

## GEOGRAPHIC VARIATION OF SIZE IN FERAL PIGEONS

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**ABSTRACT.**—Even though they originated from phenetically and genetically heterogeneous domestic stocks, feral pigeons (*Columba livia*) today show significant interlocality variation in size of skeletal elements. About 30% of the size variation in European feral pigeons is owing to interlocality effects, compared to about 20% for American ferals. Additionally, size varies positively with latitude. Owing to the independent origin and long-term geographic isolation of American and European feral pigeons, the organization of size variation necessarily was developed independently in the two stocks. This instance of replicate size clines is probably a result of natural selection by environmental variables on common heritable variation in size. Received 10 September 1992, accepted 13 January 1993.

THE ROCK DOVE (*Columba livia*) is widely distributed in Europe, southwestern Asia, and northern Africa, where the species shows significant plumage color and size variation (Cramp 1985, Johnston 1992a, Vaurie 1965). Clinal patterns of color variation have become obscured in recent decades because wild Rock Doves no longer occur over much of western Europe and the Mediterranean Basin. Many original populations have been replaced by feral pigeons, which are free-living descendants of domestic pigeons. Domestic varieties were produced by humans using artificial selection on captive Rock Doves at many localities in Europe, Asia, northern Africa, and elsewhere in the past 5,000 to 7,000 years (Sossinka 1982, Mallowan and Rose 1933, Curtis 1982). Domestic pigeons have been sold to and traded among aviculturalists throughout the world (e.g. Darwin 1868, Hollander 1983). Consequently, genetically distinctive feral populations originating from domestic sources could not preserve either the size or color characteristics of their wild ancestors (e.g. Endler 1977). Partly because of this, feral *C. livia* are rarely studied and often are considered to be simply domestics (e.g. Welty and Baptista 1988), fundamentally distinct from wild Rock Doves and of little interest for the examination of evolutionary mechanisms.

Feral pigeons nevertheless live under conditions in which differential productivity and survival occur naturally, conditions from which domestics are largely exempted. Perhaps as a consequence, much of the variation in size and shape of contemporary North American and European feral pigeons is shared with that of wild Rock Doves (Johnston 1992b). However,

geographic variation in size and shape of feral pigeons has been noted only in passing (Johnston 1990). In this paper I examine the relationship between body size and latitude for feral pigeons of Europe and North America.

### METHODS

The skeletons used in this study were assembled either through fieldwork in which specimens were collected with traps, nets, or firearms for preparation later at the University of Kansas, or by loans of prepared specimens from museums in North America and Europe (Table 1). Fieldwork began in 1984 and continued through 1989, with samples taken at: Lawrence, Kansas; Baca County, Colorado; Washington Beach, Durham, England; Basel and Zürich, Switzerland; Bolzano, Italy; and Sassari and Fertilia, Sardinia. A significant problem in the use of museum material was the identification of specimens as wild, feral or domestic. Identities of specimens collected specifically for this study were not a problem, because each was taken from local flocks of discernable phenetic status (i.e. wild, feral, or domestic). A few specimens from a wild colony were conspicuous in some non-wild plumage, and some individuals in feral colonies, as well as some from other museums, were obviously domestics. Most of the specimens recognizable as domestics were racing homers bearing leg bands. In addition, two females from Gainesville, Florida, were suspected of being homers, but were unbanded; segregation of the two specimens was based on their large body size, a characteristic of racing homers (Johnston 1990, Levi 1974).

Measurements of 16 size variables of the skeleton over 11 North American and 7 European localities provided the basic data matrices. Measurements were taken with dial calipers as described in Johnston (1990), Johnston and Selander (1971), and McGillivray (1985). Replicate sets of raw data showed that measurement

error for some variables ranged from 0.1 to 0.2 mm in some specimens; however, locality means for replicate sets of measurements were never significantly different (ANOVAs,  $P = 0.99$ ).

Specimens from some North American localities having small samples were pooled; such samples are clearly evident in Table 1. Pooling usually increased within-sample variances and reduced the power of interlocality comparisons. Principal-components analysis (PCA) was based on covariance matrices of the raw individual skeletal measurements for each continental set of each sex (Table 2). The PC scores, based on standardized data, then were treated as ordinary variables. PC-1, which generally was a positive composite of all the measurements, was considered to represent over-all sizes of individuals (cf. Rising and Somers 1989). The relationship between sexual size dimorphism (SSD) and interlocality variation in each continent was examined using two-way ANOVAs employing locality mean scores taken from PCAs with sexes pooled.

