



# Avian nuptial plumage coloration changes differently when exposed to urban and rural areas

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## Abstract

Avian plumage coloration could be altered by external factors like dust accumulation, but the effect of environmental conditions on such post-moult colour changes are poorly studied. Here, we investigated how exposure to the atmosphere in habitats of differing anthropogenic pressures modifies UV/blue structural plumage coloration — a sexually selected trait in eastern bluebirds *Sialia sialis*. We collected feather samples from live birds and distributed them in three types of habitats: (i) urban roads with low traffic, (ii) urban roads with high traffic, and (iii) rural roads with low traffic. After 4 weeks, the brightness of feathers decreased in all types of habitats—resulting in less-ornamented coloration. Changes in UV and blue chroma, however, varied with habitat type; chroma decreased in urban areas (becoming less ornamented), but increased in rural locations (becoming more ornamented). According to physiological models of avian colour vision, however, these changes in coloration tended to be below perceptual thresholds. Our results underscore the importance of how human activity can influence plumage colour of individual birds during the period between moult cycles which could have an impact on avian visual signalling. The study opens venues for further studies focusing on how the optical properties of specific airborne particles can influence coloration of wild-living animals.

## Significance statement

Plumage coloration plays an important role in avian visual communication. In addition to moult-based change, coloration may change between moult cycles due to exposure to external factors like, for example, dust accumulation. Ecological factors modifying a passive plumage change, however, remains poorly studied. We collected samples of structurally coloured feather from a species wherein plumage colour is sexually selected and exposed them to outdoor conditions. We demonstrate that UV/blue chroma of coloration changes differently in urban and rural habitats. It increased in rural and decreased in urban areas. On the other hand, brightness decreased in both habitat types. Using physiological models of avian colour vision, however, we found that these colour changes were likely not perceptible to birds. Our study provides the first evidence that changes in coloration of fully grown feathers may be habitat dependent.

**Keywords** Eastern bluebirds · *Sialia sialis* · Reflectance spectrophotometry · RNL colour discrimination models · Sexual selection

## Introduction

The vivid colours of avian plumage often play important roles in intraspecific communication. One prominent function is to convey information about the quality of potential breeding mates (Griffith and Pryke 2006) and the resource holding potential of individuals (Senar 2006). As a result,

elaborate plumage colours are often the subject of the intense sexual selection (Hill 2002, 2006; Dale et al. 2015).

The two main mechanisms behind plumage coloration are: the deposition of pigments (so called pigmentary colours, McGraw 2006a, b) and the organization of microstructure in barbs or barbules, which interact with incident light (so called structural colours, Prum 2006). As both processes take place only during feather growth, it was traditionally assumed that plumage coloration is static between successive moults (e.g. McGraw and Hill 2004; Delhey et al. 2006; Surmacki et al. 2011a, b). A number of studies,

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however, have demonstrated gradual changes in plumage coloration (both structural and pigment-based) of wild living bird during the period between moults (Örnborg et al. 2002; McGraw and Hill 2004; Figuerola and Senar 2005; Delhey et al. 2006; Hasegawa et al. 2008). Field and lab-based experiments using feather samples and feathers on living birds have revealed some mechanisms responsible for between-moult colour changes including: dirt and preen oil deposition (Surmacki and Nowakowski 2007; Pérez-Rodríguez et al. 2011), photo-bleaching (Surmacki 2008; Surmacki et al. 2011a, b), mechanical abrasion (Surmacki et al. 2011a, b), keratin-degrading bacteria (Shawkey et al. 2007). Moreover, in some cases, birds may actively control the colour change process, e.g., by applying exogenous and endogenous substances on feathers surface, so called “cosmetic coloration” (Delhey et al. 2007). More often, however, between-moult colour changes occur completely passively (so called “adventitious colours”, Montgomerie 2006).

Surprisingly, little is known about ecological factors governing between-moult changes in plumage coloration. It might be assumed that particular habitats should promote certain colour changes. For example, more intense photobleaching could be expected in open, well-lit areas, compared to in woodland shade. Analogously, changes driven by dirt accumulation are more likely to occur in urban areas where air-borne particles are abundant due to e.g., road transport or coal-fuelled power plants (Garcia et al. 2013; Pastuszka et al. 2015; Vlasov et al. 2022). Indeed, the structurally based coloration of European Starlings *Sturnus vulgaris* in a highly polluted Italian city revealed a gradual decrease in total plumage brightness, which could be prescribed to industrial dust accumulation (Griggio et al. 2011). This and other studies showed that dust accumulation is especially detrimental to reflectance in the UV range of light spectrum (Zampiga et al. 2004; Griggio et al. 2010, 2011; D’Alba et al. 2011), which is important in sexual selection of species with structural coloration (e.g., Bennett et al. 1997; Zampiga et al. 2004; Siefferman and Hill 2005a, b). Thus, populations that occur in habitats with abundant airborne particles might be particularly prone to altered signals which could influence sexual selection.

Large-scale urbanization has resulted in larger numbers of birds living in cities or in close proximity to urban environments and some species have adapted so well to urban ecosystems that it has become their main habitat (Isaksson 2018). Although proximity to urban environments comes with some benefits to birds, e.g., increased access to food (e.g., Tryjanowski et al. 2015) or nest building opportunities (James Reynolds et al. 2019) and reduced predation (e.g., Eötvös et al. 2018), there are also obvious costs for urban birds. Air pollution may directly affect the health of birds and other animals (e.g., Gorriz et al. 1994; Llacuna et al. 1996) or alter their food resources (e.g., Eeva et al.

