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Plumage Polymorphism in a Feral Population
of the Rock Pigeon

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ABSTRACT: A sample (n = 647) of feral rock pigeons collected in Syracuse, New York, between July, 1964 and February, 1965 revealed the presence of polymorphism of plumage color and wing pattern in the population. Five mutant phenotypes each comprised more than 2.5% of the sample, and apparently are being maintained by unknown selective advantages. Proportions of two common phenotypes changed significantly during the winter months. Estimates of mutant gene frequencies at five loci ranged from .037 to .239.

INTRODUCTION

The rock pigeon, *Columba livia* Gmelin, offers interesting opportunities for population studies of its plumage polymorphism. Large numbers of feral and wild populations occur in many parts of North America, Europe, North Africa, India and western Asia. Feral flocks have been derived almost exclusively from domestic pigeons and/or pigeons of domestic origin. These feral populations are generally static within their rural and urban environs, with little interbreeding between them. A few European reports on plumage polymorphism in the rock pigeon are available (Petersen and Williamson, 1949; Goodwin, 1952; Buzzati-Traverso in Huxley, 1954), but none from American observers.

The genetic basis of the common plumage colors and wing patterns occurring in domestic stocks of rock pigeons was elucidated by Cole (1914), Cole and Kelley (1919), Jones (1922), Horlacher (1930), Hawkins (1931), Steele (1931), and Hollander (1938 a, b). The type coloration of *C. livia* is known as "blue bar" (bluish-gray plumage with two parallel black bars on each wing). Since Darwin (1897), this type has served as the standard in genetical studies. The most common plumage color and wing pattern phenotypes normally found in the rock pigeon are produced by two multiple allele systems. The first system is autosomal and consists of three mutant alleles, c, C, and C^T, that produce the wing patterns called barless, checker, and T-pattern, respectively. The second system is sex-linked and consists of two mutant alleles, b and B^A, that produce the plumage colors brown and ash-red, respectively. Two other mutant genes at nonlinked autosomal loci are commonly represented in feral populations: grizzle (G) and spread (S). Occasionally pigeons carrying the mutant sex-linked alleles dilute (d) and pale (d^P) and the nonlinked autosomal genes milky (my)

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and smoky (sy) are seen. At least 20 color and pattern mutants are now recognized in the rock pigeon. They are described in Levi (1963) and pictured in color in Levi (1965).

Goodwin (personal communication, 1965) believes that truly wild populations of rock pigeons in mainland Europe and the British Isles contain the blue bar phenotype exclusively, with the highly probable occurrence of occasional blue checker pigeons. Petersen and Williamson (1949) found mostly blue bar and a few blue checker pigeons on one of the Faeroe Islands. On the other hand rural populations, at least in this country, contain several mutants (C, C^T, S, and G, and perhaps others), whereas urban flocks show all the mutants discussed in this paper, and others. The genetic differences among the three kinds of populations may indicate the differential effects of infusion of mutant domestic pigeons into rural and urban populations, as influenced by natural selection.

Unfortunately, little information is available on the local and geographic distribution of rock pigeon phenotypes in the United States and elsewhere. The present study is an attempt to analyze plumage color and wing pattern polymorphism in an urban population in America.

MATERIALS AND METHODS

Seven walk-in wire traps were placed conspicuously on the tops of flat-roofed buildings within two areas of Syracuse, New York. Each trap was supplied continuously with whole corn bait, water, and one or more live decoys. Five traps were located on or near the Syracuse University Campus and operated for varying periods between early July and early December, 1964. The other two traps were placed in

TABLE 1.—Percentages of color and pattern phenotypes

Color phenotype	Number captured	Percentage of total sample	95 percent confidence limits of percentage
Blue-Black	619	95.7	94.2-97.4
Ash-Red	19	2.9	1.9- 4.6
Recessive Red	5	0.8	0.3- 1.8
White	3	0.5	0.1- 1.3
Bronze	1	0.2	0.0- 0.9
TOTAL	647	100.0	
Pattern phenotype			
Bar	190	29.8	26.3-33.9
Checker	185	29.0	25.4-32.8
T-Pattern	148	23.2	19.7-26.7
Spread	88	13.8	11.3-17.1
Grizzle	22	3.5	2.6- 5.9
Sooty	5	0.8	0.3- 1.8
TOTAL	638	100.0	

the downtown business section of the city and operated between late December, 1964, and early February, 1965. The smallest and largest distances between traps were 0.4 and 2.6 airline miles, respectively.

