifies the statistical analysis and interpretation, and is well supported by behavioural evidence as it predicted the likelihood of nightjar nest predation in the same study system³⁷ and human detection times of hidden targets⁶⁶. Our approach here is most relevant to the concept of background-matching, where we expect the irregular patterns of the target to match the size and contrast of those in the irregular background across a range of spatial scales. It does not test a masquerade hypothesis where one would predict that the sample should be recognized as a different class of background object (i.e. an object recognition task); this would require the development of methods to analyse and interpret the phase components of the Fourier spectra, or another type of analysis altogether.

Colour analysis was based on a log form of the Vorobyev-Osorio receptor noise model of colour discrimination⁴¹ for estimating “just noticeable differences” (JNDs). Versions of this model are commonplace in studies of animal coloration (reviewed by⁶⁹). As is convention, JNDs describe colour differences between two objects in predicted discrimination values, whereby values less than 1.00 can be interpreted that two objects are indiscriminable, and increasing values above this likely to result in a greater likelihood of detection. Colour differences for both adult nightjars and the eggs of all bird groups was the mean difference (in JNDs) between the most abundant colour in the camouflaged object and all the colours found in its surrounds, weighted by coverage, as in our previous work^{37, 51}. This approach is in principle, therefore, fairly straightforward: first we find the dominant colour in the prey, and then we test how close this was on average to its background colours with a weighting for the proportion of the background composed of that colour (so if the colour of the prey was a good match to a very small patch of the background, this would not count as much as being a good match to a colour covering a larger proportion of the background). This method is able to downplay the influence of small objects in the background images that were highly different colours to the prey (such as the occasional green leaf), focussing on the matching of the larger background sections. We have used this approach previously in a study of nest covering behaviour in plovers, and shown it to be one of the best predictors of nest material selection in those birds⁴⁵. Overall, this approach allowed us to compare object and background colours, using some of the most advanced models of visual discrimination currently available.

Controlling for Effects of Nest Scrapes

Nightjars and Temminck's coursers lay their eggs directly on the substrate, making no modification to the surrounds. Plovers and bronze-winged coursers often make a shallow scrape, sometimes containing material from the immediate surrounds. Three-banded coursers sometimes partially bury their eggs during early incubation. While the subjective visual impression of the modified nest area in these latter species is minimal, its modification could potentially affect our habitat selection results. However, this is highly unlikely to have affected the majority of our findings, for two reasons. First, the nightjars and Temminck's coursers do not undertake any nest modification, meaning that this could not have contributed to those results at any spatial scale for these species. Second, we re-ran our analysis for the conspecific comparisons and for the intermediate scale (patch choice at a scale of several meters) for plovers and coursers while excluding data from the immediate

nest area. To do so, we compared egg camouflage for the conspecific comparisons and comparisons at the m scale after excluding the area potentially containing any scrape (based on the largest scrape area we could detect from our dataset), and the conclusions were unchanged. Therefore, at most, nest modification could only have influenced the results for certain plover and courser species at the finest (cm) scale (see Supplementary Information).

