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Feral pigeon melanism may vary with local climate; an example from the West Carpathians

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Abstract. Local pigeon populations surveyed in Slovak towns are intricately linked to the anthropogenic environment of their particular habitat. In the past, this has generally been more limited to historical, commercial areas, and agricultural areas, but more recently, pigeons are also expanding into newly built neighbourhoods and housing estates. The group of melanic pigeons was largely dominant in terms of abundance in 1998 and 1999 (in 1998 its lowest abundance was 42 %, and in 1999, 49 %). The second most numerous was the blue-bar phenotype, whose abundance ranged from 15 to 40 % in 1998 and from 17 to 34 % in 1999. The group of red and brown pigeons was the least numerous. The relationship between altitude and the abundance of the individual phenotypes was statistically significant only in the case of the melanic group. When examining the influence of weather factors, it was statistically proven that more melanic pigeons were found in mountainous areas with lower temperatures, higher humidity and precipitation. On the other hand, the abundance of pigeons with red plumage is statistically significantly higher in conditions of warm but humid weather in lower-lying urban areas.

Key words: feral pigeons, phenotype, abundance, melanism, Slovakia

Introduction

In all places where feral pigeon populations exist, a feather polymorphism has developed (Murton *et al.* 1973). According to Dunmore (1968), at least 20 colours and patterns were recorded in populations of the rock pigeon *Columba livia* L., which were well described by Levi (1963). Domestic pigeons also have a large variability of colours and patterns, which are characterised by human selection. Therefore, the variability of colour and pattern in feral pigeons is the result of an interaction between repeated mutations, and stems directly from their domestic ancestors (Podhradský 1953; Hollander 1983; Johnston and Janiga 1995) as well as selection pressure (Cole 1969). Variability in feral pigeon populations could be also partially affected by mixing with messenger pigeons (Leiss and Haag-Wackernagel 1999). Generally, feral pigeons have two or three times higher genetic variability than other bird species and likely have the highest known colour variability among wild birds (Johnston and Janiga 1995), as well as diversity, which results from the actions of pigeon breeders (Murton *et al.* 1973). Different colour and pattern variants are associated with different ecological and physiological properties (Murton *et al.* 1973, Janiga 1991a, Johnston and Janiga 1995) such as long-lasting conditions that have the effect of limiting the ability to form pigment in the body or fission of chromatophores (Podhradský 1953).

The default type for colour deviations is the plumage pattern of the wild rock pigeon *Columba livia* L. (Podhradský 1953; Malík and Štefka 1970; Havlín 1983; Tureček 1985). It has greyish-blue wings, the chest is medium grey, lighter on the abdomen, and the feathers on the neck have a green-violet metallic lustre. The lower part of the back (coccyx) is white. Two black parallel bands stretch across the wings and the tail feathers are bluish-grey with a black band. The claws and beak are black, and the leg feathers are bluish-grey. The iris is orange-red with a blue-grey orbital ring (Podhradský 1953). This default rock pigeon plumage colour pattern is called blue-bar or wild type among geneticists and breeders (Podhradský 1953; Lofts *et al.* 1966; Dunmore 1968; Cole 1969; Murton *et al.* 1973; Hollander 1975; Ferianc 1982; Hollander 1983; Janiga 1991a; Johnston and Janiga 1995; Leiss and Haag-Wackernagel 1999). It has a black pigment (eumelanin) deposited in the form of microscopic granules which are produced by specialized melanocytes (Hollander 1983).

The overall plumage of a pigeon is composed of three factors; basic colour, basic pattern, (Ferianc 1982; Johnston and Janiga 1995) and additional factors (Gibson 1995). According to Johnston and Janiga (1995) and Leiss and Haag-Wackernagel (1999), pigeons have three basic colours: dominant red, blue (black) and brown. In the United States, Dunmore (1968) performed the first analysis of phenotypes and gene frequencies, thus allowing a geographical comparison with other localities. His results from Syracuse in the state of New York are followed by Cole (1969), who compares the number of basic phenotypes in the Arizona city of Tempe. In terms of colour, 96 % of Syracuse pigeons were identified as black. In Tempe, this colour accounted for just under 85 % of the total number (Cole 1969). Following these comparisons in two American localities, Cole (1969) assumes that the differences in the abundance of individual phenotypes are caused by unspecified environmental factors. In the 1990s, Glissmeyer (1996) investigated the abundance of individual phenotypes in the American cities of Boston, Los Angeles, and Salt Lake City. The feral pigeons that inhabited the Salford Shipyard in Manchester were dominantly melanic individuals (C, C^T, S), this wild type, or blue-bar represents only 21 % of the local population (Murton *et al.* 1973). A similar situation occurs in urban areas of many European cities. Meinertzhagen (1954) studied the polymorphism of pigeons and its distribution in London and found a decline in individuals with the blue-bar phenotype in favour of melanic pigeons until 1954. On the other hand, Lofts *et al.* (1966) found only 24 % of melanic phenotypes in the wild pigeon population in Flamborough Head in Yorkshire. The same author compared these results with the proportion of individual phenotypes of feral pigeons in Leeds and Liverpool, in which, on the contrary, he found a predominance of melanic individuals. In the Far East, the colour and pattern of pigeons plumage are different from those in Western Eurasia (Johnston and Janiga 1995). In Russia, polymorphism in feral pigeon populations was observed by Obukhova and Kreslavskii (1984), who determined that the proportion of melanic individuals was 87 % out of 1500 studied individuals in Moscow in 1979-83. Similar proportions were observed by Pechenev (1984) in Moscow in 1978-82. In Slovakia, Podhradský (1953) investigated the influence of various factors on the plumage of the feral pigeon in Bratislava. He also determined the ratio of phenotypes in a group of 497 individuals. Later, between 1981 and 1985, Janiga (1991a) determined the proportions of selected phenotypic groups (wild type, melanic group, group of "red" pigeons and group of white pigeons) in Bratislava, and compared these data with parameters of weight, wing length and other properties for each phenotypic group. The phenotypic composition of feral pigeons was also determined in Vienna in 1989 by Leiss (1989) and later in Vienna and Basel by Leiss and Haag-Wackernagel (1999). In the cities of southern Europe, Ballarini *et al.* (1989) found that 56 % of individuals identified as blue-bar phenotype, along with a much smaller percentage of melanic individuals in Piacenza. This was also confirmed by Ragionieri *et al.* (1991) in both Fertilia and Barcelona. Both authors also studied the proportion of phenotypes in the city of Bolzano, where the melanic group significantly predominated. The phenotype data from all mentioned sites was summarized by Johnston and Janiga (1995), who, based on the comparison of the phenotype ratios, tried to determine the factors influencing their changes.