Pigeons were collected from the traps two or more times each week, sacrificed and frozen whole. Recognition and scoring of certain phenotypes were based on descriptions in Levi (1963) and assistance from W. F. Hollander, Iowa State University. Unmeasurable errors in scoring of certain phenotypes probably occurred, since the phenotypes of C and C^T, and C^T and S sometimes overlap.

ANALYSES AND RESULTS

COLOR PHENOTYPES AND PATTERN PHENOTYPES

Table 1 gives the proportions of plumage colors and wing patterns in the total sample, data pooled for all months and all traps. Almost all pigeons were of the wild type pigmentation: blue-black, including spread (black) pigeons. Specimens with red pigment (recessive red and ash-red) constituted less than 4% of the sample. Brown-pigmented pigeons were not seen; white individuals were rare.

"Bar," the wild-type wing pattern, occurred approximately equally with the mutant wing pattern "checker." The percentage estimates for c^+, C, and C^T are probably low, because spread (n = 88), recessive red (n = 5) and white (n = 3) are usually completely epistatic to these wing patterns. The barless (c) phenotype was not observed.

COLOR-PATTERN PHENOTYPES

The proportions of all color-pattern phenotypes, data pooled for all traps and all months, are presented in Table 2. The wild-type blue

TABLE 2.—Percentages of all pigeons scored for color-pattern phenotypes

Phenotype	Mutant gene(s)	Number scored	Percentage of total scored
Blue Bar	$+$	188	29.1
Blue Checker	C	182	28.1
Blue T-Pattern	C^T	138	21.3
Spread (black)	S	85	13.1
Blue Grizzle	G	22	3.4
Blue Sooty	?	3	0.5
Dilute T-Pattern	d C^T	1	0.2
Ash-Red Bar	B^A	2	0.3
Ash-Red Checker	B^A C	3	0.5
Ash-Red T-Pattern	B^A C^T	9	1.4
Ash-Red Spread	B^A S	3	0.5
Ash-Red Sooty	B^A ?	2	0.3
Recessive Red	e	5	0.8
White	?	3	0.5
Bronze	?	1	0.2
TOTAL		647	100.0

bar was the most common phenotype in the sample. Each specimen was placed in only one color-pattern class for the purposes of this table, although some pigeons exhibited more than two genetic plumage characters. The presence of partially white (pied) plumage is not indicated in the table, although it occurred on 17.6% of the scored specimens. Sooty, a darkening factor of the plumage, occurred on some blue checker and ash-red pigeons. The combination of ash-red (B^A) and spread (S) was observed on at least three specimens.

MONTHLY CHANGES OF COLOR-PATTERN PHENOTYPES

The monthly percentages of three common phenotypes are presented in Table 3 (data pooled for all traps). The possibility of significant month-to-month changes in these percentages was tested by chi square. The null hypothesis assumes no difference between any of the monthly percentages of the mutant, and the average percentage of the mutant, based on seven months' data. I assume the summer data (from the Syracuse University area) and the winter data (from the business section of Syracuse) are both samples of the same population of phenotypes.

The first test, of blue bar data (n = 185) from Table 3, yielded a significant value: chi square = 18.0, .01 > P > .005, 5 df. The month-to-month percentages of the blue bar phenotype are not within expected error limits of sampling. The two largest parts of this statistic are produced by the months of December and February, implying a significant change from the average percentage during the winter months. The December-February decreases may be indicators of selection against blue bar during the coldest months of the year.

The second test, of blue T-pattern data (n = 133) from Table 3, yielded a significant value: chi square = 12.4, .10 > P > .05, 5 df. The data of December and January were two of the largest contributors

TABLE 3.—Monthly percentages of three common color-pattern phenotypes

	BLUE BAR		BLUE T-PATTERN		BLUE CHECKER	
Month	Number	Percentage of monthly sample	Number	Percentage of monthly sample	Number	Percentage of monthly sample
Jul.	68	34.2	32	16.1	51	25.6
Aug.	28	36.4	13	16.9	28	36.4
Oct.	27	34.2	15	19.0	21	26.6
Nov.	13	38.3	6	17.7	9	26.5
Dec.	10	15.9	19	29.8	16	25.0
Jan.	19	24.1	24	30.4	19	24.1
Feb.	18	19.2	24	25.5	31	33.0
TOTAL	183	29.2	133	21.2	175	28.0

to the calculated statistic, implying a significant change in the proportion of blue T-pattern in the winter months. The increases of the phenotype may indicate a selection for it during the coldest months of the year.

The third test, of blue checker data (n = 175) from Table 3, yielded a nonsignificant value: chi square = 5.2, .75 > P > .50, 5 df. The month-to-month percentages of blue checkers do not deviate significantly from the average.