Statistical Methods

All statistical tests were performed in R v3.0.264. Due to repeated measures using three predator visual systems, linear mixed-effect models were run using the lme4 package v1.1-570 with a Gaussian error structure and fitted with restricted maximum likelihood⁷⁰. Species identity was included in each model as a fixed effect in order to statistically eliminate any between-species differences and detect camouflage effects shared between all species, rather than explicitly testing for between-species differences (which would require phylogenetically controlled statistics, and test different hypotheses to those that we investigate in this study). Full interaction models were specified with the above image metrics as response variables, and then simplified using the fitLMER function of the LMERConvenienceFunctions v2.5 using AIC to backwards-fit the fixed effects on maximum likelihood models and forward-fit the random effects. Year and nest ID were specified as random factors, although year was removed because it explained little variance and did not improve the model fit. Comparisons of camouflage matching to the nest sites of conspecifics were based on large matrices in which each clutch or adult was compared to each other nest's surroundings, under all three predator visual systems. We controlled for this pseudoreplication in models by specifying both the adult/clutch identity, and each nest surrounding's identity as random factors, and predator visual system as a fixed effect. A variable denoting whether the comparison was between an individual's phenotype and its own nest surroundings, or a different individual's nest surroundings, was then used as a fixed effect for the type of comparison ('sameOrDifferentNest' in the following example). An example of the full mixed model structure was therefore: $\text{lmer}(\text{PatternDifference} \sim \text{nightjarSpecies} * \text{predatorVisualSystemSpecies} * \text{sameOrDifferentNest} + (1|\text{nestID}) + (1|\text{nestSurroundID}))$. Model residuals were checked to verify assumptions of homogeneity of variance and a normal error structure, and variables were log-transformed to meet these assumptions. Conservative degrees of freedom were used to calculate *P*-values from maximum likelihood models⁷⁰. To ensure the structure of these models did not create a lack of independence, causing type I or II errors, we fitted the models to randomly generated dependent variables. The *p*-values for the 'sameOrDifferentNest' variable when repeated on normally distributed random data 1000 times demonstrated a flat distribution, implying model structure did not affect our results. In light of the evidence suggesting a potential trade-off between egg pattern matching and luminance matching in plover/courser eggs and nightjar eggs, we ran two additional linear mixed models to test whether there was a negative correlation between pattern-matching and luminance-matching metrics in the patches selected for nesting. The following model structure was specified: $\text{lmer}(\log\text{PatternDifference} \sim \log\text{LuminanceDifference} * \text{Zone} + \text{predatorVisualSystemSpecies} + (1|\text{nestID}))$.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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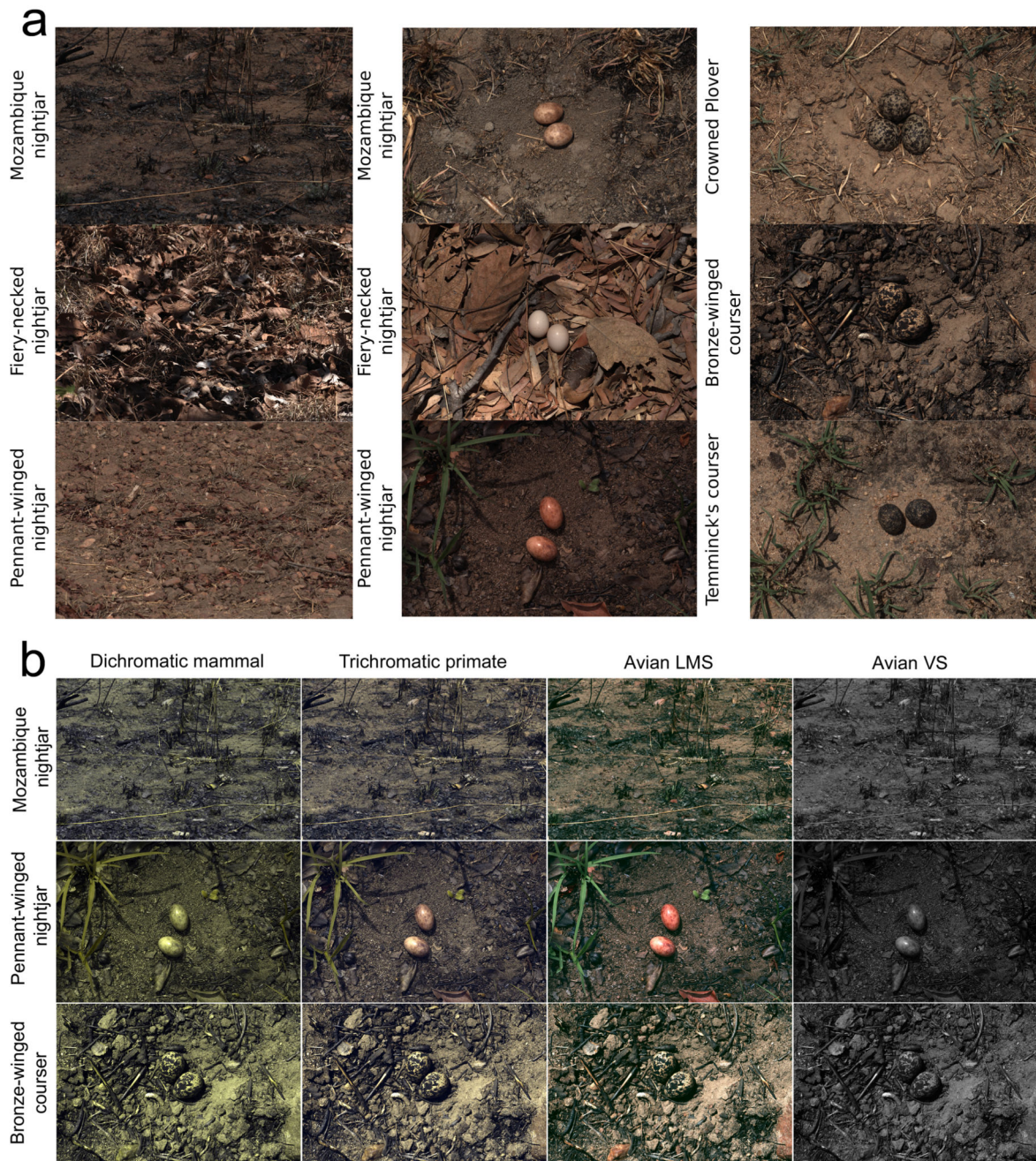