According to Goodwin (1976), environmental factors can be different in various natural environments, which may eventually create different types of selection pressure affecting feral pigeons. According to Podhradský (1953) and Ferianc (1982), the same genotypes produce different phenotypes in changed conditions. Podhradský (1968) dealt with the way factor changes affect the plumage of the feral pigeon in experimental conditions, in addition to Johnston and Janiga (1995) who showed that the adaptation of melanin expression can be caused by experimental conditions influencing the environment.

The abundance of some phenotypes in local populations is influenced by certain abiotic environmental factors, but in particular by their interconnected complex. Podhradský (1968) experimentally found a change in the colour of some phenotypes during moulting due to changes in external factors like temperature and humidity. In urban environments, this would mean that local populations of feral pigeons are affected by local climatic characteristics, which in a small area of Slovakia, depend on orographic conditions. This issue of the influence of altitude and altitude-based climatic factors was raised by Johnston and Janiga (1995), who found a statistically significant deviation in the number of melanic individuals with declining northern latitudes in the alpine Italian town of Bolzano and in some Eurasian localities. The ideas of these authors lead to the assumption that climatic factors related to altitude can replace the influence of latitude. Therefore, the main aim of this paper is the determination of the possible dependence of individual phenotypic groups' abundance on altitude as well as specific climatic factors.

Material and Methods

Study sites

Polymorphism and regional differences in plumage colour and pattern of feral pigeons was studied in nine Slovak cities (Trnava, Leopoldov, Piešťany, Trenčín, Nové Mesto nad Váhom, Žilina, Martin, Ružomberok and Liptovský Mikuláš) during the winter (February and March) in 1998 and 1999 (Fig. 1). In both years, local populations of pigeons were observed in the same parts of the cities and their outskirts. An SVHS video camera recorder (Panasonic, Japan) or binocular was used to record footage.

In Trnava, the aggregation of 99 individuals was observed on the buildings close to as well as inside the Figaro complex in 1998. Video of these pigeons was easily captured by a video camera, as the pigeons gradually settled on the roofs of the objects in the evenings. In 1999, the observation area in Trnava extended to populations of pigeons nesting on the rocky river bank of the Trnávka river, at the buildings close to the sugar factory, and in the recesses of old buildings on Schneidera-Trnavského Street. As such, the number of pigeons observed in Trnava increased to 156 individuals. After several surveys in Leopoldov, we identified one local group of feral pigeons on the roof of the railway station. Similarly to Leopoldov, in Nové Mesto nad Váhom, Trenčín and Žilina, the local population of pigeons was concentrated at one site. In Nové Mesto nad Váhom, pigeons were largely observed at a silo close to the railway station. In Trenčín, pigeons were concentrated at Mierové námestie

