

Environmental correlates of spatio-temporal patterns of colour variation in a bird of prey: The common buzzard (*Buteo buteo*)

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High colour variability in animals has been associated with adaptability to environmental change. Establishing how such variability is distributed in time and space, and identifying environmental correlates, can help understand the processes driving it. Common Buzzards *Buteo buteo* (herein buzzards) show extensive variation in plumage colour, ranging from dark brown to largely white, yet the factors maintaining or underlying this variation remain poorly understood. Previous studies showed that intermediate-coloured buzzards have higher fitness and have increased in abundance over time in a Dutch population. We compiled a large citizen science dataset to map buzzard colour variation across Europe, assess temporal changes and test for potential environmental drivers. Buzzard colour variation is geographically structured: light-coloured buzzards are mainly found in North-Central Europe, intermediates in South-East Europe and the British Isles, and darker buzzards in Iberia and Brittany. Lighter coloured buzzards are found in areas with lower temperatures and UVB radiation, and few volcanic soils (andosols), while darker birds are more common in forested areas. Between 2000 and 2022, the proportion of dark- and light-coloured buzzards declined, while intermediates increased, reducing colour variation over time. The temporal decrease in light-coloured buzzards is stronger in regions with a strong increase in temperature. Conversely, the decrease of dark morphs and the increase in intermediates are steeper where forest cover declined. Our results suggest that photoprotection and camouflage can partly explain spatial variation in buzzard colour, and that sulphur-rich soils may foster increased pigmentation. However, these effects only explain small amounts of colour variation ($R^2 < 0.01$), suggesting that historical contingency (phylogeography) may be more important than local adaptation. Temporal increases in intermediate-coloured buzzards at the expense of the extremes match the trend reported for a Dutch population, indicating widespread selection against colour extremes. Future studies should identify the mechanisms responsible for colour-related variation in fitness.

Keywords: Accipitridae, *Buteo*, colour, ecogeographical rules, melanin, polymorphism.

INTRODUCTION

Colour fulfils many functions in animals: camouflage, signalling, thermoregulation, protection against harmful radiation (e.g. ultraviolet (UV)) and

other biotic and abiotic factors (e.g. parasites, abrasion) (Cuthill *et al.* 2017). While most colour variation is found between species, substantial variation can also be observed within species (Dale 2006). Intraspecific colour variation can take different forms, from discrete morphs to continuous variation (Dale 2006), and can fluctuate in time and space (Karell *et al.* 2011, McLean & Stuart-Fox 2014,

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Delhey *et al.* 2020). High intraspecific colour variability has been linked to adaptability (Forsman *et al.* 2008), and comparative analyses suggest that highly colour-variable populations and species occupy broader environmental niches, have larger ranges and are less likely to be threatened (Delhey *et al.* 2013, Ducatez *et al.* 2017).

Given that populations with high variability should cope better with environmental variation, it is important to identify the factors that promote and maintain variation in colour (Sanderson *et al.* 2023). Most species show some degree of intraspecific variation in colour, but measuring this variation can be difficult in practice. Colour variation can be more easily quantified in polymorphic species, providing useful model systems to study the potential drivers of colour variability (Karell *et al.* 2011, Burri *et al.* 2016, Leighton *et al.* 2016, Amar *et al.* 2019). Highly variable or polymorphic species are particularly common among birds of prey (Galeotti & Rubolini 2004, Roulin 2004a), where colour variation is mainly caused by differential deposition of melanin, the most common pigment type in birds and other vertebrates (D'Alba & Shawkey 2019). Studies on birds of prey have provided key insights into the mechanisms behind colour polymorphism (reviewed in Robinson *et al.* 2024).

Robinson *et al.*'s (2024) review suggests that the best-supported hypotheses to explain the occurrence of colour polymorphism in birds of prey relate to disruptive selection along spatial gradients in abiotic (temperature, precipitation) or biotic (vegetation) variables. These associations between environmental variables and colour are best described by two ecogeographical rules that also apply more broadly across animals. The first one is Gloger's rule, which in its simple interpretation predicts that animals should be darker in more humid and warmer environments (Rensch 1929). In general, the effects of humidity are better supported than those of temperature (Delhey 2019, Delhey *et al.* 2019). Several species of polymorphic raptors (and other taxa) seem to follow this rule (Galeotti *et al.* 2009, Amar *et al.* 2014, Romano *et al.* 2019), but exceptions exist (Amar *et al.* 2019, Koskenpato *et al.* 2023). The selective mechanisms are not fully established (Delhey 2019), but darker animals may be better camouflaged in more humid environments, because they are typically more densely vegetated, and thus have darker backgrounds. In addition,

darker, melanized feathers may be more impervious to bacterial degradation, which is more prevalent in humid environments (Burt Jr & Ichida 2004). We note that while some authors suggest keeping the effects of vegetation structure separate from Gloger's rule (Marcondes *et al.* 2021), others suggest that vegetation is the main driver behind it (Zink & Remsen Jr 1986).

The other ecogeographical rule of colour, the thermal melanism hypothesis, predicts that animals are darker in colder environments (Clusella-Trullas *et al.* 2007). Darker individuals should be favoured in colder environments because they absorb more solar radiation and hence warm up faster. Conversely, lighter animals should have an advantage in warmer environments (Clusella-Trullas *et al.* 2007). This rule seems to apply broadly to bird colour variation, both when considering between- (Galván *et al.* 2018b, Delhey *et al.* 2019, Marcondes *et al.* 2021) and within-species variation (Rising *et al.* 2009, Marcondes *et al.* 2020), including in birds of prey (Amar *et al.* 2014, Romano *et al.* 2019). Warmer regions are usually closer to the Equator, and melanin deposition could also protect from exposure to UV radiation (Jablonski & Chaplin 2010, Nicolai *et al.* 2020). If melanin deposition in plumage helps to reduce UV damage to the underlying skin, we expect darker, more melanized birds in regions with higher UV levels, as has been shown in Golden Eagle *Aquila chrysaetos* nestlings (Galván *et al.* 2018a).

In addition, recent studies identified other environmental correlates of raptor colour associated with melanin synthesis, specifically with pheomelanin, which colours plumage rufous-brown (as opposed to eumelanin which is mainly black). Pheomelanin synthesis requires high levels of glutathione, an important antioxidant. Galván and Alonso-Alvarez (2011) hypothesized that pheomelanin synthesis would be curtailed in regions where high antioxidant levels are required. They found that spatial variation in natural radioactivity (gamma radiation), which causes oxidative stress, was negatively associated with pheomelanin deposition in Barn Owls *Tyto alba* (Galván & Alonso-Alvarez 2011) and Golden Eagle nestlings (Galván *et al.* 2018a). In Barn Owls, darker pheomelanin-rich plumage is also more prevalent in regions with volcanic soil (Romano *et al.* 2023). Pheomelanin contains sulfhydryl groups, and therefore the high sulphur abundance in volcanic

soil could foster the deposition of phaeomelanin in the plumage. Finally, associations between environmental variation and plumage colour may be a result of selection on other traits, such as behaviour, immunocompetence, stress responses and hormone levels, that are pleiotropically linked to colour (Ducrest *et al.* 2008).

