

VARIATION IN SIZE AND SHAPE IN PIGEONS, *COLUMBA LIVIA*

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ABSTRACT.—Morphometric studies of Rock Doves and feral pigeons (*Columba livia*) are enhanced by knowing that variation in size and shape has a well-studied genetic causation in domestic pigeons. Size distributions of skeletal elements of the sexes approximate normality; males are significantly larger than females. Size as measured by principal component I of feral females shows significant interlocality variation, and tends to increase with latitude in North America. Size of males shows no such geographic patterning. Relative limb lengths vary inversely with core size in feral pigeons. Large pigeons have proportionately shorter wings, heavier wing-loading, and are likely to fly faster than small ones. This may explain why homing pigeons tend to be larger than feral pigeons, which are more like wild Rock Doves than homers. Since feral colonies could be colonized by domestics of all sizes, the absence of very small and very large birds probably reflects results of interbreeding of colonizers with resident ferals, and ultimately natural selection for intermediate sizes. Received 24 April 1989, accepted 26 Aug. 1989.

Variation in size and shape in Rock Doves² (*Columba livia*) is in some ways more interesting to examine than that of many other kinds of birds because humans have been modifying size and shape of domestic and feral pigeons by artificial selection for thousands of generations (Levi 1974, Sossinka 1982). Captive stocks have been genetically modified for a wide range of sizes (Wexelsen 1937); feral populations may be expected to show evidence of this, variably depending on recency of colonization and genetic composition of the early sources, the frequency and genetic composition of current immigrants, the nature of any directional natural selection, and the magnitude of environmental induction of size. Such conditions could well lead to idiosyncratic size variation in feral pigeons in contrast to patterns found in other species (Jackson 1970; Power 1970; James 1970, 1983; Johnston and Selander 1971; Calder 1984).

Information on sizes of feral pigeons has long been generally available (e.g., Olson and Miller 1958, Levi 1974). Additionally, sexual size dimorphism was noted in studies of the genetics of size (e.g., Wexelsen

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² This is commonly accepted by North Americans as the vernacular name of wild and feral *C. livia* (but see British Ornithologists' Union Records Committee [1988] for current British usage). Even so, names of domestic and feral derivatives of Rock Doves have a long history in English, antedating any codification of vernacular nomenclature, as *pigeon*, *domestic pigeon*, *dovecote pigeon*, and *feral pigeon*, among others; wild *C. livia* has always been called Rock Pigeon by some (e.g., Darwin 1868). In this paper the name Rock Dove will be reserved for specimens of wild *C. livia*, and the expressions feral pigeon and domestic pigeon will be used for specimens of feral and domestic sources.

TABLE 1
 SCORES ON THE FIRST PRINCIPAL COMPONENT OF VARIATION IN SKELETAL SIZE OF
COLUMBA LIVIA FROM NORTH AMERICA AND EUROPE

Localities	Principal Component I*					
	Males			Females		
	N	Mean	SD	N	Mean	SD
Lawrence, KS	11	4.12	0.53	12	2.70	0.72
Chicago, IL–Madison, WI	16	4.49	0.60	10	3.52	0.54
Edmonton, Alta.	21	4.57	0.56	9	3.94	0.68
Ann Arbor, MI–Pittsburgh, PA	9	4.10	0.76	10	3.54	0.75
Ottawa–Toronto, Ont.	10	4.75	0.75	5	3.51	0.13
New Haven, CT–New York, NY	7	4.10	0.58	17	3.42	0.51
Washington, DC–Gainesville, FL	15	4.27	0.62	9	3.64	0.76
Berkeley, CA	2	4.12	1.07	5	3.13	1.02
North-central Italy	4	3.13	0.83	3	2.53	0.49
Rock Doves	2	3.64	0.88	4	2.51	0.60
Racing Homers	8	6.16	2.50	5	5.38	0.14

* Of 16 skeletal variables of size, computed from the ln-transformed data and the covariance matrix of the pooled sexes.

1937) and has been examined at least twice for population samples (Burley 1981a, Johnston and Johnson 1989). Differences in sizes of the sexes have also been documented for Rock Doves in faunal works (e.g., Witherby et al. 1940). Shape of pigeons has been examined in studies of bird flight (e.g., Rayner 1988).