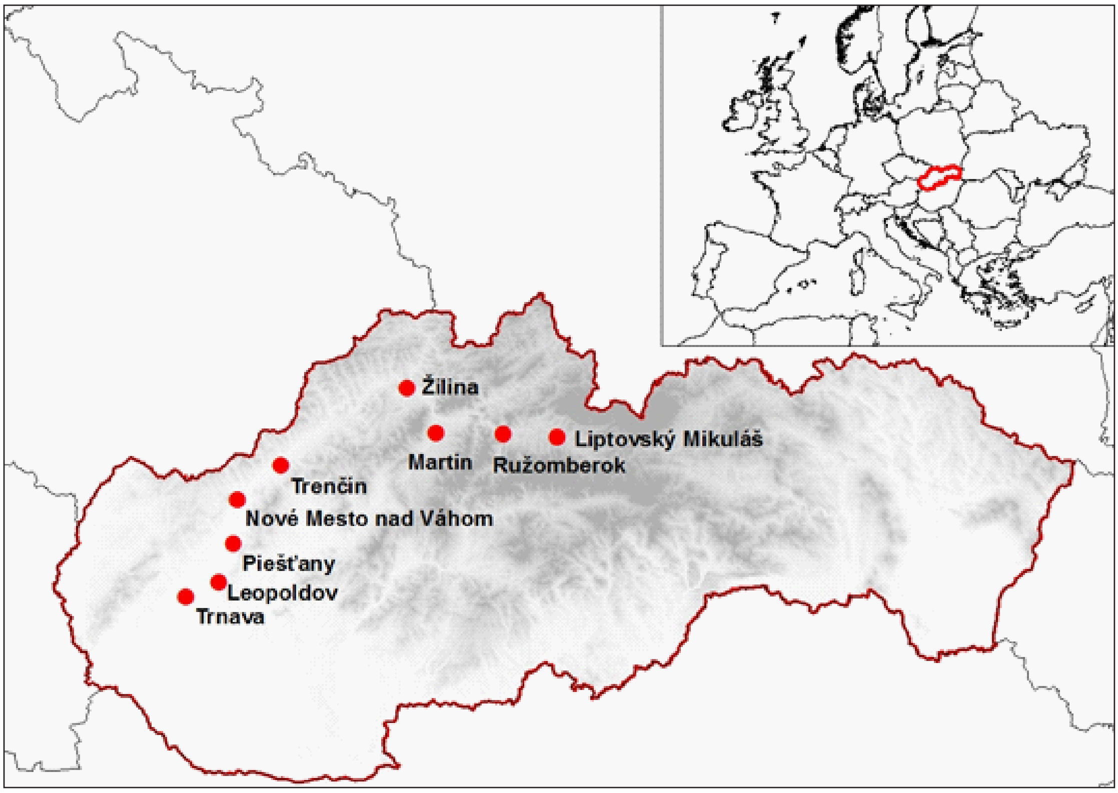

Fig. 1. Studied cities of Slovakia, where proportions of individual phenotype of feral pigeon were counted.

in the historical city centre, and in Žilina they resided in the main square in the commercial and historical part of the city. In Piešťany, several scattered aggregations of pigeons were observed during both years. The most abundant one was found in the city centre on the bank of the Váh River and surrounding buildings, where pigeons were fed as a result of people feeding seagulls and swans. Two other relatively large groups were observed in two housing estates on the outskirts of the city. In Martin, more groups were recorded; in the commercial centre of the city, in a housing estate on the outskirts of the city, and also at a silo where the number of pigeons was the largest, but access was not granted during either year of the study. In Ružomberok and Liptovský Mikuláš, pigeons were concentrated in several groups, but only in the historical and commercial centre of the city.

The above descriptions of pigeon habitats show that feral pigeons are closely linked to the anthropogenic environment, populating mostly historic parts of the city suitable for nesting and with a high concentration of people. Other locations include silos and food processing facilities, representing an important food source. However, they are already expanding to the surrounding newly built parts too, as is it in the case of Martin and Piešťany.

Determination of phenotypic composition of local populations

Descriptions and classification using Leiss and Haag-Wackernagel (1999) was used to distinguish the most common phenotypes occurring in urban populations. Pigeons were divided into four phenotypic groups (blue-bar, melanic, red, pied) based on the pattern and colour of their plumage. These groups were chosen so that the number of melanic (dark) individuals and their ratio to other groups was immediately apparent.

The first group includes pigeons with a plumage pattern similar to wild rock pigeons. This is called wild type or blue-bar phenotype. The second group is a group of melanic individuals with blue-checker, blue-T-pattern and spread phenotypes. The third group consists of pigeons that have plumage that is primarily red and brown. Pigeons that have varying degrees of their body covered with red or brown colours were also added to this group. Pigeons assigned to this group belong mainly to the following phenotypes: ash red-bar, ash red-checker, ash red-T-pattern and recessive red. The fourth group consists of white pigeons. This group includes all-white individuals or individuals with plumage containing white colour. The presence of white is conditioned by a complementary factor (Gibson 1995) to the main colour and pattern. These are the phenotypes: pencilled, grizzle, tiger-grizzle and recessive white. Not reliably categorized phenotypes were included in the fifth group of unidentified phenotypes.

Statistical evaluations

For each studied city, the relative abundance of each of the four main phenotype groups of feral pigeons were evaluated and statistically processed with factors of environment, especially altitude and weather conditions. The list of weather factors measured during the study can be found in Table 1. The relationship between abundance of phenotype groups and altitude was evaluated by correlation using linear regression. Altitude with weather variables converted to factors by principal component analysis (PCA). Resulting component scores were correlated with the data reflecting abundance each phenotype group.

Results

The total number of individuals and the relative percentage within each phenotypic group (see methodology) recorded in 1998 and 1999 in selected Slovak cities is shown in Table 2. The group of melanic (hyperchromatic) pigeons (Fig. 2a,b) was significantly dominant in all cities and in both years. The prevalence of this melanic group was 42 % at minimum in the first year, and 49 % at minimum in the second year (Table 2). Individuals from this phenotype group represent more than half of the local population in most cities. Their higher abundance occurred mainly in cities at higher altitudes (except Liptovský Mikuláš).

The second most abundant phenotype group was the wild type/blue-bar pigeons. The abundance of this group was less in cities with higher altitude (except Žilina, Martin and Liptovský Mikuláš). Values representing the relative abundance of this phenotype range from 15 % to 40 % in the first year and from 17 % to 34 % in the second year of the study (Table 2). Pigeons with basic red and brown patterns were merged into the phenotype group of red pigeons. This group had low relative abundance in all examined cities.