Here, we study geographical variation in colour in the nominate race of the Common Buzzard *Buteo buteo buteo* (herein buzzards). This widespread, medium-sized bird of prey is an excellent model to study how colour variation is generated and maintained, as it is mostly sedentary (although some populations are partially migratory; Cramp & Simmons 1977), and is one of the most colour-variable European bird species (Cramp & Simmons 1977). Colour in buzzards varies from almost entirely dark brown to largely white individuals (Fig. 1; Cramp & Simmons 1977, Kappers *et al.* 2017). This variation can be scored into different categories directly in the field, which has allowed detailed studies on the function of colour in populations in Germany and in the Netherlands (Krüger *et al.* 2001,

Krüger & Lindström 2001, Krüger 2002, Chakarov *et al.* 2008, Boerner & Krüger 2009, Kappers *et al.* 2018, 2020).

These studies revealed that colour variation is linked to fitness, with the most abundant intermediate-coloured buzzards having higher fitness (lifetime reproductive success and survival) than the rarer dark or light extremes (Krüger *et al.* 2001, Krüger 2002, Kappers *et al.* 2020). Colour is highly heritable ($h^2 = 0.82$) and likely to be a quantitative polygenic trait (Kappers *et al.* 2018), raising the question of how colour variation is maintained over time. This is relevant because at least in one population in the Netherlands the proportion of intermediate birds has increased over the last few decades at the expense of the extremes (Kappers *et al.* 2020). Krüger and Lindström (2001) hypothesized that phenotypic variation is maintained owing to heterozygote advantage, but this is unlikely given the polygenic nature of the trait (Kappers *et al.* 2018). Instead, colour variation may be maintained by local adaptation (Kappers *et al.* 2018), which can be assessed by studying geographical variation in colour.

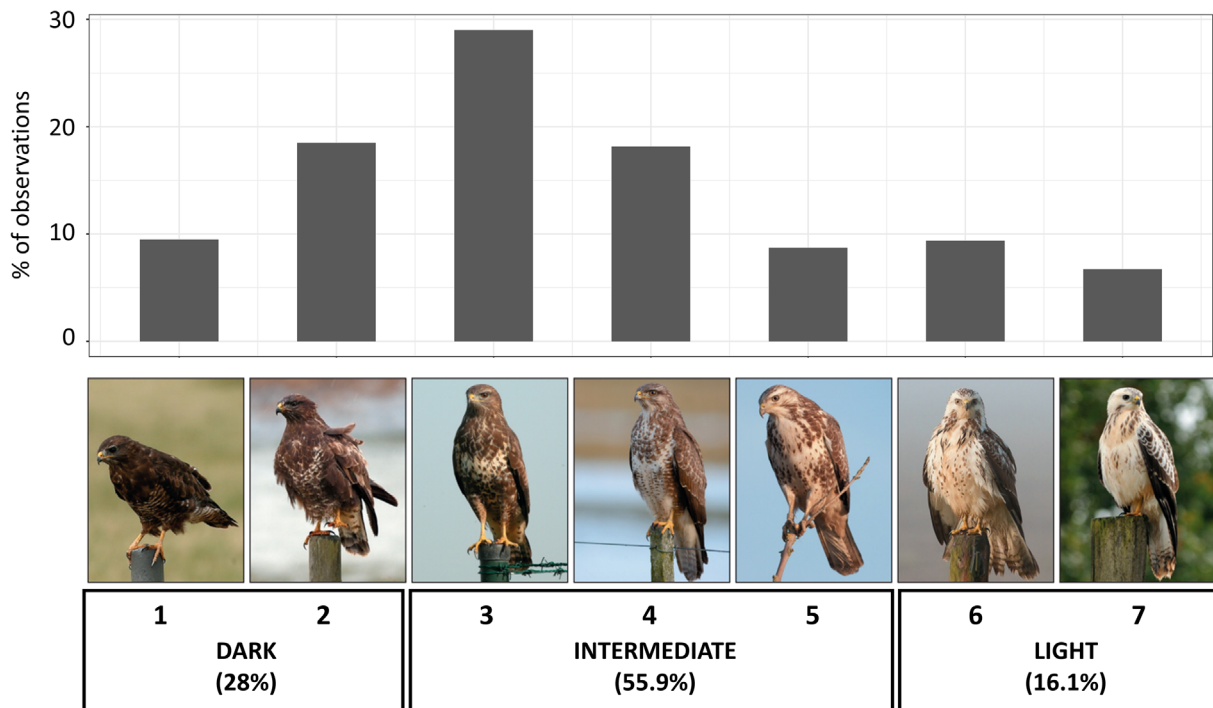


Figure 1. Colour variation in Common Buzzards across Europe. Histogram based on 99 343 observations of buzzard colour obtained from citizen science databases (see [Methods](#)). Pictures show a representative example of each colour category used to score colour variation. The continuous variation can be further subsumed into three different categories: dark (1–2), intermediate (3–5) and light (6–7), following (Kappers *et al.* 2017, 2018). Images reproduced with permission from Ardea/NOU.

Surprisingly little is known about geographical variation in buzzard colour. It has been suggested that extensive within-population variation may obfuscate spatial patterns (Cramp & Simmons 1977). Available evidence suggests that (1) buzzards are lighter and more colour-variable in a Dutch than in a Swiss population (van Bergen & Riem Vis 2015), (2) within Germany, lighter birds are less common in the south (Krüger *et al.* 2001), and (3) in Sweden, light-coloured buzzards are more common in the southern tip of the country (Ulfstrand 1977). Here we collate a large citizen science dataset to quantify geographical variation in buzzard coloration across Europe.

Our study has three aims: (1) to describe spatial variation in Common Buzzard colour across Europe and (2) to test whether this variation follows spatial environmental gradients. Specifically, Gloger's rule predicts lighter buzzards in dry and cold regions with open vegetation; conversely, the thermal melanism hypothesis predicts lighter birds in warmer regions. Alternatively, or in addition, we expect lighter buzzards in regions with low UV radiation, high gamma radiation and low abundance of volcanic soil. Our third aim (3) is to evaluate whether buzzard colour has changed over time across Europe, consistent with previously documented temporal patterns (Kappers *et al.* 2020), and whether temporal changes in colour can be linked to temporal changes in environmental variables. Specifically, we predict an increase in light plumage over time as a result of global warming, but an increase in dark plumage in places where precipitation (Delhey *et al.* 2020), forest cover and UV radiation have increased. Temporal changes in coloration have been documented in other raptors (Galeotti *et al.* 2009, Karrell *et al.* 2011, Koskenpato *et al.* 2023), but they do not always align with expectations. We address these aims analysing colour variation both as a continuous variable and in three categories (dark, intermediate, light) to allow comparison with previous work and document changes over time.

METHODS

Data compilation

We compiled citizen science data on buzzard colour variation from six different sources (NL, BE, Observation, IT, Buteo Morph, iNaturalist). Three sources of data (NL, BE and Observation data) are part of

the [Observation.org](https://www.observa.org) platform, a global biodiversity platform for citizen science and monitoring (websites: www.Waarneming.nl, www.Waarnemingen.be and www.Observation.org). One data source (IT) corresponds mainly to Italian observations hosted at www.Ornitho.it, a common platform for Italian ornithologists and birdwatchers that is used for citizen science projects and for the creation of distribution atlases. Observations entered by users on the [Observation.org](https://www.Observation.org) and [Ornitho.it](https://www.Ornitho.it) platforms are vetted by taxonomic experts. From 2015 onwards, observers obtained information about the seven colour categories depicted in Figure 1. For NL, BE and Observation, observers were offered a pop-up option to select one of the seven pictures (Fig. 1), which would be recorded alongside the observation with date and location. For IT, observers were given a digital flyer with the seven pictures (Fig. 1) and instructions in the news section of the website. Observers could then add colour information in the remarks field with the 1–7 code (Fig. 1). For all four sources, data on observations before 2015 were subsequently derived from user notes or from pictures. Buteo Morph data were collected using a custom-made website launched in 2015 and functional until 2019 (hosted by the Max Planck Society). The user could choose among the seven pictures (Fig. 1) and add information on date and location. Observations were vetted by BK.

