

Genetic analysis of the domestic pigeon (*Columba livia*) through feather colour-associated markers in Montería, Córdoba, Colombia



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Abstract

The species known as the domestic pigeon, scientifically *Columba livia*, has managed to establish itself successfully in urban environments of numerous cities around the world. This expansion has become so significant that it has triggered concerns related to its tendency to nest in human-built structures. This nesting behaviour has contributed to the deterioration of these buildings. The distinctive presence of these birds in neighbourhoods and plazas has generated a growing interest in better understanding the genetic patterns that encode their varied coloration and plumage designs. The aim of this study was to investigate the genetic variability of the population of domestic pigeons (*Columba livia*) in Montería, Colombia, using phenotypic markers of plumage. Random sampling was conducted between March and April 2023 on 21 flocks of pigeons within the municipality of Montería. Through urban excursions, direct observation, and photographic records, 1570 individuals were phenotypically classified. Autosomal markers encoding coloration and plumage design

were studied: *Checker* (C), *Grizzle* (G), *Spread* (S), and *Ash-Red* (B). The genetic profiles of subpopulations of domestic pigeons were established using the following genetic population indices: expected heterozygosity (H_e), total genetic diversity (H_T), diversity within populations (H_S), diversity between populations (D_{ST}), coefficient of genetic diversity (G_{ST}), gene flow (Nm), and genetic distance between populations. It was found that the most common allele in the studied populations is *Checker*, allelic frequencies ranged from 0.315 for the *Checker* gene to 0.005 for the *Spread* marker. Total genetic diversity was moderate, and genetic differentiation between populations was low, accompanied by a high gene flow. An excess of heterozygotes was also observed, and low genetic distance values were found between populations. The results indicate limited genetic differentiation among populations, leading to the conclusion that pigeon populations in Montería are highly related.

Key words: *Columba livia*; genetic diversity; gene flow; heterozygosity; Montería

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Introduction

The domestic pigeon, *Columba livia* (Gmelin, 1789), belongs to the *Columbidae* family, which likely evolved through selection processes from ancestral bird species. The domestic pigeon is native to the Mediterranean Basin and the Middle East. Due to its widespread introduction to various parts of the world, it is considered cosmopolitan. Its migratory patterns are linked to processes of domestication, during which this species served various purposes such as a food source, messenger pigeon, and even pets in pigeon racing, among other activities (Haag-Wackernagel et al., 2006). The similarities between human-made structures and the natural habitats of domestic pigeons, such as cliffs, have allowed them to adapt to human environments. Additionally, the absence of natural predators has contributed to this adaptation (Stock and Haag-Wackernagel, 2016). Domestic pigeons typically have an average size ranging from 30.5 to 35.5 cm, a medium-length tail, and weigh between 180 to 360 g. They exhibit predominantly light blue coloration with two black stripes on their wings, reddish or pink legs, and a dark beak. However, natural monogenic variations in their phenotype are also observed (Mosco, 2021).

In urban areas, domestic pigeons feed on scattered grains and seeds found on the ground. As a result, they tend to rely on humans for food, as a significant portion of their diet consists of edible waste left by humans in streets, parks, or garbage bins (Pardo et al., 2018). In their wild state, their diet is based on seeds, berries, and invertebrates, leading to some studies considering them as omnivores. While in their natural habitat, they nest on cliffs and in caves (Carbia-Rodríguez, 2022). In urban environments, they have adapted to nesting on rooftops, drainage pipes, and other building structures,

constructing their nests from grass and dry branches placed on a simple base (Olalla et al., 2009).

Multiple bird species, especially domestic ones, exhibit variations in feather and skin coloration as well as in plumage patterns (Price-Waldman and Stoddard, 2021). *Columba livia* is no exception, with 60 hereditary factors identified that encode for its plumage patterns and coloration. This extensive set of genetic factors serves as a crucial tool in population genetic studies, offering information about a large number of individuals with less effort and investment, while also enabling swift identification and characterisation (Pardo et al., 2018).