This report examines the size and shape of skeletons of feral pigeons and Rock Doves from a number of localities. Analyses of univariate and multivariate sexual size dimorphism are presented; specific characteristics of locality samples are displayed, along with geographic variation in sexual size dimorphism; and shape differences among pigeons of different sizes are noted.

MATERIALS AND METHODS

Skeletons of pigeons were assembled in the course of field work or through loans from several institutions; adults providing measurements totaled 105 males and 89 females (Table 1). Geographic sources included parts of the Mediterranean Basin and northwestern Europe, Canada, and the United States. Most of the specimens came from feral populations, but six were Rock Doves.

A small set of birds of "homing pigeon" stock ("homers") was separated from several of the locality samples. The birds were identified as homers if they had been fitted with leg bands used by persons who raise and fly homing pigeons. These collectively were treated as a sample in some of the analyses described below, although they came from widely separated sources in both North America and Europe. In this study, homer characters were of large size. Unidentified large individuals might have been homers, might have had recent

TABLE 2
SUMMARY STATISTICS FOR SKELETAL MEASUREMENTS FOR THE SEXES OF *COLUMBA LIVIA*,
LOCALITIES POOLED

Character	Males (105)		Females (89)		<i>F</i> ^a	<i>P</i> ^b
	Mean	SD	Mean	SD		
Premaxilla length	22.3	1.17	21.6	1.27	17.72	<0.002
Premaxilla width	3.0	2.09	2.9	1.77	8.58	0.06
Skull length	33.2	1.20	32.1	1.14	46.87	<0.002
Skull width	19.4	0.59	18.6	0.51	91.51	<0.002
Mandible width	4.5	0.22	4.3	0.22	12.63	0.008
Scapula length	44.7	1.95	42.8	1.85	48.47	<0.002
Coracoid length	34.3	1.39	32.7	1.47	62.68	<0.002
Sternum length	66.0	2.79	63.4	2.79	44.03	<0.002
Sternum depth	35.4	1.67	33.6	1.90	48.27	<0.002
Keel length	70.4	3.27	69.1	3.18	50.88	<0.002
Femur length	39.1	1.70	37.1	1.71	63.69	<0.002
Tibiotarsus length	58.1	2.52	56.0	2.47	32.32	<0.002
Tarsometatarsus length	31.7	1.47	30.2	1.45	51.57	<0.002
Humerus length	45.4	1.78	43.5	1.81	58.02	<0.002
Ulna length	54.9	2.29	52.6	2.19	49.93	<0.002
Carpometacarpus length	33.6	1.84	32.3	1.46	29.50	<0.002

^a ANOVA *F*-values computed on ln-transformed characters of the total sample.

^b Bonferroni correction applied.

homer ancestry, or might have been large for other reasons. Four males and eight females fell into the subset of possible homers by discriminant function analysis, but were analyzed as parts of the locality samples in which they were received.

Sixteen bony size variables were measured with dial calipers to 0.01 mm (Table 2); most measurements were obtained as per protocols of Johnston and Selander (1971) or McGillivray (1985), but mandible width was taken as the least distance across the articular surface.

Computations were done on an IBM 3081 KX3 mainframe computer using BMDP (Dixon 1988) or on a hand calculator. Size over the 16 variables was summarized by principal component analyses (PCA; BMDP4M). For assessment of size generally and within each sex, the data for both sexes were pooled, ln-transformed and the covariance matrix employed; use of both sexes generates large size variance and thus produces a common size component (PC-I), with shape being partialled over subsequent axes (Hamilton and Johnston 1978, Somers 1986). For PCA comparisons of shape the raw data were handled through the correlation matrix. PC scores vary around a mean of zero, so in order to enhance comparison of individuals 4 was added to each score, making them all positive.

Descriptive statistics were computed using BMDP2D. Geographic variation in size was assessed through one-way analysis of variance (ANOVA, BMDP7D) and discriminant function analysis (BMDP7M). Possible interaction between sexual size dimorphism (SSD) and interlocality size variation was examined by two-way ANOVA. Differences between means were examined by *t*-tests (BMDP3D) or ANOVA *F*s. Regressions were performed by means of BMDP2R. Degree of SSD for individual characters is presented either in the form of