Pigeons with basic red and brown patterns were merged into the phenotype group of red pigeons. This group had low relative abundance in all examined cities. In the examined Slovak cities, their average relative abundance was only 4.5 % in 1998 and 3.7 % in 1999, meaning that pigeons with red and brown patterns were relatively rare in urban populations (Fig. 2a,b). White or partially white pigeons (pied) were also rare or moderately rare (Fig. 2a,b).

Using linear regression, we observed statistically significant dependence on altitude in the case of the melanic phenotype group (Fig. 3). The correlation coefficient (Table 3) indicates a close connection between the above variables. In cities at higher elevations there was an increased abundance of melanic pigeons. Blue-bar and red pigeon abundance was not significantly correlated to altitude ($p > 0.05$).

The weather factors and altitude were processed by analysis of principal components. The resultant factors, especially PC 1, describe different weather conditions in mountainous areas (humid, rainy with low temperature) and in lowland areas (warmer and

	Average air temperature in °C					
	year 1998			year 1999		
	February	March	1998	February	March	1999
Trnava	4.9	4.3	10.8	-0.2	6.9	10.9
Leopoldov	4.0	3.7	10.6	-0.4	6.7	10.6
Piešťany	3.7	3.4	10.0	-0.4	6.6	10.0
Nové Mesto nad Váhom				-0.6	6.2	9.8
Trenčín	2.9	3.0	9.4	-0.8	6.1	9.7
Žilina	2.0	1.4	8.0	-1.3	4.5	8.5
Martin	2.0	1.5	8.2	-1.6	4.0	8.6
Ružomberok	2.4	1.4	8.0	-1.5	3.4	8.7
Liptovský Mikuláš	1.0	0.5	7.2	-2.7	3.4	7.6
	Average air humidity in %					
Trnava	60	54		65	60	
Leopoldov	61	59		78	65	
Piešťany	72	67		84	72	
Nové Mesto nad Váhom				82	73	
Trenčín	78	70		82	73	
Žilina	81	74		84	76	
Martin	83	76		87	78	
Ružomberok	69	75		77	75	
Liptovský Mikuláš	77	71		92	90	
	Monthly and annual total precipitation in mm					
Trnava	0	10	493	34	12	522
Leopoldov	1	15	516	50	26	632
Piešťany	2	14	626	38	20	615
Nové Mesto nad Váhom				67	37	706
Trenčín	2	27	627	60	31	689
Žilina	18	38	756	59	29	763
Martin	25	44	804	61	31	743
Ružomberok	13	42	764	59	30	604
Liptovský Mikuláš	12	46	644	59	19	719

Table 1. Values of weather factors used in the study.

Cities	lat. N	alt. m asl	Total number of individuals 1998	Total number of individuals 1999	year 1998 (II,III) in % Blue	mel.	Red	Wht	ndf	year 1999 (II,III) in % Blue	mel.	Red	Wht	ndf
Trnava	48˚	146	99	156	33	42	4	10	11	34	49	4	10	3
Leopoldov	48˚	151	130	217	33	50	4	11	2	32	50	2	11	5
Piešťany	49˚	162	73	91	30	51	3	8	8	29	51	7	11	2
Nové Mesto nad Váhom	49˚	195		198						19	51	9	16	5
Trenčín	49˚	211	60	140	22	53	8	10	7	17	53	7	13	10
Žilina	49˚	344	45	45	27	60	2	11	0	27	58	0	15	0
Martin	49˚	390	86	66	40	51	6	3	0	30	62	2	6	0
Ružomberok	49˚	490	41	77	15	63	7	15	0	18	65	1	14	1
Liptovský Mikuláš	49˚	590	60	197	30	52	2	6	10	21	59	1	8	11

Table 2. Relative abundance of pigeons according phenotype in selected Slovak cities with regards to altitude (lat. = latitude, alt. = altitude, Blue = blue-bar, mel. = melanic, Wht = white, ndf = non defined).

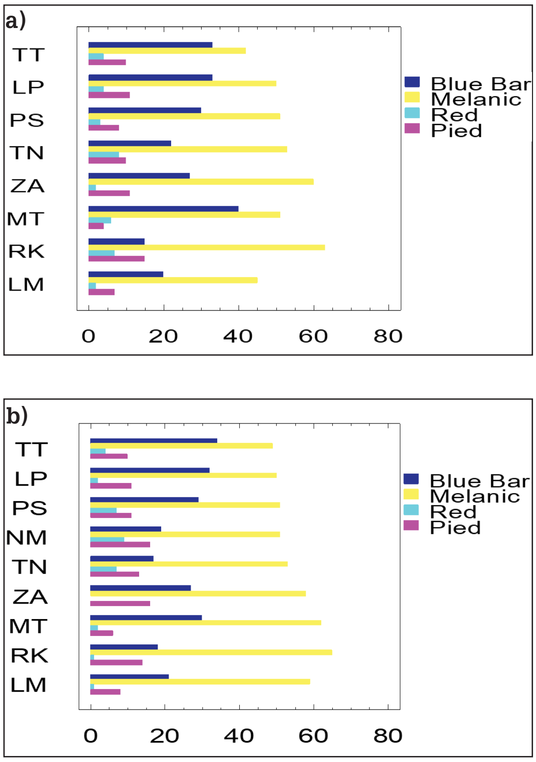

Fig. 2. Relative abundance of pigeons according phenotype in selected Slovak cities; **a)** 1998, **b)** 1999; TT = Trnava, LP = Leopoldov, PE = Piešťany, NM = Nové Mesto n. Váhom, TN = Trenčín, ZA = Žilina, MT = Martin, RK = Ružomberok, LM = Liptovský Mikuláš.