Phenotypic markers associated with coloration are valuable tools for deciphering the genetic profiles within natural populations; the gathered information allows us to deduce the existing genealogical relationships among members of a population, assess the genetic exchange between different populations, estimate the effective population size, and mitigate the adverse impacts stemming from reproduction among close relatives (Eiroa, 2016).

In Colombia, there are records of genetic diversity and variability through phenotypic markers in cities such as Llorica, Ciénaga de Oro, Sincelejo and Cotorra (Causil et al., 2016, 2017; Pardo et al., 2018; Rodríguez and Causil, 2022) yielding heterogeneous results. High frequencies of melanic individuals were found in the populations of Llorica and Ciénaga de Oro, while Sincelejo exhibited the lowest interpopulation differentiation. Additionally, Ciénaga de Oro and Llorica displayed an excess of heterozygotes (Causil et al., 2016, 2017). However, for Montería, there are only records of the abundance and distribution of *Columba livia* pigeons (Begambre and Pardo, 2015). Due to the lack of knowledge regarding the genetic diversity

of pigeons in Montería, the current study aimed to establish the genetic structure of *Columba livia* and the genetic relationships among subpopulations in Montería, Córdoba, using plumage coloration markers.

Materials and methods

Study Area

The study was conducted in the urban area of Montería city, situated at (8°44'52.73" N, 75°52'54.15" W), with an approximate elevation of 18 meters. The climate is characterised as tropical dry, with an average annual daytime temperature of 32.9°C. Samples were collected from 21 flocks: Granja 1, Granja 2, San Martín, Mercado 1, Ed. López 1, Mercado 2, Calle 21 Cra 2, Calle 27 Cra 4, Calle 37 Cra 1, Sucre, Calle 41 Cra 8, Calle 32 Cra 8, Pradera, Cantacclaro, El Dorado, Alma Viva, Ed. López 2, Limonar, Sta. Helena 1, Sta. Helena 2 and Terminal.

Data Collection

Incidental sampling was conducted through urban excursions and photo-

graphic documentation between the months of September and October 2022. During this period, the phenotypic classification of each individual within the 21 distinct pigeon flocks found in Montería was performed ($n=1570$). Each route was used only once to prevent resampling.

Study Variables

To estimate the genetic diversity of the *Columba livia* populations in Montería, the following autosomal markers (Table 1) were examined, which encode for plumage pattern and colouration: Ash-Red (B), Grizzle (G), Spread (S), Checker (C).

Population Analysis

The estimation of allele frequencies for each marker at both population and global levels, along with Nei's (1973) genetic diversity measures (i.e., expected heterozygosity (H_e), total genetic diversity (H_T), diversity within populations (H_S), diversity between populations (D_{ST}), coefficient of genetic diversity (G_{ST}), gene flow (Nm), and genetic distance between populations) was con-

Table 1. Description of the studied markers

Locus	Alleles	Characteristic
<i>B</i> (<i>sex linked gene</i>)	<i>B</i>	Mutant; produces red pigeons.
	<i>b</i>	Wild; originates non-red pigeons Silvestre;
<i>G</i> (<i>autosomal gene</i>)	<i>G</i>	Mutant; produces widespread white patches around the head or body.
	<i>g</i>	Wild; no White spots.
<i>S</i> (<i>autosomal gene</i>)	<i>S</i>	mutant; originates black pigeons.
	<i>s</i>	Wild; non-black pigeons.
<i>C</i> (<i>autosomal gene</i>)	<i>C</i>	mutant; produces a pattern of light grey or blue triangular spots on the back of the wings on a dark background.
	<i>c</i>	Wild; no triangular spots.

B: Ash-Red; *G*: Grizzle; *S*: Spread; *C*: Checker

ducted using the PopGene 1.31 software (Yeh et al., 1999). The genetic structure of populations was determined using the FSTAT v. 2.9.3.2 software (Goudet, 2002). The construction of the dendro-

gram representing the estimated genetic distance values was performed using the Neighbour-Joining method through the MEGA 11.0.13 software (Tamura et al., 2021).

