EVOLUTION IN THE ROCK DOVE: SKELETAL MORPHOLOGY

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ABSTRACT.—Domestic pigeons were derived from Rock Doves (*Columba livia*) by artificial selection perhaps 5,000 ybp. Feral pigeon populations developed after domestics escaped captivity; this began in Europe soon after initial domestications occurred and has continued intermittently in other regions. Ferals developed from domestic stocks in North America no earlier than 400 ybp and are genealogically closer to domestics than to European ferals or wild Rock Doves. Nevertheless, North American ferals are significantly closer in skeletal size and shape to European ferals and Rock Doves than to domestics. Natural selection evidently has been reconstituting reasonable facsimiles of wild size and shape phenotypes in feral pigeons of Europe and North America. *Received 17 April 1991, accepted 13 January 1992.*

Man, therefore, may be said to have been trying an experiment on a gigantic scale; and it is an experiment which nature during the long lapse of time has incessantly tried [Darwin 1868].

Of the many kinds of animals examined for the study of variation under domestication by Charles Darwin, only for pigeons (*Columba livia*) did he describe fully the chief domestic strains, along with "their history, the amount and nature of their differences, and the probable steps by which they have been formed" (Darwin 1868: 1 [vol. 1]). He did artificial selection and studied inheritance of plumage colors, color patterns, and body size and shape in domestic pigeons; the results of these studies were important to his work on natural selection (Darwin 1859, 1868). Darwin's findings supported the idea that the range of colors, patterns, sizes, and shapes shown by domestic strains had antecedents in the variation of wild Rock Doves. He also thought that feral pigeons were an understandable consequence of domestic birds escaping captivity. In the late 1850s, however, Darwin was heavily involved in writing his "big book" (Stauffer 1975), so origins of ferals from domestics were barely mentioned. Details of such origins, involving character variation molded presumably by natural selection, are nevertheless of interest to thinking concerning population differentiation; some details inferred from skeletal morphology are reported here.

Rock Doves were domesticated in the period 10,000 to 5,000 ybp, earlier than has been previously suggested (e.g. Sossinka 1982). Domestications evidently occurred many times throughout the Mediterranean Basin, Near East,

and southwestern Asia; this is known to be true in more recent time (Darwin 1868; N. E. Baldaccini, pers. comm.). Later, pigeons escaping captivity either rejoined wild colonies or became feral, and are now found in most of the world (Long 1981). European, North African, and Asiatic ferals may have histories of several thousand years.

North American ferals have a significantly shorter history, stemming from British dovecote pigeons (the earliest of which were brought to Britain by the Romans; Levi 1974) introduced by Scottish and English immigrants to American Atlantic seaboard localities in 1600–1610 (Schorger 1952). North American ferals, therefore, are not directly lineally related to ferals of the Old World (Fig. 1). Additionally, founder gene frequencies seemingly departed significantly from those of European domestics, judging from allozymes of North American and European ferals (Johnston et al. 1989).

Thus, the evolutionary derivation of ferals is more complex than it might have been. The complexity is most useful—it is, for example, important that feral pigeons were derived from domestics more than once, because the development of ferals in North America can be viewed as an independent replicate of the natural experiment in ferality tried in Europe and Asia. Without the replicate, this study would almost certainly not have been undertaken, nor would it in any event have a satisfactory conclusion. Getting to that conclusion employs assessment of skeletal similarities and differences among wild, domestic, and the two feral lines of Rock Doves, and approximating how the similarities and differences could have occurred.
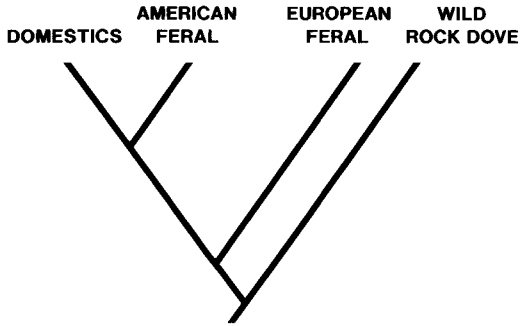
**AMERICAN   EUROPEAN   WILD
DOMESTICS   FERAL   FERAL   ROCK DOVE**

Fig. 1. Tree diagram depicting genealogical relationships of wild Rock Doves, domestic pigeons, and two lineages of feral pigeons.

TABLE 1. Sample sizes of wild, feral, and domestic pigeon skeletons used in different analyses.[a]

Wild Rock Doves.—Total sample (22 M, 23 F); Capo Caccia, Sardinia (19 M, 19 F).
North American ferals.—Total sample (111 M, 86 F); Lawrence, Kansas, USA (26 M, 22 F).
European ferals.—Total sample (49 M, 61 F); Durham, Co., Durham, England (16 M, 27 F).
Domestic pigeons.—Total sample (64 ?); large specimens (36 ?); small specimens (28 ?); racing homer (11 M, 7 F); tumbler (5 M, 4 F); runt (5 ?); pouter (4 ?); English carrier (5 ?); turbit (5 ?); jacobin (3 ?); fantail (2 ?).

[a] M = male; F = female; ? = sex unknown.

MATERIALS AND METHODS

The geographic region of this study is chiefly Europe and North America. Specimens come from Canada, the United States, the British Isles, Switzerland, Italy, Egypt, Israel, and Yemen. Wild *C. livia* are found from the Faeroes, Shetland, Scandinavia and Russia south to Ghana, northern Chad, eastern Sudan, Yemen, Pakistan, and India. Ferals occur in most cities worldwide, extensively in agricultural and maritime habitats, and on many isolated oceanic islands (Long 1981).

Darwin appreciated the value and uses of biological collections, so at the conclusion of his work with pigeons his captive birds were preserved and stored at the British Museum of Natural History, along with his other pigeon specimens. Fifty-three now exist as whole skeletons, and are included below, one as a wild specimen from Shetland and the remainder as part of the domestic samples.