	Altitude			
	r	P	F	n
Melanic	0.68	0.002	13.2	17
Blue-bar	-0.31	0.23	1.6	17
Red	-0.39	0.1	2.76	17

Table 3. Results of testing the relationship between altitude and the abundance of phenotypic groups.

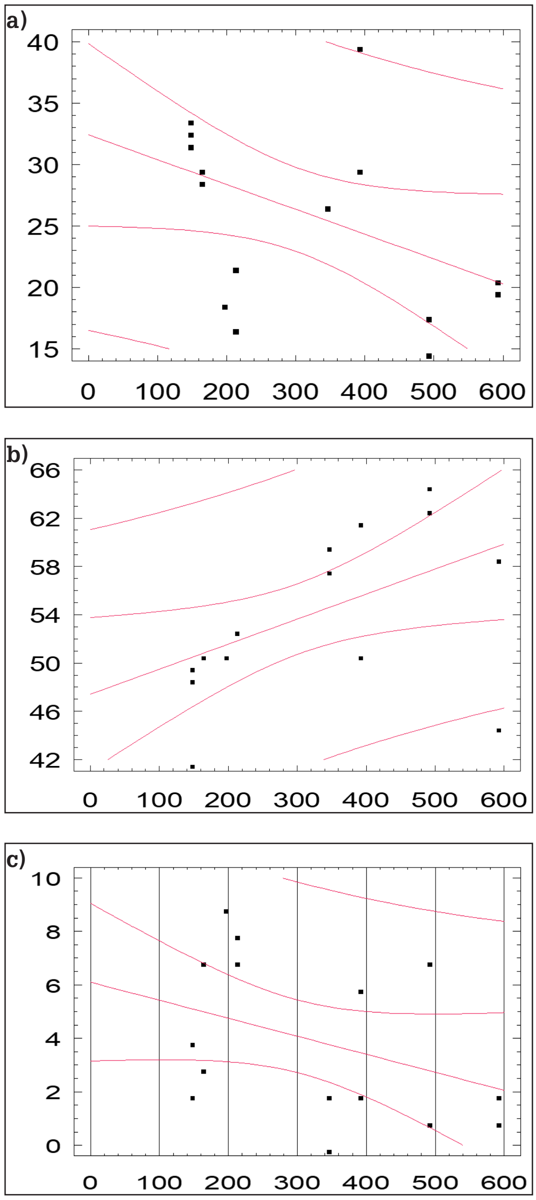

Fig. 3. Statistical dependence of phenotype groups abundance with altitude; **a)** - melanic, **b)** - blue-bar, **c)** - red.

drier conditions) of Slovakia (Table 4). The component score (Table 5) of PC 1 was considered as an independent variable in linear regression, when changes in the abundance of individual (melanic, blue-bar and red) phenotype groups with weather factors were examined. The significant correlation (Table 6) was found in the case of the melanic phenotype group, which indicates that, in mountainous areas of Slovakia with predominantly lower temperature, high humidity and higher precipitation, melanic pigeons are more abundant (gen. symbol C, C^T). Blue-bar and red phenotypes did not have a significant correlation with PC 1. None of the phenotype groups were significantly correlated with principal components PC 2 and PC 4. However, PC 3 correlated strongly with an abundance of the red phenotype group. The PC 3 component separates cities with warmer weather and higher precipitation in the lowlands from those with colder weather and low precipitation in mountainous areas. The abundance of pigeons in the red phenotype group was significantly higher in lowland cities with warmer weather and higher precipitation (Table 6).

Discussion

In all studied Slovak cities, a melanic (hyperchromatic) group of pigeons prevailed in both years, as well as in the cities listed in Table 7, with the exception of London in 1921. Even in this case, representation of the blue-bar phenotype decreased in favour of melanic individuals towards 1954 (Table 7), and in 1954 up to 81 % of pigeons at this site were identified as melanic (Meinertzhagen 1954). More recent data from eastern Slovakia (Košice 53.5 %, Svidník 56.4, Stropkov 59.6 %) has also confirmed melanic phenotypical dominance in terms of abundance (Čanády and Mošanský 2013, 2016). From a broader perspective, sites compared in Table 7 (g), at Flamborough in Yorkshire (a peripheral coastal area), show that blue-bar phenotypes (70 %) were more abundant than melanic phenotypes (24 %) in wild pigeon populations (Lofts *et al.* 1966). Podhradský (1953), Murton *et al.* (1973) and Janiga (1991a) also suggest that phenotypes showing varying degrees of melanism tend to dominate in cities. According to Johnston and Janiga (1995), there are also more melanic pigeons in the cities of European Russia and northern Central Europe. According to Goodwin (1954), the most common colour among feral pigeons in Great Britain is the blue-checker and blue-T-pattern phenotype, which belong to the melanic group. In 1951, Podhradský (1953) observed 497 pigeons in Bratislava, of which 20 % had the wild pigeon pattern and 63 % were melanic (Table 7). In 1981-85, the number of wild phenotype pigeons rose to 23 % and the number of melanic pigeons remained unchanged (Janiga 1991a). The phenotypic composition of pigeons in Brno is similar to Bratislava (Podhradský 1953). In the Gdansk wild, Hetmański and Jarosiewicz (2008) found that blue-bar pigeons were the dominant phenotype, especially in the old city centre, while melanic birds were most common in buildings constructed after WW II. This is not the case in most southern European cities, where the blue-bar phenotype predominates over others (Table 8) (Johnston and Janiga 1995). Compared to others, "red" phenotypes are usually less common in Slovak cities, as well as in other European and American localities. In Syracuse, the "red" group (ash red-bar, ash red-checker, ash red-T-pattern and recessive red) represented less than 4 % of the total population (Dunmore 1968), which

