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The Eurasian Treecreeper (*Certhia familiaris*) has an effective camouflage against mammalian but not avian vision in boreal forests

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A well-known example of visual camouflage in birds is the plumage coloration of the Eurasian Treecreeper *Certhia familiaris*, yet this species' camouflage has never been objectively quantified. Here, we quantify Treecreeper camouflage in its boreal forest habitat, test whether Treecreepers better match tree backgrounds at nest-site, territory or habitat spatial scales, and explore which common tree species provide the best background match. Using photographic data of the birds and forested backgrounds, we test their background match using human, ferret and avian vision modelling. We found that a Treecreeper's wing and mantle provided the closest background matching, whereas the wing stripe and tail were more conspicuous against tree trunks. Vision modelling also suggests that Treecreeper camouflage provides a better protection against mammalian than against avian vision. The matching was not significantly different across spatial scales in local spruce forests. However, the background match was better on conifers than on deciduous trees. Our results support the long-standing conjecture of Treecreeper camouflage but also suggest that the camouflage is an adaptation especially against mammalian predators, which are important nest predators of Treecreepers.

Keywords: background matching, habitat selection, QCPA, vision model.

Camouflage is an anti-predatory adaptation that hinders detection and recognition by increasing prey resemblance to its visual environment (Poulton 1890, Cott 1940, Endler 1980, Bond & Kamil 2002, Ruxton *et al.* 2004, Stevens & Merilaita 2011, Troscianko *et al.* 2013, Hultgren & Mittelstaed 2015, Duarte *et al.* 2018, Nokelainen *et al.* 2019). The examples of camouflage are numerous, including birds (Troscianko *et al.* 2016), mammals (Boratyński *et al.* 2017), lizards (Marshall *et al.* 2016), fish (Cortesi *et al.* 2016), crustaceans (Price *et al.* 2019), insects (Kang *et al.* 2015) and many more. One of the earliest illustrations of camouflage concerned birds (Thayer 1896), where the colour pattern of the Ruffed Grouse *Bonasa umbellus* and American Woodcock *Scolopax minor* were described as resembling their natural habitat for reasons of concealment. Although quantitative

assessments of concealment versus conspicuousness have been explored in many taxa (Endler 1978, 1984, Endler & Théry 1996, Théry & Casas 2002, Håstad *et al.* 2005, Stuart-Fox & Moussalli 2009), systematic demonstrations of camouflage in adult birds have been scarce. In birds, the first quantifications of camouflage (i.e. objective demonstration of animal-to-background similarity rather than subjective anecdote) occurred fairly recently (Troscianko *et al.* 2016, Wilson-Aggarwal *et al.* 2016), although egg mimicry has been studied in detail previously (Spottiswoode & Stevens 2011, Stoddard & Stevens 2011, Stevens *et al.* 2013).

Although the concept of camouflage (i.e. that something that resembles its surroundings is difficult to detect) is intuitive, it has proven challenging to study camouflage in naturally variable environments. One of the main constraints of camouflage is that it renders an organism's appearance such that it is associated with specific visual characteristics in its habitat (Thayer 1896, Cott 1940, Ruxton *et al.* 2004, Stevens & Merilaita 2009,

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Hughes *et al.* 2019). A particular appearance may therefore not provide ideal camouflage in other habitats where concealment requires matching different lightness, colour or pattern texture. This may either constrain habitat use to a narrow 'visual' niche (Merilaita *et al.* 1999, 2001, Kjærnsmo & Merilaita 2012, Michalis *et al.* 2017) or, alternatively, animals may have adopted a more general resemblance to a preferred habitat type. In terms of camouflage, an animal may thus either be a specialist within a small visual niche or a generalist across a larger niche (Nokelainen *et al.* 2020, Briolat *et al.* 2021). The latter can be considered an imperfect compromise to match different backgrounds (Hughes *et al.* 2019), which provides flexibility to animals' visual niche.

From an ecological standpoint, it must also be acknowledged that relevant receivers (e.g. predators or conspecifics) may have different visual perception to ours. Generally, it should not be assumed that animals that are well camouflaged against humans' trichromatic visual system are also well camouflaged against ecologically relevant predators. For example, birds are tetrachromatic and can process wavelengths in the ultraviolet range, whereas mammals are often di- or trichromats, having a narrower spectral sensitivity range (Endler 1978, Kelber *et al.* 2003, Endler *et al.* 2005, Kelber 2019). The differences in visual perception of animals can cause us to over- or underestimate the relative value of camouflage in nature (Håstad *et al.* 2005). Thus, state-of-the-art demonstrations accompanied with vision modelling are needed to increase our understanding of how camouflage works in nature (Rosenblum 2006, Troscianko *et al.* 2016, Wilson-Aggarwal *et al.* 2016).

The Eurasian Treecreeper *Certhia familiaris* (hereafter 'Treecreeper') is a small passerine bird, specialized to feed on insects and spiders that it searches for in bark crevices (Gibb 1954, Norberg 1986, Kuitunen & Helle 1988). It is sedentary, prefers old-growth forest stands and is found in coniferous forests across the boreal zone (Suorsa *et al.* 2004, Jäntti *et al.* 2007, Aho *et al.* 2009), although it has a broad range and may also occupy deciduous woodlands (typical of western Europe where habitat lacks conifers). A long-standing hypothesis posits that it has an effective camouflage, because to humans it is apparently hard to detect against tree trunks, yet its camouflage has never been documented apart from subjective observations of its background resemblance (Gibb 1954, Bursell & Dyck

2003). Previous work on Treecreepers has not considered the effect of variation in visual backgrounds on camouflage or analysed camouflage from the predator perspective (e.g. using vision models). Consequently, it is not known whether Treecreepers are camouflaged to non-human receivers such as birds, which are able to process visual input in the ultraviolet range where humans lack sensitivity (Kelber *et al.* 2003). Feeding on the bark of different trees also means that Treecreepers may be exposed to potential detection against a range of diverse backgrounds and achieving good camouflage against all of these might be difficult. This makes the species suitable for investigating the effectiveness of camouflage by testing how the colours of different body parts match natural backgrounds at different habitat scales as perceived by different visual systems of predators.

