BEING DARK IS BETTER: A FERAL PIGEON PLUMAGE POLYMORPHISM AS A RESPONSE TO URBAN ENVIRONMENTS IN SLOVAKIA

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Received: 26 July 2020 / Accepted: 3 September 2020

Abstract

Csanády A., Duranková S.: Being dark is better: A feral pigeon plumage polymorphism as a response to urban environments in Slovakia. *Ekológia (Bratislava)*, Vol. 40, No. 1, p. 54–61, 2021.

The purpose of this study was to determine the distribution and plumage phenotypes of the feral pigeon, *Columba livia* forma *urbana* (Gmelin, 1789), in Slovakia. Censuses carried out in the built-up areas of 16 towns and cities from November to February (2012–2018) counted and evaluated 3,123 individual birds. The most frequent were melanic colored birds (checker, T-pattern and spread phenotypes), which predominated in the population (51.6%, $n = 1,613$), followed by paler ones (42.1%, $n = 1,316$) and other types (6.2%, $n = 194$). A statistically significant difference was confirmed among the melanic and paler plumage phenotypes ($\chi^2 = 81.49$, $df = 15$, $p < 0.0001$). Correlation confirmed the different importance of city area and human density on the maintenance of dark and/or pale pigeons living in cities.

Key words: color, feather variability, urbanization process.

Introduction

The feral pigeon, *Columba livia* forma *urbana* (Gmelin, 1789), is one of the most numerous urban bird species in many European and American cities (Janiga, 1991; Johnston, Janiga, 1995; Saari, 1997; Obukhova, 2001, 2007, 2011; Sacchi et al., 2002; Hetmański, Jarosiewicz, 2008; Ferman et al., 2010; Kowalski et al., 2011; Jacquin et al., 2010; Čanádý, Mošanský, 2013, 2016; Vickrey et al., 2018; Pardo et al., 2018). The mentioned authors showed that large concentrations of these birds were primarily observed in old town centers, in church towers, museums, theatres, railway stations, and attics. The pigeons nest and breed mainly under roofs and in niches of old houses, on the balconies of panel blocks of flats, and in factories and bridge constructions. Moreover, the mentioned authors confirmed the significant diversity in pigeon plumages among the populations and reported adaptation mechanisms and a direction of selection favoring different morphs.

Changes in the phenotype distribution in populations were also associated with changes in the social structure of the human population (Obukhova, 2007). Urbanization is the most dynamic phenomenon worldwide, and many species colonize urban environments. The urbanization process introduces important changes in habitats or creates new urban ecosystems where ecological functions are affected by human activities (e.g., Čanádý, Mošanský, 2017; Tryjanowski et al., 2017). The higher frequency of some phenotypes in urban

versus rural/wild areas has led to the assumption that directional selection occurs in urban habitats and may thereby favor some behavioral and physiological traits in urban animal populations compared to rural ones (Jokimäki, Suhonen, 1998; Obukhova, 2007; Jacquin et al., 2011, 2012, 2013a,b; Przybylska et al., 2012; Récapet et al., 2013; Čanádý, Mošanský, 2017; Tryjanowski et al., 2017). Obukhova (2007) showed that the blue color was more adaptive in natural habitats. This morph was found in rural populations more frequently than in urban ones. Moreover, constant and rich sources of food in urban habitats. Melanistic birds were accumulated, because their behavioral characteristics make them more resistant to a high population density. She assumed, that new possibilities for the formation and maintenance of polymorphism appeared when an increase in population density was accompanied by changes in behavioral stereotypes. The ability to spread to new subniches leads to ecological segregation of the species, thereby increasing its resistance to sudden fluctuations of environmental conditions. Behavioral adaptation in colonies of the blue rock pigeons results in a structured community in which genetic exchange between groups is maintained at a certain level and the gene pool of the total population is preserved.

In this context, melanin-based coloration is a good candidate trait to investigate the effect of urbanization process (i.e., selection forces associated with urbanization), because it has a strong genetic basis (Roulin, 2004). A number of studies

Table 1. Basic characterisation of the studied cities with feral pigeons (*Columba livia f. urbana*) in eastern Slovakia.