The study of geographic variation used the null hypothesis that no interlocality size variation existed in either sex. The hypothesis, as it concerned the 16 size variables as well as PC-1, was examined using one-way ANOVAs. The Student-Newman-Keuls multiple-range procedures were employed in *a posteriori* comparisons of ranked means. Linear least-squares regression analyses were used to examine the relationships in each sample between locality mean PC-1 scores and latitude. The percent of the total variation owing to interlocality effects was computed by the relationship

$$IV = 100s_g^2 / (s_g^2 + s^2), \quad (1)$$

where: IV refers to percent interlocality variation;  $s_g^2$  is the mean square among groups minus the mean square within groups, with the difference divided by the mean locality sample size; and  $s^2$  is the mean intralocality variance. BMDP statistical programs (Dixon 1990) were used on an IBM 3081 KX3 mainframe at the University of Kansas Academic Computing Service.

## RESULTS

*Interlocality variation.*—Because feral pigeons show significant SSD (Burley 1981, Johnston 1990), relationships between SSD and interlocality variation for the two continental sets of specimens were examined by two-way ANOVAs (Table 3). Both sources of variation are appreciable, and SSD is responsible for most of the variation in size; that owing to differences in sizes between localities is nevertheless significant. No statistical, or nonlinear, interaction between the two sources of variation is evident.

American males show significant interlocal-

TABLE 1. Localities and numbers of skeleton specimens used in this study.

North America (85 females and 109 males)	
Lawrence, Kansas (LAWR; 22 females, 26 males);	
Chicago, Illinois, and Madison, Wisconsin (WILL; 10, 16);	
Flagstaff County, Alberta (FLAG; 4, 4);	
Edmonton, Alberta (EDMN; 4, 17);	
southern Michigan and western Pennsylvania (MIPA; 10, 9);	
Ottawa and Toronto, Ontario (OTTO; 5, 10);	
Connecticut and New York (CONY; 17, 7);	
Washington, D.C. and northern Virginia (VADC; 6, 7);	
Gainesville, Florida (GAIN; 0, 8);	
Berkeley, California (BERK; 5, 2);	
Baca County, Colorado (BACA; 2, 3).	
Europe (69 females and 54 males)	
Fertilia (Alghero), Sardinia (FERT; 2, 8);	
Sasari, Sardinia (SASS; 12, 8);	
Bolzano, Italy (BOLZ; 10, 10);	
Zürich, Switzerland (ZRCH; 11, 6);	
Basel, Switzerland (BASL; 2, 3);	
vicinity of London, England (LOND; 5, 3);	
Durham, England (DURM; 27, 16).	

ity variation by ANOVA for only 4 of the 16 original characters, whereas significant variation exists in 14 of the 16 variables of American females and in all 16 for both sexes of the European samples. Likewise, both sexes of Rock Doves from both continents show interlocality variation in general size as rendered by PC-1 (Table 4; European males, ANOVA  $F = 5.43$ ,  $P = 0.0002$ ; European females, ANOVA  $F = 4.65$ ,  $P = 0.0006$ ; American males,  $F = 1.33$ ,  $P = 0.23$ ; American females,  $F = 2.79$ ,  $P = 0.007$ ). Translated to more meaningful terms, 32% of the variation in PC-1 of European males is due to interlocality effects, with 30% found in European females, 19% in American females, and only 6% in American males.

The degree of differentiation in size over the localities sampled is greater in the European samples than in the American, and the variation in PC size of American males fails to achieve statistical significance. A conservative examination shows the scores for American males to occupy one statistically homogeneous set (Table 4; SNK analysis,  $P = 0.05$ ); the other three samples show two significant subsets by SNK, and the subsets for Europe have appreciably less overlap than those for the American females. Thus, whether examined by a multivariate summation of body size, or by serial examination of the original size variables, geographic variation is found in both continental sets, and is less in the American than in the European samples.