	PC 1	PC 2	PC 3	PC 4
Altitude	0.36	0.22	-0.52	0.27
Annual temperature	-0.39	-0.26	0.18	-0.01
February temperature	-0.27	0.45	0.25	-0.27
March temperature	-0.18	0.56	0.14	0.07
Annual precipitation	0.38	0.05	0.52	-0.24
February precipitation	0.23	-0.50	0.00	0.31
March precipitation	0.32	0.22	0.55	0.58
February humidity	0.37	-0.24	0.14	-0.45
March humidity	0.41	-0.09	-0.17	-0.40
Total variability %	**56.7**	**28.5**	**7.2**	**4.7**

Table 4. Vectors (component weights) of the first four components derived from the correlation matrix of altitude and weather factors (average).

local.	year	PC 1	PC 2	PC 3	PC 4
TT	1998	-4.40	1.06	-0.47	0.01
TT	1999	-3.07	-1.53	-0.63	0.63
LP	1998	-3.64	1.10	-0.38	0.03
LP	1999	-1.17	-1.84	0.66	0.42
PE	1998	-2.10	0.90	0.02	-1.15
PE	1999	-0.70	-1.79	0.09	-0.60
NM	1999	0.57	-1.80	1.18	0.52
TN	1998	-0.90	1.09	0.32	-0.76
TN	1999	0.37	-1.75	0.70	-0.22
ZA	1998	1.40	1.66	0.68	-0.04
ZA	1999	1.72	-1.05	0.21	-0.93
MT	1998	2.03	1.58	1.11	-0.02
MT	1999	2.09	-1.04	0.003	-0.63
RK	1998	1.34	2.43	0.28	0.48
RK	1999	1.17	0.49	-1.24	0.98
LM	1998	1.83	2.57	-0.65	1.07
LM	1999	3.47	-1.10	-1.86	-1.08

Table 5. Component scores of weather conditions for individual cities where feral pigeons were recorded (the score determines each of the listed cities in the vector matrix described in Table 11) TT - Trnava, LP - Leopoldov, PE - Piešťany, NM - Nové Mesto nad Váhom, TN - Trenčín, ZA - Žilina, MT - Martin, RK - Ružomberok, LM - Liptovský Mikuláš.

		PC 1		
Melanic	**r**	**P**	**F**	**n**
	0.73	0.001	16.9	17
		PC 3		
Red	**r**	**P**	**F**	**n**
	0.55	0.02	6.5	17

Table 6. Results of testing the relationship between weather factors and the abundance of phenotypic groups.

					Main phenotype groups						
					wild	melanic		other			SUM
Author	**Locality**	**year**	**lat.**	**alt.**	**Bb**	**Bch**	**BT**	**S**	**Red**	**Wht**	
Dunmore (1968)	Syracuse	?	42°	?	29 %	28 %	21 %	13 %	4 %	1 %	647
Cole (1969)	Tempe	1963	34°	?	20 %	38 %	24 %	1 %	13 %	2 %	93
Cole (1969)	Tempe	1968	34°	?	18 %	33 %	26 %	3 %	15 %	4 %	273
Glissmeyer (1996)	Los Angeles	?	34°	103	26 %	42 %	27 %			5 %	?
Glissmeyer (1996)	Salt Lake City	?	41°	?	10 %	38 %	23%			7 %	?
Glissmeyer (1996)	Boston	?	42°	?	16 %	59 %	18 %			7 %	?
Meinertzhagen (1954)	London	1921	51°	?	37 %	12 %	2 %	?	?	?	100
Meinertzhagen (1954)	London	1954	51°	?	14 %	36 %	45 %	?	?	?	100
Lofts *et al.* (1966)	Liverpool	1963	54°	?	23 %	37 %	27 %	7 %	3 %	1 %	305
Lofts *et al.* (1966)	Leeds	1963	54°	?	24 %	27 %	31 %	9 %	2%	5 %	265
Lofts *et al.* (1966)	Flamborough	1963	54°	?	70 %	16 %	8 %	0	4%	1 %	102
Murton *et al.* (1973)	Manchester	1966	54°	?	21 %	26 %	35 %	7 %		11 %	2843
Podhradský (1953)	Brno	?	49°	227	12 %	19 %	33 %	29 %	1%	3 %	89
Podhradský (1953)	Bratislava	1951	48°	133	20 %	20 %	32 %	11 %	11%	6 %	497
Janiga (1991a)	Bratislava	1981	48°	133	23 %			63 %	2%	12 %	276
Leiss (1989)	Vienna	1989	48°	171	30 %	23 %	22 %	5 %	5%	7 %	?
Leiss and Hague-Wackernagel (1999)	Vienna	?	48°	171	24 %	25 %	18%	7 %	?	?	7682
Leiss and Hague-Wackernagel (1999)	Basel	?	48°	259	25 %	22 %	16 %	6 %	?	?	327