Data from iNaturalist were downloaded for 2008–2022 using the function *get_inat_obs* in the package 'rinat' (Barve & Hart 2022). We only used research-grade observations with location data. The 'rinat'-specific limit was 10 000 observations per year (only reached in 2022). The same observer (KD) used the scale in Fig. 1 to score the colour categories of 22 057 images of 33 832 downloaded observations. The rest could not be scored owing to: (1) poor-quality photographs (e.g. bird too small in frame, too dark/light exposure, blurred image, obscured parts of the body); (2) images depicted only feathers or degraded carcasses; (3) multimedia link corresponded to an audio instead of an image file; or (4) broken or missing image link. When more than one buzzard was depicted in the image, we scored the left-most scorable individual. As long as the quality of the image allowed it, we scored both perched and flying buzzards.

We summarized the colour variation described above into three categories (Fig. 1) based on (Kappers *et al.* 2017, 2018): dark (scores 1–2),

intermediate (scores 3–5) and light (scores 6–7). This enabled comparison with previous studies that analysed colour variation using these categories (Krüger *et al.* 2001, Krüger & Lindström 2001, Krüger 2002, Kappers *et al.* 2020). Furthermore, only this coding system allows us to test whether the reported temporal increase in the intermediate colour category at the expense of the extremes (light and dark; Kappers *et al.* 2020) constitutes a general pattern across Europe. Previously, Kappers *et al.* (2017) showed that the scores correlated well with quantitative image analyses ($r = 0.70$) and that inter-observer repeatability was high ($r > 0.84$). In sum, we used four colour variables: a continuous variable (colour score, 1–7) and three binary variables (0,1) indicating the probability that an individual belongs to the dark (P_{dark}), intermediate ($P_{\text{intermediate}}$) and light (P_{light}) categories.

The combined dataset contained 99 343 observations collected year-round and covering nearly the entire European range of *Buteo buteo buteo*. The contribution of the different datasets was uneven (NL: $N = 38\,085$, 1967–2020; BE: $N = 21\,810$, 1974–2020; IT: $N = 4571$, 2010–2020; Observation: $N = 2098$, 1983–2020; Buteo Morph: $N = 10\,722$, 2015–2019; iNaturalist: $N = 22\,057$, 2008–2022). NL, BE, IT and Buteo Morph data largely (but not exclusively) comprised observations from the Netherlands, Belgium, Italy and Germany, respectively. Thus, many more observations are available for some parts of the range (such as the Netherlands and Belgium) than for others (Fig. S1A). Some observations were within the range of subspecies *Buteo buteo arrigonii* (Corsica and Sardinia), and a few observations in the east (e.g. Baltic countries) may correspond to *Buteo buteo vulpinus*. These few observations are unlikely to bias patterns of colour variation. We excluded the few observations from before the year 2000 (0.25%, of which 93% were from the Netherlands and Belgium) to avoid problems with temporal analyses (see below), resulting in a final dataset of 99 088 observations from 2000 to 2022, which is the temporal range considered in this study.

Spatial analyses

The large sample size precluded running spatial models on the entire dataset for the binomial colour variables (P_{dark} , $P_{\text{intermediate}}$, P_{light}) owing to computational limits. Moreover, analysing all

observations may bias our sample towards the most sampled regions (Fig. S1A). To alleviate these issues, we used spatial thinning (Aiello-Lammens *et al.* 2015), a method where subsets of observations are randomly selected while ensuring that observations are separated by a user-specified distance. We used the *thin* function in the ‘spThin’ package (Aiello-Lammens *et al.* 2015) to generate 25 subsets of the data, with observations separated by at least 10 km. We used this threshold distance to obtain sample sizes sufficiently large to detect biologically relevant effects ($N = 6485$), while allowing reasonable computational times (~4 h per generalized linear spatial model).

For each buzzard observation we extracted the mean value for the environmental variables from a buffer area of 5-km radius (using the function *st_buffer* from the R package ‘sf’ (Pebesma 2018)). We extracted two climatic variables associated with ecogeographical rules of colour: annual mean temperature (Bioclim: Bio 1, °C) and annual precipitation (Bioclim: Bio 12, mm) from Karger *et al.* (2017) using the function *exact_extract* in the R package ‘exactextract’ (Baston 2023). Similarly, we computed the average amount of tree cover (data from Defries *et al.* 2000, based on NOAA’s Advanced Very High Resolution Radiometer (AVHRR)), the proportion of andosol (i.e. volcanic) soil (using the R package ‘geodata’, interfacing with a soil database at <https://soilgrids.org>), the intensity of UVB radiation (data from Beckmann *et al.* 2014) and the intensity of gamma radiation (data from Tollefsen *et al.* 2016) (see Fig. S2 for the spatial distribution of these predictors). As a consequence of limits in the spatial extent of some of these environmental data, 1043 observations had missing environmental data, reducing the sample for the spatial analyses to $N = 98\,045$.

For visual purposes, we also summarized the dataset by overlaying a hexagonal grid (preferred for plotting; Birch *et al.* 2007) over the study region and computing representative colour variables for each cell. We chose a hexagonal grid with a 150-km distance between hexagon centroids to balance sample size within each cell (important for temporal analyses, see below) with number of available cells. We used the R package ‘sf’ (function *st_make_grid*; Pebesma 2018) to create the grid and computed four different summary colour variables per cell: mean colour score (average within the cell), and the proportion of dark, intermediate and light individuals.

To analyse spatial colour variation as a continuous variable (colour score, 1–7), we used the function *splm* in the package ‘*smodel*’ (Dumelle *et al.* 2023) with an exponential anisotropic spatial covariance structure and Gaussian error distribution. To analyse spatial variation in P_{dark} , $P_{\text{intermediate}}$ and P_{light} , we used the function *spglm* from the same package, setting family = binomial and using an exponential anisotropic spatial covariance structure. Models included the environmental variables annual mean temperature, annual precipitation, forest cover, UVB and gamma radiation, and the proportion of andosols as predictors. All variables were scaled and centred to make effects comparable. Predictors were not so strongly correlated to cause collinearity problems, except for annual mean temperature and UVB radiation ($r = 0.7$), so we fitted these in separate models (each including all other predictors, henceforth temperature and UV models). We compared alternative models using the corrected Akaike information criterion (AICc). We also included year of observation as a predictor to account for possible temporal trends in colour variation (Kappers *et al.* 2020). Note that these spatial models do not account for potential temporal autocorrelation effects. Thus, we specifically explored temporal trends in a set of separate analyses (see next section; the results of the models described here led to similar conclusions). Models also included the random factors observer ID (because observers may record the same individuals repeatedly or score higher or lower than others), month (to account for seasonal movements; Ulfstrand 1977, Kjellén 1999) and dataset ID (to account for potential differences between datasets).