1998, 2008). Less obvious impacts of urban living, however, could include the degradation of optical properties of nuptial plumage, which, in turn, alters the sexual selection process.

Studies measuring the effect of environmental factors on bird plumage often use collected feathers instead of living birds (examples include: the effect of microorganisms (Shawkey et al. 2007), sun irradiation (Surmacki 2008), dust (Surmacki and Nowakowski 2007), and preen oil (López-Rull et al. 2010)). Such studies have limitations because birds may actively moderate the effect of these agents via preening (applying preen oil and removing dust) or by avoiding direct sunlight by seeking shade. Nevertheless, there are many advantages of experiments that use collected feathers, arguably the most important is that it allows researchers to limit the number of potential agents and uncover the mechanisms behind colour change in living birds. Moreover, experiments on feathers are easier to conduct and reduce stress to live birds.

This study is the first attempt to investigate whether colour changes of fully grown feathers vary along an urbanization and traffic-intensity gradient. To answer these questions, we used a design incorporating structurally UV/blue feather samples collected from wild birds and then exposed to atmospheric conditions in neighbouring urban and rural areas. In urban locations, we placed samples along paved roads with high and low traffic. In rural areas, we placed samples along mainly gravel roads with low traffic. We expected that changes in plumage coloration to be the greatest in urban areas with high traffic, intermediate in urban areas with low traffic, and the lowest in rural areas with low traffic. In addition, using physiological models of avian colour vision, we tested whether these colour changes are perceivable by birds.

## Methods

### Feather samples

We used UV/blue rump feathers collected from live breeding male eastern bluebirds *Sialia sialis*. This plumage trait is known to play an important role in sexual selection; males with more elaborate coloration (those with brighter and greater UV chromatic plumage) acquire higher-quality territories (Siefferman and Hill 2005a), are more socially threatening (Mercadante and Hill 2014) and provision offspring at higher rates (Siefferman and Hill 2003). Analogous plumage in female eastern bluebirds also reflects individual condition and mate quality (Siefferman and Hill 2005b). We collected feathers from 60 males in Auburn (Lee County) Alabama, USA, as part of other projects. From each individual, we collected 8–24 feathers. Until beginning of the experiment, feather samples were stored in sealed plastic

envelopes. Next, feathers were cleaned following D'Alba et al. (2011); feathers were placed in 40% ethanol for 5 min and then rinsed with distilled water and left at room temperature to dry. Finally, we taped all feathers collected from each individual onto matt black plastic cards in a fashion that mimicked the way the feathers naturally lay on birds (Siefferman and Hill 2003).

Catching birds and collecting feathers were done with the approval of the ethics committee (2008–1341, MB167551-0). It was not possible to record behavioural data blind because our study involved focal animals in the field.

## Reflectance measurements

We measured reflectance using a USB4000 spectrophotometer connected to a pulsed xenon lamp PX-2 with reflection probe R200-7-UV/VIS (Ocean Optics, Dunedin, FL, USA). The probe was fitted with a black plastic tip to keep a fixed distance of 1.5 mm and to eliminate ambient light. The angle between the probe and the feather's surface was 90°. Before measuring each sample, measurements were standardized using a white standard (WS-1-SL, Labsphere, North Sutton, NH, USA), while the dark standard was taken by covering the probe with a black velvet. We took five readings of each sample that were spaced ~1 mm apart.

We processed spectral data using the *pavo* package in R (Maia et al. 2013). First, we averaged the reflectance data obtained for each bird. Then, we calculated three reflectance variables: UV chroma, blue chroma, and brightness. UV and blue chroma were calculated as the ratio of the reflectance of UV (300–400 nm) and blue (400–510 nm) regions to total reflectance (300–700 nm, S1U and S1B in *pavo*). Brightness was the mean reflectance for each wavelength (step 1 nm) between 300 and 700 nm (B2 in *pavo*). UV chroma and brightness are standard colour variables used in studies of eastern bluebirds, which play important role in within-species communication (Siefferman and Hill 2003, 2005a, b). We additionally calculated blue chroma, because it represents a significant portion of the reflectance and may potentially respond differently to the dust accumulation. All feather samples were measured twice: before and after field exposure.

To assess repeatability (sensu Lessells and Boag 1987) of spectrometer measurements, we calculated within-sample repeatability (R) of first (I) and second (II) measurements in both years (in each year  $n = 57$ ). All colour variables were significantly repeatable: UV chroma I:  $F_{1,56} = 292891.5$ ,  $R = 0.74$ ; UV chroma II:  $F_{1,56} = 244507.3$ ,  $R = 0.72$ ; blue chroma I:  $F_{1,56} = 386632.7$ ,  $R = 0.56$ ; blue chroma II:  $F_{1,56} = 312646.1$ ,  $R = 0.58$ ; brightness I:  $F_{1,56} = 17732.23$ ,  $R = 0.56$ ; brightness II:  $F_{1,56} = 12219.5$ ,  $R = 0.47$ , in all cases  $p < 0.001$ ).