City	GPS coordinates	City area (km ²)	Human density (inhab./km ²)	Height m a.s.l.
Košice	48°43'12"N/21°15'29"E	237.05	984.87	208
Stropkov	49°12'18"N/21°39'05"E	24.67	431.86	202
Svidník	49°18'20"N/21°34'04"E	20.20	549.31	230
Prešov	49°00'00"N/21°14'00"E	70.43	1265.63	255
Bardejov	49°17'32"N/21°16'35"E	72.39	450.16	323
Medzilaborce	49°16'15"N/21°54'14"E	47.48	139.26	326
Giraltovce	49°06'42"N/21°31'00"E	11.4	377.55	195
Vranov nad Topľou	48°52'51"N/21°40'24"E	34.36	657.42	132
Michalovce	48°44'57"N/21°54'05"E	52.81	741.36	114
Trebišov	48°38'01"N/21°43'02"E	70.16	350.44	109
Humenné	48°56'09"N/21°54'24"E	28.76	1 168.04	157
Moldava nad Bodvou	48°36'23"N/21°00'01"E	19.77	573.70	216
Rožňava	48°39'30"N/20°31'51"E	45.61	420.65	313
Štútník	48°39'28"N/20°21'54"E	34.54	44.01	284
Revúca	48°40'59"N/20°06'48"E	38.87	315.13	318
Veľký Šariš	49°02'18"N/21°11'30"E	25.73	240.38	269

have reported differences in pigeon melanin-based coloration between urban and rural areas (Obukhova, 2001, 2007, 2011), and it has been frequently reported to covary with other phenotypic traits, such as immunity, behavior, or reproduction (Ducrest et al., 2008; Jacquin et al., 2010, 2011; 2012, 2013a,b; Récapet et al., 2013).

In consequence, more dark, that is, melanic pigeons were observed in city centers than on their peripheries. These differences were demonstrated in Gdańsk (Poland) by Hetmański, Jarosiewicz (2008), who confirmed that blue-bar birds were dominant in the old city center, while melanic individuals prevailed in the more recently built housing estate districts surrounding the city center. Čanády, Mošanský (2013) showed for Košice's populations (Slovakia) that melanic birds were more common than blue-bars. Similar ratio in color were observed between the center and the periphery of a city.

Several authors (Lofts et al., 1966; Hetmański, 2008; Kowalski et al., 2011) have devoted greater attention to ecological processes related to the maintenance of coloration polymorphism. Lofts et al. (1966) showed that melanic birds were seen more often in cities because their gonads are active even in winter in contrast to blue-bars, and they thus produce more pups during the longer breeding season. In contrast, Kowalski et al. (2011) disproved the thesis that climatic conditions significantly shaped the polymorphism of feral pigeons. Hetmański (2008) considers the *founder's effect*, that is, the different history of each population and varying environmental conditions in cities, to be the most important factor determining the frequency of color and phenotypic forms in the feral pigeon population.

On the other hand, several authors (Gasparini et al., 2011; Jacquin et al., 2011, 2012, 2013a,b; Récapet et al., 2013) reported an adaptation to the urban environment which brings some benefits based on melanin-based coloration. It was confirmed that checkered and T-pattern pigeons had higher fre-

quencies of successful fledging from the nest and longer (up to year-round) breeding seasons; in addition, they are able to sequester more toxic heavy metals in plumage pigments through chelation (Lofts et al., 1966; Janiga, 1991; Chatelain et al., 2014, 2016; Vickrey et al., 2018).

According to the cited studies, the properties associated with darker coloring are consistent with those of individuals in urban and/or stressful areas. All the findings suggest that melanin-based coloration reflects adaptations to different environmental conditions (Roulin, 2004). Therefore, directional selection could be expected to affect this property. The suitability of dark individuals of several bird species should be higher than that of paler individuals in urban areas, which could result from differences in survival, reproductive success, and habitat selection (Roulin, Altwegg, 2007; Roulin et al., 2000, 2008, 2010; Van den Brink et al., 2012; Saino et al., 2013).

The aim of this study was to evaluate the plumage phenotype of feral pigeons in the urban areas of 16 towns and cities in eastern Slovakia. If melanin-based coloration reflects an adaptation to the urban environment, we assumed that melanic birds would occur in higher numbers than paler birds.