I secured recent samples and prepared the specimens at the University of Kansas. They include: wild Rock Doves from Capo Caccia, 25 km W Alghero, Sardinia, November, 1989; ferals from Fertilia and Sassari, Sardinia, November, 1989; Zurich and Basel, Switzerland, November, 1989; Washington, 17 km E Durham, England, January, 1989; Lawrence, Douglas County, Kansas, 1983 to 1989; and Baca County, Colorado, June, 1987. The remaining specimens were examined either at the British Museum (Natural History), Tring, England, or at Kansas on loan from a number of other museum collections (listed in the acknowledgments). Sample sizes employed in the study are listed in Table 1.

Point-locality specimens as noted above were sometimes used as discrete analytical units. For most analyses, samples were pooled (Zink and Remsen 1986), owing to a need for a relatively high level of generality: 15 locality or regional samples provide the "North American feral" sample, and seven were used for the "European ferals." One large and several fractional samples were used for "wild Rock Doves." Eighteen specimens with leg bands identifying them

as racing homers, a post-Darwinian, artificially selected strain of domestic pigeon (Levi 1974), were removed from locality samples and used as one of the varieties of domestic pigeon. Domestic samples have a great range in size and shape, so they (depending on the analysis) were sorted to various subsets: pooled large domestics (keel length > 69 mm); small domestics (keel length < 69 mm); and a number of domestic strains maintained and identified by Charles Darwin (runts plus pouters, jacobins plus fantails, English carriers, turbits, and tumblers). These strains are composed of substrains and some, such as tumblers, are more variable morphologically than others (Darwin 1868). Most of the domestics from the Darwin collection were prepared without sex being recorded; there is no reliable way in which to estimate sex for these specimens, forcing the use of both sexes in many analyses. Although the wild and feral samples are satisfactory in sample sizes, associated label data, and methods of preparation, the domestic specimens are suboptimal in some of these respects. In samples with sexes pooled, however, their size and shape information seems to be satisfactory.

The 16 skeletal variables employed are listed in the Appendix for some representative samples; I took measurements for all specimens, which was consistent with past practice (Johnston 1990). Except for purely descriptive purposes (as in the Appendix) or in cluster analysis (for which the data were standardized), variables were transformed to natural logarithms. Statistics were processed on an IBM mainframe computer using BMDP (Dixon 1988) and NTSYS (Rohlf 1985), or on an MS-DOS 80286/287 personal computer using BMDP PC90 (Dixon 1990). Missing data were computed for specimens lacking no more than two variables by means of maximum-likelihood estimation in which missing values were estimated by regressing the variable on all variables of specimens of the same sex and locality that had acceptable values in the specimen with the missing value.

Three ways to examine similarities and differences in wild, domestic, and feral samples were used. For each sample, univariate product-moment correlation coefficients were computed for the 16 variables of the

Table 2. Abbreviations used in tables.

Abbreviation	Full name
MAXL	Premaxilla length
MAXW	Premaxilla width
SKLL	Skull length
SLKW	Skull width
MAND	Mandible width
SCAP	Scapula length
CORA	Coracoid length
STRL	Sternum length
STRD	Sternum depth
KEEL	Keel length
FEMR	Femur length
TIBI	Tibiotarsus length
TARS	Tarsometatarsus length
HUML	Humerus length
ULNA	Ulna length
CARP	Carpometacarpus length

basic data matrices, and the coefficients were then examined by cluster analysis; the fit of a phenogram back to its correlation matrix was indicated by the cophenetic correlation coefficient, r_{cs} (Rohlf 1985). Second, principal components (PC) of variation over the 16 variables for each of five samples were computed; correlations of the variables to PC1 were examined by rank correlation coefficients for the three classes of specimens. Third, discriminant-function analyses (DFA) were performed on nine samples. Because of the serial replication involved in this comparative study, statistical significance was judged by Bonferroni standards.

The DFA was performed using the following input groups with sexes pooled: North American ferals (n = 297), European ferals (110), wild Rock Doves (45), homers (18), runts + pounters (9), English carriers (5), jacobins + fantails (5), turbits (5), and tumblers (9). The samples vary in degree of homogeneity; to increase the sample sizes of some groups of domestics, more than one strain was included, and the assumption of equality of variance-covariance matrices over the nine groups probably was not met. The results nevertheless are reasonably consistent with those of the correlation and PC analyses. Males are larger than females (Burley 1981, Johnston 1990), so that samples with sexes pooled have inflated variances. Consequently, the degree of discrimination between groups is reduced. Use of samples with sexes pooled is a necessary procedure because of the unsexed specimens from the Darwin collection.

The tree diagram (Fig. 1) depicting genealogical relationships among the wild, feral, and domestic pigeons of this study is based on the known history of domestication of Rock Doves (Levi 1974) and the inferred history of ferals. Position of nodes is based on information concerning: (1) time of origin of Mediterranean domestic pigeons (ca. 5,000 ybp); (2) time of origin of European ferals (ca. 100 years later); and (3) time of origin of North American ferals (ca. 400 ybp).

Results

Sample statistics.—Descriptive statistics for males and females over the 16 variables for five subsamples of pigeons are shown in the Appendix. Individual wild Rock Doves average smaller in size than ferals and homers, and significantly so for about one-half the characters for each sex (t-tests, $P < 0.05$). North American and European ferals are similar in sizes and differ only in sternum length (females) and sternum depth (males; t-tests, $P < 0.05$). The homers, not the largest of the domestics in this study, average larger than the others listed in the Appendix, differing from all in all characters except skull length of European feral females and skull width of European and American feral females. The tumblers are smallest of all (t-tests, $P < 0.05$), differing in all characters except skull length of wild females.

Coefficients of variation.—To compare character variation in wild, feral, and domestic samples, coefficients of variation (CV) are shown in Table 3. The ferals from Lawrence, Kansas, and Durham, England, tend to have CVs similar to those for Sardinian Rock Doves, so feral character variability is of the same order of magnitude as in the wild birds. Male racing homers have large CVs as may be expected, but this is not true of the females.