European localities with large males tend to have large females (Spearman's  $r = 0.67$ ,  $P <$

TABLE 2. Correlations of original variables with first two principal components of variation in 16 skeletal characters for two samples of female and two samples of male *Columba livia*.<sup>a</sup>

Variable	Females				Males			
	PC-1		PC-2		PC-1		PC-2	
	America	Europe	America	Europe	America	Europe	America	Europe
Premaxilla length	0.438	0.655	0.076	0.046	0.459	0.618	0.088	-0.053
Premaxilla width	0.429	0.437	-0.067	0.047	0.372	0.415	-0.081	-0.003
Skull length	0.674	0.686	0.242	-0.184	0.655	0.736	0.000	0.021
Skull width	0.596	0.104	0.086	0.013	0.429	0.269	-0.063	0.122
Mandible length	0.430	0.425	0.130	-0.033	0.586	0.513	-0.124	0.053
Scapula length	0.878	0.834	0.003	0.090	0.837	0.888	0.128	-0.172
Coracoid length	0.919	0.871	0.091	0.059	0.825	0.838	0.264	-0.143
Sternum length	0.866	0.926	-0.394	-0.263	0.833	0.840	-0.462	0.444
Sternum depth	0.770	0.730	-0.134	-0.081	0.736	0.665	-0.044	0.222
Keel length	0.881	0.881	-0.423	-0.429	0.825	0.757	-0.519	0.613
Femur length	0.839	0.830	0.428	0.425	0.849	0.873	0.321	-0.146
Tibiotarsus length	0.912	0.864	0.291	0.363	0.818	0.859	0.489	-0.323
Tarsometatarsus length	0.840	0.836	0.265	0.306	0.797	0.853	0.440	-0.185
Humerus length	0.901	0.888	0.337	0.323	0.862	0.949	0.338	-0.100
Ulna length	0.923	0.916	0.302	0.287	0.856	0.799	0.421	-0.440
Carpometacarpus length	0.871	0.826	0.247	0.231	0.711	0.881	0.229	-0.162
Character variance explained	9.765	9.345	1.058	0.958	8.612	9.188	1.485	1.104

<sup>a</sup> Analyses performed on individual specimens using raw measurements.

0.05). The relationship, however, does not hold for the North American localities (Spearman's  $r = 0.44$ , ns).

*Organization of variation in size.*—Gradient variation in PC-1 scores is evident in both sexes from both North America and Europe; the variation is weakly expressed in North American males. Scatterplots of locality means on latitude show reasonably strong linearity. For seven localities, European feral pigeons have positive regressions of size on latitude ( $R = 0.836$  [males], and  $R = 0.883$  [females]; Fig. 1). For North American samples (Fig. 2), females show a positive regression of size on latitude (10 localities;  $R =$

0.692), but the males show considerable scatter (11 localities;  $R = 0.533$ ).

*Variation in shape.*—The correlations of variables with PC-1 indicate that all contribute information to this axis of variation, although some from the skull and bill are not as well represented as those from other parts of the body. This implies that some shape information is carried on PC-1. Skull and bill variables nevertheless have only minor correlations with PC-2. Correlations on PC-2 tend to show a contrast between body core and limbs, a relationship dictated by the body core-limb length allometry in which larger individuals have proportionally shorter limbs, and vice versa (Johnston 1990). ANOVA shows no significant interlocality variation in PC-2, although that for North American females comes close ( $F = 1.65$ ,  $df = 9$ ,  $P = 0.063$ ). European females (based on fewer localities) are farther from significant variation ( $F = 1.61$ ,  $df = 6$ ,  $P = 0.160$ ), and both sets of males fall far short ( $P > 0.90$ ).

## DISCUSSION

The lineages of North American feral pigeons are independent of those for European ferals, and this is important to the conclusions reached in this paper. The origins of feral pigeons from Eurasian domestics could have begun perhaps

TABLE 3. Relationship between sexual size dimorphism and interlocality variation in feral pigeons.<sup>a</sup>

Source of variation	Sum of squares	df	F-value	P
<b>European ferals</b>				
Sex	17.82	1	36.1	<0.0000
Interlocality variation	23.69	6	4.0	0.030
Interaction	0.89	6	0.5	0.820
<b>North American ferals</b>				
Sex	27.53	1	63.8	<0.0000
Interlocality variation	20.38	9	3.1	0.007
Interaction	6.71	9	1.2	0.373

<sup>a</sup> Two-way ANOVA. European ferals, 7 samples (123 specimens); North American ferals, 10 samples (197 specimens).