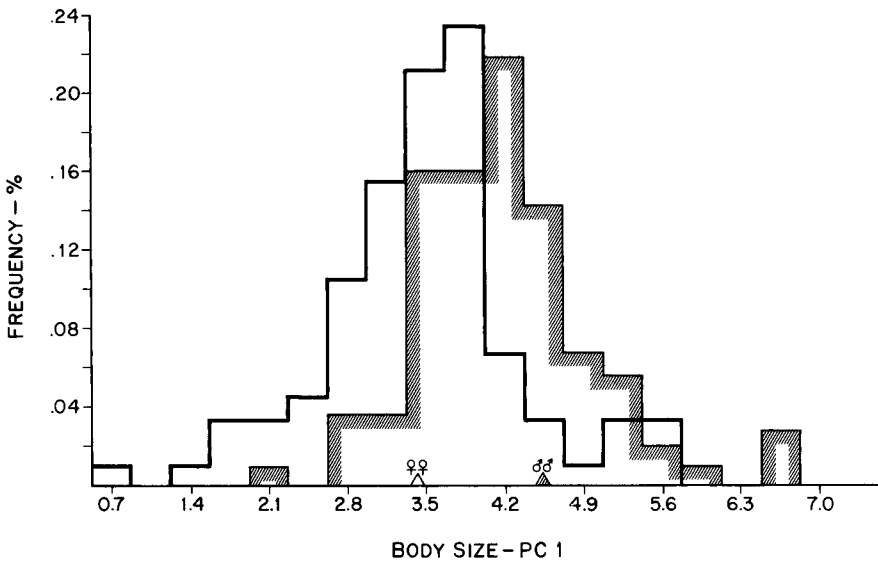


FIG. 1. Frequency distribution of sizes of 194 specimens of females (left histogram) and males (right histogram) of *Columba livia*. The principal component I scores for individuals were obtained from a PCA over 16 variables of skeletal size using ln-transformed data and the variance-covariance matrix for the pooled sexes. An ANOVA of the two samples provided $F = 64.26$ ($df = 1, 192, P = 0.0001$), describing highly significant size dimorphism.

F -values from an ANOVA or of the dimorphism index (DI) of Storer (1966). The DI is calculated as a percentage of the means for each sex ($100(\bar{X}_m - \bar{x}_f)/(\bar{x}_f + \bar{x}_m)/2$), in which \bar{x}_f and \bar{x}_m symbolize means of females and males.

RESULTS

Variation in size.—The distribution of sizes of adult males and females using scores of individuals on PC-I is shown in Table 1 and Fig. 1. Considerable sexual size overlap is displayed, and males are larger than females. The distribution of the entire sample (not shown) is normal (Shapiro and Wilk's [1965] $W = 0.99, P = 0.69$); that for the females is likewise normal ($W = 0.98, P = 0.61$), but that for the males is skewed to the right ($W = 0.95, P = 0.005$); the latter finding reflects the comparatively few small individuals relative to the numbers of large individuals in the sample of males.

Univariate SSD is given in Table 2; differences in sizes of the sexes for any one of the variables run around 2 to 4 percent. Interlocality variation also occurs, but does not statistically interact with SSD (Table 3, for North American specimens). Males are larger than females in all but two vari-

TABLE 3
SEXUAL SIZE DIMORPHISM AND INTERLOCALITY VARIATION IN SIZE OF CHARACTERS OF THE
SKELETON OF NORTH AMERICAN *COLUMBA LIVIA*^a

Character	F-Value		
	Sexual dimorphism	Localities	Interaction of SD and loc.
Premaxilla length	13.79**	1.42	0.33
Premaxilla width	5.78	5.31**	0.92
Skull length	38.84**	4.50**	0.65
Skull width	54.09**	3.10*	0.66
Mandible width	7.34*	2.82*	0.81
Scapula length	24.14	0.66	0.73
Coracoid length	33.92*	0.72	0.46
Sternum length	36.22**	1.20	1.21
Sternum depth	25.11*	1.14	0.28
Keel length	41.53**	2.28	1.61
Femur length	49.59**	3.06*	0.99
Tibiotarsus length	19.73**	3.68*	1.36
Tarsometatarsus length	25.90**	3.65*	0.63
Humerus length	44.15**	2.22	1.33
Ulna length	36.69**	2.86*	1.07
Carpometacarpus length	18.69**	2.52	1.01
PC-I	58.38**	3.66*	1.24

^a The ln-transformed data for 91 males and 77 females from 8 localities were analyzed in a two-way ANOVA (BMDP 7D; Dixon 1988) in which sex and locality were the independent variables. Statistical significance: * = <0.05, ** = <0.01 (Bonferroni correction applied).

ables of skeletal size as well as PC-I; 9 of the 17 show significant interlocality variation.