We ask whether the Treecreeper coloration provides camouflage in the forest habitats they live in. More specifically, we (i) quantify the camouflage of bird topography (i.e. mantle, tail, wing and wing stripe) in its natural habitat, (ii) test whether Treecreepers better match the nest-site (i.e. home tree), specific trees within their territory or different between-habitat patches (i.e. scale-dependent camouflage) and (iii) explore which common tree species provide the best background match with respect to plumage coloration. An analysis of background matching with multispectral image analysis was performed to quantify the chromatic and achromatic contrast between plumage and backgrounds. We focused on the dorsum, as the species is most likely to be viewed from this side by potential predators. We predicted that the back (mantle) should have the closest background match as being the most visible part of bird when foraging against tree trunks, and it evidently has the best match from the perspective of human vision (Fig. 1). If Treecreepers seek backgrounds against which they are hardest to detect (Kang *et al.* 2012, Duarte *et al.* 2016, Marshall *et al.* 2016, Stevens *et al.* 2017, van Bergen & Beldade 2019), then the match should be best at the nest-site or within the home territory. Alternatively, species may have adapted to match a broader range of habitat patches and tree species (Merilaita *et al.* 2017, Michalis *et al.* 2017, Hughes *et al.* 2019). Finally, we used visual modelling of three visual systems (dichromatic – ferret *Mustela furo*, trichromatic – human, tetrachromatic – avian) to test whether Treecreeper coloration provides substrate-

specific camouflage against visually guided predators.

METHODS

Treecreeper field sites

The Eurasian Treecreeper has a large distribution over the Western Palaearctic region ranging from

western Europe to Japan in the east. Across the boreal forest belt, it prefers old-growth forest stands (Fig. 1a–c), typically coniferous forests, although the species also occurs in deciduous and mixed forest stands (Kuitunen & Helle 1988, Suorsa *et al.* 2004, Jäntti *et al.* 2007). The study areas were located in Finland, where woodlands comprise predominantly conifers (spruce and pine), although mixed woodlands and deciduous