Table 2. Allele frequencies of *Columba livia* populations in Montería

	<i>N</i>	<i>B</i>	<i>G</i>	<i>S</i>	<i>C</i>
Granja 1	43	0.048	0.012	-----	0.380
Granja 2	34	0.015	0.030	-----	0.222
San Martin	57	0.045	0.045	0.018	0.192
Mercado 1	70	0.014	0.044	-----	0.198
Ed. López 1	37	0.056	0.027	-----	0.239
Mercado 2	92	0.016	0.011	0.005	0.176
Calle 21 Cra 2	80	-----	-----	-----	0.243
Calle 27 Cra 4	356	0.008	0.003	0.003	0.185
Calle 37 Cra 1	187	0.022	0.013	0.005	0.242
Sucre	36	0.028	0.014	-----	0.425
Calle 41 Cra 8	26	0.059	0.019	-----	0.352
Calle 32 Cra 8	70	0.014	0.022	-----	0.359
Pradera	25	0.020	0.020	-----	0.402
Cantaclaro	107	0.053	0.014	-----	0.328
El Dorado	120	0.021	0.030	-----	0.332
Alma Viva	32	0.032	-----	0.016	0.361
Ed. López 2	17	0.061	0.061	0.030	0.323
Limonar	92	0.022	0.011	-----	0.408
Sta. Helena 1	43	0.024	0.048	0.012	0.347
Sta. Helena 2	27	0.019	0.077	0.019	0.549
Terminal	19	-----	0.054	-----	0.345
Total	1570				
Promedio		0.193	0.026	0.005	0.315
DE		0.019	0.021	0.009	0.096

N: Number of individuals. *B*: Ash-Red; *G*: Grizzle; *S*: Spread; *C*: Checker

Results

Allelic Frequencies

When analysing allelic frequencies in each population (Table 2), it was observed that the *Checker* allele (C) exhibited the highest frequency, with an average of 0.315. Among these populations, Santa Helena 2 shows the highest frequency, recording a value of 0.549. Following in frequency were the Barrio Sucre and Limonar populations, with frequencies of 0.425 and 0.408, respectively.

On the other hand, the *Grizzle* (G), *Spread* (S), and *Ash-Red* (B) markers showed the lowest frequencies, and these markers were not recorded in several populations, including Calle 21 Cra 2, Terminal, El Dorado, Sucre.

Genetic Diversity

In the pigeon population in Montería, the total heterozygosity (Table 3) showed an average of $H_T = 0.184$, with the *Checker* marker ($H_T = 0.621$) presenting the highest diversity and the *Spread* marker showing the lowest diversity ($H_T = 0.010$). The genetic diversity within populations revealed $H_S = 0.178$, and the diversity among populations showed $D_{ST} = 0.006$. The coefficient of genetic diversity ($G_{ST} = 0.031$) revealed that 3.1% of the genetic diversity is found among populations and 96.9% is within populations. The number of migrants obtained for Montería was 15.7, a value much higher than 4, indicating high gene flow among the studied local populations (Slatkin, 1981) and the existence of low

Table 3. Genetic diversity of the *Columba livia* population in Montería

Markers	H_T	H_S	G_{ST}	D_{ST}	Nm
<i>Checker</i>	0.621	0.600	0.034	0.021	14.216
<i>Ash-Red</i>	0.053	0.053	0.013	0.001	37.643
<i>Spread</i>	0.010	0.010	0.010	0.000	50.000
<i>Grizzle</i>	0.051	0.051	0.016	0.001	31.563
<i>Media</i>	0.184	0.178	0.031	0.006	15.707

H_T : total genetic diversity; H_S : diversity within populations; D_{ST} : diversity between populations; G_{ST} : coefficient of genetic diversity; Nm : gene flow

Table 4. Values of the F statistics for four markers (*Checker*, *Ash-Red*, *Spread* and *Grizzle*) in the global population