Correlations among characters.—Intercharacter correlations (r_p) for the pooled sexes of several samples are examined in correlation matrices and phenograms. The phenogram for the wild sample (Fig. 2) provides the basic description of character relationships in the species and serves as a standard for comparison of the feral and domestic samples. The phenogram is derived from a character correlation matrix by the unweighted pair-group method using arithmetic averages. The phenogram distorts relationships in the matrix only slightly ($r_{cs} = 0.791$); it shows two main branches, each with one-half the variables. In one branch, the appendicular elements, scapula and coracoid are grouped, thus keeping leg, wing and pectoral girdle elements together. The second major group includes the core, skull, and bill characters.

This division of the character set is maintained by consistent and strong negative correlations between the six limb and three core elements. Additionally, the two bill characters each show five negative correlations with the limb elements, and skull width shows four. Since mandible width is highly correlated with pre-

TABLE 3. Coefficients of variation for skeletal characters in some locality samples of Rock Doves.

Character[e]	USA[a]		England[b]		Homers[c]		Sardinia[d]	
	M	F	M	F	M	F	M	F
MAXL	3.61	4.04	3.57	3.19	5.15	1.67	3.52	6.43
MAXW	7.21	6.79	4.90	4.70	8.55	5.86	3.09	3.79
SKLL	3.26	2.35	2.26	2.34	3.51	2.45	2.03	1.84
SKLW	3.03	2.79	2.27	2.25	2.90	1.93	2.10	1.81
MAND	4.32	3.78	4.42	4.85	2.82	3.81	3.49	4.41
SCAP	3.09	3.90	2.33	2.63	4.30	3.09	4.11	2.88
CORA	2.63	3.85	2.54	3.43	3.80	1.16	3.47	3.25
STRL	2.98	3.00	2.58	3.30	4.26	1.50	3.26	2.97
STRD	3.27	5.89	3.03	3.19	4.85	3.33	3.27	5.60
KEEL	3.36	3.68	2.91	4.13	5.31	3.93	4.06	3.41
FEMR	2.65	4.46	5.61	3.43	4.24	1.33	2.52	2.68
TIBI	2.39	3.91	2.99	3.56	3.79	1.88	2.22	3.44
TARS	3.00	4.58	2.52	3.44	3.76	1.43	2.36	2.72
HUML	2.12	3.69	2.20	2.95	3.36	1.14	2.72	2.58
ULNA	2.56	3.81	2.26	3.08	3.48	1.75	2.99	2.90
CARP	2.80	4.14	2.77	3.67	2.74	1.31	3.05	2.92

[a] Lawrence, Douglas County, Kansas.
[b] 17 km NE Durham, Co. Durham, England.
[c] Italy, England, Canada, and USA.
[d] Capo Caccia, 25 km W Alghero, Sardinia.
[e] Full names indicated in Table 2.

maxillary width, and skull length with skull width, they join the other six as a group.

A near duplicate of the above set of correlations is obtained from an analysis of the entire 416-specimen sample. This is worth noting while examining other subsets for their approximation to correlations of the wild birds, because coincidence or departure from the wild condition is not a simple function of degree of pooling of samples.

The correlation phenogram for the European ferals is almost a duplicate of that of the wild birds (but $r_{cs} = 0.862$). The split of characters into two groups as a consequence of strong negative correlations is preserved.

The North American ferals differ from the correlation phenograms noted above (although $r_{cs} = 0.862$). The major difference is that, even though the six limb elements form a distinct cluster, scapula and coracoid join the group of core, bill, and skull characters. A second difference is that depth of sternum, strongly correlated with length of sternum in wild pigeons, clusters apart from other core characters and only weakly with others. Some of the functional character pairs that are strongly correlated in the wild and European feral sets are no longer as strongly correlated in these ferals (Table 4). However, this varies in locality samples; for instance, the sample from Lawrence, Kansas (not depicted here) has character correlations more

similar to those of the wild pigeons than to North American ferals as a group.

The domestic specimens are examined as large domestics, small domestics, homers, runts, runts + pouters, carriers, and tumblers. The phenogram of the small domestics presents covariant subsets similar to those of the North American ferals ($r_{cs} = 0.822$); the appendicular elements cluster together and are joined only by premaxillary length. The other cluster has the remaining nine characters reasonably linked, save for skull width and scapula, which as a pair join skull length; the three then join the coracoid. A tendency for functional character pairs to show lesser levels of correlation is evident.
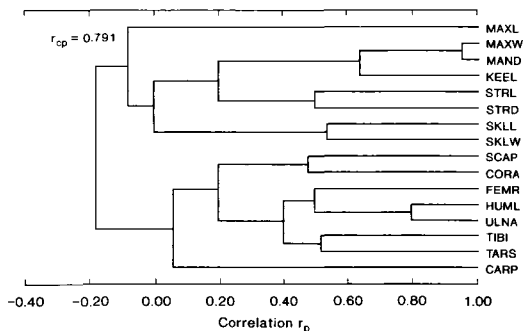

Fig. 2. Phenogram of character correlations derived from correlation matrix of 16 skeletal characters in sample of wild Rock Doves.

TABLE 4. Correlation coefficients (r_p) for functional character pairs in several subsets of wild, feral, and domestic pigeons.[a]

Characters	Wild Rock Dove	North American feral	European feral	Domestic	
				Homer	Tumbler
SKLL and SKLW	0.498 *	0.257 *	0.382 *	0.379 ns	0.450 ns
MAXW and MAND	0.913 *	0.861 *	0.805 *	0.909 *	−0.379 ns
SCAP and CORA	0.449 *	−0.126 ns	0.278 *	0.203 ns	0.415 ns
STRL and STRD	0.463 *	0.132 ns	0.324 *	−0.407 ns	0.188 ns
STRL and KEEL	0.321 ns	0.421 *	0.406 *	−0.386 ns	0.481 ns
STRD and KEEL	0.266 ns	−0.175 ns	0.126 ns	0.057 ns	0.210 ns
HUML and ULNA	0.763 *	0.622 *	0.300 *	0.702 *	0.788 ns
ULNA and CARP	0.201 ns	0.292 *	0.231 *	0.591 *	0.069 ns
FEMR and TIBI	0.189 ns	0.409 *	0.154 ns	0.581 ns	0.077 ns
TIBI and TARS	0.471 *	0.500 *	0.510 *	0.441 ns	0.691 ns

[a] Sexes pooled (see Appendix). Bonferroni correction applied: *, $P < 0.01$; ns, $P > 0.01$. Character abbreviations as in Table 2.