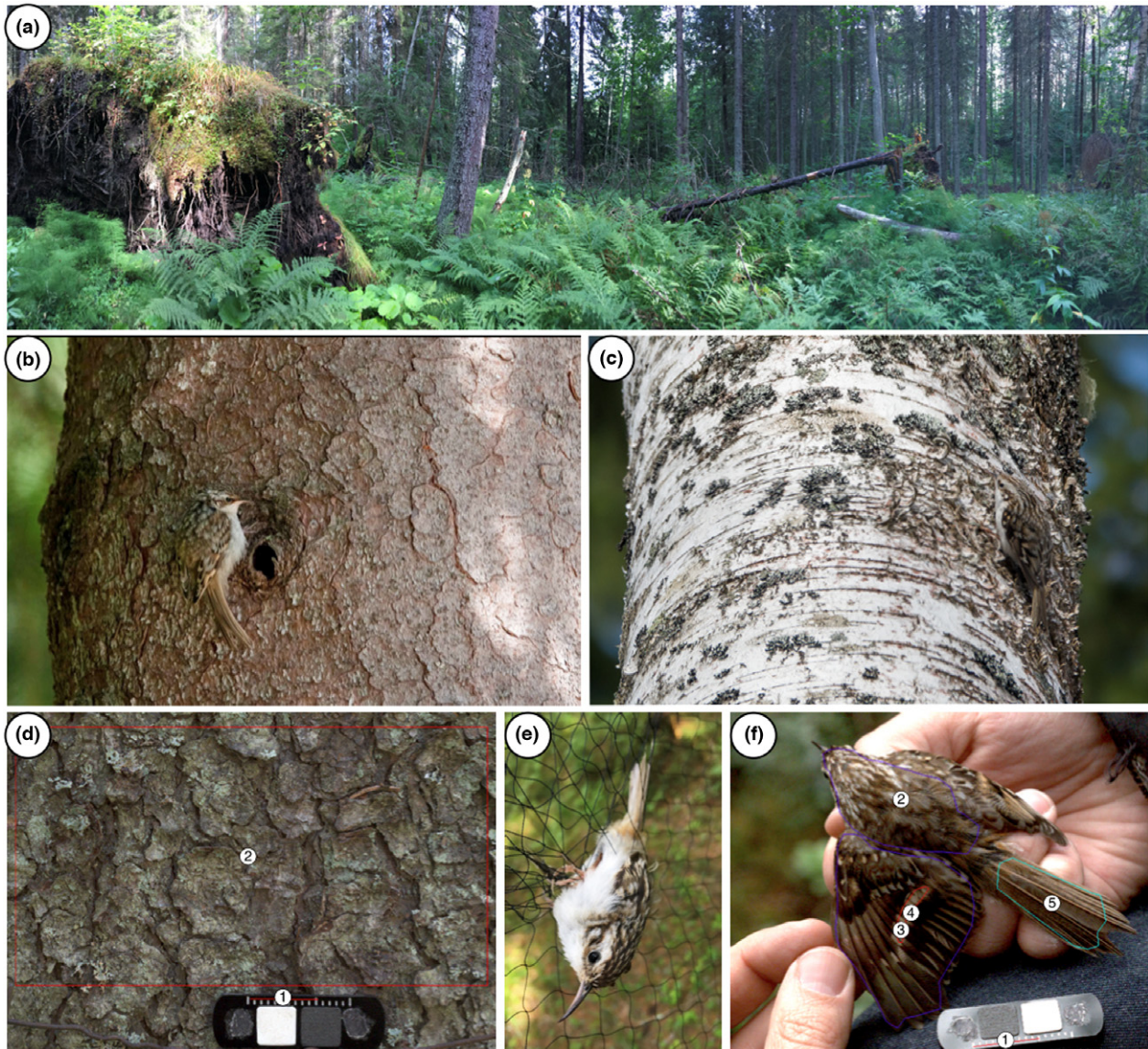


Figure 1. Camouflage of the Eurasian Treecreeper. The figure shows examples of variation in the visual environment. Photos starting from top left: (a) boreal forest habitat with an ample amount of old-growth spruce trees; (b) a Treecreeper against a spruce; (c) a Treecreeper against a birch; (d) an example of the photographic scene where white standards are photographed against spruce background (1 standard, 2 background); (e) Treecreepers were caught using mist-nets; (f) after which they were photographed and the regions of interests in the bird topography were defined in the image analysis (1 standard, 2 mantle, 3 wing, 4 stripe, 5 tail). All animals were captured and photographed at the site after which they were ringed and released unharmed. [Colour figure can be viewed at wileyonlinelibrary.com]

forests are not uncommon. Birds were caught near their nest-sites (Fig. 1f) using mist-nests (9 m long with 19-mm mesh size) during May–July 2018–2019.

Bird-to-background comparisons

First, to quantify the background match with respect to bird topography (i.e. back or mantle, tail, wing and wing stripe – Fig. 1f), we computed the chromatic and luminance match against nest trees of all birds captured. All nest trees in our study area were conifers (spruce *Picea abies* or pine *Pinus sylvestris*).

Secondly, we investigated the match of Treecreeper plumage (we only used the ‘mantle’ in the subsequent analyses) to the background with respect to focal, territory and global habitats. At each site we photographed the nest tree; the closest (typically *c.* 5 m away) eight trees on each of the main compass headings (N–E–S–W; two trees each) were then photographed, always facing the nest tree. Focal refers to the specific background of the nest tree (i.e. or ‘home’ tree, representing small-scale microhabitat), ‘territory’ refers to the home forest trees (i.e. core territory) and ‘habitat’ refers to all backgrounds in which other members of the same species were found (i.e. representing larger scale macrohabitat within the locality).

Thirdly, we obtained an independent comparison of animal-to-background match to potential Treecreeper habitat. We photographed the bark of the five most common tree species from a different site at which Treecreepers were known to be present but where no Treecreeper photography took place. The five common boreal tree species chosen for comparison were *Pinus sylvestris* (Pine), *Picea abies* (Norway Spruce), *Betula pendula* (Silver Birch), *Populus tremula* (Aspen) and *Alnus incana* (Grey Alder). Five bark samples of the same-sized trees (minimum 30 cm diameter, measured at a height of 1.5 m) were haphazardly chosen to represent these tree species. Then, we compared the background match of the Treecreepers to each of these bark type representatives.

Photography and image processing

To quantify Treecreeper camouflage, we photographed both the birds and their visual backgrounds (i.e. tree trunks). In total, 17 birds from

11 sites, and 99 trees were documented; one individual was excluded from comparisons due to poor photograph exposure. All were photographed under natural daylight. No light diffusor was used but care was taken to ensure that light fell similarly across the scene. Photographs were taken from similar height (*c.* 1.5 m). A calibration standard was included in the photographic scene for further use in the image analysis (Fig. 1d). The area of the visual backgrounds (tree trunks) photographed was approximately 30 cm in width and 25 cm in height, which corresponds to a 1 : 3 animal-to-background ratio. The specific spot from where the photograph was taken of the trees was from a height of 150 cm and facing the nest tree, which in turn was photographed from the opposite side of the tree to the nestbox. The bird regions of interest (ROIs: wing, stripe, tail, mantle) were measured as entire areas from the respective dorsal side. We did not measure the ventrum, as the species characteristically ‘creeps’ up the tree trunk while foraging, which effectively hides the ventrum, making it less obvious in camouflage function.

Photographs were taken with a customized full-spectrum Samsung NX1000 digital camera equipped with Nikon EL-80-mm lens. For the human visible spectrum, we placed a UV and infrared (IR) blocking filter in front of the lens, which only transmits wavelengths between 400 and 680 nm (Baader UV/IR Cut Filter). For the UV images (to gain the ultraviolet spectral range required for avian vision modelling, see further below), a UV pass filter was used (Baader U filter), which transmits between 320 and 380 nm. Grey reflectance standards which reflect light equally at 7% and 93% between 300 and 750 nm were used. The images were saved in RAW format with manual white balance.

All image analyses were carried out in ImageJ (Abràmoff *et al.* 2004) with the multispectral image analysis toolbox (Troscianko & Stevens 2015). During calibration in ImageJ, images were converted to uncompressed TIFF files, and the images of each animal comprised bandpass layers corresponding to the long-wavelength (LW, i.e. red), medium-wavelength (MW, i.e. green), short-wavelength (SW, i.e. blue) and ultraviolet (UV, i.e. ultraviolet) parts of the spectrum. The proportional channel ‘reflectance’ values were calculated from these channel values (e.g. LW/

(LW + MW + SW + UV)), thus representing the relative (non-receiver-dependent) distribution of colour. These are reported as descriptive reflectance values (Fig. 2).