TABLE 4. Interlocality variation in PC-1 size for two continental sample sets of feral pigeons.<sup>a</sup>

Sample	Females		Sample	Males	
	PC-1 ± SD	SNK <sup>b</sup>		PC-1 ± SD	SNK <sup>b</sup>
<b>North America</b>					
LAWR	-0.67 ± 0.10		GAIN	-0.45 ± 0.86	
BERK	-0.13 ± 1.11		CONY	-0.43 ± 1.02	
VADC	-0.08 ± 1.02		LAWR	-0.32 ± 0.76	
BACA	-0.05 ± 0.35		BERK	-0.28 ± 1.90	
CONY	0.11 ± 0.73		VADC	-0.08 ± 1.16	
MIPA	0.14 ± 1.06		MIPA	-0.01 ± 1.04	
OTTO	0.18 ± 0.20		FLAG	0.05 ± 0.65	
WIIL	0.37 ± 0.95		BACA	0.08 ± 1.34	
FLAG	0.80 ± 0.85		WIIL	0.20 ± 0.94	
EDMN	1.26 ± 1.07		EDMN	0.36 ± 1.06	
			OTTO	0.65 ± 1.23	
<b>Europe</b>					
FERT	-1.01 ± 0.05		FERT	-1.21 ± 0.69	
SASS	-0.27 ± 0.68		ZRCH	-0.36 ± 0.67	
ZRCH	-0.12 ± 0.73		SASS	-0.34 ± 0.87	
BOLZ	0.00 ± 0.77		BASL	-0.04 ± 1.62	
LOND	0.39 ± 0.91		LOND	0.18 ± 1.08	
BASL	0.48 ± 0.62		BOLZ	0.30 ± 0.82	
DURM	0.84 ± 0.89		DURM	0.67 ± 0.63	

<sup>a</sup> Abbreviations of sample localities as in Table 1.

<sup>b</sup> 95% confidence level.

6,500 years ago, but those for North America only about 400 years ago (Schorger 1952, Johnston 1992b). Subsequently, European feral pigeons had long-term opportunity to interbreed with wild pigeons and both lines still interbreed with domestics, but the degree of intercontinental feral exchange is small or nonexistent.

Three additional points aid discussion of morphometric variation in feral pigeons. First, the genetic basis of size variation in *C. livia* is well understood. If a breeder controls the sizes of the parents in a cross of domestic pigeons, the sizes of the offspring are, within the limits of classical quantitative genetics, predictable (Wexelsen 1937); there is no reason to suppose that feral pigeons are different in this respect. Second, sizes of offspring of free-living feral pigeons in Kansas are positively correlated with the sizes of their parents (Johnson and Johnston 1990); again, there is no reason to suppose that other feral pigeons are different in this respect. Third, broad-sense heritability varies from season to season in Kansas, and it is clear that environmental variation modifies the degree to which parental size is approximated by offspring (Johnson and Johnston 1990); other feral pigeons may be expected to be similar.

*Geographic variation in shape.*—The idea that

the allometric differences between limb lengths and body core contained in PC-2 might show interlocality variation comes from the rough interlocality variation shown by SSD, decreasing with size, which varies positively with increase in latitude (Johnston 1990). If specimen samples of 15 to 20 for each sex from perhaps

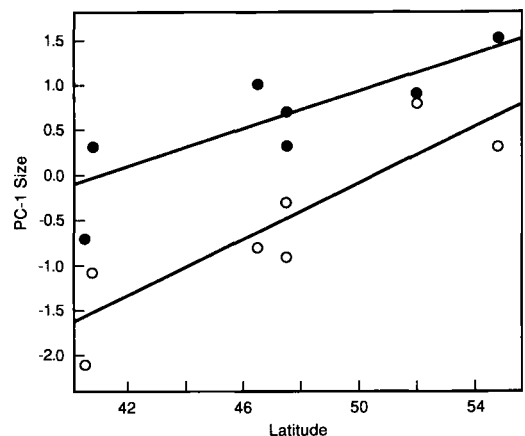


Fig. 1. Scatterplot of scores on PC-1 for European specimens of feral pigeons against latitude of localities at which they were collected. Solid circles represent males, for which  $R = 0.836$  ( $n = 7$ ); open circles represent females, for which  $R = 0.883$  ( $n = 7$ ). PCA based on locality means of samples with sexes pooled.