We ran each model on the 25 subsets of thinned data and averaged the results using Rubin’s rules (Nakagawa & De Villemereuil 2019) as implemented by the function *pool* from the R package ‘*mice*’ (van Buuren & Groothuis-Oudshoorn 2011). We confirmed that using 25 subsets of the data was enough by computing ‘relative efficiency’ (using formula 12 in Nakagawa & De Villemereuil 2019) for each parameter. In all cases efficiency exceeded the recommended threshold of 0.99. For the continuous variable ‘colour score’ we also ran the analyses using the entire dataset for comparison. The spatial thinning procedure, together with the explicit modelling of spatial autocorrelation in the statistical analyses, successfully accounted for biases associated with

the extreme spatial sample size imbalance in the original dataset. We found no spatial signature in the model residuals.

Temporal analyses

We used the approach described in Romano *et al.* (2024) to quantify temporal changes in colour for different subregions (each hexagonal cell in the grid depicted in Fig. 2) and combined these temporal trends using meta-analyses. Thus, for each colour variable, we obtained an overall estimate of temporal changes over the 2000–2022 period. Before 2015, all observations were entered retrospectively based on photographs or field notes for all datasets except iNaturalist. Because these earlier records could be biased in favour of rare or extreme colour categories, they could potentially bias temporal trends. Thus, we repeated the temporal analyses including only observations within the 2015–2022 range.

We calculated temporal effects on colour variation separately for each hexagonal cell (Fig. 2) and plotted them in Figure S3. To obtain meaningful estimates, we only tested the effect of year on colour in a grid cell with a minimum of 50 observations spread across a minimum of 5 years ($N = 132$ grid cells; see Fig. S1B for the spatial variation in temporal range). For each cell we fitted models with one of the colour variables as the dependent variable, and with year (centred on the cell-specific median) as a fixed-effect covariate, while accounting for temporal autocorrelation using the function *glmmTMB* from the homonymous R package. We also included the random factors dataset ID, observer ID and month in the models.

Models analysing variation in colour score had Gaussian error distribution, while models analysing P_{dark} , $P_{\text{intermediate}}$ and P_{light} were binomial. We started with the most complex model, but if this model failed to converge, we fitted alternative or simplified models in a step-wise fashion (see Supporting Information). Even after simplification, models in some cells failed to converge (see Results) and these cells were excluded from further analyses, together with cells where there was no variation in the focal colour variable (only P_{light}).

For each successful model we extracted the effect of year – thus, the temporal slope and its standard error. These values were then summarized using meta-analysis with the R package

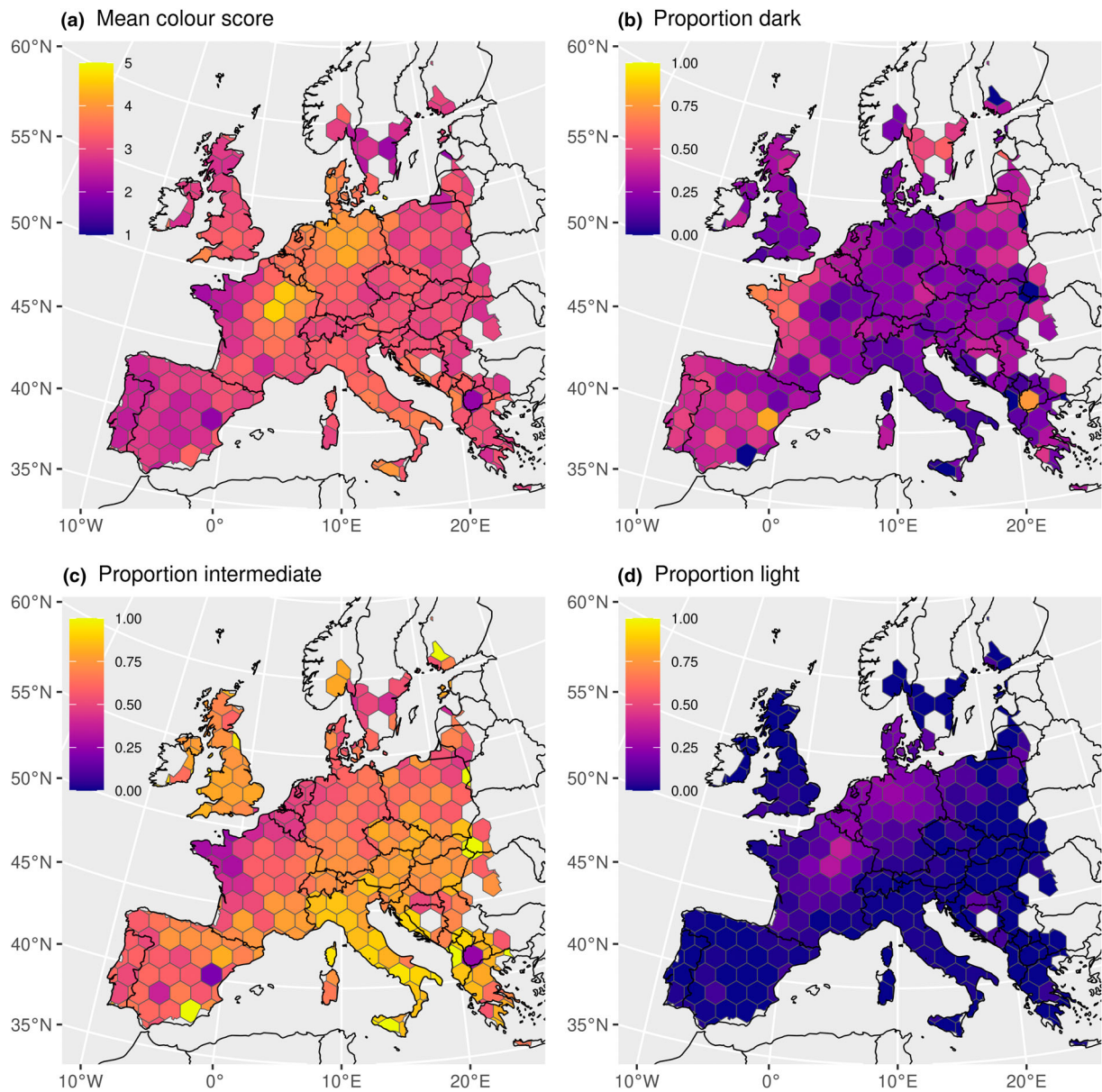


Figure 2. Geographical variation in Common Buzzard colour across Europe. Panels depict geographical variation on a 150-km hexagonal grid in mean colour (a), and in the proportion of dark- (b, colour scores 1–2), intermediate- (c, colour scores 3–5) and light-coloured (d, colour scores 6–7) buzzards.

‘metaphor’ (Viechtbauer 2010, 2015). For each colour variable (colour score, P_{dark} , $P_{\text{intermediate}}$ and P_{light}) we obtained an overall effect of year (the meta-analytical mean) using a random effect meta-analysis (function *rma*), which weighs each effect by its variance (se_{slope}^2). We checked for residual spatial autocorrelation in the temporal effects using Moran’s I-test implemented in the R package ‘ape’ (Paradis & Schliep 2019). These

tests indicated significant spatial autocorrelation only in the temporal meta-analyses for colour score, but not for P_{dark} , $P_{\text{intermediate}}$ or P_{light} . The meta-analysis on temporal effects for P_{light} (the least frequent colour category) showed large variation in slope errors and hence results need to be interpreted with caution.