Vision modelling

Vision modelling, image calibration and analysis followed previously described methods (Stevens *et al.*

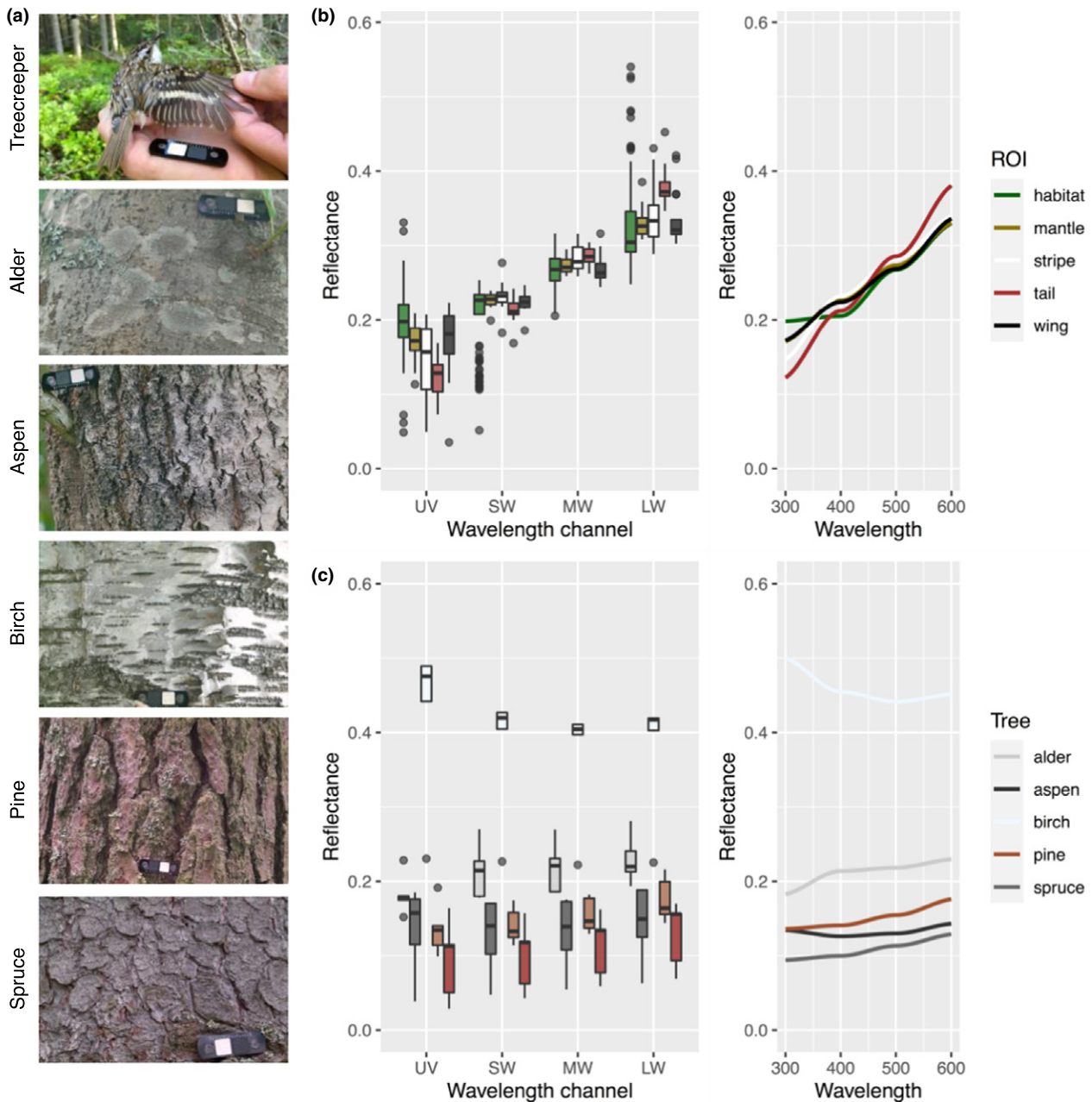


Figure 2. Descriptive reflectance data of Eurasian Treecreeper and examples of common boreal tree species (a). Boxplots show camera-obtained reflectance values (y-axis) against wavelength channel (x-axis). The reflectance of Treecreeper topography (mantle, wing, stripe, tail) for each region of interest (ROI) in the spruce-dominated habitat (b), where boxplots represent habitat (green), mantle (orange), stripe (white), tail (red) and wing (black) from left to right. Bark reflectance of five common boreal tree species (c) show alder (grey), aspen (black), birch (white), pine (brown) and spruce (dark-red) from left to right. One outlier (birch) was excluded from plots. Line plots show the same data plotted along the spectrum by smoothing the reflectance values between channels (i.e. bandwidth of each channel is 100 nm). [Colour figure can be viewed at wileyonlinelibrary.com]