Although no interaction between SSD and geographic variation is found in Table 3, the dimorphism index for localities computed on PC-I varies widely but without pattern. Some interplay between sex and locality, or sex and size, is noted in a comparison of SSD in different samples (Table 4). A consistent and high-level SSD, similar to that in the overall specimen set, is found in the sample from eastern Kansas. Specimens from Alberta, Canada, and the heterogeneous set of homers, however, show a lesser degree of dimorphism. Only for male homers, among which one specimen is exceptionally small (for a homer, that is; it is still larger than 85% of all specimens), are inflated variances noted for any variable. The patterning of dimorphism of the 16 variables in the sample from Edmonton and the homers is similar; correlating the rank-ordered variables in degree of dimorphism from large to small across the two samples produces a coefficient of $r_s = 0.47$ ($N = 16$; $P < 0.05$). The specimens of the two

TABLE 4
COMPARISON OF SEXUAL SIZE DIMORPHISM OF VARIABLES IN THREE SAMPLES OF SKELETONS
OF *COLUMBA LIVIA*

Variable	Dimorphism index ^a		
	Homers	Alberta	Kansas
Premaxilla length	0.9	1.0	1.7
Premaxilla width	4.3	1.9	1.9
Skull length	0.9	0.3	1.4*
Skull width	1.7	0.7	1.7**
Mandible width	2.1	2.0	2.8
Scapula length	0.8	0.5	1.6**
Coracoid length	0.9	0.6	2.0**
Sternum length	0.5	0.5	1.4**
Sternum depth	0.7	0.8	2.0*
Keel length	1.0	0.5	1.7**
Femur length	1.0	0.8	1.9**
Tibiotarsus length	0.4	0.5	1.5**
Tarsometatarsus length	0.8	1.2	1.8**
Humerus length	1.0	0.8	1.6**
Ulna length	0.8	0.8	1.8**
Carpometacarpus length	1.2	0.9	1.7**

^a Indexes were calculated on means of the ln-transformed male and female data for each locality; significance of the differences between means was tested by *T* and is indicated by the following levels: * = <0.05, ** = <0.01 (Bonferroni correction applied).

samples are not only similar in reduced size dimorphism, but also in the degree to which each variable shows dimorphism.

Patterning of interlocality size variation is weak in the present samples. North American males from 8 localities show significant variation for only 5 of the 16 individual variables. North American females from 9 localities, however, show significant variation in PC-I scores and in 13 of the 16 individual variables. A regression of scores of females on PC-I with latitude for 9 North American localities was marginally significant ($r = 0.66$; $F = 5.33$; $df = 1, 7$, $P = 0.06$).

Variation in shape.—Lengths of limb elements vary inversely with central-core sizes in this sample. Most of the correlations are not statistically significant, but the patterning is clear: the six limb elements (as well as the coracoid and scapula) have negative correlations on PC-II, and the body core elements, (along with those of the skull) have positive correlations (Table 5). Scores on PC-II failed to regress on latitude in either sex. The scores also showed no sexual dimorphism (ANOVA $F = 0.81$; $df = 1, 192$, $P > 0.37$).

The change in relative limb lengths with “size” is usually described as

TABLE 5
CORRELATIONS^a OF THE ORIGINAL VARIABLES WITH PRINCIPAL COMPONENTS I AND II FROM
MATRICES OF SIZE CHARACTERS OF SKELETONS OF *COLUMBA LIVIA*

Variable	Females (89)		Males (105)	
	PC I	PC II	PC I	PC II
Premaxilla length	0.612	0.114	0.738	0.079
Premaxilla width	0.489	0.544	0.493	0.560
Skull length	0.777	0.087	0.800	0.153
Skull width	0.611	0.063	0.560	0.378
Mandible width	0.566	0.370	0.780	0.332
Scapula length	0.899	-0.006	0.866	-0.058
Coracoid length	0.929	-0.175	0.915	-0.220
Sternum length	0.884	0.186	0.857	0.231
Sternum depth	0.760	0.411	0.781	0.006
Keel length	0.843	0.209	0.843	0.281
Femur length	0.743	-0.292	0.901	-0.168
Tibiotarsus length	0.919	-0.267	0.902	-0.212
Tarsometatarsus length	0.902	-0.163	0.890	-0.158
Humerus length	0.935	-0.208	0.925	-0.245
Ulna length	0.950	-0.197	0.929	-0.275
Carpometacarpus length	0.921	-0.158	0.821	-0.180
Eigenvalue	10.484	1.026	10.807	1.048
% of Variance	0.66	0.06	0.68	0.06