Figure 1.

a: Examples showing camouflage of eggs and adults of six of the species of nightjar and plover/courser included in the study (individuals/clutches are in the centre of each image). This shows the variation in camouflage match among species, and some of the different colours and markings found in the eggs and adults used for concealment. **b:** Images of one adult nightjar, one nightjar clutch, and one courser clutch to predator vision. These images (see Methods) correspond to a dichromatic mammal, which sees colours that to humans are yellows and blues, a trichromatic primate with equivalent colour perception to humans, and

a tetrachromatic bird. The latter has colour vision involving four cone types, including ultraviolet, and because there is no standard way to illustrate the range of colours birds may see (conventional images being restricted to three channels), we here present separate trichromatic images (based on the avian LW, MW, and SW cones), and greyscale UV (violet; VS) cone images (whereby brighter pixels correspond to greater UV information).

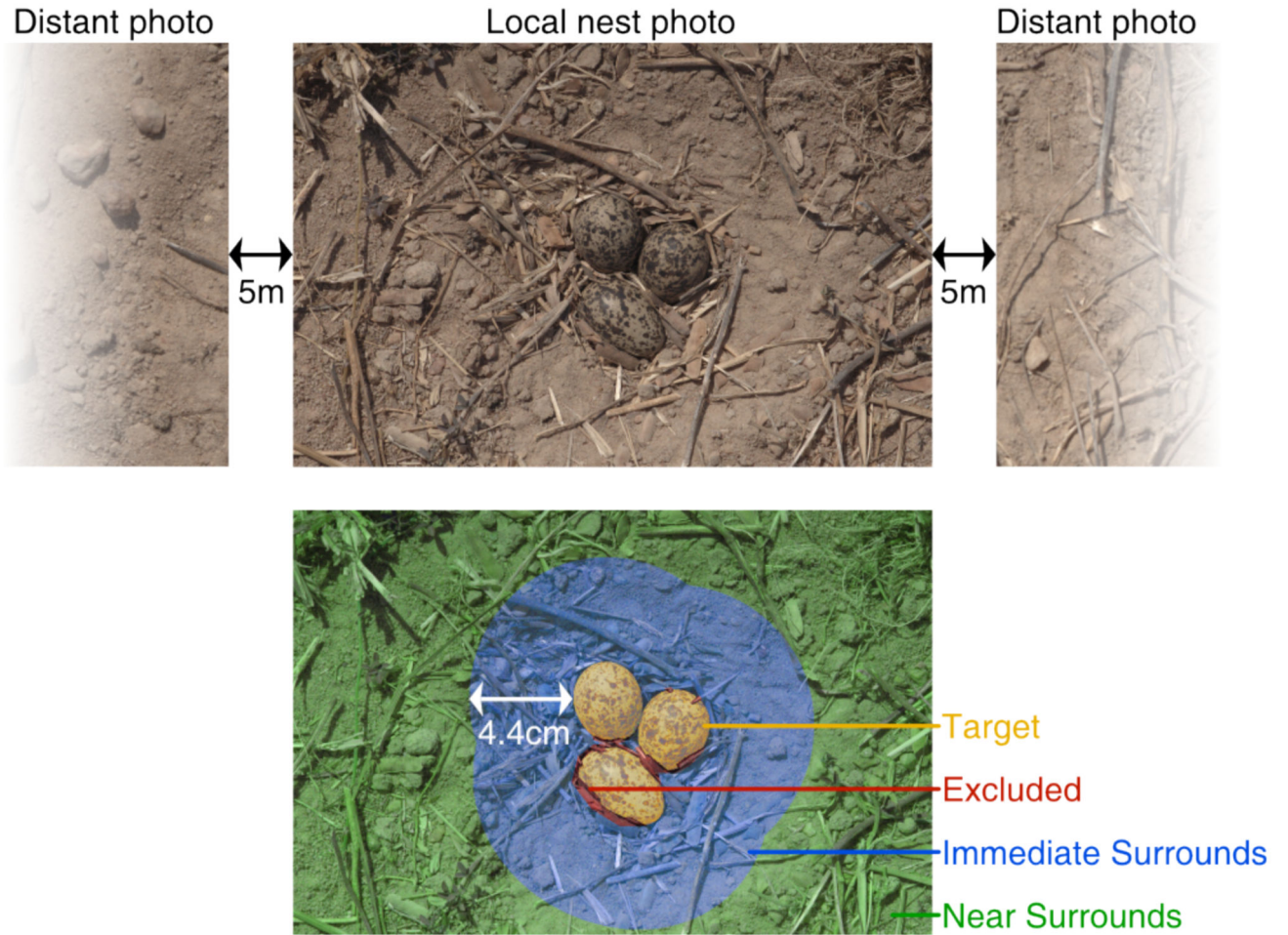


Figure 2.

Analysis of egg camouflage between chosen nest sites and potential other sites. We compared the camouflage of eggs or adult nightjars at three spatial scales. At the finest cm scale (or zone), we compared egg or plumage camouflage to the chosen ('immediate' = comparison within a few cm) background surrounding the eggs (400 pixels, or approximately 4.4 cm radius) to a ('near') background immediately adjacent to this. Next, we compared target camouflage to the chosen nest background ('local', comprising the combination of the 'immediate' and 'near' areas) to potential backgrounds in the same area 5 m away ('distant' = comparison within 5 m). Finally, we compared the camouflage of targets to the chosen nest background of each individual to the sites chosen by other conspecifics.