We used another set of meta-analyses with moderators (environmental moderator meta-analyses)

to test whether temporal changes in colour were associated with temporal changes in annual mean temperature, annual precipitation, forest cover and UV radiation (changes in soil type and gamma radiation are unlikely during the period considered in our study), following the approach in Romano *et al.* (2024). For each hexagonal cell we obtained mean values of each environmental variable for each year covering the period for which we had observations in that cell, based on data generated using Copernicus Climate Change Service information 2025 (Copernicus Climate Change Service, Climate Data Store 2019, Copernicus Climate Change Service (C3S), Climate Data Store (CDS) 2024). To estimate the temporal change in temperature, precipitation, forest cover or UV for each cell, we ran a simple linear model with year as the sole predictor. These temporal slopes were then used as scaled predictors (moderators) in the meta-analyses (see Fig. S4 for tsatial distribution of temporal effects in environmental variables). We also tested whether the strength of the temporal changes correlated with spatial variation in colour (mean colour score, and the proportion of dark, intermediate and light buzzards in each cell, Fig. 2), by including them as moderators as well. Finally, we assessed whether the conclusions were affected by: (1) the extent (year range) or (2) the recency of the temporal range (median year) and (3) whether model structures accounted for temporal autocorrelation (yes/no). To this end, we included these factors as moderators in another set of meta-analyses (technical moderator meta-analyses).

RESULTS

General patterns of spatial variation in plumage colour

Buzzards were lighter in North-Central Europe (Netherlands, Belgium, northern Germany, north-east France, Denmark), and darker in Brittany (France) and the Iberian Peninsula (Spain and Portugal; Fig. 2a). The proportions of the dark (overall 28% of observations) and light (16.1%) category revealed similar respective patterns (Fig. 2b,d), whereas the proportion of the most abundant intermediate-coloured birds (55.9%) was highest in South-East Europe (Italy, Balkans, Greece) and on the British Isles (Fig. 2c).

Environmental correlates of spatial colour variation

Models analysing colour as a continuous variable (colour score) using thinned data revealed a significant effect of UVB radiation (Fig. 3; UV model: $R^2 = 0.005$, $AICc = 22\,708$). As predicted, buzzards were darker in areas with higher UV radiation. None of the other environmental variables, including temperature, had a significant effect on colour (Fig. 3; temperature model: $R^2 = 0.0027$, $AICc = 22\,717$). Analysis of the entire dataset including all observations led to similar effects, but the negative effects of temperature and andosols were statistically significant (temperature model: $R^2 = 0.0027$, $AICc = 369\,279$), while only the effect of UVB remained significant in the UV model ($R^2 = 0.0027$, $AICc = 369\,181$). Comparing $AICc$ values suggests that the UV model fitted the data better than the temperature model (thinned datasets: $\Delta AICc = 9$, entire dataset: $\Delta AICc = 98$). In both models, the predictors only explained small amounts of the observed colour variation (low R^2 values).

Models analysing spatial variation in P_{dark} revealed a significant positive effect of forest cover in the UV model (Fig. 3; $R^2 = 0.0028$, $AICc = 18\,977$), but this effect was nonsignificant in the temperature model ($R^2 = 0.003$, $AICc = 18\,974$). $P_{\text{intermediate}}$ showed a positive correlation with temperature (Fig. 3, temperature model; $R^2 = 0.0016$, $AICc = 19\,930$). None of the other variables had a significant effect (UV model: $R^2 = 0.0018$, $AICc = 19\,923$). UVB radiation had a significant negative effect on the probability that a buzzard belonged to the light category (UV model: $R^2 = 0.0045$, $AICc = 15\,484$), but no other environmental variable had a significant effect (temperature model: $R^2 = 0.0004$; $AICc = 15\,509$, Fig. 3).

Temporal variation in plumage colour

Meta-analyses summarizing temporal trends across all grid cells with sufficient data (Fig. 4) indicate that colour score has increased over time, suggesting that buzzards have become lighter over the 2000–2022 period. However, this effect was mainly driven by an increase in the proportion of intermediate buzzards, because the proportion of both dark and light buzzards decreased over time

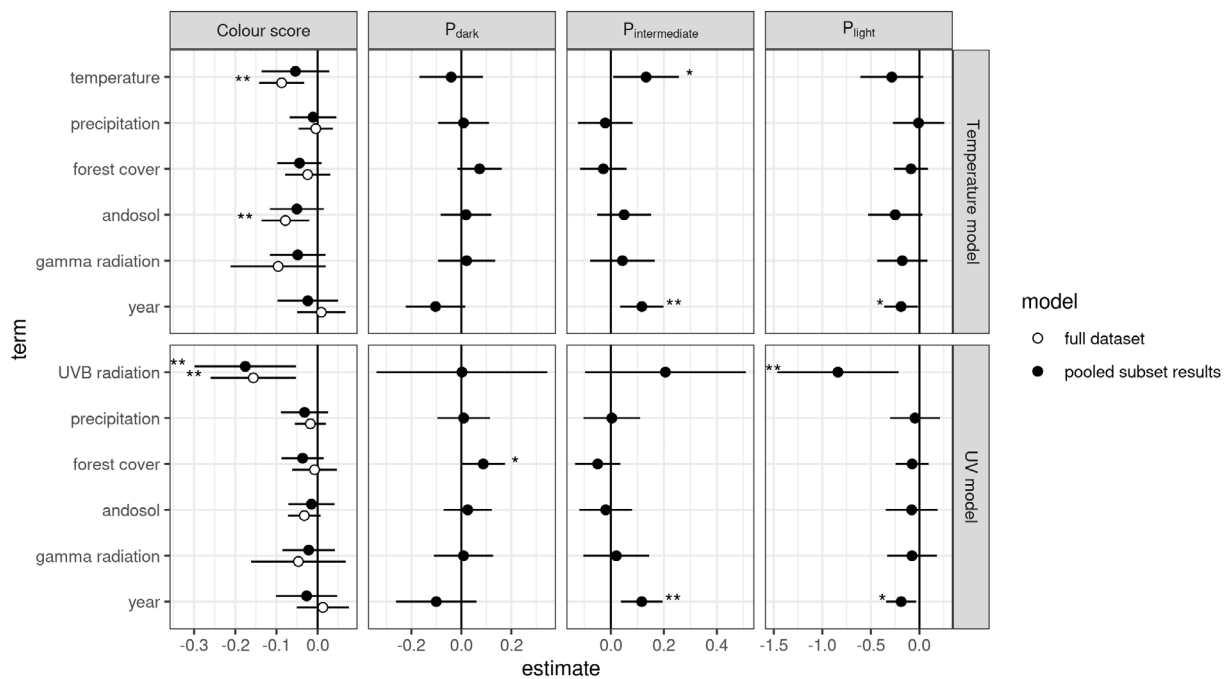


Figure 3. Environmental correlates of spatial variation in Common buzzard colour. Forest plots depict effects of environmental variables on colour variables (response variables: colour score, proportion of dark (P_{dark} , colour scores 1–2), intermediate ($P_{\text{intermediate}}$, colour scores 3–5) and light (P_{light} , colour scores 6–7) birds) for two alternative models (one including temperature, one including UVB radiation, both variables are strongly correlated; see [Methods](#)). Dots and whiskers represent the effect sizes and 95% CIs. White symbols represent model results using all observations ($N = 98\,045$, only for colour score owing to computational limits; see [Methods](#)); black symbols are mean effects from analyses of 25 thinned datasets (each $N = 6485$) combined using Rubin’s rules (see [Methods](#)). Statistical significance is indicated as: * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$. The effects of year are shown for completeness, but only interpreted in separate models that account for temporal autocorrelation (Fig. 4). Full model results can be found in Table S1.