^a Computed from raw data and the correlation matrices. Correlation for PC-II larger than ± 2.66 (99) or ± 2.53 (95) are significant at the 0.01 level, and are printed in bold-face type.

allometric. As noted before, body size in feral pigeons is satisfactorily summarized by PC-I. If wing bone elements of individuals are plotted against their PC-I scores, a strongly linear relationship is evident (Fig. 2, for humerus length). PC-I evidently increases more rapidly than length of humerus, because ratios of humerus length to PC-I are smaller for large than for small individuals.

DISCUSSION

Size. — Classical assessment of size in Rock Doves of Europe and North Africa shows variation to be clinal, small to the south and larger to the north (review in Cramp 1985). Variation in size of feral pigeons is less predictable than in wild birds, and only that of North American females varies in accordance with accepted ecogeographic theory (James 1970, Murphy 1985). Given that North American ferals have had in excess of 400 generations in which to adjust to environmental pressures acting on variation in size, the lack of size patterns might indicate a slow response to selection. The conclusion probably is unwarranted, however, in part

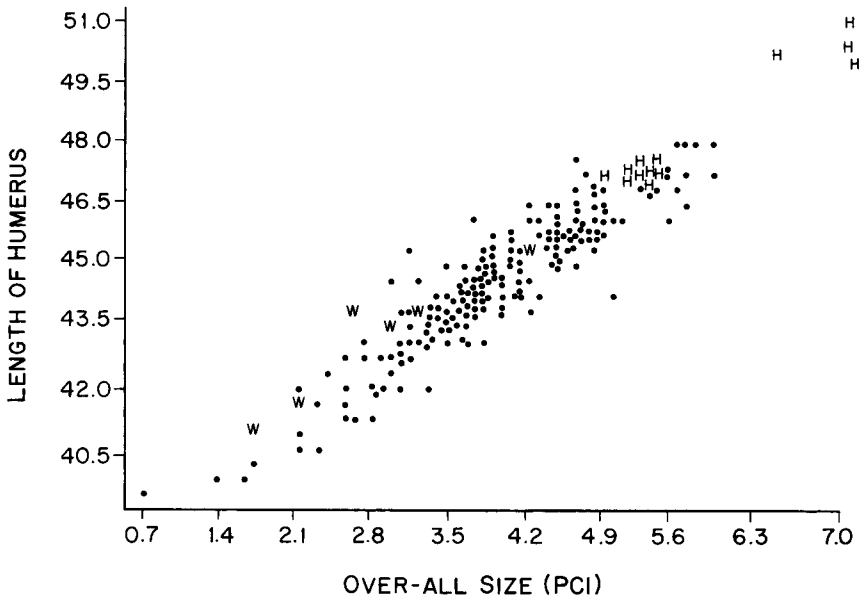


FIG. 2. Length of humerus as a function of over-all size for 194 specimens of *Columba livia* from North America and Europe. The dots represent feral pigeons from the USA, Canada, and Italy; the W's represent Rock Doves from the Mediterranean Basin; the H's represent homing pigeons from northern Italy and several North American localities. The correlation is $r_p = 0.94$; $P = 0.001$.

because genes from domestic stock are still entering feral gene pools. It is impossible to know the number of such immigrants, but racing homers regularly join feral colonies. Size of the ancestors of ferals (i.e., domestics) has long been under artificial selection by humans (Levi 1974), so it is inevitable that intrusions of domestics into feral colonies introduce otherwise uncharacteristic variation in size into feral populations.

Even if rates of immigration of domestics to feral colonies are unknown, some nontrivial deductions about size of ferals can be made. For example, if ferals from Edmonton are significantly larger than those from Kansas, this is likely to be genetically based because the birds at Edmonton are large in the same aspects of the skeleton as homers, and artificial selection is responsible for the large size of homers. Notable also is the reduction, when compared to populations of smaller birds, of number of elements showing significant SSD and the degree of SSD in each of the elements in both the Edmonton sample and the homers. Again, this may reflect selection, though of different sorts, in both samples. It is parsimonious

to assume that the similarities in size and SSD between birds from Edmonton and homers are owing to similar causes, as is examined beyond.