2007, Troscianko & Stevens 2015, van den Berg *et al.* 2020), which have proven effective in quantifying camouflage in natural settings (Nokelainen *et al.* 2017, 2018, Stevens *et al.* 2017). We used a receptor-noise-limited visual discrimination model (Vorobyev *et al.* 1998). Dichromatic ferret, trichromatic human and tetrachromatic avian (Blue Tit *Cyanistes caeruleus* – UV-sensitive) vision models were used as proxies, as visual systems of these are well characterized (Stoddard *et al.* 2019). Thus, sensitivity to ultraviolet wavelengths probably corresponds to conspecific avian (Treetreepeeper) vision, as UV-vision is considered to be conservative among passerines (Ödeen *et al.* 2011). Raptors (e.g. Eurasian Sparrowhawk *Accipiter nisus*) may possess more V-type vision (Håstad *et al.* 2005, Lind *et al.* 2013), but also rely more on motion sensitivity as ambush predators. The vision models were run under D65 irradiance. We used a commonly applied 0.05 Weber fraction for the greatest abundant chromatic contrast for the most abundant cone type for all vision models, although we note that a 0.1 Weber fraction may be more appropriate with wild birds (Olsson *et al.* 2018, Silvasti *et al.* 2021). The use of the latter (0.1 Weber fraction) would result in half the lower contrast values (i.e. effectively closer animal-to-background match). The cone ratios used were those provided by default in the MICA toolbox: avian cone ratios 1 : 1.92 : 2.68 : 2.7 uv/sw/mw/lw (Hart 2001), ferret cone ratios 1 : 14 sw/lw (Calderone & Jacobs 2003) and human cone ratios 0.057 : 0.314 : 0.629 sw/mw/lw (Hofer *et al.* 2005). The vision model yields discrimination values as ‘just noticeable differences’ (JNDs), although before behavioural validation these should be considered predicted contrast values (dS). By definition, values lower than one (<1 JND) are indistinguishable, whereas larger values are increasingly discriminable (Siddiqi *et al.* 2004, Kang *et al.* 2015, Nokelainen *et al.* 2019). The luminance (or achromatic) contrast values were modelled using a 0.1 Weber fraction (Olsson *et al.* 2018). A double cone receptor was used for bird vision, whereas an mw-receptor (i.e. the longest wavelength-sensitive receptor in ferret) was used for ferret, and an lw-receptor was used for human to compute achromatic contrast under each vision model.

Statistical analyses

We used linear mixed effects models (lmer-function) in the lme4 R-package (Kuznetsova *et al.*

2017) and all models were run with normal (Gaussian) error structure. In all models we set chromatic contrast (dS) or achromatic luminance contrast (dL) as the response variable, and the vision model (‘vismod’: human, ferret, bird) plus the variable of interest (see below: i, ii, iii) and their interaction were set as factors. Bird ID was set as a random factor to control for data structure in all models. All analyses were done with the program R (3.2.1).

- i. To test whether Treetreepeepers are camouflaged with respect to bird topography, we used ‘ROI’ (mantle, tail, wing and wing stripe) as a factor [$\text{lmer}(\text{dS or dL}) \sim \text{ROI} * \text{vismod} + (1|\text{ID})$].
- ii. To test scale-dependency of chromatic match, we used the background comparison variable (home nest-site, territory, habitat) as a factor [$\text{lmer}(\text{dS or dL}) \sim \text{habitatscale} * \text{vismod} + (1|\text{ID})$]. We used the ROI ‘mantle’ against which the match was tested here and in the subsequent analysis.
- iii. To test the match against different tree species, the latter (alder, aspen, birch, pine, spruce) was set as factor [$\text{lmer}(\text{dS or dL}) \sim \text{treespecies} * \text{vismod} + (1|\text{ID})$]. The significance of the factors included in the final model was tested using *F*-test ratios in analysis of variance (ANOVA).

Full factorial models were tested and reduced by backward-stepwise model simplification removal of non-significant terms in all cases. Full lmer results are reported in the Supporting Information Tables S3–S8. Post-hoc analysis was done using Tukey’s HSD pairwise test (Figs S1–S6).

RESULTS

Camouflage and bird topography

There was a notable resemblance in the camera-obtained reflectance values of birds and their backgrounds (Fig. 2). Also, the vision-modelled animal-to-background contrast values were in a similar range for chromatic and achromatic contrasts (Supporting Information Tables S1 and S2). With respect to bird topography (i.e. plumage features: mantle, tail, wing and wing stripe), we found a significant interaction between plumage parts (ROIs) and the vision model for both chromatic and achromatic contrast (Table 1). The avian vision model showed

Table 1. Eurasian Treecreeper camouflage with respect to bird topography. Linear mixed effects model (LMER) analyses of the animal-to-background contrast were used, and the ANOVA table with Satterthwaite's method is reported here. Contrast was measured as chromatic (dS) and achromatic (dL) contrast between bird and background (i.e. a lower value indicates a closer match to the background) and modelled through human (trichromatic), ferret (dichromatic) and Blue Tit (tetrachromatic) vision models. The chromatic match of Treecreeper plumage topography was tested against all nest trees across the conspecifics.

Model term	SS	MS	d.f.	F	P
CHROMATIC dS					
ROI	3046.70	1015.60	3	100.74	<0.001
vismod	28125.90	14063.0	2	1395.03	<0.001
ROI*vismod	2230.80	371.80	6	35.88	<0.001
ACHROMATIC dL					
ROI	1463.03	487.68	3	31.59	<0.001
vismod	41.84	20.92	2	1.35	0.258
ROI*vismod	400.36	66.73	6	4.32	<0.001

Vismod, vision model; ROI, region of interest.

significantly higher chromatic contrast values in comparison with mammalian vision models (Fig. 3a). For the mammalian vision models (human and ferret), only the tail contrast was detectable from background (Fig. 3a, Table S3). The mantle and the wing were least separable from the background (Fig. 3a, Tables S2–S4, Figs S1 and S2). The achromatic contrast was on average similar across the comparisons (Fig. 4a), although the wing contrasted with the mammalian vision model more than the others (Fig. 3a).