(Fig. 4). These effects remain similar if the temporal range is restricted to 2015–2022 (colour score: slope = 0.012, $se = 0.005$, $z = 2.19$, $P = 0.028$, $N = 131$; P_{dark} : slope = -0.068 , $se = 0.008$, $z = -8.73$, $P < 0.0001$, $N = 131$; $P_{\text{intermediate}}$: slope = 0.078, $se = 0.009$, $z = 7.93$, $P < 0.0001$, $N = 131$; P_{light} : slope = -0.035 , $se = 0.019$, $z = -1.81$, $p = 0.07$, $N = 99$).

We assessed whether temporal changes in colour were more or less marked in cells where these colours were more common. $P_{\text{intermediate}}$ increased more strongly over time in cells with a high proportion of intermediate individuals, while P_{light} decreased less in cells with a higher proportion of light individuals (Fig. 5). We tested whether changes in buzzard colour over time are correlated with changes in environmental variables in each hexagonal cell. Over the period 2000–2022, changes in temperature were negatively correlated with changes in colour score (Fig. 5), suggesting

that plumage lightness increased less in areas that warmed up more during 2000–2022. Decreases in forest cover from 2000 to 2022 correlated with increases in intermediate- and decreases in dark-coloured buzzards, but did not affect P_{light} (Fig. 5). Changes in precipitation or UV radiation were not significantly correlated with changes in colour variables (Fig. 5). Including the effects of other technical moderator variables (accounting for temporal autocorrelation, year range and median year) did not change the conclusions (see [Supporting Information](#) for details).

DISCUSSION

Spatial variation in plumage colour

Common Buzzard colour shows clear geographical variation, with lighter birds in North-Central Europe (Fig. 2a). This pattern is mainly driven by

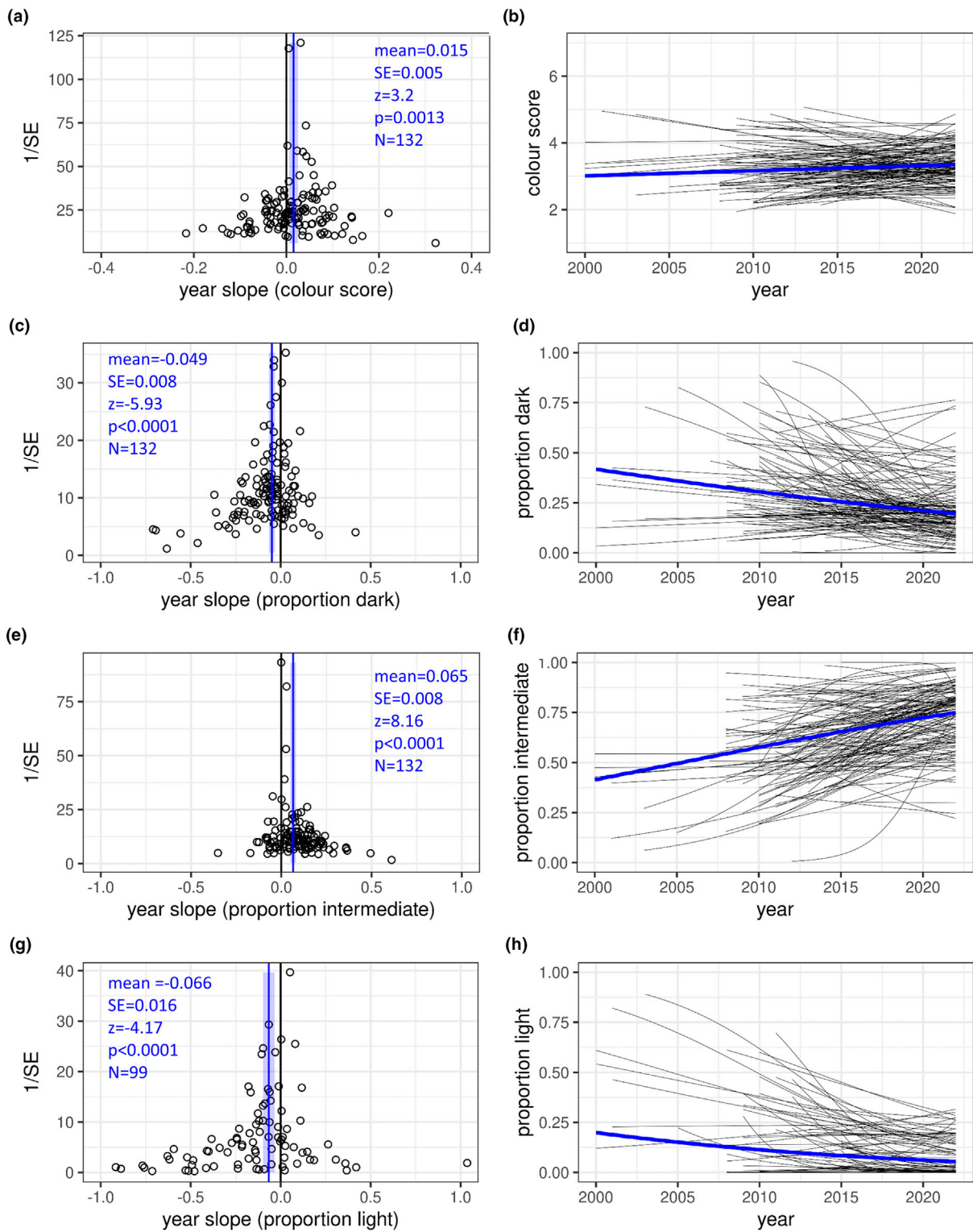


Figure 4. Temporal changes in Common Buzzard colour variables from 2000 to 2022. Depicted on the left are funnel plots for temporal effects on mean colour score (a), proportion of dark (c, colour scores 1–2), intermediate (e, colour scores 3–5) and light (g, colour scores 6–7) buzzards. Black circles indicate temporal effects for each cell, whereby the effect size is depicted on the x-axis (year slope) and its precision (1/se) on the y-axis. The vertical blue line indicates the meta-analytical mean and the shading represents its 95% CI. In (g) extreme effects have been left out of the plot for visual purposes but mean effect and 95% CI were computed on the whole sample. On the right, we show predicted temporal trends for each cell (thin black line) and the predicted line from the meta-analytical mean (thick blue line), for mean colour score (b), and for the proportion of dark- (d), intermediate- (f) and light-coloured (h) buzzards.