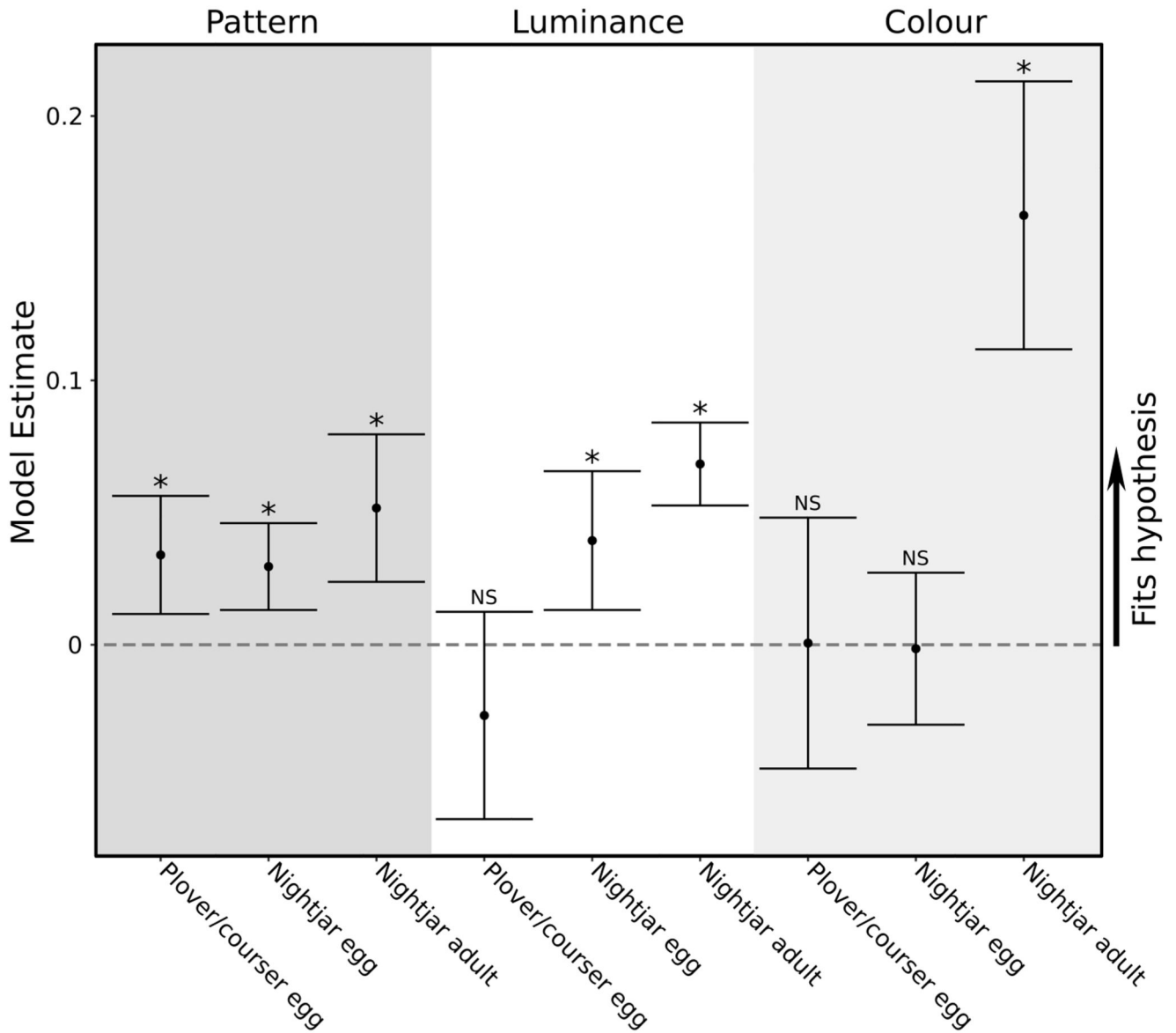


Figure 3.

Model estimates of planned comparisons comparing the match between each subject (egg or adult bird) and its chosen nest background versus its match to backgrounds chosen by its conspecifics. Error bars show 95% confidence intervals. Estimates above zero indicate that the chosen background is a better fit than non-chosen conspecific backgrounds, supporting the hypothesis that females select backgrounds that match their own camouflage, rather than a species-specific habitat preference. The y-axis (model estimates) shows the model estimate multiplier for pattern, luminance, or colour matching. For example, this shows that on average a nightjar's chosen nest has a (logged) JND value 0.16 times lower than that of a conspecific's.