Only three of the familiar functional character pairs are found in the correlation phenogram of the large domestic specimens ($r_{cs} = 0.832$; Fig. 3). Importantly, the wing elements are clustered apart from the leg elements, the former appearing with skull length, premaxilla length, scapula, and coracoid. Additionally, skull width (which in the wild sample pairs with skull length) joins sternum depth (which normally pairs with sternum length). Compared to wild Rock Doves, the large domestic strains present novel character correlations, resulting in loss of some covariant character pairs noted above and providing levels of character relationship not found in wild pigeons and European ferals. Some characters are paired with other pairs of characters, rather than with single characters.

Examples from other groups of domestics may be briefly noted. Homers show correlations similar to those of wild pigeons except for negative correlations for sternum length with sternum depth and with keel length. Runts show neg-

ative correlations between the wing elements and two of those of the legs, and the character pairs are distorted relative to wild pigeons. Tumblers have all appendicular and pectoral girdle elements clustered together, but the character pairs are not those of associated elements; premaxilla width and mandible width are negatively correlated. Pooled jacobins and fantails show negative coefficients for skull length and width, but the appendicular elements cluster together.

Ten character pairs functionally associated with each other are examined by means of their correlation coefficients r_p in Table 4 for five subsets of specimens just discussed. Significance levels of the coefficients are included, but their utility is mitigated, first by variation in sample sizes and second by Bonferroni adjustments. Some of the differences generated by significance levels could be spurious. For instance, it is difficult to ignore the fact that the overall pattern of variation in character correlations is relatively uniform from one specimen set to another (Fig. 4).

In Figure 4, North American ferals and the large domestics depart conspicuously from the values for wild Rock Doves. Among large domestics, three pairs of characters show high positive correlations: humerus and ulna; tibiotarsus and tarsometatarsus; and femur and tibiotarsus. A large negative correlation is found for sternum length and keel length. North American ferals show small negative correlations between scapula and coracoid and between sternum depth and keel length. Jacobins + fantails have a negative correlation for skull length and skull width.

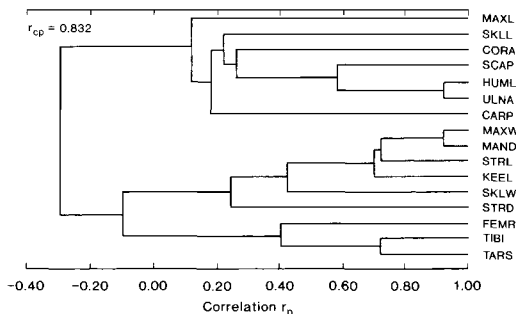*Principal-components analysis.*—This analysis

Fig. 3. Phenogram of character correlations derived from correlation matrix of 16 skeletal characters in sample of large domestic pigeons.
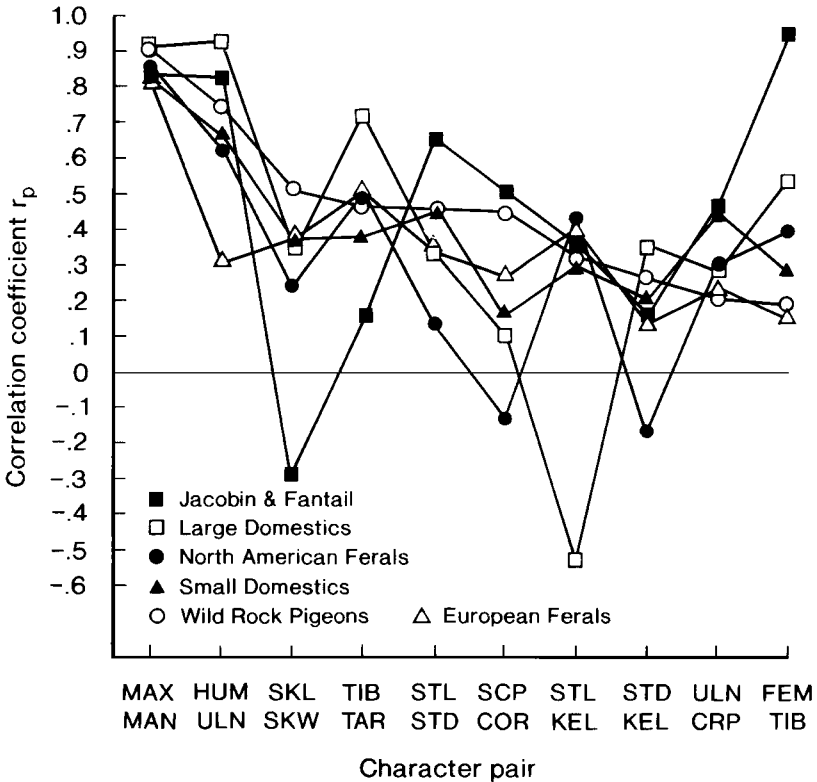
Fig. 4. Correlation coefficients r_p for 10 functionally-paired skeletal characters in five samples of pigeons.

provides orthogonal axes of variation that are linear combinations of the originally measured variables. Concerning the present specimens, independently computed PC1 axes for the five samples summarize from 81% to 92% of the total variation in the 16 variables of each set (Table 5). The percentage is large and all correlations are positive in all samples, suggesting that each group is characterized by a strong "size" component.