F_{IS}	F_{ST}	F_{IT}
-0.378	0.022	-0.421
-0.279	0.015	-0.279
-0.193	0.020	-0.218
-0.149	0.019	-0.131
-0.248	0.018	-0.261

Table 5. Genetic distance matrix (Nei, 1972) between populations

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	
A																						
B	0.0070																					
C	0.0097	0.0005																				
D	0.0083	0.0007	0.0010																			
E	0.0058	0.0005	0.0007	0.0017																		
F	0.0121	0.0066	0.0069	0.0033	0.0080																	
G	0.0048	0.0015	0.0028	0.0011	0.0023	0.0030																
H	0.0124	0.0082	0.0089	0.0045	0.0097	0.0002	0.0037															
I	0.0090	0.0094	0.0108	0.0060	0.0105	0.0013	0.0040	0.0008														
J	0.0014	0.0130	0.0168	0.0133	0.0122	0.0146	0.0083	0.0140	0.0091													
K	0.0003	0.0059	0.0080	0.0064	0.0048	0.0091	0.0036	0.0094	0.0065	0.0019												
L	0.0013	0.0074	0.0104	0.0083	0.0069	0.0097	0.0037	0.0096	0.0071	0.0023	0.0014											
M	0.0051	0.0174	0.0212	0.0155	0.0173	0.0122	0.0102	0.0109	0.0060	0.0018	0.0047	0.0051										
N	0.0012	0.0060	0.0080	0.0055	0.0053	0.0061	0.0027	0.0062	0.0037	0.0023	0.0004	0.0016	0.0036									
O	0.0009	0.0031	0.0053	0.0041	0.0029	0.0089	0.0022	0.0096	0.0077	0.0035	0.0009	0.0021	0.0074	0.0015								
P	0.0005	0.0067	0.0094	0.0072	0.0062	0.0091	0.0035	0.0091	0.0062	0.0013	0.0004	0.0006	0.0037	0.0006	0.0011							
Q	0.0049	0.0038	0.0047	0.0069	0.0026	0.0171	0.0068	0.0191	0.0180	0.0109	0.0053	0.0082	0.0187	0.0076	0.0031	0.0066						
R	0.0044	0.0168	0.0207	0.0153	0.0166	0.0126	0.0099	0.0114	0.0064	0.0013	0.0042	0.0043	0.0001	0.0033	0.0068	0.0032	0.0177					
S	0.0010	0.0055	0.0079	0.0055	0.0054	0.0082	0.0031	0.0084	0.0057	0.0020	0.0007	0.0023	0.0041	0.0009	0.0007	0.0007	0.0057	0.0038				
T	0.0095	0.0298	0.0353	0.0308	0.0286	0.0339	0.0242	0.0328	0.0243	0.0049	0.0115	0.0131	0.0072	0.0132	0.0137	0.0105	0.0214	0.0068	0.0103			
U	0.0016	0.0042	0.0068	0.0050	0.0045	0.0101	0.0032	0.0107	0.0085	0.0035	0.0017	0.0032	0.0070	0.0024	0.0004	0.0017	0.0038	0.0066	0.0006	0.0117		

A: Granja 1. B: Granja 2. C: San Martín. D: Mercado 1. E: Ed. López 1. F: Mercado 2. G: Calle 21 Cra. 2. H: Calle 27 Cra. 4. I: Calle 37 Cra. 1. J: Sucre. K: Calle 41 Cra. 8. L: Calle 32 Cra. 8. M: Pradera. N: Contactlaro. O: El Dorado. P: Alma Viva. Q: Ed. López 2. R: Limonar. S: Sta. Helena 1. T: Sta. Helena 2. U: Terminal

genetic distance among them (Piñero et al., 2008).

Population Structure

The negative values for each marker and on average for the F_{IS} and F_{IT} statistics (Table 4) revealed an excess of heterozygotes in individuals within each population and individuals relative to the total population. On the other hand, the average value of F_{ST} was low (0.018), indicating limited genetic differentiation among the populations.

Genetic Distances

The genetic distance between populations was low, with Pradera and Limonar

showing the smallest distance (0.0001), while Santa Helena 2 and San Martin exhibiting the highest distance (0.0353), a value of little significance as it did not surpass 5% of the genetic differentiation among the studied populations (Table 5).