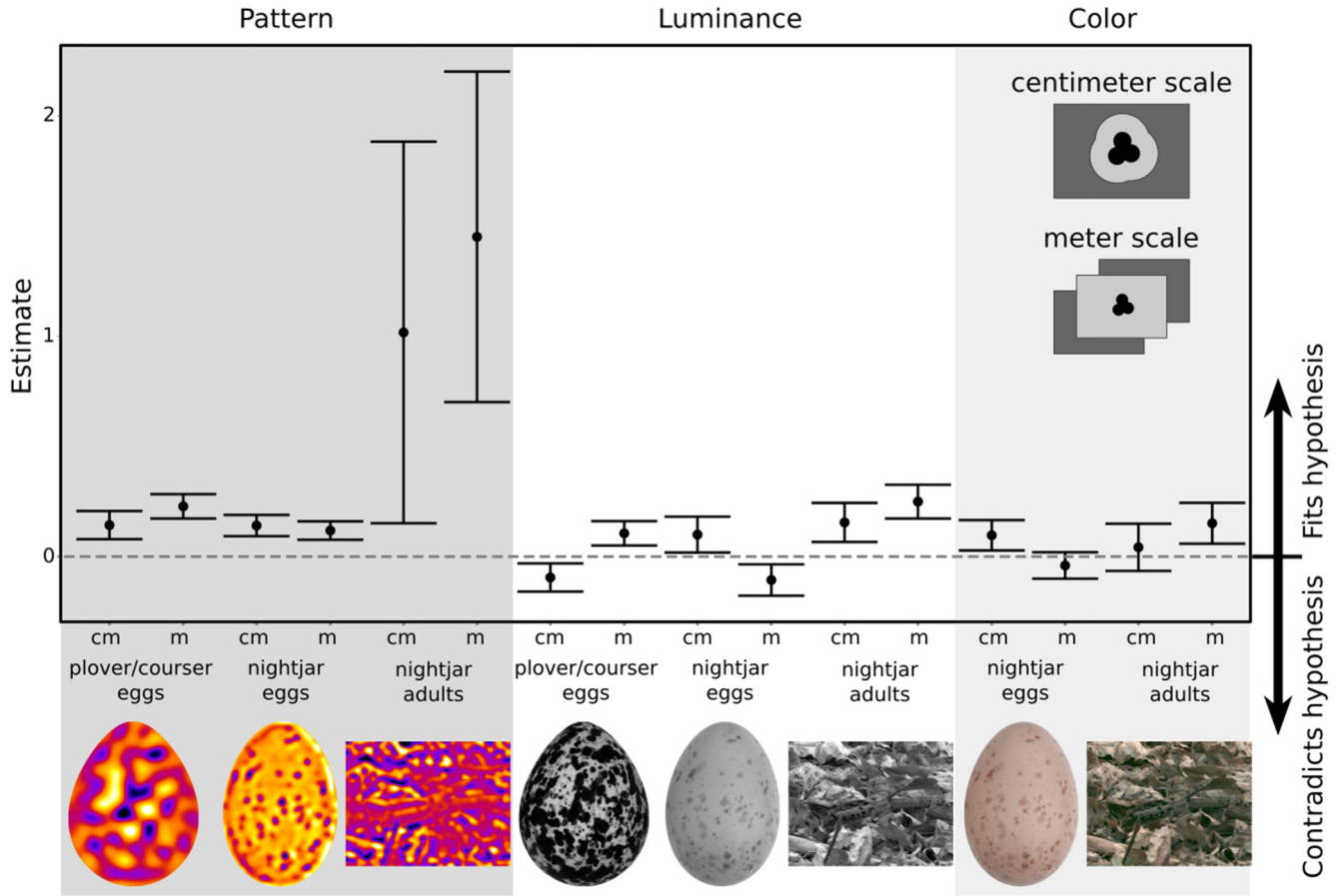


Figure 4. Model estimates of planned comparisons in pattern, luminance, and colour camouflage matching between zones with 95% confidence intervals. Estimates greater than zero show that the zone nearer the clutch matches the eggs or adult better than the zone further away. Estimates below zero show the opposite effect, matching the more distant zone better than the nearer zone. Colour matching for plover and courser eggs did not differ between zones, so is not included.

Table 1

Summary of results comparing camouflage match to the chosen versus non-chosen locations for all three metrics. The code '+' corresponds to when camouflage was a better match to the chosen background than other locations, '-' corresponds to a better match to the non-chosen background, and 'O' corresponds to no significant difference. The majority of results show support for microhabitat selection, especially for pattern. Where a model did not retain zone as a predictor, Chi-square model comparison results are shown. F-statistics are shown for conspecific comparisons as the variable has two levels (same or different nest). T-values for planned contrasts are shown for fine scale and local scale results (Tukey Post-hoc test).