Table 7. Frequencies of phenotypes of feral pigeon coloration from various European and North American localities (lat. = latitude, alt. = altitude, Bb. = blue-bar, Bch = blue-checker, BT = blue-T-pattern, S = spread, Red = red, Wht = white).

is comparable with the ratios presented in our survey of Slovak cities. This finding was not confirmed in Tempe, Arizona, where the number of red pigeons were 13 % and 15 % over the two years of the study Cole (1969). These outliers could be explained by environmental factors related to latitude.

Lichard (1981) claims that the hyperchromatic portion of the population in Bratislava is developmentally the oldest, which is also confirmed by the results of Podhradský (1952, 1953), but domesticated individuals are mixed into the group. It is predominantly a group of white phenotypes, which according to Podhradský (1952) and Goodwin (1957), represent immigrants from domestic farms. White-coloured pigeons are more abundant than red in most Slovak cities and their numbers are close to the values found in Bratislava by Janiga (1991a). In terms of the overall ratio, they are usually under-represented, which is in agreement with Johnston and Janiga (1995), but they are not uncommon, and can be observed in other cities (Table 7) where they make up 1 % -3 % of the total population.

According to Obukhova and Kreslavskii (1985a, 1985b), plumage polymorphism in feral pigeons largely reflects their abilities, and particularly their adaptability to changes in conditions. According to Murton *et al.* (1973), adaptation played an important role in the phenomenon of increased melanism in most European cities compared to the wild type phenotype that persists in natural (native) habitats. Lofts *et al.* (1966) also states that melanic phenotypes are selectively favoured in urban habitats. The authors give several reasons why this trend is generally valid in many cities. According to Obukhova and Kreslavskii (1985a), the melanic individuals have a survivability rate twice as high among urban biotopes, when compared to the wild-type phenotype; and therefore, higher presuppositions that they will reach adulthood (Murton *et al.* 1973; Janiga 1991a). Dunmore (1968) determined that there is statistically, the blue-T-pattern phenotype, belonging to the melanic group, constitutes the majority, and there is a significant decrease in "blue-bars" during the winter months (December and January) compared to the summer

				MAIN PHENOTYPE GROUPS						
				wild	melanic			other		SUM
Author	**Locality**	**year**	**lat.**	**Bb**	**Bch**	**BT**	**S**	**Red**	**Wht**	
Ragionieri *et al.* (1991)	Barcelona	?	41°	75 %	6 %	0	3 %	2 %	?	405
Ragionieri *et al.* (1991)	Fertilia	?	41°	84 %		6 %	?	0	?	17
Ballarini *et al.* (1989)	Piacenza	?	45°	56 %		29 %	1 %	4 %	3 %	?
Ballarini *et al.* (1989)	Bolzano	?	47°	8 %			85 %	2 %	1-2 %	%
Ragionieri *et al.* (1991)	Bolzano	?	47°	17 %			64 %	1 %	?	102

Table 8. Frequencies of colour phenotypes of some southern European cities (lat. = latitude, Bb = blue-bar, Bch = blue-checker, BT = blue-T-pattern, S = spread, Red = red, Wht. = white).

or autumn. This demonstrates the selection advantage of the blue-T-pattern phenotype during winter. The increase in the number of melanic individuals in the winter months of the year was also confirmed by Johnston (1984). Burley (1977) discusses the preference for dark phenotypes when pigeons choose partners, and according to Murton *et al.* (1973), melanic phenotypes have a higher chance of forming pairs with other phenotypes. The blue-bar phenotype is most prone to disease in cities (Obukhova and Kreslavskii 1985b). In a later study, Jacquin *et al.* (2011) found that melanic pigeons were less likely to be parasitized due to better immunocompetence. Therefore, a hypothesis exists that immune capacity and pathogen pressure play a potential role in maintenance colour polymorphism in bird species (Gangoso *et al.* 2011). These are likely the main factors contributing to the dominance of melanic phenotypes. The phenomenon of adaptation of melanic phenotypes to urban conditions and their advantage in such an environment is indicated by the opposite tendencies of these individuals in rural populations, where melanic individuals have a higher mortality rate than blue-bar phenotypes (Petersen and Williamson 1949). Lofts *et al.* (1966) state that in rural localities, individuals that experience regression of gonads in winter are mostly melanic. Corbel *et al.* (2016) observed a higher corticosterone response in melanic pigeons from rural habitats; but not in urban habitats, due to adaptation.