Each of the five PC1 axes shows positive correlation with all others on the basis of Spearman rank correlation coefficients (Table 6). Thus, the relative load of any character is approximately the same from one sample to another. PC1 for the wild sample is significantly correlated with those for the two feral sets; PC1 for the American ferals is correlated with those for the European ferals and both domestic sets; and the two domestic samples are correlated with each other. The other coefficients achieve significance at the 0.05 level, but are not here interpreted as statistically significant by Bonferroni standards.

PC2 summarizes an additional fraction of

variation—11% in the wild specimen set, but only 5% to 8% in the feral and domestic samples (Table 7). PC2 for the wild set includes information on allometry involving body core and limb length; this relationship also is marginally discernable in the loadings of the two feral sets and, perhaps, is biologically significant.

Discriminant analysis.—The specimens were segregated into nine subsets that were the input groups for stepwise discriminant analyses using the 16 skeletal variables. Resultant multivariate distances are summarized by a bivariate plot of group centroids in canonical space (Fig. 5), and by F-statistics computed from pairwise values of Mahalanobis D^2 (Table 8). All values of Mahalanobis D^2 are statistically significant at the 0.001 level. Domestic samples of most body sizes are highly significantly differentiated from wild and feral samples, but the jacobin + fantail sample shows D^2 values similar to the ferals. Specimens in the tumbler sample average smallest in size, and those in the runt + pouter sample average largest; there is an evident geometric similarity of departure by the larger and smaller domestic specimens from wild and feral sam-

TABLE 5. Correlations with original variables of first principal component of variation based on 16 skeletal characters in five samples of Rock Doves.[a]

Character	Wild Rock Dove	European feral	American feral	Large domestic	Small domestic
MAXL	0.554	0.741	0.593	0.761	0.887
MAXW	0.336	0.620	0.540	0.848	0.652
SKLL	0.703	0.795	0.779	0.910	0.892
SKLW	0.626	0.394	0.696	0.776	0.652
MAND	0.573	0.555	0.597	0.829	0.537
SCAP	0.856	0.901	0.881	0.955	0.889
CORA	0.886	0.918	0.911	0.883	0.836
STRL	0.834	0.879	0.834	0.848	0.874
STRD	0.579	0.748	0.823	0.902	0.844
KEEL	0.882	0.821	0.837	0.769	0.892
FEMR	0.855	0.874	0.911	0.945	0.913
TIBI	0.777	0.887	0.898	0.902	0.957
TARS	0.852	0.895	0.882	0.891	0.918
HUML	0.932	0.945	0.926	0.925	0.977
ULNA	0.881	0.860	0.929	0.947	0.982
CARP	0.885	0.907	0.803	0.918	0.955
Eigenvalue	9.45	10.50	10.55	12.33	11.91
Proportion of variance explained	81%	86%	92%	83%	82%

[a] Sexes pooled (see Appendix). Character abbreviations as in Table 2.

ples. Nevertheless, wild birds and the two feral samples, all of intermediate sizes, also are significantly different from one another.

The discriminant axes are defined by 15 variables; the first axis evidently incorporates substantial size information—the sample centroids plot as a reflection of their general sizes as perceived from information in the Appendix. Other axes receive different proportions of information from the same variables, and evidently summarize aspects of shape.

DISCUSSION

Nevertheless, I do not doubt that the simple fact of animals and plants becoming feral does cause some tendency to reversion to the primitive state, though this tendency has been much exaggerated by some authors [Darwin 1868].

The remarks beyond are based on two assumptions: that Rock Doves 5,000 to 10,000 ybp possessed much the same bony morphology as wild Rock Doves today; and that English and Scottish domestic dovecote pigeons were largely domestic, not feral, birds. The first assumption has modest support, in the form of isolated pigeon bones from cave deposits of Pleistocene age (310,000 to 60,000 ybp) from the Near East; many are readily identifiable as those of C. livia

(Tchernov 1962, 1968). But, population samples of whole skeletons of Rock Doves prior to the development of domestics will probably never be available and, since the rates at which bony sizes and shapes of pigeons can change are known to be rapid, the assumption must be kept in mind.

The second assumption is not testable, as no records exist concerning the kinds of pigeons settlers brought by ship to North America. However, the birds would have been adjusted to confinement, a necessary condition for a sea voyage on sailing ships, so the number of ferals in the transoceanic shipments was possibly zero.

Given the assumptions, the results of my study on body size and shape similarities and differences in wild, domestic, and feral Columba livia are almost straightforward. The two feral sam-

TABLE 6. Rank correlation coefficients r_p for first principal component based on 16 skeletal variables in five samples of pigeons.[a]

Sample	Wild	European feral	American feral	Large domestic
European feral	0.812			
American feral	0.756	0.706		
Large domestic	0.476	0.521	0.629	
Small domestic	0.579	0.594	0.688	0.644

[a] Coefficients above 0.601 significant at 0.01 level.

TABLE 7.   Correlations with original variables of second principal component of variation based on 16 skeletal characters in five samples of Rock Doves.[a]

Character	Wild Rock Dove	European feral	American feral	Large domestic	Small domestic
MAXL	0.179	0.137	0.077	−0.566	−0.406
MAXW	−0.065	0.771	0.821	−0.094	0.619
SKLL	−0.020	0.103	0.090	−0.070	0.103
SKLW	0.111	0.094	−0.020	−0.022	0.102
MAND	−0.130	−0.118	0.205	−0.146	−0.141
SCAP	−0.139	−0.114	−0.146	0.077	−0.047
CORA	−0.280	−0.177	−0.224	−0.112	−0.012
STRL	0.355	−0.095	−0.023	0.406	0.189
STRD	0.771	0.114	−0.019	0.175	0.166
KEEL	0.157	0.009	0.043	0.446	0.136
FEMR	−0.115	−0.126	−0.148	0.163	0.028
TIBI	−0.312	−0.129	−0.141	0.295	0.149
TARS	−0.359	−0.093	−0.123	0.332	0.157
HUML	−0.237	−0.130	−0.172	−0.112	0.076
ULNA	−0.337	−0.142	−0.184	−0.108	0.050
CARP	−0.301	−0.138	−0.209	−0.021	0.029
Eigenvalue	1.41	0.79	0.98	1.02	0.73
Proportion of variance explained	11%	7%	8%	6%	5%