The dendrogram (Figure 1) illustrates the genetic similarity between the Pradera and Limonar colonies, with the associated Sucre colony. Similarly, a connection is observed between the Mercado 2 and Calle 27 Cra 4 colonies. Additionally, the Santa Helena 2 colony appears distinct from the others but with a relatively insignificant distance value, implying that the populations are closely related as a whole.

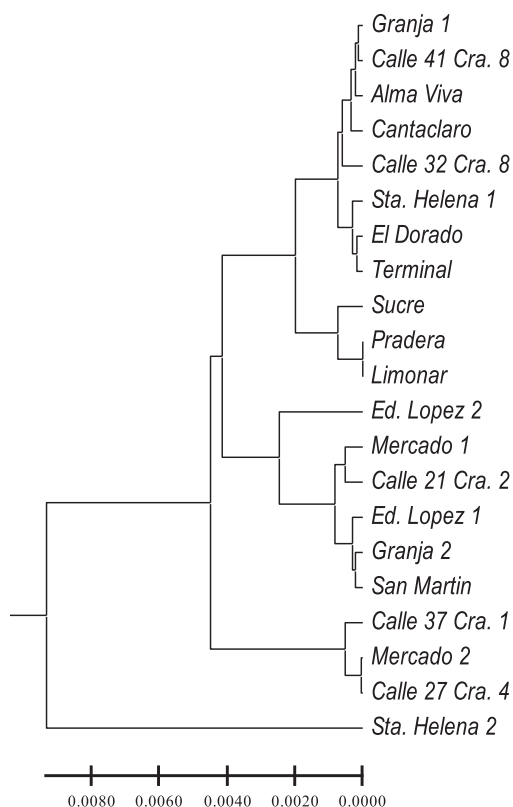


Figure 1. UPGMA dendrogram obtained from the genetic distances of Nei (1972) of populations of domestic pigeons from Montería, Córdoba

Discussion

The high frequency of the *Checker* marker (Table 2) reported in this research coincides with other studies (Ěanádý and Mošanský, 2013; Csanádý and Duranková, 2021). The melanin coloration could indicate better adaptation to urban habitats, which is then passed on to future generations (Roulin, 2004; Jacquin et al., 2013a), greater stress resistance (Almasi et al., 2010) caused by factors such as anthropogenic disturbances in cities, and improved survival (Van den Brink et al., 2012; Saino et al., 2013). Additionally, melanin in the plumage of *Checker* pigeons has the property of binding to toxic metals, which can enhance the detoxification of harmful metals by retaining them away from the bloodstream (Chatelain et al., 2016). Gasparini et al. (2011) demonstrated a better immune response in melanin-rich birds, along with greater resistance to parasites (Jacquin et al., 2013a,b). Burley (1977) suggests that melanin coloration could provide advantages in sexual selection, as both female and male pigeons tend to prefer darker mates. It is also important to mention that during periods of food scarcity, females with melanin phenotypes tend to produce a greater number of eggs, and the offspring born under restricted food conditions show a higher body mass due to being descendants of darker parents (Jacquin et al., 2012). These findings were similar to reports by Ěanádý and Mošanský, (2013), Pardo et al. (2015, 2019), and Causil and Causil, (2019).

The Spread allele (Table 2) was found in only eight of 21 flocks, which might suggest that this marker could be undergoing negative selection. Angelier (2020) previously reported that Spread pigeons, when exposed to sunlight, raised the temperature of their plumage, resulting in increased energy costs for cooling, compared to pigeons with lighter coloration. Furthermore, Obukhova (2007) observed

a latitudinal gradient where populations closer to the equator had fewer Spread pigeons compared to populations closer to the poles, a condition that is present in Montería. This could potentially affect the population increase of these pigeons.