The plumage patterns of feral pigeons do not only reflect the phenomenon of urbanisation (Jacquin *et al.* 2013), but also domestication, or its elimination (Johnston and Janiga 1995). Albino pigeons, and partial-albino pigeons, which are present in greater numbers in cities than in native habitats, will likely grow extinct in subsequent generations (Podhradský 1952). They face decreasing numbers in Slovakian cities, as well as others (Table 7,8). Janiga (1991a) found a decreased similarity between young and their parents in white individuals in Bratislava, which indicates a decrease in the population of pigeons that were originally domesticated. Alleles for white plumage persist for a long time as recessive (Johnston and Janiga 1995). White nestlings had empty crop more often than the nestlings of other phenotypes (Janiga 1991b). Their white plumage, attracts the attention of predators, likely due to its uniqueness (Mueller 1975), and attacks of predators on pigeon aggregations with white plumage has been experimentally confirmed by Pielowski (1961).

One of the factors explaining the differences in the abundance between pigeon phenotypes found in European cities is the climatic characteristics caused by latitude. According to Johnston and Janiga (1995), there is a statistically significant relationship between rising northern latitudes and rising numbers of melanic individuals in the populations of 21 Eurasian localities ($n = 22$, $r = 0.745$, $P = 0.001$). An exception to this trend is the southern Italian city of Bolzano (Table 8), where a larger group of melanic individuals (85 %, 64 %) was recorded, compared to other Italian cities (Table 8). According to Johnston and Janiga (1995), the reason for this deviation could be the high altitude of this city.

The effect of altitude and associated climatic factors on the plumage pattern phenotypes of feral pigeons is not well covered in current studies on pigeon polymorphism. Findings of our study support the possible relationship between altitude and weather with the abundance of individual phenotypes of feral pigeons. Higher altitude often determines the specifics of climatic conditions in Slovak cities, and affects the ratio of individual phenotypes in favour of melanics. However, similar altitudes in different European cities determine different climatic characteristics. For example, in Basel (259 m asl.), it was found that the proportionate abundance of phenotypes (Table 7) is not identical to Slovak cities with a similar altitude (Table 2). On the other hand, in Vienna, the relative abundance of melanic phenotype individuals did not differ significantly, though it shares a similar altitude and climate with the Slovakian cities studied (Table 7). This phenomenon would be clearer if abundance phenotype data from European cities could be compared to weather characteristics.

C-series alleles determine the distribution of eumelanic (black) pigment or pheomelanic (red) pigment (Johnston and Janiga 1995). Derelle *et al.* (2013) by sequencing the melanocortin 1 receptor gene (MC1R), and showed that feral pigeon polymorphism is most likely not attributable to amino acid variation at the MC1R locus, as it is in case of some wild bird populations (Theron *et al.* 2001; Mundy *et al.* 2004; Baiao *et al.* 2007; Johnson *et al.* 2012). Later, Vickrey *et al.* (2018), discovered through whole-genome scans, that the NDP gene drives polymorphism, and post-domestication introgression supplies potentially advantageous melanistic alleles to feral pigeons. Podhradský (1953) compared the effect of the environment to changes in pigmentation in pigeons from both domestic farms (n = 430), and feral pigeons (n = 497) in Bratislava. He found that hyperchromatic individuals are predominant in cities and hypochromatic ones are predominant in domestic farms. Podhradský (1953) noticed that, although feral pigeons originate from domesticated pigeons, they are affected by significantly different biological and ecological conditions (changes in climate, food, nesting). He comments that factors such as heat, light, humidity, etc. affect plumage phenotype. Podhradský (1968) verified his claims by conducting experiments on pigeons that originated from the Bratislavan population of feral pigeons, with an unknown genetic disposition that he interbred panmictically. He kept the pigeons under variable temperature and humidity conditions. Blue-bar and ash red-bar phenotypes did not change plumage colour under the stress of these experimental conditions. However, the blue-checker and blue-T-pattern phenotypes reacted significantly, and while their plumage pattern changed by getting more intense or fading, the basic pattern did not change. Johnston and Janiga (1995) concur with Podhradský, that the feather pattern of some feral pigeons may depend on the environmental conditions at the time of moulting. Our findings of the statistical significance of the dependence of rising melanism on rising altitude and the relation of weather factors are in accord with Podhradský (1968). Increased humidity and decreased temperature support an increase in the number of melanic individuals in areas characterized by this trend in the weather; predominantly in Slovak highlands and mountainous areas.

The possible effect of climatic factors on the abundance of some phenotypes or phenotypic groups is also mentioned by Dunmore (1968), who observed feral pigeons in Syracuse, New York State. blue-bar phenotype was the dominant group of individuals there. Cole (1969) suggests that cold winters played a role in the selection of resistant genotypes. However, Dunmore (1968) found decreasing abundance of "blue bars" when compared to other phenotypes during the coldest months. On the other hand, the success of melanic phenotypes (C, C^T) in the coldest months was confirmed by their reduced mortality during this period, and thus, their greater resistance to cold (lower temperatures).

Pigeons belonging to a 'red' phenotype group were also subject to the effect of environmental factors. The number of red-coloured pigeons may increase from north to south (Dunmore 1968, Cole 1969, Johnston and Janiga 1995). Pigeons with ash red base colour were rare in Syracuse (Dunmore 1968), but accounted for more than 12 % of all individuals in Arizona, which Cole (1969) claims could reflects Arizona's mild climate. The increase in abundance of red pigeons from north to south (Johnston and Janiga 1995), including n in Slovak cities, may confirm their sensitivity to some weather factors.

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