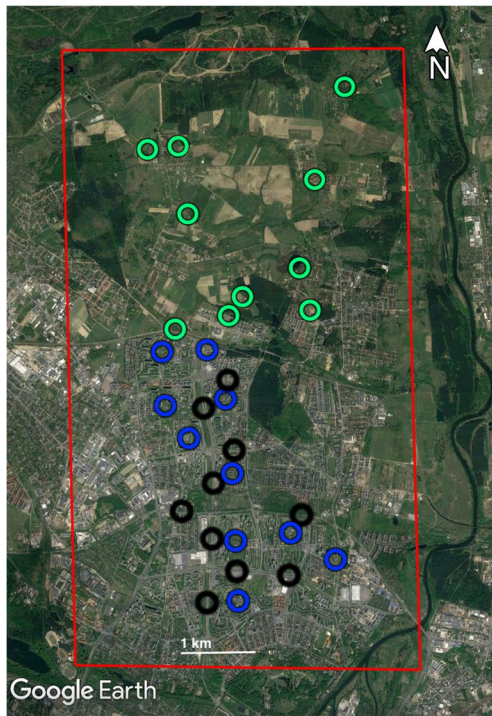
## The experimental procedure

We conducted the feather placement experiment in 2012 and 2013 at the end of May for 4 weeks. This time frame corresponds the timing of single breeding event (incubation + nestlings' period) of eastern bluebirds (28–40 days; Gowaty and Plissner 1998) and many other temperate zone passerines that raise multiple broods per season. Earlier studies show that females may change breeding partners between successive broods, or engage in extra-pair mating according to short-term colour changes (Safran et al. 2005). Thus, the 4-week time frame is relevant to sexual selection.

We exposed the feather cards in the field in 6×6×6 cm boxes, made of white non-transparent white plastic (back, top, and bottom) and white 1×1 mm plastic mesh (front and sides, Fig. 1.). We placed the feathers cards at ~30° angle to the box bottom. The design of the boxes was intended to reduce the impact of sunlight and rain, while allowing airborne particles to flow freely. We randomly selected 30 sites, 10 in each of three habitat types: (1) urban roads with a high traffic, (2) urban roads with a low traffic, and (3) rural roads with a low traffic. The first two groups were distributed in largely overlapping fashion in the northern part of the city of Poznań, Poland (Fig. 2). The rural area was north of the city adjacent to urban sites (Fig. 2). The total area of the study was ~47 km<sup>2</sup>. Roads with high traffic are major urban four-lane routes that are heavily used throughout the day. Low-traffic urban roads are one- or two-lane local roads



**Fig. 1** Example of a feather sample and box used in the exposure experiment



**Fig. 2** The map with location of feather samples in a three traffic zones. Explanations: black circles: urban high traffic, blue circles: urban low traffic, green circles: rural low traffic, red frame: approximate study area

leading to small residential areas, which are used mainly in the morning and afternoon. Rural low-traffic roads connect small villages with paved roads and have low use throughout the day.

Feather samples were randomly assigned to sites. In both study years, different feather samples were located in the same sites. Thus, in 2012–2013, 60 samples were distributed over 30 sites. Boxes with feathers were attached to various industrial posts (e.g., lampposts, traffic signs) at approximately 2 m high, 2–5 m from the edge of roads, with the front side facing the road. To reduce the impact of organic matter fallout, samples were not placed under tree canopies. Three samples disappeared during the experiment; therefore, they were not remeasured after the exposure.

In our study, we exposed feathers of a North American species to Central European habitats. Eastern bluebirds occur mainly in open rural areas, but will breed in city parks with open grassy areas (Gowaty and Plissner 1998). Our intention was not to extrapolate results from a single species experiment conducted Poland to Alabama USA, as natural conditions in both regions are obviously different. Instead, we use the eastern bluebird as a model species for birds with structurally based plumage colour living both in rural and urban habitats. In both Europe and North America, there are species with structurally based plumage colour that inhabit

both habitats, e.g., blue tit, Eurasian jay *Garrulus glandarius*, European starling, and blue jay *Cyanocitta cristata*.

## Visual models

To test whether the observed colour changes and the within-population variation in coloration are perceivable according to the avian visual system, we employed the receptor noise-limited (RNL) colour discrimination model (Vorobyev et al. 1998, 2001). Using the `vismodel ()` function in *pavo* (Maia et al. 2013), we calculated receptor quantum catches. We used averaged cones  $\lambda_{\max}$  values for species with UV visual system (`visual = "avg.uv"`) and standard daylight illumination (`illum = "D65"`). Data on European Starling double cone sensitivity was used to calculate luminance (achromatic) receptor stimulation (`achromatic = "st.dc"`). In the last step, we employed *pavo* `coldist ()` function to calculate chromatic and achromatic colour contrasts ( $dS$  and  $dL$ , respectively) between spectra of clean and polluted feathers. Weber fraction for cones (`"weber"` in *pavo*) and double cones (`"weber.achro"` in *pavo*) were set to 0.1 and 0.34, respectively. These values equal chromatic noise for LWS (long-wave sensitive) cones in the Red-billed Leiothrix *Leiothrix lutea* and an achromatic vision noise in the European starling, respectively (Olsson et al. 2018).

In the way described above, we calculated two kinds of colour contrasts. The first one, hereafter “within-individual colour contrast,” was to assess difference between colour of the same feather sample before and after the exposure to the weather conditions. It was calculated for all individuals in which both reflectance measurements were available ( $n = 57$ ). The second kind of colour contrast one, hereafter “between-individual colour contrast,” was calculated to assess variation in feather coloration at population level. It was obtained by calculating chromatic and achromatic contrasts from the first ( $n = 1770$ ) and the second ( $n = 1596$ ) measurement for all possible pairs of samples.

## Statistical analysis

We used general linear mixed models (GLMM) to investigate the effect of time and location on feather colour change. We built separate models for the following dependent variables: UV chroma, blue chroma, and brightness. The explanatory factors were location (“habitat”) and the year of the study (“year”). The “time” was the colour change between measurements made on the same feather sample at the beginning and end of the exposition. We also introduced two-way interactions between `time * habitat` as well as `time * year` of research into the model to investigate whether the degree of colour change was similar across habitats and years. In all models, bird ID was added as a random factor. We performed analyses using the Jamovi (v 2.3). All data

used in analyses are available as Supplementary Information (Supplementary Information file 1).