[a] Sexes pooled (see Appendix). Character abbreviations as in Table 2.

ples tend to be more like one another and the wild birds than any of the domestics, aside from the pooled sample of jacobins + fantails. This is a tendency that could not have been predicted from knowledge of the phyletic relationships of these birds (Fig. 1)—North American ferals could be expected to be more similar to domestic samples than to European ferals, if recency of common ancestry is a basis on which to judge. Note that a study of allozyme variation using feral specimens from Kansas and northern Italy found a Nei's genetic distance of 0.11 over 49 presumed loci between the two samples (Johnston et al. 1988), which is not inconsistent with the genealogical tree. Furthermore, the genetic distance over the same loci between North American and wild birds is 0.31, and that for Italian ferals and wild birds is 0.13.

Discrepancies between morphological similarity and phylogenetic relationships will have
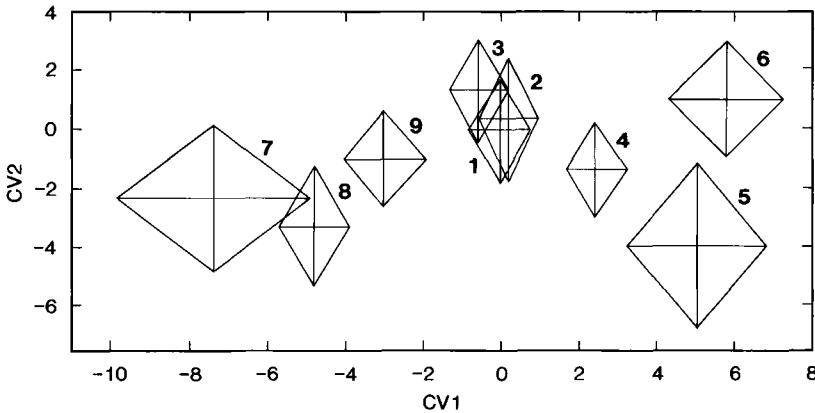

Fig. 5.   Plot of first two canonical variates of skeletal characters for nine samples of *C. livia* (sexes pooled). Centroids of samples indicated by numbers at centers of quadrilaterals, apices of which show one standard deviation to either side of mean on each axis. Identifications: (1) North American ferals; (2) European ferals; (3) wild Rock Doves; (4) racing homers; (5) pooled runts and pouters; (6) English carriers; (7) tumblers; (8) turbits; (9) pooled jacobins and fantails.

TABLE 8. Pairwise morphologic distances as Mahalanobis D^2 statistics in canonical analysis of skeletal characters for nine samples of pigeons.[a]

	WILD	EURF	NAMF	HOMR	PUNT	CARR	TUMB	TURB
EURF	5.27							
NAMF	9.89	4.21						
HOMR	15.45	9.41	11.56					
PUNT	30.07	23.79	25.41	8.31				
CARR	17.78	15.58	16.72	9.47	10.94			
TUMB	30.90	37.23	34.80	40.59	46.58	39.98		
TURB	11.22	11.51	10.52	13.03	19.64	23.26	4.46	
JACB	5.41	6.21	5.41	10.09	17.07	15.62	6.76	4.29

[a] Sexes pooled (see Appendix). Entries evaluated as F-statistics; at $\alpha = 0.001$ with df = 15 and 379, all are statistically significant. Codes for samples: WILD, European wild *Columba livia*; EURF, European ferals; NAMF, North American ferals; HOMR, racing homers; PUNT, combined runt and pouter domestics; CARR, English carrier domestics; TUMB, tumbler domestics; TURB, turbit domestics; JACB, combined jacobin and fantail domestics.

occurred as a result of some strong nonrandom process, because North American ferals have had only about 400 years in which to have their domestic morphology modified toward that of European ferals. The most likely nonrandom process causing the intercontinental resemblance of ferals is natural selection on size and shape variables of the escaped domestics and their descendants. Another possible cause of the resemblance is that pigeons of only a certain range of sizes and shapes, such as jacobins and fantails or captive European ferals, escaped captivity to become feral in North America.

The latter prospect probably can be rejected as a significant cause. No evidence exists that domestic pigeons of different shapes and sizes have different rates of successful escape from captivity; it is implied that domestics of unusual or bizarre plumage characteristics would have low survival fitness in the wild (Levi 1974, Janiga 1991). Both jacobins and fantails, which prove similar to ferals and wild stock in bony size and shape, are show birds of ancient origin. Jacobins have trouble seeing through their feather hoods (breeders clip the hoods outside the show season), are reputed to be difficult to breed (Levi 1974), and are likely to be of low fitness in the wild. Fantails are bred exclusively for show and also have bizarre plumage—more than 30 rectrices is considered desirable by breeders—and lack uropygial glands. Aside from size, these varieties do not seem to be the stuff of feral ancestors. Recaptured ferals could escape captivity at the same rates as domestics, and could be at higher survival fitness than domestics; they also could account for size resemblances between American and European ferals if they were significant components of the original inoculations; there is no information on presence or absence of European ferals in the inoculations.

In any event, escapes of large, intermediate-sized, or small dovecote birds could have done well as the ancestors of American ferals; if large, intermediate, and small domestics escape and interbreed, their offspring, regressing toward the mean, will be of intermediate sizes (Wexelsen 1937), and little trace of large or small parents will later exist. Racing homers are a case in point. Today they escape captivity more often and have greater chances to join feral colonies than any other domestic strain; yet, ferals are significantly smaller than homers.

Moving to a consideration of natural selection being a causal part of current feral sizes and shapes, do the results of correlation, component, and discriminant analysis support the idea? The examination can be made serially.