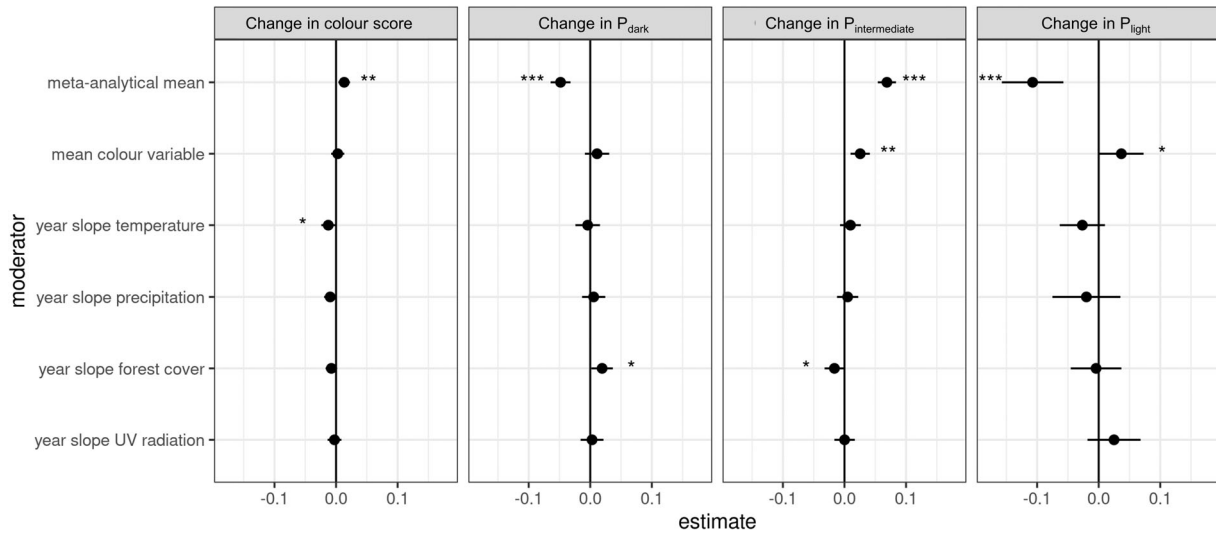


Figure 5. Forest plots depicting how changes in buzzard plumage colour in each area (cell) from 2000 to 2022 relate to the mean colour in that area and to concurrent changes in environmental variables. Shown are the results of meta-analyses with moderators for the four colour variables: colour score, the proportion of dark (P_{dark} , scores 1–2), the proportion of intermediate ($P_{\text{intermediate}}$, scores 3–5) and the proportion of light (P_{light} , scores 6–7) buzzards. Dots and whiskers represent the effect sizes and 95% CIs. Statistical significance is indicated as: * $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$. Full model results are given in Table S2.

the proportion of light buzzards, which is highest in central France, Belgium, The Netherlands and northern Germany (Fig. 2d). Dark-coloured buzzards are most common in Brittany and Iberia, and intermediate-coloured individuals in the eastern Mediterranean region and the British Isles (Fig. 2b, c). The patterns of spatial variation that we describe here generally agree with the limited earlier information (Ulfstrand 1977, Krüger *et al.* 2001, van Bergen & Riem Vis 2015), but do not closely match patterns observed in other polymorphic birds of prey in Europe. For example, the Barn Owl becomes darker towards the east and north, with the lightest individuals found in Iberia (Burri *et al.* 2016, Romano *et al.* 2019). The darker brown morph of the Tawny Owl *Strix aluco* is more common in temperate parts of Europe and less common in boreal and mediterranean regions (Koskenpato *et al.* 2023). In Booted Eagles

Hieraetus pennatus, darker birds become more common towards the east (Bosch 2019), while for several other diurnal raptors the pattern is reversed with lighter birds being more common towards the north and east (e.g. *Aquila chrysaetos*, *Accipiter gentilis*, *Buteo lagopus*, *Falco peregrinus*; Cramp & Simmons 1977). This latter pattern somewhat resembles buzzard colour variation, although the lightest buzzards were found in central Europe and not further north or east (see also Ulfstrand 1977). However, direct, quantitative comparisons are difficult because the nature of colour variation differs between species (e.g. light to dark, grey vs. brown morph, degree of melanin spottiness) and colour has been quantified using different approaches.

Based on general ecogeographical rules of colour and on previous studies on colour variation in birds of prey, we predicted that spatial variation in

buzzard colour would be associated with environmental gradients in climate, soil type, forest cover, and UVB and gamma radiation. We found that buzzards tended to be lighter-coloured in regions with lower temperatures, but colour was not correlated with variation in precipitation (Fig. 3). Temperature was significantly and positively associated with the probability of occurrence of intermediate-coloured buzzards, but not with the occurrence of light or dark buzzards (Fig. 3). Overall, the temperature effect does not support the hypothesis that plumage colour in buzzards is involved in thermoregulation. However, UVB radiation was the strongest predictor of colour. In accordance with the prediction, buzzards were darker in areas with higher UV radiation, matching the pattern previously detected in Golden Eagle nestlings (Galván *et al.* 2018a). This suggests that dark coloration in buzzards may function in photo-protection (Nicolai *et al.* 2020). However, note that temperature and UVB radiation are strongly correlated, which makes it difficult to disentangle their effects. In addition, exposure to solar radiation can be mediated by changes in behaviour and habitat use (e.g. seeking shade), factors that could not be accounted for in our study.

Our results provide limited support for an effect of forest cover: as predicted, buzzards were darker in more forested regions, but this effect was only statistically significant when analysing the proportion of dark-coloured individuals and only in the model that included UV radiation instead of temperature (Fig. 3). It is possible that the effect of forest cover is underestimated because this variable was only quantified in a coarse way. Thus, more subtle and complex estimates of vegetation type and density could reveal further associations between colour and habitat. The most likely mechanism linking darker buzzards to forested environments is camouflage, either to be less visible to prey or to avoid being detected by a predator. Given established links between colour variation and preferred prey types in other polymorphic raptors (Roulin 2004b, Romano *et al.* 2021), the former may be more likely. Buzzards also tended to be lighter in regions with lower proportions of volcanic soil (Fig. 3). However, soil type did not have a significant effect on the proportions of the three colour categories. Nevertheless, the effect of soil type on the colour score matches results from a study on Barn Owls, whereby lighter individuals were found in

andosol-poor soils (Romano *et al.* 2023). Finally, we did not find any effect of gamma radiation on buzzard colour.

Overall, the environmental variables explained only small amounts of variation (all models: $R^2 < 0.01$), suggesting that spatial patterns of colour distribution in buzzards may have been shaped by other environmental drivers, or by historical contingency. Phylogeographical studies on the Barn Owl show that patterns of colour variation result from a combination of colonization history and local adaptation (Antoniazza *et al.* 2014, Burri *et al.* 2016, Cumer *et al.* 2022, Machado *et al.* 2022). Studies on geographical patterns of genetic variation in buzzards are scarce. Two studies in Germany, using allozyme variation (Schreiber *et al.* 2001) or microsatellites (Boerner *et al.* 2013), revealed no evidence of isolation-by-distance at smaller scales, and no genetic divergence between colour categories (Boerner *et al.* 2013). A more comprehensive study, at a broader geographical scale and including other *Buteo* taxa, suggests that Iberia and South-East Europe functioned as potential refugia for Common Buzzards during the last glaciation (Jowers *et al.* 2019). Afterwards, recolonization of Europe may have taken place from these areas; however, genetic differences between buzzard populations in Europe are relatively low (Pârâu & Wink 2021), complicating further inference.