To test the effect of the initial colour on the degree of colour change, we calculated Pearson's correlations between the first measurement colour value (i.e., brightness, blue chroma, and UV chroma) and the percentage of colour change caused by exposure. To test whether the feather exposure affected variation in coloration, we used Levene's tests to assess the equality of the variance of the colour variables (i.e., brightness, blue chroma, and UV chroma) between feathers before and after the exposure. Pearson's correlations and Levene's tests were calculated for all habitats and years combined, and also separately for each year (in case of brightness) and habitat (for blue and UV chroma). This is because the changes in brightness were year specific, while changes in blue and UV chroma were habitat specific (Table 1).

## Results

Blue chroma and brightness of feathers decreased over the course of the exposure, whereas no significant effect of time was observed in UV chroma (Table 1; Figs. 3 and 4). Colour change significantly interacted with a habitat: in the urban areas (low and high traffic), UV and blue chroma decreased, whereas in the rural area (low traffic site), UV and blue chroma increased (Table 1; Figs. 3 and 4). Moreover, changes in brightness depended on the year of the study: in 2012, we detected no clear trend, whereas in 2013, brightness decreased (Table 1; Figs. 3 and 4).

**Table 1** Results of GLMM assessing variation of plumage coloration (blue chroma, UV chroma, brightness) caused by exposure to atmospheric conditions in three different traffic zones. Statistically significant interactions ( $p < 0.05$ ) are marked in bold

Factor	Predictor	<i>F</i>	<i>df</i>	<i>p</i>
Brightness	<b>Time</b>	<b>9.88</b>	<b>1, 53.8</b>	<b>0.003</b>
	Habitat	1.86	2, 56.1	0.509
	Year	2.83	1, 56.1	0.098
	Time * Habitat	3.41	2, 53.8	0.937
	<b>Time * Year</b>	<b>8.51</b>	<b>1, 53.8</b>	<b>0.005</b>
UV chroma	Time	0.34	1, 53.7	0.564
	Habitat	0.95	2, 56.3	0.391
	Year	0.03	1, 56.3	0.860
	<b>Time * Habitat</b>	<b>4.98</b>	<b>2, 53.7</b>	<b>0.010</b>
	Time * Year	1.55	1, 53.7	0.218
Blue chroma	<b>Time</b>	<b>4.83</b>	<b>1, 53.2</b>	<b>0.032</b>
	Habitat	1.38	2, 55.4	0.260
	Year	2.85	1, 55.4	0.097
	<b>Time * Habitat</b>	<b>6.08</b>	<b>2, 53.2</b>	<b>0.004</b>
	Time * Year	0.31	1, 53.2	0.583

These trends were driven by changes in reflectance at particular wavelengths across habitats; at high-traffic urban roads, reflectance decreased mainly in the shorter wavelengths (300–500 nm; Fig. 5). At low-traffic urban roads, reflectance decreased relatively evenly across all wavelengths (Fig. 5). At rural roads, reflectance decreased more in the longer (500–700 nm) than shorter (300–500 nm) wavelengths (Fig. 5).

Results from RNL colour discrimination models revealed that in the most cases, chromatic (70.2%) and achromatic within-individual contrast (78.9%) were below 1.0 just noticeable difference and this was true for all three habitats surveyed (Fig. 6). These results suggest that birds are unlikely to perceive the differences in coloration between the majority of intact and exposed feathers but could distinguish differences in 21.1–29.8% of the samples. Moreover, the differences in site-specific patterns of colour change likely would not be visible by birds. Additionally, neither chromatic nor achromatic contrasts varied with habitat type (Kruskal–Wallis test,  $H=0.04$ ,  $p=0.98$  and  $H=2.06$ ,  $p=0.35$ , respectively, Fig. 6).

Between-individual colour contrast for the first measurements was significantly higher than within-individual colour contrast (see above). This was due to the higher ratio of contrasts with JND values exceeding 1.0, which was true for both chromatic (47.6%;  $\chi^2=11.10$ ,  $df=1$ ,  $p=0.01$ ) and achromatic colour contrast (43.2%;  $\chi^2=6.98$ ,  $df=1$ ,  $p=0.01$ ). Moreover, mean values of dS and dL were significantly higher for between-individual colour contrasts ( $Z=4.21$ ,  $p<0.01$ ;  $Z=3.24$ ,  $p<0.001$ , respectively), and in case of dS, they approached the level of 1.0 JNDs (Supplementary Information file 2). Between-individual chromatic contrast was significantly higher for the second measurement compared to the first measurement ( $Z=-2.38$ ,  $p=0.02$ ; Supplementary Information file 2), whereas no significant differences were found for achromatic contrast ( $Z=0.12$ ,  $p=0.90$ , Supplementary Information file 2).