Character correlations.—Character correlations should trace functional character complexes that are developmentally, and presumably genetically, linked (Darwin 1868, Wright 1968, Gould and Johnston 1972, Baker 1985). Such complexes include bony character pairs in these pigeons. The characters are, to judge by quantitative studies of inheritance, genetically based (Wexelsen 1937). Thus, there is no necessary reason for functional character pairs of wild pigeons to be somehow changed in domestics and ferals; however, that is what is indicated.

Consequently, the character correlation phenogram for wild Rock Doves (Fig. 2) is worth examining in detail. The diagram sets off one main branch with the following pairs: premaxilla and mandible widths, sternum length and depth, and skull length and width; keel length joins premaxilla and mandible widths, and premaxilla length is the odd character out. In the

second main branch, scapula and coracoid lengths, humerus and ulna lengths, and tibiotarsus and tarsus lengths are paired; femur length joins humerus and ulna lengths, and carpometacarpus length is the odd character out. Appendicular and pectoral-girdle characters, thus, are set off from those of the head, bill, and, most importantly, the core. This topology pays appropriate respect to the allometric reduction in length of appendages relative to body size that ought to be found in pigeons showing variation in size (Johnston 1990; B. McGillivray, pers. comm.). This core-to-limb topology also is found in a character correlation analysis of the pooled sample of 416 specimens; it very nearly duplicates that for the wild Rock Doves.

Striking departures from the correlations just listed exist in the pooled large domestics. Here the forelimbs and hindlimbs are negatively correlated, so that wing and leg elements appear in different main branches of the phenogram (Fig. 3). The large domestic strains were subjected to strong selection for large size or its covariates, so the dissolution of the correlation between wings and legs could be an inadvertent consequence of artificial selection. This is not to say that there is no structure in the correlation matrix of the large domestics, only that the structure is different. In fact, these birds show high positive correlations for some functional character pairs from the appendages, and a remarkable high negative correlation between lengths of sternal basin and sternal carina. However, it is not the same set of relationships as depicted for wild Rock Doves.

Similarly, the pattern of character correlation for the jacobin + fantail pool departs from expectation based on the wild sample. The exceptional character pair is skull length and width, which have strong negative coefficients.

Overall, the correlation study provides little evidence for a common structure of functional character pairs. Of those found in wild Rock Doves (Table 4), only some are evident (less closely linked) in domestic samples, and in large domestics they may even disappear. However, the functional pairs tend to be found in feral samples, especially those from Europe. All this is consistent with a hypothesis that character correlations of the functional pairs are being reconstituted in ferals after having been lost in some domestics.

Principal-components analysis. —Character loadings on PC axes occasionally have been used to compare size and shape in specimen samples of birds. Similarity in character loadings within each of PC1 and PC2 (and, thus, of size and shape) has been found for populations of House Sparrows (*Passer domesticus*) from Europe and North America, separated for perhaps 130 years (Johnston 1973), and from Europe and New Zealand, separated for 110 years (Baker 1980). Much the same story is found for New Zealand populations of the Common Myna (*Acridotheres tristis*; Baker and Moeed 1979, 1980). On this basis, we could expect pigeons to show a similar conservatism in component structure.

The five samples of pigeons examined heie in fact show marked similarity in character loadings on PC1; this is to some extent evident in the raw loadings (Table 5), and is quantified in Table 6 by means of nonparametric correlation coefficients for 10 possible pairs of vectors of loadings. As in the correlation analysis, however, the patterns of character loadings in Table 5 show strong phenetic relationships between the two feral sets and wild pigeons, as well as between the two feral sets themselves. These relationships are in all cases stronger ($P < 0.01$) than those between the three and either domestic set ($P > 0.01$).

The only PC2 axis that reaches nominal significance is that for the wild specimens (Table 7). This axis reflects the core/limb inversity imposed by size allometry. One would expect such allometric relationships to be preserved in working domestic pigeons, as they are in homers (Johnston 1990), which (aside from the cere) probably have escaped arbitrary artificial selection for bizarre morphology. Similarly, if ferals have escaped the yoke of domesticity and are now subject to natural selection, they too should display the allometry of wild pigeons. Both feral samples and the large domestics actually suggest the presence of the core/limb inversity by means of the pattern of positive and negative loading on PC2, although the trace of variance is trivial.

Summarizing the component study, character loadings on PC1 show American ferals to be less strongly phenetically allied than are European ferals to wild pigeons; however, they have a distinctly stronger correlation of PC1 loadings with wild pigeons than with either domestic set. PC2 weakly suggests the reconstruction in ferals of the allometry of body core and limb length characteristic of wild pigeons but lacking in small domestics.

Discriminant analysis.—All groups compared in this analysis are statistically differentiable from one another (Table 8; Fig. 5). And, as in other analyses, even though they are not identical, the two samples of ferals are phenetically closer to one another and to the wild sample than to domestics (excepting the jacobin/fantail sample). The artificially selected birds have size and shape characters clearly different from those of birds living beyond human confinement.

Conclusions.—As a preamble, please recall that domestic strains of Rock Dove are genetically based. Strains are identifiable by their bony and plumage morphology, their behavior, and their physiology, because many of these characteristics are what were selected by human breeders for hundreds of generations. Some of the domestic phenetic characteristics could have appeared initially as a result of genetic drift and fixation in small captive populations (often in which $n = 2$), variation in captive population structure, pleiotropism, and interstrain hybridization, aside from strictly environmental components (James 1983). The negative character correlations found in large domestics and the jacobin + fantail sample could have arisen in captivity in a number of ways, including drift coupled with artificial selection. Later, when domestic strains reverted to living in the wild in the absence of artificial maintenance of strains, genetic changes affecting size and shape of free-living domestics would had to have been caused by other factors. These could have been as simple as the breaking up of homozygous recessives through cross-matings, or as complex as major changes in allele frequencies in response to selection.