Background matching across spatial scales

When comparing mantle coloration against the coniferous forest habitat, there was a significant effect of the visual model on chromatic and achromatic contrast (Table 2, Tables S5 and S6, Figs S5 and S6) but interactions with spatial scale were not significant. Both mammalian vision models (ferret and human) predicted significantly closer chromatic similarity of plumage coloration to background compared with the avian vision model (Fig. 3b, Table 2). In terms of achromatic contrast, the ferret vision model showed higher animal-to-background contrast values than the human vision model (Fig. 4b). However, we did

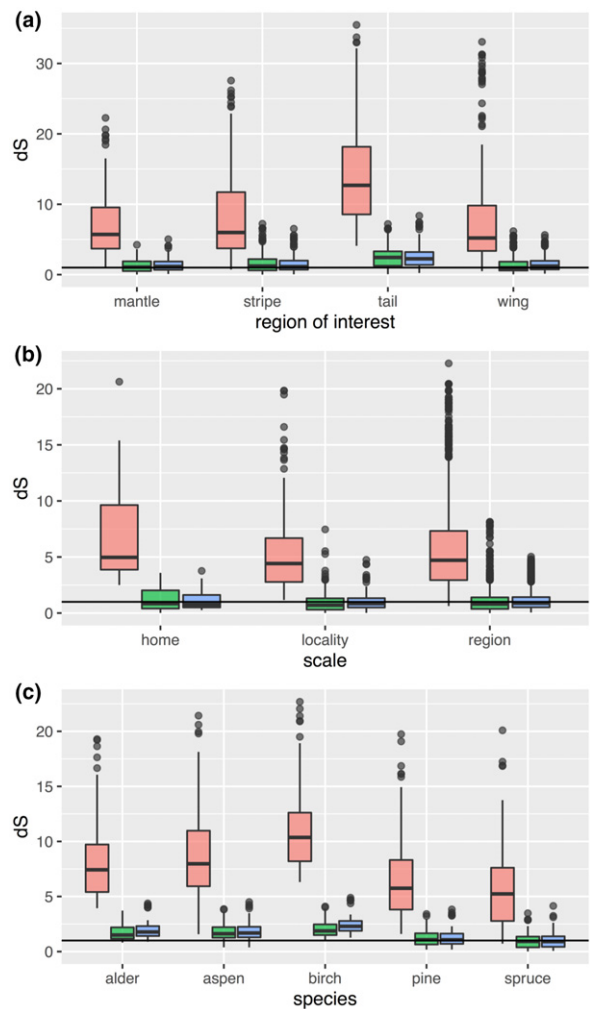


Figure 3. Vision modelling Eurasian Treecreeper camouflage: chromatic contrast. Boxplots show discrimination values for avian (red), ferret (green) and human (blue) vision models. (a) Modelled chromatic contrast values (in 'dS' units) plotted on the y-axis and across bird topography for each region of interest (ROIs) on the x-axis. Contrast values <1 are considered indistinguishable and values above this are increasingly easy to distinguish. (b) Camouflage at different scales. Vision-modelled contrast values across scales ('home' nest-site, locality, region) are plotted on the y-axis and separately for each scale on the x-axis. (c) Treecreeper camouflage against different tree species. Modelled contrast values are plotted on the y-axis and tree species on the x-axis. The black horizontal line indicates dS = 1, corresponding to the threshold of being able to perceive the contrast difference. [Colour figure can be viewed at wileyonlinelibrary.com]

not detect scale-dependent background matching with respect to spruce-dominated forests occupied by the Treecreepers (Tukey pairwise comparisons across scale $P > 0.05$, Figs S3 and S4, Tables S5 and S6).

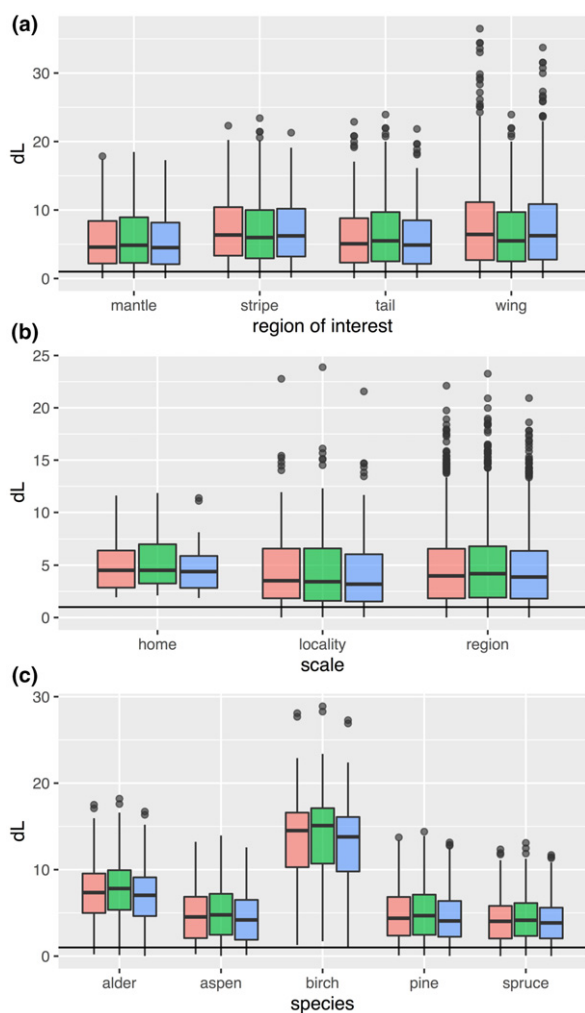


Figure 4. Vision modelling Eurasian Treecreeper camouflage: achromatic contrast. Boxplots show discrimination values for avian (red), ferret (green) and human (blue) vision models. (a) Modelled achromatic contrast values (in 'dL' units) plotted on the y-axis and across bird topography for each region of interest (ROIs) on the x-axis. Contrast values <1 are considered indistinguishable and values above this are increasingly easy to distinguish. (b) Camouflage at different scales. Vision-modelled contrast values across scales ('home' nest-site, locality, region) are plotted on the y-axis and separately for each scale on the x-axis. (c) Treecreeper camouflage against different tree species. Modelled contrast values are plotted on the y-axis and tree species on the x-axis. The black horizontal line indicates $dL = 1$, corresponding to the assumed threshold of being able to perceive the contrast difference. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