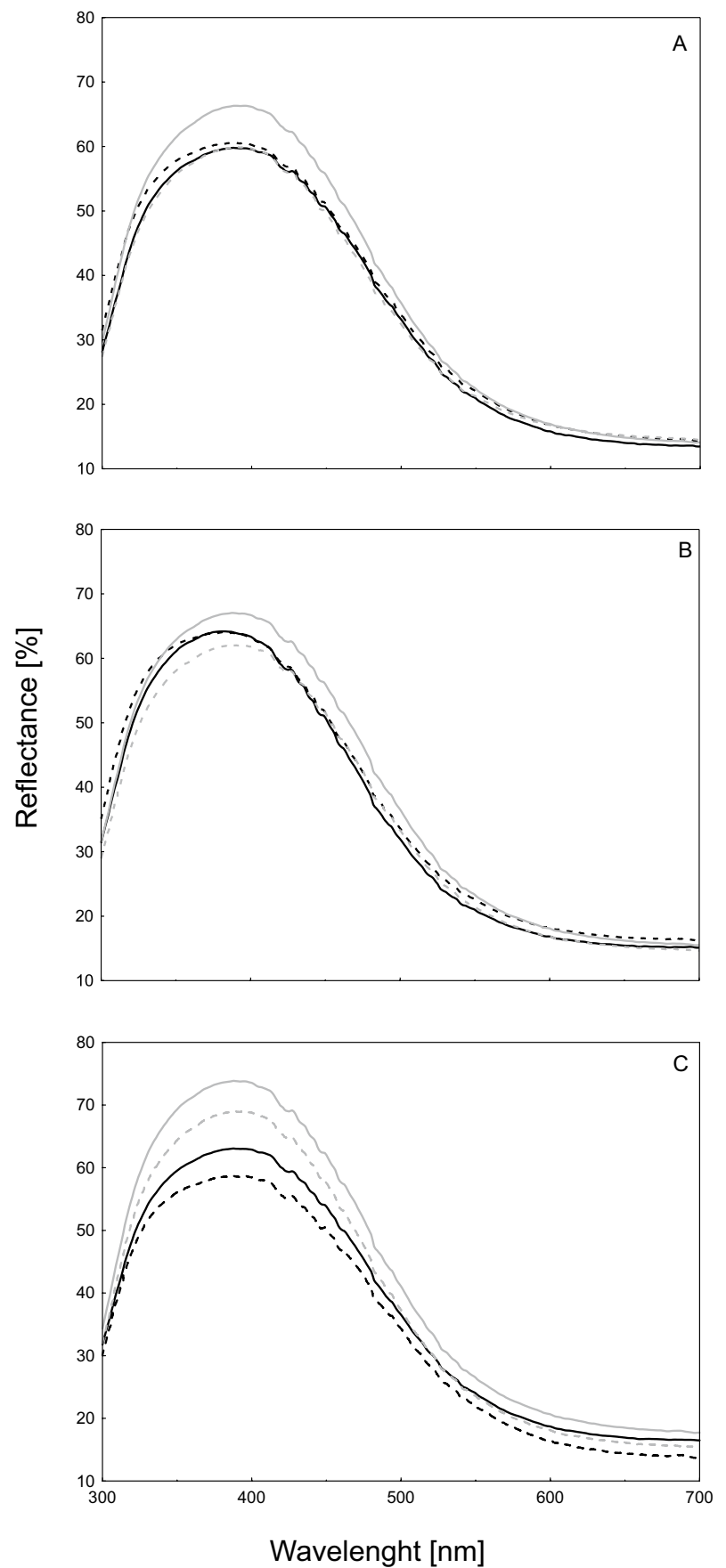
We found that overall initial brightness and blue chroma were both significantly and negatively correlated with the degree of colour change (Table 2). In case of the brightness, the correlation was significant for feathers exposed in 2011, but not in 2012 (Table 2). When tested separately for each of three habitats, there were no significant correlations between blue chroma and the degree of colour change (Table 2).

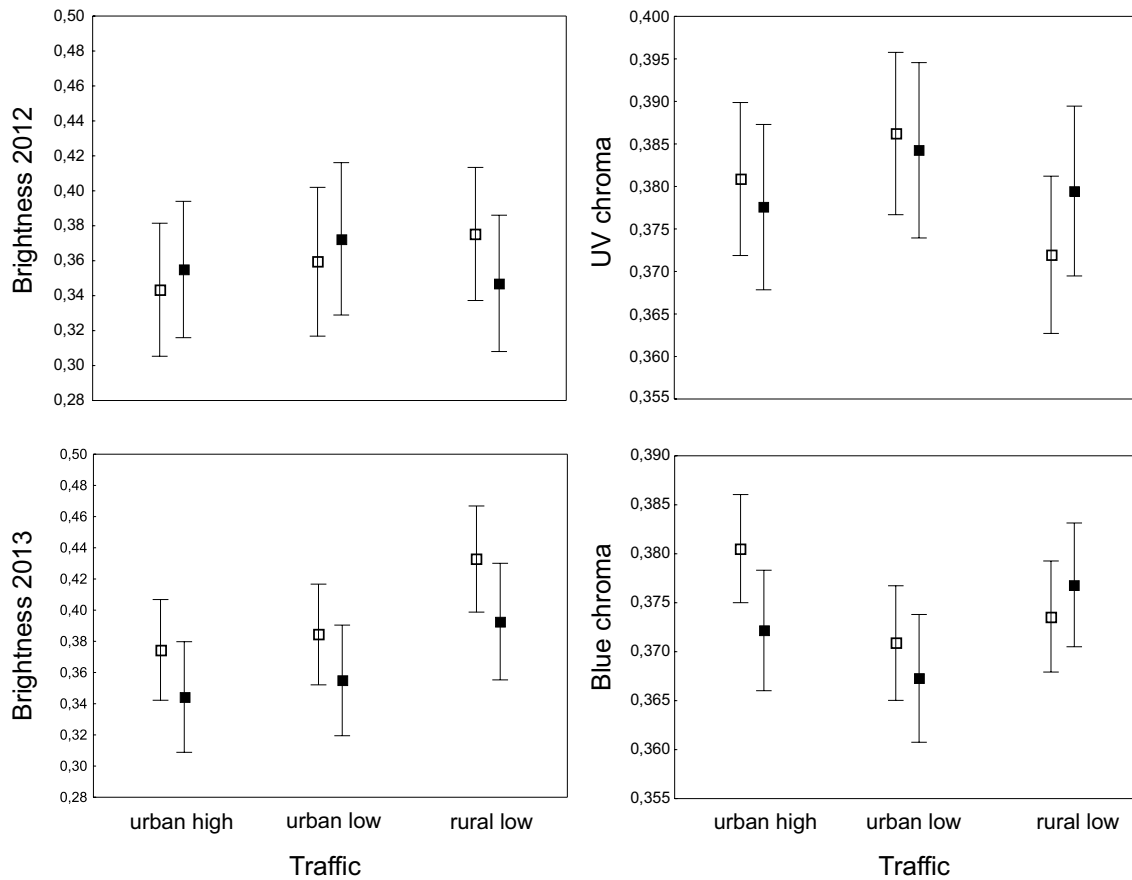
There were no statistically significant differences in the variance of any of the colour parameters tested between measurements before and after the exposure (Table 2).