Material and methods

The study was conducted within the administrative borders of 16 cities or towns in eastern Slovakia (Table 1). With the exception of Košice, which represents one of the three largest cities in Slovakia in terms of area, all the other cities were medium or smaller in size based on the area in km². In this study, we also used our previously published data from Košice (see Čanády, Mošanský, 2013) and the towns of Stropkov and Svidník (see Čanády, Mošanský, 2016). Censuses of pigeons were conducted by walking through cities in built-up areas during the autumn and winter seasons, that is, from November 2012 to February 2019. According to Hetmański, Jarosiewicz

Table 2. The number of phenotype forms distinguished in feral pigeon (*Columba livia* f. *urbana*) populations in the urban environments of eastern Slovakian cities.

City	Date	Blanc	Wild	Checker	T-pattern	Spread	Rufous	Other	Summary
Košice	2013*	10	431	246	335	73	22	104	1 221
Stropkov	2016**	2	11	5	13	7	1	3	42
Svidník	2016**		15	13	15	3	4	5	55
Prešov	18-20 October 2018	12	205	49	168	12	6	6	458
Bardejov	26 October 2018	2	24	10	18		3		57
Medzilaborce	27 October 2018		23	1	20	8	2		54
Giraltovce	27 October 2018		11	4	8	11	1		35
Vranov nad Topľou	27 October 2018		75	4	22		5	1	107
Michalovce	27 October 2018	2	51	4	34	10		1	102
Trebišov	27 October 2018	8	177	20	184	31	20		440
Humenné	9 February 2019	2	17	14	14	1	1		49
Moldava nad Bodvou	16 February 2019	3	134	82	55	12	6		292
Rožňava	17 February 2019	1	46	9	22	1	2		81
Štitník	17 February 2019		15	25	10				50
Revúca	17 February 2019		11	2	22	1			36
Veľký Šariš	21 February 2019	3	25	10	5			1	44
Summary		45	1 271	498	945	170	73	121	3 123

Notes: * – Čanády, Mošanský, 2013; ** – Čanády, Mošanský, 2016.

(2008), this period represents the best time to study plumage phenotype distribution and the numbers of pigeons in cities, because only a few birds are breeding, or breeding has stopped altogether. Moreover, at this time, pigeons are found away from buildings at foraging sites. Pigeons were observed and counted for 1 hour at sites where these were abundant, for example, railway or bus stations, squares, marketing places, and other places where a pigeon flock was found. All the pigeons with different phenotypes were counted.

The urban areas of all the evaluated cities were characterized by panel housing blocks, tall buildings, churches, cafés and shops, which create an ideal synanthropic environment for feral pigeons. The fact that a significantly greater number of pigeons occupy older buildings in the city centers than areas in the outskirts of the city was confirmed (Sacchi et al., 2002). Plumage phenotypes in all the cities were recorded and determined using binoculars (Bresser Hunter 10x50, Grossfeld 119/1000 m) according to the previous studies (see Čanády, Mošanský, 2013, 2016).

On the basis of our observations, six color plumage phenotypes and one group of individuals that had not been classified with any of these forms were distinguished (Čanády, Mošanský, 2013, 2016): (1) the *blue-bar* or *wild* phenotype, that is, a gray mantle with two dark wing bars, but many birds had a lilac shade, and the bands on the wings were brown instead of black; (2) the *blanc* or *white* phenotype, that is, white or almost white individuals; (3) the *spread* or *black* phenotype, that is, a completely melanic plumage; (4) the *checker* or *lightly checker* phenotype, that is, a checkered mantle with moderate dark spots; (5) the *T-pattern* or *dark checker* phenotype, that is, a dark mantle with small gray marks; (6) the *rufous* phenotype, that is, beige-and-grey plumage, sometimes with

white elements, two brown stripes on the wings but no stripe on the tail, and a gloss on the neck; and finally (7) the *others* group, which included individuals with phenotypes that had not been classified with any of these forms. These patterns are all primarily determined genetically (Jonhston, Janiga, 1995) and differ by the surface of the dark area on the wings, which corresponds to different melanin deposition in the feathers (Haase et al., 1992).

Plumage phenotypes were firstly treated separately and then pooled as *melanic* (i.e., checker, T-pattern and spread phenotypes) or *paler* (wild and blanc) compared using the chi-square (χ^2) test. The relationships among city area and human density and color phenotypes were also explored with Spearman's correlation analysis (r_s).