Background matching against common boreal tree species

When we compared the chromatic contrast of the mantle against five common tree species in boreal

Table 2. Linear mixed effects model (LMER) analyses of the animal-to-background contrast for Eurasian Treecreepers with respect to nest-site, territory, habitat and their relation to predator vision, with the ANOVA table with Satterthwaite's method reported here. Contrast was measured as chromatic (dS) and achromatic contrast (dL) between bird mantle and background (i.e. a lower value indicates a closer match to the background) and modelled through human (trichromatic), ferret (dichromatic) and Blue Tit (tetrachromatic) vision models. Only vision model ('vismod') was left in the final model after model simplification.

Model term	SS	MS	d.f.	F	P
CHROMATIC dS					
vismod	23070.00	11535.00	2	2408.70	<0.001
ACHROMATIC dL					
vismod	100.92	50.46	2	6.31	0.001

Vismod, vision model.

Table 3. Eurasian Treecreeper camouflage against five common boreal tree species. Linear mixed effects model (LMER) analyses of the chromatic contrast with respect to tree species and their relation to predator vision, with the ANOVA table with Satterthwaite's method reported here. Contrast was measured as chromatic (dS) and achromatic contrast (dL) between bird mantle and background (i.e. a lower value indicates a closer match to the background) and modelled through human (trichromatic), ferret (dichromatic) and Blue Tit (tetrachromatic) vision models.

Model term	SS	MS	d.f.	F	P
CHROMATIC dS					
tree	929.20	232.30	4	69.74	<0.001
vision	11701.20	5850.60	2	1757.70	<0.001
tree*vision	490.90	61.40	8	18.42	<0.001
ACHROMATIC dL					
tree	15516.40	3879.00	4	437.93	<0.001
vision	83.80	41.90	2	4.73	0.008

Vismod, vision model; tree, tree species comparison.

forests, we found a significant interaction between vision models and tree species (Table 3, Fig. 3c, Table S7, Fig. S5). The colour match was significantly closer to conifers (pine and spruce) but lower for deciduous trees (alder, aspen and birch). Also, chromatic background matching was significantly closer for trichromatic human and dichromatic ferret vision models than for the tetrachromatic avian vision model (Fig. 3c). In terms of achromatic contrast, only the main effects of tree species and vision model were significant (Fig. 4c, Table 3). Again, the conifers provided

significantly the lowest animal-to-background contrast values (i.e. facilitating background matching), whereas in terms of vision models, achromatic values were higher for the ferret vision model than for the human or avian vision model (Table S8, Fig. S6).

DISCUSSION

Our results support the long-standing conjecture of the camouflage hypothesis in the Eurasian Treecreeper. The colour match of plumage to the respective backgrounds, however, seems most effective for mammalian visual perception, as vision modelling suggests the chromatic match to be less effective for avian vision.

When tested separately against Treecreeper nest trees (i.e. spruces), bird plumage features (wing, wing stripe, tail and back) were differently associated with birds' chromatic contrast to the background. We found that Treecreeper wing and back (or mantle) matched background coloration more effectively, whereas wing stripe and tail were more conspicuous. This suggests that the colour match of the back and wing parts are the most important for achieving an effective camouflage in boreal forests, which is a typical habitat of the species (Suorsa *et al.* 2004). Moreover, Treecreepers feed predominantly against tree trunks (Jäntti *et al.* 2001, Bursell & Dyck 2003, Adamík & Korňan 2004), where matching the mantle and wing coloration to the immediate surroundings is important. In comparison, the more conspicuous wing stripe may be used for some other function such as intraspecific communication (Gluckman & Cardoso 2010) or may perhaps be a disruptive or distractive marking against predator attacks (Cott 1940). The tail, on the other hand, could serve as a target for the predators and raptors. Thus, the different plumage regions of the Treecreeper may serve different adaptive functions.

Plausibly, adopting a generalist camouflage would provide flexibility in Treecreeper habitat use (Michalis *et al.* 2017, Hughes *et al.* 2019, Nokelainen *et al.* 2020, Briolat *et al.* 2021). Here, Treecreeper contrast to the background was similar across habitat scales (i.e. nest-site, territory, habitat) within the study areas, which could suggest that Treecreeper camouflage supports their habitat use within their own niche in boreal forests rich in coniferous trees (Kuitunen & Helle 1988, Jäntti *et al.* 2007). It has been reported (Huhta

et al. 2003) that the habitat classes of Treecreeper nest-sites in Finland comprise spruce forests (34.8%), mixed forests (20.5%), pine forests (14.5%), sapling stands (3.3%), deciduous forests (2.1%), spruce mires (1.3%) and pine mires (0.7%) in addition to unforested habitat types (22.8%). Our study reported that both chromatic and achromatic match (i.e. bird-to-background similarity) were highest on spruce, followed by pine, aspen, alder and birch. Notably, Treecreepers do not occupy the birch belt in northernmost Europe, which could potentially be due to a lack of efficient camouflage and/or suitable wintering conditions. Nevertheless, in our study Treecreepers seem best matched to conifers, their preferred trees in Fennoscandia.