Regarding the total genetic diversity (H_T) estimated in Montería (Table 3), it was found to be moderate. This is because most of the genetic diversity is within populations (H_S), and only a small amount of differentiation was detected among populations (D_{ST}). This indicates that the analysed populations share a high degree of overall diversity. The limited genetic diversity observed within each population could be attributed to the high gene flow between the populations ($Nm = 15.7$; Table 3). This suggests a close relationship between populations, where significant gene exchange exceeds the effects of genetic drift, preventing local differentiation (Aguilar et al., 2021). As a result, the level of genetic differentiation among populations was low ($G_{ST} = 0.031$). It is worth noting that genetic diversity is closely related to the level of gene flow, which significantly influences genetic distances (Glesmann et al., 2013). There is a direct relationship between these genetic variables, reflected in the low distance values and reduced diversity among populations. This implies that the limited levels of genetic diversity reported here had a decisive impact on the obtained distance values.

The deficit of homozygotes observed when using fixation indices (F_{IS} and F_{IT}) for each population (Table 4) indicates a nearly homogeneous structure. This could be attributed to the substantial gene flow between populations facilitated by their geographical proximity. Given that high gene exchange prevents inbreeding events within populations (Szczecińska et al., 2016), an increase is observed in heterozygous genotypes, suggesting the presence of panmictic crossbreeding within populations. The F_{ST} values between the studied

populations exhibited a low level of genetic differentiation, falling within the interpretation ranges formulated by Wright (1965), which ranged from 0.015 to 0.022.

Regarding the genetic distance results (Table 5) and the obtained dendrogram (Figure 1), it is important to emphasise that these are a result of the significant gene flow between populations due to their geographic proximity. Additionally, it has been reported that domestic pigeon populations (Carlen and Munshi-South, 2021) behave as a single population, regardless of the demographic area, as long as urbanisation in the landscape is continuous. The genetic similarity is directly proportional to geographic closeness (Cruz and Ruiz, 2020).

Conclusions

The marker with the highest frequency was Checker, which could be related to better adaptation to the urban habitat, while the gene with the lowest frequency was Spread. The genetic diversity observed in Montería was limited, possibly due to the high gene flow, leading to a strong genetic cohesion among pigeon populations. The obtained dendrogram illustrates that the geographic proximity of populations is directly proportional to their genetic closeness.

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Genetska analiza gradskih golubova (*Columba livia*) kroz markere povezane s bojom perja u općini Montería, Córdoba, Kolumbija

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Cilj ove studije bio je istražiti genetsku varijabilnost populacije gradskih golubova (*Columba livia*) u općini Montería, Kolumbija, uporabom fenotipskih markera perja. Nasumično uzorkovanje je provedeno između ožujka i travnja 2023. na 21 jatu golubova u općini Montería. Kroz urbane ekskurzije, izravno promatranje i fotografsku evidenciju, fenotipski je klasificirano 1570 jedinki. Proučavani su autosomni markeri koji određuju boju i dizajn perja: *Checker* (C), *Grizzle* (G), *Spread* (S), i *Ash-Red* (B). Genetski profili subpopulacija gradskih golubova su utvrđeni uporabom sljedećih genetskih indeksa populacije: očekivana heterozigotnost (H_e), ukupna genetska raznolikost (H_T), raznolikost unutar populacija (H_S), raznolikost između populacija (D_{ST}), koeficijent ge-

netske raznolikost (G_{ST}), genski tok (Nm) i genetska udaljenost između populacija, procijenjeno pomoću PopGene 1.31 programa. Frekvencije alela kretale su se od 0,315 za *Checker* gen do 0,005 za *Spread* marker. Ukupna genetska raznolikost bila je umjerena, a genetska diferencijacija između populacija bila je niska, popraćena visokim genskim tokom. Zamićen je i višak heterozigota te su pronađene niske vrijednosti genetske udaljenosti između populacija. Rezultati ukazuju na ograničenu genetsku diferencijaciju između populacija, što dovodi do zaključka da su populacije golubova u općini Montería u vrlo visokom srodstvu.

Ključne riječi: *Columba livia*, genetska raznolikost, genski tok, heterozigotnost, Montería