Data on city area (km²) and human density (inhab./km²) were obtained from the Wikipedia web site (www.wikipedia.org). All the traits were coded in quantitative (number of pigeons for phenotype morphs) or ranked scales, that is, for city area (1 – less than 70 km²; 2 – 70–140 km²; 3 – more than 140 km²) and for human density (1 – less than 500 inhab./km²; 2 – 500–1000 inhab./km²; 3 – more than 1000 inhab./km²). Such a division was subjective and served only to simplify further analyses.

The chi-square (χ^2) test and Spearman's correlation analysis (r_s) were performed using MS Excel 2003 for Windows XP and the statistical analysis system GraphPad Prism, version 5.01 (Graph-Pad Software, Inc., San Diego, California, USA).

Results

The censuses counted a total of 3,123 feral pigeons, which were evaluated for plumage polymorphism (Table 2). The

Fig. 1. Two plumage phenotypes (melanic and paler) distinguished in the population of feral pigeons (*Columba livia f. urbana*) in the urban environments of Slovakian cities showed by (a) city area and (b) human density.

census of plumage patterns showed different frequencies for each of the studied cities (Figs 1a, b), with a predominance of paler pigeons for 11 cities. The distribution of both morph groups were also different according to pigeons, city area, and human density. Nevertheless, overall melanistic birds predominated (51.6%, $n = 1.613$), while paler birds (42.6%, $n = 1.316$), were the second most frequent group. The frequency of birds with aberrant plumage color, that is, *rufous* and *other* phenotypes, varied and was higher in some cities. However, this prevalence was not influenced only by city size or population density (see Fig. 1). Rufous pigeons comprised 2.3% of the population, and 3.9% of the pigeon populations were not classified with any of the distinguished phenotypes (Table 2).

The chi-square test confirmed statistically significant differences between color phenotypes (Table 3) as well for the melanistic and paler plumage phenotypes in pigeons occupying different cities ($\chi^2 = 81.49$, $df = 15$, $p < 0.0001$). Our results

confirmed the positive and significant relationships between melanistic feathers and city area as well with human density in the cities (Table 4).

Discussion

Several authors showed that traits associated with darker coloration match those found in individuals exploiting urban and/or stressful areas. Melanin-based coloration might reflect an adaptation to the urban environment because it brings some benefits that are also transmitted to future generations (Roulin, 2004; Jacquin et al., 2013a). Therefore, it represents a good precondition for investigating some ecological issues. According to this assumption, directional selection should favor this property, and the frequency of darker individuals should be higher than that of pale individuals in urban areas, which could result from differences in survival, reproductive success, and habitat

Table 3. Chi-square test (χ^2) between the plumage color of feral pigeons (*Columba livia f. urbana*) from cities in Slovakia. Significant values were evaluated in level * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(a)

	Stropkov	Svidník	Bardejov	Medzilaborce	Giraltovce	Humenné	Rožňava	Štítник	Revúca
Svidník	8.63								
Bardejov	16.41*	12.85*							
Medzilaborce	11.36	20.62**	17.62**						
Giraltovce	6.61	15.19*	21.20***	8.31					
Humenné	12.62*	9.68	3.78	19.76**	16.95**				
Rožňava	24.79***	25.32***	8.36	18.16**	27.38***	11.13*			
Štítник	26.85***	16.59*	15.40**	37.07***	26.21***	7.79	24.50***		
Revúca	13.72*	16.77*	12.46*	8.86	21.52***	13.39*	12.63*	24.07***	
Veľký Šariš	21.86**	21.75**	8.78	28.57***	23.13***	8.30	9.14	12.54*	25.06***

(b)

	Košice	Prešov	Vranov nad Topľou	Michalovce	Trebišov
Prešov	76.86***				
Vranov nad Topľou	65.48***	33.16***			
Michalovce	32.00***	17.32**	24.04***		
Trebišov	123.4***	37.36***	40.72***	13.23*	
Moldava nad Bodvou	47.22***	57.94***	40.58***	37.39***	105.9***

selection. This assumption has also been supported by the results observed in some birds (Roulin, Altwegg, 2007; Roulin et al., 2010; Van den Brink et al., 2012; Saino et al., 2013).