## Discussion

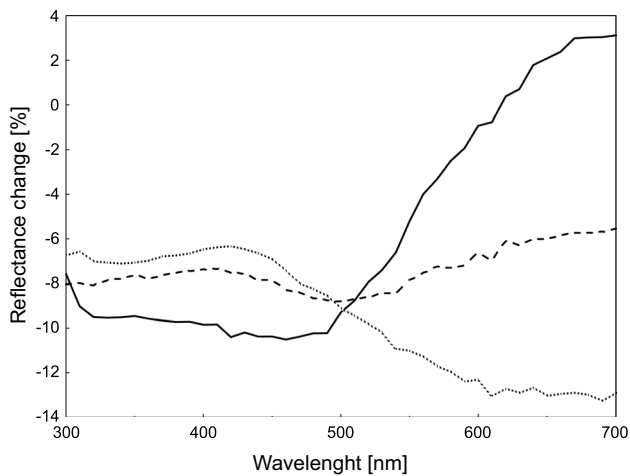
We found that feathers exposed to the air in urban and rural areas exhibited colour change over time. Although the exact mechanism behind spectral changes remains unknown,

**Fig. 3** Reflectance of bluebird feathers before (solid line) and after (dashed line) exposure to atmospheric conditions in each of three traffic zones. Explanations: **A** high urban, **B** low urban, **C** rural low traffic; black lines — 2012, gray line — 2013





**Fig. 4** Changes of brightness, UV chroma, and blue chroma of feathers exposed to the atmospheric conditions in a three traffic zones. Explanations: filled squares — after exposition, empty squares — before exposition. Shown are means and 95% confidence limits