Group	Scale	Camouflage Metric		
		Pattern	Luminance	Colour
Plover/courser eggs	Conspecific	+	O	O
		$F_{5,7854} = 4.77, p < 0.001$	Model comparison Chi-square $p = 0.982$	Model comparison Chi-square $p = 0.981$
	Local scale (5 m)	+	+	O
		$t = 10.56, p < 0.001$	$t = 4.90, p < 0.001$	Model comparison Chi-square $p = 0.795$
	Fine scale (< 5 cm)	+	-	O
		$t = 5.73, p < 0.001$	$t = -3.81, p < 0.001$	Model comparison Chi-square $p = 0.795$
Nightjar eggs	Conspecific	+	+	O
		$F_{1,13187} = 12.46, p < 0.001$	(X for one species) $F_{2,13185} = 7.02, p = 0.001$	Model comparison Chi-square $p = 0.919$
	Local scale (5 m)	+	-	O
		$t = 7.26, p < 0.001$	$t = -3.83, p < 0.001$	$t = -1.72, p = 0.085$
	Fine scale (< 5 cm)	+	+	+
		$t = 7.49, p < 0.001$	$t = 3.14, p = 0.002$	$t = 3.60, p < 0.001$
Nightjar adult	Conspecific	+	+	+
		$F_{1,11738} = 13.19, p < 0.001$	$F_{1,11734} = 72.87, p < 0.001$	$F_{1,11688} = 7.49, p < 0.001$
	Local scale (5 m)	+ t = -3.01, p = 0.003	+	+
			$t = 8.33, p < 0.001$	$t = 4.18, p < 0.001$
	Fine scale (< 5 cm)	+	+	O
		(O for one species) $t = -4.96, p < 0.001$	$t = 4.49, p < 0.001$	$t = 1.00, p = 0.313$