Our results confirmed that the distribution of color phenotypes was rather heterogeneous for each studied city. Although the chi-square (χ^2) test confirmed the overall predominance of the melanic type across cities and towns, the paler pigeons prevailed in 11 of them. These findings were in accordance with the observations made by Obukhova (2001, 2007) that pigeon populations were characterized by a polymorphism of color patterns with different phenotype frequencies. She also showed the existence of different conditions for the origin of the urban populations of feral pigeon and consequent high genetic heterogeneity of this species. On the basis of these findings, she assumed that the key aspect of color polymorphism in feral pigeon was synurbization, that is, anthropogenic evolution. Later, she also demonstrated changes in the frequency of distribution of several plumage color phenotypes during the 30-year dynamics (from 1978 to 2008) in Moscow (Obukhova, 2007). Mainly she showed that, the frequency of the melanic phenotype decreased as a result of a decrease in the total pigeon population size and, consequently, population density in colonies. This change led to increased proportions of wild type and aberrantly colored birds throughout the city and an increased frequency of transitory phenotypes in the central region. An increase in the proportion of aberrant phenotypes suggests an increase in the genetic heterogeneity of the populations. The proportion of strongly melanic pigeons was higher in urbanized area, suggesting different selective pressures along an urbanization gradient.

Pigeons colonize cities from their center to the periphery and live in a highly urban environment, where they utilize the resources provided by the urban environment. They depend directly on processes that take place in the social structure of the human population, and changes in the structure of the urban

Table 4. Spearman's correlation coefficients (r_s) between the plumage color of feral pigeons (*Columba livia f. urbana*) and city area and human density in Slovakia. Significant values were evaluated in level * $p < 0.05$, ** $p < 0.01$.

	city area (km ²)	human density (inhab./km ²)
Blanc	0.42	0.18
Wild	0.51*	0.08
Checker	0.36	0.06
T-pattern	0.58*	0.19
Spread	0.74**	0.62
Rufous	0.68*	0.32
other	0.83*	0.31

pigeon population reflect changes in the human population and vice versa. Pigeon populations respond adaptively to dramatic alterations in environmental conditions, such as changes in the amount and accessibility of food and nesting places. When feeding resources are poorer due to social anthropogenic factors, the pigeon population size decreases. This leads to changes in the phenotype frequencies, which are an adaptive response of the population to environmental changes (Obukhova, 2007).

Nevertheless, our results, as well as the above-cited studies, show that paler morphs also represent a very significant part of the pigeon population in urban areas. Jacquin et al. (2011) assumed that despite benefits in term of blood parasite resistance, being darker also entails some costs. Gasparini et al. (2009) showed a stronger immune response in melanic birds but at the cost of a greater body mass loss. Similarly, darker morphs could be more resistant to endoparasites, such as blood parasites, but more susceptible to other parasites, such as ectoparasites

(Chakarov et al., 2008). According to these findings, different selection pressures by parasites may lead to the favoring of intermediate morphs (e.g., heterozygous advantage) in a population, thus promoting the maintenance of polymorphisms in environments with both types of parasites. This is because each morph could be better adapted to different types of parasites or to alternative exposure levels (Roulin, 2004). The positive relationships between immune responsiveness and parasite intensity with different coloration (e.g., Jacquin et al., 2011; Gasparini et al., 2011) suggests that melanin-based coloration could also play an important role in sexual selection (Burley, 1977), that is, in captivity, females and males of feral pigeons tend to prefer darker-colored partners. Therefore, it cannot be totally excluded that mate choice according to coloration could also depend on the presence of parasites in the environment (Jacquin et al., 2011).

All the above-mentioned observations give a partial explanation of why the less amount in dark forms was confirmed in 11 Slovakia cities (see Fig. 1) but coupled with a higher frequency of aberrant color types. This is also highlighted by the fact that a decrease in the feral pigeon population in the historical center of Košice city over the last decades was confirmed (Čanádý, Mošanský, 2013). However, this explanation seems to be too simple, and there is likely to be a combination of multiple factors affecting the overall maintenance of individual color phenotypes (Roulin, 2004, 2009; Roulin, Altwegg, 2007; Roulin et al., 2000; 2001, 2008, 2010; Obukhova, 2001, 2007; Ducrest et al., 2008; Gasparini et al., 2011; Jacquin et al., 2011, 2012, 2013a,b; Van den Brink et al., 2012; Saino et al., 2013).