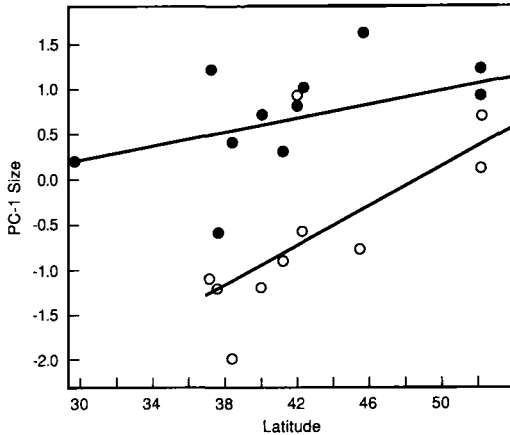


Fig. 2. Scatterplot of scores on PC-1 for North American specimens of feral pigeons against latitude of localities at which they were collected. Solid circles represent males, for which  $R = 0.533$  ( $n = 11$ ); open circles represent females, for which  $R = 0.692$  ( $n = 10$ ). PCA based on locality means of samples with sexes pooled.

15 to 20 localities were available, PC-2 would show statistically significant variation for both sexes on both continents. Given the small sample sizes in the current study, the degree to which American females show PC-2 shape variation is surprising.

*Geographic variation in size.*—It is important to find the cause or causes of geographic size variation in Rock Doves. Possible causes include at least (a) environmental gradients in natural selection, (b) neutral character diffusion for populations in contact, (c) gradients in environmental induction, or (d) any combination of the three.

Gradients in environmental variables are common in the natural world, but tying them causally to selective agencies for character gradients in organisms is difficult (Endler 1986). In the present case, feral pigeons are known to have domestic pigeons as ancestors (Darwin 1868). That is, the ancestors were birds in which size and shape were modified by artificial selection on genetic variation (Wexelsen 1937). Also, domestics that try or are forced to live under natural conditions experience heavy mortality (Janiga 1991), which could include selective deaths based on variation in body size. Thus, if feral pigeons have departed from domestic character states, it is tempting to think that selection is responsible—what selection has done to produce domestics can by selection be

undone to produce ferals. This, however, must be a prediction, not a conclusion, a state of affairs that has persisted in one form or another since the late 1850s (cf. Darwin 1868).

Neutral diffusion of size characters between populations in contact with each other probably occurs in feral pigeons, but this is taken as a matter of faith rather than a consequence of scientific study. However, when size covaries with an environmental variable, drift is difficult to invoke.

Gradients in environmental induction have never been implicated in any large-scale instance of clinal size variation, but local induction of character states by environmental variation is known for feral pigeons in Lawrence, Kansas (Johnson and Johnston 1990), and its potential importance to interlocality variation cannot be ignored (James 1983). Controlled transplant experiments have not been done for feral pigeons. Nevertheless, simple transplants have been performed countless times by breeders buying and selling pure-strain stocks of domestic birds. Results of such transplants are that environmental induction is not easy to see—such stocks “breed true” in color, pattern, size, and shape (or else the trade in pure strains would no longer exist). Details of size variation in offspring from these informal transplants have never been published, but one assumes that, if departures from expectation had occurred with any regularity, documentation would be available. Therefore, it is difficult to imagine that the present case of replicate clinal size variation could have come about without any genetic changes.

One is tempted to think of the North American size cline as paralleling that found for Europe. To justify use of that term, however, the causalities should be shown to be parallel, and that case is impossible to marshal at present. Specimens from Europe come from lowland, maritime localities, as well as from montane regions; those from North America are mostly from lowland localities, but these span the continent. Climatic coincidences probably are not important, and do not appear to be parallel. Furthermore, the other possible causes for generation of clinal size variation also do not appear to parallel one another.

In any event, over the past 400 years American feral pigeons have had sufficient size variation, and whatever physiologic relations to environment are required (James 1970), to produce

a case of clinal size variation descriptively consistent with that found in European feral pigeons. This has been done in North America beginning with undifferentiated domestics and has included persistent infusion of genetic noise from domestics of varying stocks and sizes, most significantly from racing homers (Johnston 1990). The organized variation is not yet assignable to any known cause of size clines, but because variation in size of feral pigeons has a significant relationship to genetic variation, it is attractive to suppose that differential survival and productivity of size classes at different localities are somehow causally involved.

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