Treecreepers appear relatively well matched to several tree species and, to a certain degree, generalizing might be beneficial, as their habitat is mixed-forest, especially towards the south of their range in Europe. Interestingly, a closely related southern relative of the Eurasian Treecreeper, the Short-toed Treecreeper *Certhia brachydactyla*, inhabits deciduous forest, a niche occupied by Eurasian Treecreeper in Britain and Ireland, where the species is associated more with deciduous woodlands than with conifers. We could thus predict that the camouflage in more southern Treecreeper populations may thus rely on different appearance to better match the deciduous forest environment (e.g. Bursell & Dyck 2003). Another study investigating habitat use of Eurasian Treecreepers in Central Europe has reported that habitat structure was markedly different than in northern boreal forests (Adamík & Korňan 2004). They reported tree dominance structure vs. Treecreeper foraging habitat preference (dominance – preference expressed as %) as beech (44.8–21.6), fir (20.2–36.8), snags (14.7–16.0), spruce (4.8–12.2) and sycamore (4.3–13.4). Thus, it appears that Treecreepers are often associated with conifers, although mixed woodlands and deciduous forests are a not uncommon niche in their range. Additionally, environmental conditions such as temperature and humidity in lower latitudes vs. higher latitudes may select for different overall appearance due to thermoregulation (Delhey *et al.* 2019), which may shape the phenotypic appearance of Treecreepers worldwide depending on local climatic conditions. More generally, habitat differences and local environmental conditions can influence intraspecific signalling in birds and

facilitate evolution of plumage coloration and speciation over time in a broader geographical context (Price 2006, 2010). More research is needed to understand the drivers of Treecreeper appearance.

We speculate that if top-down selection by visual predators has been shaping Treecreeper appearance, it may have evolved more against nest predators rather than to protect adults per se (i.e. predators might detect adults and so locate the nest tree, whereby adult plumage could be exposed at the nest). According to vision modelling results, Treecreeper camouflage is more effective against di/trichromatic mammalian predators and may be less so against avian tetrachromatic vision. Kuitunen and Aleknonis (1992) found that 30–40% of Treecreeper nesting attempts may be unsuccessful and considered that the most likely nest predators of Treecreepers are Red Squirrels *Sciurus vulgaris* and small mustelids such as the Least Weasel *Mustela nivalis* and Stoat *Mustela erminea*, but also birds such the Great Spotted Woodpecker *Dendrocopos major*. It is plausible that the camouflage would be effective against other dichromatic predators, which lack the chromatic sensitivity in the LW range (e.g. Van Hooser & Nelson 2006). Against dichromatic vision, it would be important for the Treecreepers to have an effective background match in short and medium wavelengths to avoid giving any nest location cues. In contrast, the ultraviolet and long-wavelength region seem to make the white patches conspicuous to the avian vision system (Vorobyev *et al.* 1998, Kelber 2019), which renders the camouflage less effective against avian predators, but may serve a purpose in intra-specific signalling, as proposed in owls (Penteriani *et al.* 2010). Nevertheless, proving the effectiveness of camouflage to predators and how different parts of bird plumage patches may function in this respect would require further behavioural assays beyond the current study.

In conclusion, our results suggest that the Eurasian Treecreeper is camouflaged particularly against mammalian predators, which can be important nest predators of the species. The effectiveness of camouflage against avian predators or conspecifics is less certain, as is the efficacy of Treecreeper camouflage across the species' range. To our knowledge this is the first computational quantification of Eurasian Treecreeper camouflage.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

Ossi Nokelainen: Conceptualization (equal); Formal analysis (equal); Resources (equal); Supervision (equal); Writing – original draft (lead). **Heikki Helle:** Methodology (equal); Resources (equal); Writing – review & editing (equal). **Juho Hartikka:** Investigation (equal); Methodology (equal); Writing – review & editing (equal). **Juho Jolkkonen:** Investigation (equal); Methodology (equal); Writing – review & editing (equal). **Janne K. Valkonen:** Conceptualization (equal); Formal analysis (equal); Supervision (equal); Writing – review & editing (equal).

ETHICAL NOTE

The birds were ringed from their nest-sites by permission from the Finnish Ringing Centre to O.N., J.H., J.J. & H.H. (Finnish Museum of Natural History).

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 The camouflage of the Eurasian Treecreeper: chromatic contrast.

Table S2 The camouflage of the Eurasian Treecreeper: achromatic contrast.

Table S3 Treecreeper camouflage with respect to bird topography: chromatic contrast.

Table S4 Treecreeper camouflage with respect to bird topography: achromatic contrast.

Table S5 Linear mixed effects model (LMER) analyses of the animal-to-background contrast with respect to home range, territory, habitat and their relationship to predator vision: chromatic contrast.

Table S6 Linear mixed effects model (LMER) analyses of the animal-to-background contrast with respect to home range, territory, habitat and their

relationship to predator vision: achromatic contrast.

Table S7 Treecreeper camouflage against five common Boreal tree species: chromatic contrast.

Table S8 Treecreeper camouflage against five common Boreal tree species: chromatic contrast.

Figure S1 Chromatic contrast (dS) and bird topography with respect to camouflage of the Eurasian treecreeper: post-hoc comparisons.

Figure S2 Achromatic contrast (dL) and bird topography with respect to camouflage of the Eurasian treecreeper: post-hoc comparisons.

Figure S3 Treecreeper chromatic camouflage in relation to home range, territory and habitat: post-hoc comparisons.

Figure S4 Treecreeper achromatic camouflage in relation to home range, territory and habitat: post-hoc comparisons.

Figure S5 Treecreeper camouflage against different tree species: chromatic contrast post-hoc comparisons.

Figure S6 Treecreeper camouflage against different tree species: chromatic contrast post-hoc comparisons.