Temporal variation in plumage colour

We found a weak but statistically significant trend suggesting that, on average, buzzards have become lighter from 2000 to 2022 (Fig. 4a). Out of context, this result may be interpreted as a potential adaptive response to climate change, because the thermal melanism hypothesis predicts that animals become lighter in colour with increasing temperatures (Delhey *et al.* 2020). However, this explanation is unlikely for the following reasons. First, spatial variation in buzzard colour does not follow temperature gradients in the expected manner (lighter birds were found in colder, not warmer regions; Fig. 3). Second, increases in lightness over the period 2000–2022 are weaker, not stronger, in regions that warmed-up more during the same period (Fig. 5). A more likely reason for the observation that buzzards have become, on average, lighter over time is that the proportion of the different colour categories has changed over time,

specifically intermediate-coloured birds having become more frequent at the expense of the extremes (Fig. 4).

Between 2000 and 2022, both dark- and light-coloured buzzards have declined in abundance, while intermediate birds have increased (Fig. 4). According to the models, intermediate birds are 33% more abundant, while dark and light buzzards were (respectively) 22% and 14% less abundant in 2022 than in the year 2000. The magnitude of these temporal changes matches those reported for a buzzard population in the Netherlands (1995–2015; Kappers *et al.* 2020), and may be a consequence of the higher fitness of intermediate compared to either dark or light birds (Krüger & Lindström 2001, Krüger 2002, Kappers *et al.* 2020). Our results indicate that the increase in intermediate-coloured buzzards is not restricted to one local population, but a more general phenomenon (Fig. 4), suggesting that the fitness advantage intermediates have over dark and light buzzards may also apply beyond the studied populations in Germany and the Netherlands (Fig. 4).

Our meta-analyses with moderators revealed that the decrease in the relative abundance of dark buzzards over time and the increase in intermediates was stronger in regions where forest cover decreased most (Fig. 5). These effects partially match the spatial association between forest cover and colour variation (Fig. 3). Although the effects are weak, they show that in more forested regions darker buzzards are more common and intermediate buzzards tend to be less common. Although UVB radiation was identified as the strongest correlate of spatial colour variation in buzzards (Fig. 3), temporal changes in this variable were not associated with changes in colour (Fig. 5). Our analyses further show that in areas that warmed up more in 2000–2022, the increase in overall colour score (i.e. in colour lightness) was less steep (Fig. 5). However, changes in temperature or precipitation from 2000 to 2022 were not correlated with changes in the relative abundance of individuals of the three colour categories (Fig. 5), unlike studies in the Barn Owl (Romano *et al.* 2024).

Taken together, our results tentatively suggest that changes in forest cover may partly be responsible for the increase in intermediate-coloured buzzards over recent times. Regardless of the reasons for the changes in colour, increases in the proportion of intermediate-coloured birds should lead to an overall reduction in colour variability. We

tested this for cells with sufficient observations (see [Supporting Information](#) for details). As expected, colour variation declined over time (meta-analytical mean: -0.014 , $se = 0.0047$, $z = -3.07$, $P = 0.002$, $N = 74$ cells). If colour variation is an indicator of underlying genetic variability, a reduction in colour variation suggests lower adaptability to future environmental change. However, this result should be considered preliminary, because the temporal effects on variability are not spatially independent (spatial autocorrelation: Moran's I , $P < 0.001$).

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

We find marked spatial variation in buzzard plumage colour. A set of environmental variables known to correlate with colour variation in other highly variable birds of prey explained only little of the colour variation in buzzards. Our results are in accordance with previous studies showing effects of soil type, UV radiation and forest cover on colour, but do not support general ecogeographical rules of colour variation. Relaxed natural selection on colour may explain considerable amounts of intraspecific colour variation in this species. An analysis of changes in colour over the last decades confirms an increase in intermediate-coloured birds at the expense of light and dark buzzards. These changes in colour are related to concurrent changes (mostly decrease) in forest cover, suggesting a potential causal link.

We suggest that future research should focus on three main aspects. First, determine whether intermediate-coloured individuals indeed have higher fitness and elucidate the underlying mechanism(s). To better understand the relationship between colour and fitness, field studies prioritizing populations in regions with a different colour composition than those in Germany or the Netherlands would be most valuable. Furthermore, behavioural studies are necessary to assess how individual buzzards of varying coloration use the landscape. Promising avenues include detailed studies of morph-specific habitat use, diet and foraging success. Just like in other birds of prey, differently coloured buzzards may specialize on different prey types and use different hunting habitats (Roulin 2004b, Charter *et al.* 2012, Tate *et al.* 2016, Romano *et al.* 2021). So far data on morph-specific diet or habitat use are lacking for

the Common Buzzard. If different morphs specialize on different prey or use different hunting grounds, changes in prey abundance or in the extent of preferred hunting habitats across the range may provide an explanation for changes in morph frequencies.

Second, it would be interesting to extend temporal series further into the past by quantifying colour variation in museum specimens (e.g. Galeotti *et al.* 2009, Koskenpato *et al.* 2023). Assuming that collections are not biased in favour of certain colour categories, such data would allow putting recent colour changes into perspective. Such a longer-term perspective is relevant because Common Buzzard populations increased markedly after DDT use and persecution were banned (Cramp & Simmons 1977), and these demographic changes could have shaped the distribution of colour variability. Note that the Swainson's Hawk *Buteo swainsoni* underwent similar population bottlenecks in North America, but demographic changes did not affect colour variation (Briggs *et al.* 2023).

Finally, we need genomic studies to reconstruct the phylogeographical history and to identify the genetic basis of colour variation. Phylogeographical studies are essential to disentangle local adaptation from historical contingency (e.g. Burri *et al.* 2016) and to understand the consequences of reductions in colour variability over time. Identifying the genetic basis of colour variation could provide new cues about potential adaptive mechanisms behind morph-specific fitness differences, because genes associated with melanin synthesis and deposition potentially have extensive pleiotropic effects (Ducrest *et al.* 2008, McNamara *et al.* 2021). Thus, it would be interesting to determine whether variation in the MC1R locus is associated with colour variation, as suggested by Boerner *et al.* (2013).

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AUTHOR CONTRIBUTIONS

Kaspar Delhey: Conceptualization; methodology; data curation; investigation; formal analysis; writing – original draft. **Elena F. Kappers:** Conceptualization; methodology; data curation; investigation; writing – review and editing. **Mihai Valcu:** Conceptualization; methodology; data curation; investigation; formal analysis; writing – review and editing. **Christiaan Both:** Conceptualization; methodology; investigation; writing – review and editing; supervision. **Bart Kempnaers:** Conceptualization; investigation; data curation; writing – original draft; funding acquisition; supervision.

CONFLICT OF INTEREST

None declared.

ETHICAL NOTE

None.

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Data Availability Statement

Data and code are available at: <https://figshare.com/s/a6c951009622b6fa1617>.

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SUPPORTING INFORMATION

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

Supplementary Text.

Figure S1. Maps depicting spatial variation in sample size (A) and temporal range (B) using a hexagonal grid (150 km between cell centroids). Note logarithmic colour scale in (A).

Figure S2. Maps depicting spatial variation in environmental predictors using a hexagonal grid (150 km between cell centroids).

Figure S3. Maps depicting variation in temporal change (year slope) in colour variables for cells in a hexagonal grid (150 km between cell centroids) with sufficient data (see [Methods](#)).

Figure S4. Maps depicting variation in temporal change (year slopes) in environmental variables for cells in a hexagonal grid (150 km between cell centroids, see [Methods](#) for more details).

Table S1. Results from spatial models quantifying the effects of environmental variables on geographical variation in Common Buzzard colour across Europe.

Table S2. Results from meta-analytical models analysing temporal variation in Common Buzzard colour across Europe.