GENE FREQUENCIES

Table 4 presents frequencies for five loci. The B^A locus is sex-linked. C, S, G, and e are autosomal. The C and S loci are weakly linked; C and C^T are allelic.

The frequency of ash-red was calculated directly from the proportion of hemizygous ash-red females (n = 11) in the sample. The sample excluded recessive red (n = 5), white (n = 3) and bronze (n = 1), since these phenotypes are completely epistatic to the expression of ash-red. The same three phenotypes were also deleted from the samples used to calculate the frequency of C, C^T, S, and G. The b allele of B^A is presumed absent from the Syracuse population, for no brown pigeons were observed.

The frequency of recessive red was taken as the square root of its phenotypic proportion in the sample. The sample excluded white (n = 3) which is epistatic to the expression of e.

The C locus possesses two mutant alleles in the Syracuse population. We may assume barless (c) is absent or present at a very low frequency, since no specimens were observed during the study. Calculation of gene frequencies at this and the S and G loci assumes that genotypes of these mutant genes are distributed according to the Hardy Weinberg formula, even though the phenotypes are being selected. Furthermore, I assume recognition of C and C^T phenotypes is fairly accurate, in spite of some overlap in their expression.

The phenotypic frequency of spread (S) is based on recognition of this gene in wild-type and ash-red (B^A) birds. This combination was seen in at least three specimens. Other B^A S pigeons may not have

TABLE 4.—Gene frequencies at five loci controlling production of pigment and wing pattern in rock pigeons

Allele	No. of pigeons with phenotype	Gene frequency	95 percent confidence limits of frequency
B^A	19	.037	.025-.061
e	5	.089	.068-.116
C	185	.239	.206-.270
C^T	148	.239	.206-.270
S	88	.186	.168-.229
G	22	.095	.076-.122

been scored as such, since S is usually less epistatic to the pattern alleles (C and C^T) in the presence of B^A. Consequently, the estimate of S may be low.

Grizzle (G) is incompletely dominant to its wild type allele, and produces a homozygous mutant phenotype that can be recognized fairly accurately by some observers. Such scoring was not attempted with the 22 grizzle specimens in this sample.

DISCUSSION

NATURAL SELECTION OF PHENOTYPES

The color-pattern diversity of feral rock pigeons in urban and rural sections of the United States and Europe is apparent to many. Ford (1964) believes that any mutant phenotype maintained at a level of 1.0% or more is so maintained by a selective advantage. The color phenotypes ash-red and spread (black), and the pattern phenotypes checker, T-pattern and grizzle, are each present at levels greater than 2.5% in the Syracuse sample. Evidently each of these components of this polymorphism is maintained by an unknown selective advantage.

The blue and ash-red phenotypes appear to exhibit balanced polymorphism, considering the low percentage of ash-red in the sample and the long time pigeons have been in Syracuse.

The mutant pattern phenotypes (checker and T-pattern), and spread may show transient polymorphism, in view of their rather high percentages (checker = 29.2, T-pattern = 23.4, spread blue = 13.0) in the sample. Mayr (1963) noted that a drastic increase occurred in the proportion of a dark wing pattern mutant (either checker or T-pattern) in the Venice, Italy, population between 1941 and 1951. This was apparently a case of transient polymorphism, where a mutant allele tended to replace its wild type allele.

Polymorphism at the C locus is significant in the Syracuse population. The two mutant phenotypes, checker (C) and T-pattern (C^T) together constitute 52.2% of the trapped sample; the frequency of the two alleles is estimated at 23.9%. Their success may relate to lessened mortality through the coldest months in Syracuse (latitude, just over $43°$ N). This hypothesis is probable for C^T and possible for C. Cryptic, unknown pleiotropic effects of this or very closely linked loci may also contribute to the fitness of C and C^T through reproductive success, differential nestling survival or disease resistance.

On the other hand, the absence of polymorphism in Syracuse for several known loci is noted. The absence of opal (o), indigo (I), reduced (r) and milky (my) may indicate a lack of ready infusion of these mutant genes from domestic pigeons, rather than a selective disadvantage. However, I do not know if these phenotypes exist within the domestic flocks in the Syracuse area. The dilute (d) and recessive red (e) genes should infuse readily into feral populations since they are not uncommon in many domestic flocks. Their very low frequencies in Syracuse and other populations may be indicators of natural selection against them.

The questions of (1) the presence of certain mutant phenotypes in urban flocks (above the level of recurrent mutations), but not in rural flocks; (2) the differences in the proportions of certain phenotypes in rural and urban populations, and (3) the ecologic-genetic maintenance of all mutants (above the level of spontaneous mutations) in free-living populations of rock pigeons are not yet answered.

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