Is natural selection a necessary or sufficient cause of the morphologic coincidences found among American and European feral pigeons? The answer to this must emphasize the differences in the founder inocula and subsequent populations of the two feral lines. Apart from the time differences, which are substantial, European ferals from the beginning have had wild Rock Doves as possible reproductive partners. Ferals still are capable of functionally joining wild colonies, as at Flamborough Head, England, and Capo Caccia, Sardinia. Moreover, some European dovecote culture has been maintained with wild Rock Doves, birds that were not domesticated (Hawes 1984), providing additional opportunities for European ferals to incorporate the genetics of size otherwise characteristic of wild Rock Doves. Thus, from a richness of background including domestic, dovecote, and wild stocks in Europe, and from a restricted background including only domestic dovecote stocks in North America, feral pigeons provide a major case of convergent morphology for which natural selection may be the only explanatory cause.

Feral pigeons have a way to go to fully fit the morphometrics of wild pigeons, but the prospect of ferals ultimately physically approximating Rock Doves is apparent. If the Rock Dove is in time rendered extinct, it will have been in part because of interbreeding with feral pigeons, and some form of feral will no doubt replace wild Rock Doves, a fate already realized in Great Britain and underway elsewhere. Long-term consequences of such a replacement are difficult to estimate, at least because feral birds come from ancestors genetically modified for tractability and tameness (see Leopold [1944] for an examination of heritable wildness in turkeys [*Meleagris gallopavo*]). Even so, as I have shown, feral *C. livia* ought to have satisfactory bony morphometrics when reverting wholly to the wild.

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APPENDIX.   Means (mm) and standard deviations (in parentheses) of skeletal characters of wild, feral, and domestic Rock Doves.

| | Sex | Wild Rock Dove | European feral | N. American feral | Domestic | |
					Homer	Tumbler
MAXL	F	21.1 (1.32)	22.0 (1.10)	21.4 (1.14)	23.7 (0.40)	12.7 (1.44)
	M	21.5 (0.76)	22.3 (1.01)	22.2 (0.91)	23.7 (0.40)	17.0 (1.08)
MAXW	F	2.7 (0.11)	2.9 (0.18)	2.9 (0.18)	3.1 (0.18)	2.4 (0.31)
	M	2.9 (0.09)	3.0 (0.15)	3.0 (0.20)	3.3 (0.40)	2.8 (0.39)
SKLL	F	31.5 (0.57)	32.4 (1.01)	31.9 (1.00)	34.7 (0.89)	26.6 (1.06)
	M	32.2 (0.65)	32.8 (0.91)	32.9 (0.97)	35.7 (1.26)	29.6 (0.82)
SKLW	F	18.6 (0.33)	18.8 (0.47)	18.5 (0.51)	19.2 (0.37)	17.4 (0.72)
	M	19.2 (0.40)	19.2 (0.49)	19.3 (0.56)	19.9 (0.58)	17.9 (0.37)
MAND	F	4.1 (0.18)	4.3 (0.24)	4.3 (0.22)	4.7 (0.18)	3.8 (0.22)
	M	4.2 (0.15)	4.3 (0.21)	4.4 (0.20)	4.8 (0.14)	4.1 (0.26)
SCAP	F	41.0 (1.15)	43.0 (1.87)	42.6 (1.61)	46.6 (1.44)	36.4 (2.89)
	M	42.0 (1.73)	44.0 (2.00)	44.6 (1.63)	47.7 (2.05)	39.5 (1.40)
CORA	F	31.9 (1.02)	32.9 (1.41)	32.6 (1.48)	35.8 (0.41)	28.2 (1.22)
	M	33.0 (1.14)	34.0 (1.34)	34.0 (1.42)	37.1 (1.41)	31.9 (1.28)
STRL	F	61.7 (1.81)	64.3 (2.37)	63.2 (2.21)	69.8 (1.05)	52.1 (3.22)
	M	64.1 (2.09)	65.6 (2.38)	65.7 (2.20)	71.8 (3.06)	57.0 (2.45)
STRD	F	32.9 (1.87)	34.0 (1.61)	33.7 (1.58)	34.4 (1.82)	27.7 (1.74)
	M	33.8 (2.37)	34.6 (1.69)	35.4 (1.36)	37.4 (1.82)	31.2 (1.79)
KEEL	F	65.5 (2.18)	68.0 (2.82)	66.8 (2.79)	74.1 (2.91)	53.5 (4.13)
	M	68.4 (2.78)	69.9 (2.97)	70.0 (2.62)	77.3 (4.10)	59.7 (3.52)
FEMR	F	36.2 (0.86)	37.5 (1.56)	37.0 (1.57)	40.6 (0.54)	31.1 (1.51)
	M	37.6 (0.95)	38.5 (1.64)	38.9 (1.37)	42.2 (1.79)	36.4 (1.82)
TIBI	F	54.5 (1.86)	56.3 (2.32)	55.6 (2.32)	61.4 (1.16)	45.5 (2.33)
	M	55.9 (1.24)	57.9 (2.32)	57.8 (2.32)	62.8 (2.38)	52.6 (1.89)
TARS	F	29.1 (0.81)	30.2 (1.23)	30.0 (1.18)	33.2 (0.48)	24.8 (1.11)
	M	30.1 (0.71)	31.2 (1.17)	31.5 (1.18)	36.0 (3.47)	29.0 (2.19)
HUML	F	42.4 (1.07)	43.8 (1.62)	43.2 (1.62)	47.2 (0.54)	38.9 (1.54)
	M	44.0 (1.20)	45.0 (1.57)	45.2 (1.35)	49.0 (1.65)	41.4 (1.23)
ULNA	F	50.9 (1.44)	52.0 (2.10)	52.3 (1.92)	57.5 (1.01)	42.2 (2.33)
	M	52.6 (1.57)	54.0 (2.52)	54.6 (1.75)	59.5 (2.07)	49.7 (1.71)
CARP	F	30.9 (0.89)	32.3 (1.41)	32.1 (1.28)	35.6 (0.46)	26.1 (1.13)
	M	31.5 (2.10)	33.1 (1.35)	33.4 (1.47)	37.1 (1.02)	30.0 (1.14)