In contrast, the directional change in the frequency of aberrant phenotypes also opens up a very interesting issue, that is, pressure from predators (see Obukhova, 2007). It was thus also due to the overall success of attacks on pigeons with different phenotypes by predatory birds, such as hawks, falcons, or packs of crows, or by town predators, such as cats or dogs, depending on how distinguishable the plumage color was from a flock. Mikula et al. (2013) noted an increase in several raptors, such as *Accipiter gentilis* (Linnaeus, 1758), *A. nisus* (Linnaeus, 1758), *Falco tinnunculus* (Linnaeus, 1758), and *Buteo buteo* (Linnaeus, 1758), in urban environments in recent decades, although urbanization has also been associated with a decreased abundance of raptors that keep a safe distance from humans (Díaz et al., 2013; Mikula et al., 2013; Mikula 2014; Tryjanowski et al., 2016). Chace, Walsh (2006) showed that this was caused by changes in the food supply, and predators' habituation to novel nesting substrates may further influence the spectrum of predators in urban habitats and subsequently change predation risk for urban birds (Chace, Walsh, 2006). Nevertheless, urban birds are threatened more often by mammalian predators, such as cats and dogs or by disturbance from humans (Møller, 2008; Møller, Ibáñez-Álamo, 2012; Mikula et al., 2013; Tryjanowski et al., 2016). According to the cited studies, urban birds are typically exposed to moving cats, dogs, or humans and, therefore, could have consistently lower flight initiation distance (FIDs) than birds from rural sites (more often threatened by avian predators). For example, Mikula (2014) estimated the FIDs for feral pigeon to be only 2.78 m.

Nevertheless, interpreting FID results this broadly can be tricky, as it is always measured as a response given to approaching humans, yet it is usually considered to be a general fear

(anti-predatory) response against any non-flying predators (including humans) – which is likely overly simplifying as a city-dweller bird can surely make a difference between a passing by human (low threat level, i.e., harmless in most of the cases) and a cat (seldom if ever harmless) see (Blumstein, 2014; Vincze et al., 2019).

Chace, Walsh (2006) assumed that avian communities could be differentially affected when city districts differ in the composition (predominantly mammalian or avian) and density of their predator fauna. This may also be a factor that is important for affecting the population size and for maintaining melanin color phenotypes in the stable and healthy pigeon population.

Also, several explanations were proposed for feral pigeons, in relation to explaining color polymorphism, such as differential adaptation to urban conditions (Johnston, Janiga, 1995), parasites (Jacquin et al., 2011, 2013a, b), or food availability (Jacquin et al., 2012). Récapet et al. (2013) showed that eumelanin-based coloration was under directional survival selection in dense populations of highly urbanized areas and that such selection occurs through the differential survival or dispersal rate of juveniles. They also assume that interactions between melanin-based coloration and population densities (see also Obukhova, 2011) could explain the observed differences in local survival. Moreover, a positive correlation between urbanization level and the proportion of dark phenotypes was found within the urban areas of several European cities (Obukhova, 2001, 2007; Jacquin et al., 2013b; Récapet et al., 2013). The results obtained in these studies confirmed the differences in fitness and/or habitat choice between dark and pale pigeons in urban areas.

To conclude, this study provides knowledge on melanin-based coloration in feral pigeons from Slovakia. Our findings thus contribute to the growing body of evidence that darker eumelanin individuals in urban environments have a higher abundance than paler ones. A current survey of color variation in pigeons from free-living populations in various cities of Slovakia may yield interesting information on the environmental correlates of coloration-dependent local survival. We also observed differences in the number of color phenotypes according to city size and/or human density, which were consistent with such effects, but future long-time studies are needed to provide sufficient data to confirm them in full. Moreover, our results are in agreement with the assumption that melanin-based coloration reflects an adaptation to the urban environment or to stressful factors to which urban birds are more exposed.

Acknowledgements

Our thanks also go to anonymous referees for their valuable comments on the manuscript and to David McLean for revising the English language.

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