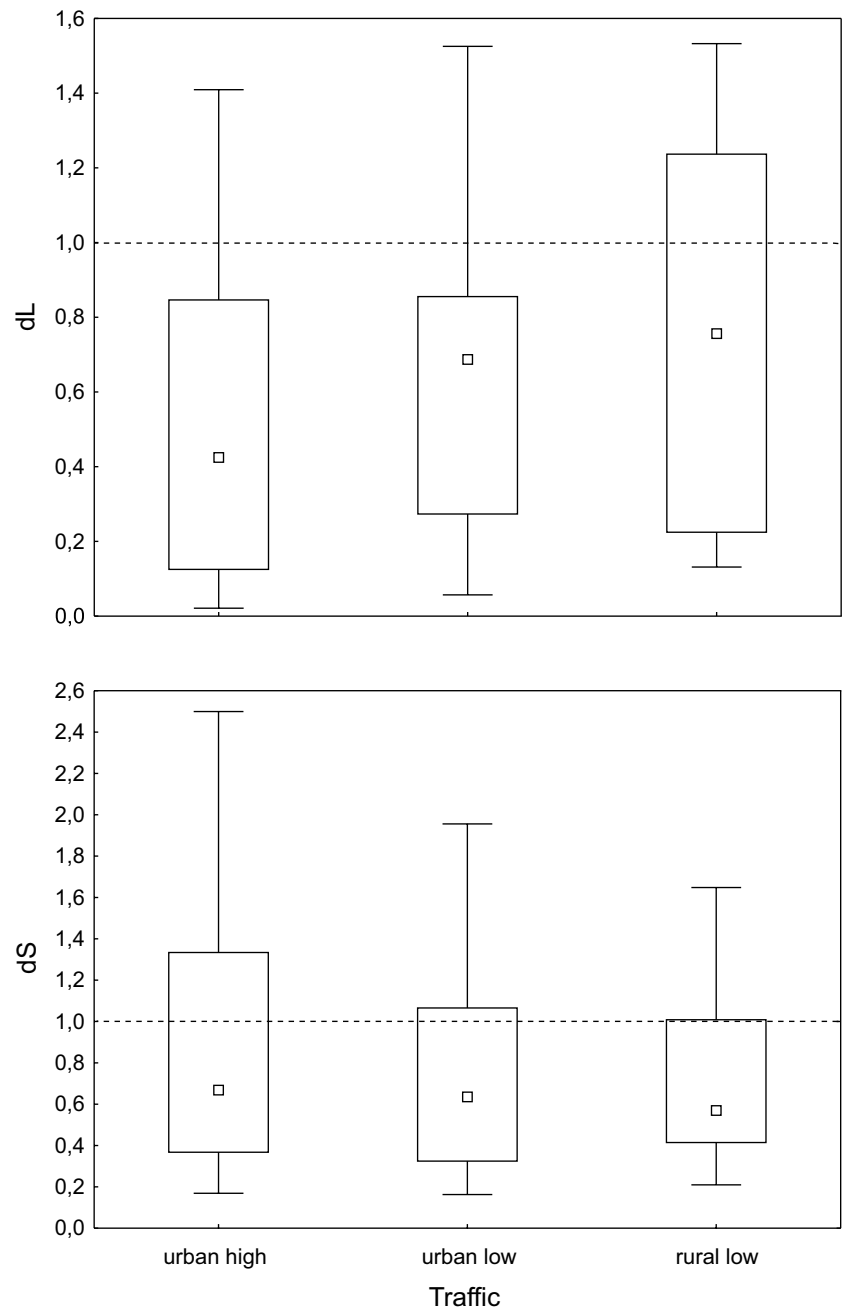


**Fig. 5** Changes in reflectance of bluebird feathers after exposition to atmospheric conditions in a three traffic zones. Explanations: thick solid line — urban high, thick dashed line — urban low, thick dotted line — rural low

there are several lines of evidence suggesting that it was mainly the effect of the deposition of airborne particles on feather surfaces, while other factors are less probable. Past research demonstrates that structurally based plumage colour is resistant to photobleaching (Surmacki et al. 2011b). Moreover, bluebird feathers were partially protected from the direct sunlight by the box in which they were exposed. Although the UV/blue feathers of eastern bluebirds harbour keratin degrading bacteria, which ultimately alters plumage reflectance (Shawkey et al. 2007), we doubt this process led to the observed colour changes because samples were in airy and well-lit conditions that are not optimal for bacteria development. Moreover, karatinolytic bacteria cause increases in overall reflectance (Shawkey et al. 2007) contrary to our trends.

In line with our predictions, we found that spectral changes varied with site location (urban vs. rural areas) and with traffic intensity (high vs. low). In high-traffic urban sites, we found a marked reduction in reflectance within UV/blue wavelengths. A similar change, albeit on smaller scale, occurred in low-traffic urban sites. On the other hand, in rural low traffic areas, the opposite colour

**Fig. 6** Colour distances between intact feathers and the same feathers after the exposure to the atmospheric conditions in three traffic zones. Explanations: dS — chromatic contrast, dL — achromatic contrast; point — median, bar — 25–75% quartiles, whiskers — min–max. Dashed line denotes colour discrimination threshold (i.e. just noticeable difference = 1.0)



change occurred: UV and blue chroma increased. The most prominent decrease of short-wave reflectance in high-traffic urban areas could be ascribed to the optical properties of air pollution. Airborne particles in urban areas generally have greater absorption index compared to rural areas (Weiss and Waggoner 1982; Liu and Smith 1995; Pastuszka et al. 2015) caused mainly by a carbon-containing compounds like soot (Bergstrom et al. 1982; Pastuszka et al. 2015). Such compounds absorb mainly short wavelengths of light (Chudnovsky et al. 2007) and are in higher abundance near highways (Pastuszka et al. 2015).

Contrary to our predictions, feather colour changes along rural roads were not markedly lower than in urban roads and affected chroma differently. This is likely because most rural roads were gravel. In dry weather, passing cars raise clouds of loose dust particles from gravel roads causing pronounced accumulation of dust on feathers. In contrast to the high-traffic urban roads, feathers exposed to rural roads exhibited decreased reflectance mainly within the longer wavelengths, which, in turn, increased UV and blue chroma. Thus, despite reduced brightness, exposure in rural locations could increase the quality of another component of UV/



**Table 2** Correlations between initial (first) measurement and variable change (%). Levene's tests for the equality of variance between first and second measurements. Statistically significant results ( $p < 0.05$ ) are marked in bold. All test were performed for all data pulled (total) and separately for each habitat (blue and UV chroma) or year (brightness). Explanation: habitat 1: high urban traffic; habitat 2: low urban traffic; habitat 3: low rural traffic

Variable	Pearson's correlation			Levene's test			
	<i>n</i>	<i>r</i>	<i>p</i>	<i>n</i>	<i>F</i>	<i>df</i>	<i>p</i>
Brightness (2011)	<b>28</b>	<b>-0.38</b>	<b>0.048</b>	30, 28	0.05	56	0.83
Brightness (2012)	29	-0.30	0.12	30, 29	0.01	57	0.91
Brightness (total)	<b>57</b>	<b>-0.40</b>	<b>0.002</b>	60, 57	0.12	115	0.73
Blue chroma (habitat 1)	20	-0.31	0.18	20, 20	0.17	38	0.68
Blue chroma (habitat 2)	18	-0.06	0.81	20, 18	0.54	36	0.47
Blue chroma (habitat 3)	19	-0.30	0.21	20, 19	0.07	37	0.79
Blue chroma (total)	<b>57</b>	<b>-0.28</b>	<b>0.037</b>	60, 57	0.13	115	0.72
UV chroma (habitat 1)	20	-0.33	0.16	20, 20	0.07	38	0.80
UV chroma (habitat 2)	18	-0.10	0.64	20, 18	0.15	36	0.71
UV chroma (habitat 3)	19	0.11	0.66	20, 19	0.21	37	0.65
UV chroma (total)	57	-0.24	0.070	60, 57	0.22	115	0.64

blue structural coloration. This contradicts results of earlier experiments showing that artificial soiling is detrimental to optical properties of nuptial structural plumage (Zampiga et al. 2004; Griggio et al. 2010). Our results also suggest that road dust in rural areas absorbs longer light wavelengths. These findings are intriguing because even natural airborne particles, like Sahara dust, absorb mainly within the short wavelengths (e.g., Rocha-Lima et al. 2018). On the other hand, a similar effect of natural soiling on UV/blue structural plumage colour (an increase of UV chroma) has been observed on the recites of Blue Tits *Cyanistes caeruleus* caught during spring migration in a rural area (Surmacki 2011). The identification of specific components of rural road dust (e.g., pesticides or fertilizers from agriculture) and their optical properties warrant further studies.

Regardless of location, we found a general trend of reduced overall reflectance. A decrease in plumage reflectance due to soiling has been repeatedly reported for many substances, including preen wax (Surmacki and Nowakowski 2007; Pérez-Rodríguez et al. 2011; Surmacki 2011), artificial organic dirt (Griggio et al. 2010), natural soiling (D'Alba et al. 2011), and industrial air pollution (Griggio et al. 2011). The most probable explanation for such uniformity is that most of the additional substances that attach to feather surfaces cause abortion or/and scattering of light, which in turn, reduces total reflectance. The year-dependent differences in colour change may reflect the complicated nature of dynamics of urban airborne particles, which is very heterogeneous and depends on local weather conditions (Liu et al. 2019).

Our study also showed that aside from habitat and the season, the initial colour may affect further colour changes. We found a negative correlation between both initial brightness and blue chroma and the extent to which these parameters changed. This means that the more-ornamented feathers (i.e., with higher brightness and blue chroma) decreased more in ornamentation compared to the less-ornamented

feathers. This result suggests that urbanization has the potential to counteract directional selection for the most colourful males by reducing the differences in coloration between males. The mechanism behind this observation remains unclear. In theory, such a correlation should reduce the colour variance after feather exposure, yet we found that the variance remained constant before and after exposure. This result was strengthened by the outcome of the avian visual models, which assessed how birds perceive differences in coloration at the population level. Achromatic between-individual colour contrast did not differ between the first and the second measurement. The chromatic between-individual contrast for the second measurement was significantly higher than for the first measurement. However, this difference was, on average, only 0.06 JND, which means it is too small to be perceived by birds. Thus, the above results suggest that the initial plumage colour is not the cornerstone of the mechanism of the colour changes that were observed in this study.

It should be noted that our experiment was performed a specific geographical location. It is possible that the result of exposing the same feathers in another place would be different, due to local climate, land use, types of crops, traffic, etc., due to the different air particles that are generated. Moreover, different local natural conditions could also promote other agents potentially responsible for feather colour change. For example, the hot and humid climate of Alabama could be a better environment for keratin-degrading bacteria.

Spectrophotometry yields very accurate measurements that capture even minute changes in plumage reflectance. However, the ability of birds to discriminate between colour signals depends on opponent photoreceptor interactions, which is limited by receptor noise (Vorobyev et al. 1998, 2001; Kelber et al. 2017). Contemporary methods enable calculations of signal-to-noise ratios using data from the spectral sensitivities of rods and cones, their relative numbers in a retina, transmittance of light spectra in a cornea, and spectrum of ambient light illuminating the

object studied (Vorobyev et al. 1998, 2001). The results of the avian visual models suggest that the patterns of colour change that we measured are hardly perceivable by birds; both chromatic and achromatic within-individual contrasts between clean and dirty feathers in all habitat types were, on average, well below 1.0 JND. This result contrasted with the mean between-individual colour contrast, which expressed how birds perceive colour differences at population level, which was significantly higher. Similar results were obtained from the UV/blue feathers of blue tits wherein natural soiling resulted in a visible effect only in achromatic contrasts (Surmacki 2011). Nevertheless, we cannot exclude the possibility that the patterns of plumage colour change described in the current study could ultimately affect avian visual communication. First, longer exposures to air may result in greater changes in colour. Indeed, the iridescent structural coloration of European starlings showed a progressive reflectance decrease over 3 weeks (Griggio et al. 2010). Second, the intensity of sedimentation of airborne particles may depend on the season. While we conducted this study in spring, we might have expected visible differences in winter when air pollution increases due to burning coal for heating buildings (Pastuszka et al. 2015).

We assume that the main mechanism behind the observed changes is the deposition of airborne particles; however, further studies need to verify this assumption. Importantly, our experiment only imperfectly mimicked the soiling effect that likely occurs in living birds. In more a realistic scenario, birds would be exposed to soiling for longer periods of time, move within their habitats, preen their plumage, and engage in many other activities that may affect dirt accumulation. Another challenging issue which warrants further studies is the quantitative and qualitative analysis of the particles that settle on bird plumages; this is important because the optical properties of particles are key for understanding how they affect plumage coloration.

This research highlights the significance of human activity on avian plumage colour change during the period between-moult cycles, which could have an impact on avian visual signalling and sexual selection. We show that land use and road traffic may have different effects on plumage coloration. This study opens the field for further studies focusing on how the optical properties of specific airborne particles can influence coloration of wild-living animals.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00265-023-03404-9>.

**Author contribution** AS conceived the project, designed methods, wrote the original draft, analysed and visualized data. LS collected the data, prepared the original draft. AP performed field work and lab analysis, visualized data, prepared the original draft. All authors read and approved the final manuscript.

**Data availability** All data generated or analysed during this study are included as supplementary information files.

## Declarations

**Ethics approval** All applicable national and institutional guidelines for the use of animals were followed. Feathers collected under two permits:

1. US federal permit to capture birds and collect feathers (MB167551-0).
2. Auburn University permit to handle birds and collect feathers (2008–1341).

**Informed consent** All authors have given consent for submission of the manuscript.

**Conflict of interest** The authors declare no competing interests.

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