This is not the same as saying that the birds at Edmonton are likely to have been derived from homers, although that is a possibility. It is more likely that the Edmonton birds have the same ancestry as the rest of North American ferals—a variety of domestic sources—so that their present approach to size and shape of homers is a consequence of natural selection for large size or covariates thereof. The earliest records of the introduction of domestic pigeons in North America actually are for Canada (1606, in Nova Scotia; Schorger 1952). Adjustments to high latitude North American environments by feral pigeons have therefore been occurring for perhaps 470 generations (figuring a generation at 9 months; Johnston and Johnson 1990), which, despite probably continual immigration of domestics throughout that time, should have been enough to allow natural selection to modify size.

Clearly, racing homers are a problem in such considerations because they are likely to be the most consistent domestic immigrants into feral colonies; their history is therefore of some consequence. Modern homers were developed in the late 19th and early 20th centuries by crosses among several domestic varieties of pigeon, including the smerle, cumulet, dragoon, horseman, and English carrier (Levi 1974). All these are (or were—the cumulet, dragoon, and horseman are extinct) known as muscular and/or deep-keeled birds, and the dragoon, horseman, and carrier were large.

Homers are not the largest variety of domestic pigeon (e.g., Riddle et al. 1932), and presently seem to be only indirectly selected for large size. Levi (1974) writes that one selects for a blocky body build with deep keel, hard or durable plumage, and for speed of return on homing flights. Selecting for speed of return should indirectly select for large size, because rapid flight is necessitated by high wing-loading (Rayner 1988). Wing-loading varies allometrically with body mass, because wing area varies as the square of linear dimensions, whereas body mass varies as the cube. If the relatively large size of homers is partly an allometric result of selecting for high speed of flight, a relatively simple genetic basis could be involved—breeders selecting for flight speed would actually be working on allelic frequencies at a few genetic size loci amenable to artificial selection.

If, as here conjectured, the feral birds in Canadian populations are large owing to selection, they will have achieved body size-wing loading characteristics of homers not artificially but as a consequence of natural selection. Thus, if the high-latitude Canadian populations have been selected for large body size, they will have recapitulated for North America the clinal size pattern found in European Rock Doves.

This wing length-body size allometry is implied in the bivariate relationship between length of humerus and body size as quantified by PC-I (Fig. 2). Most specimens occur in the mid-range of the two axes, at or slightly above the locations of the wild specimens. Homers plot in the upper right of the graph and are joined by 20 of the largest birds in various samples, of which a third come from Edmonton. All these individuals have shorter humeri relative to body size than do Rock Doves or most ferals. My argument necessarily assumes that shorter wing bones relative to body size increases wing-loading.

Sexual size dimorphism.—The present samples of feral pigeons suggest that degree of SSD is geographically localized, but that variation in SSD has no interlocality pattern. Should the pattern of size variation shown by the female samples—increasing size on latitude—be supported by larger samples, then we may find SSD to decrease with latitude. Based on present samples, SSD of feral pigeons appears to decrease either with latitudinal increase or with body size increase. If the latter, the decrease in SSD could be a consequence of allometry; if only the former, the decrease would be difficult to interpret, and could involve unlikely scenarios such as relaxation of sexual selection.

Sexual shape dimorphism.—Lack of sexual dimorphism on PC-II, the component representing variation in shape, conforms to the null hypothesis. This means that variation in the shapes of pigeons from large to small is the same for both sexes—the allometric relationships are evident in males and females alike. This is necessary to demonstrate in the data set, because no theoretical basis for the sexes of pigeons having different allometries has ever been advanced.

Conclusions.—Within the limits of these samples, it appears that the variation in size of feral birds is similar to that of Rock Doves. Since it is unlikely that very large and very small domestic pigeons are differentially prevented from escaping to feral populations, their absence from the samples must stem from causes other than capability of escape. Possible scenarios include the following:

(1) Under the assumptions that some very large or small birds living in feral colonies are of high or adequate fitness and that most other individuals are of average size, the large or small birds will probably mate with, respectively, smaller or larger ferals. They would thus tend to leave offspring of intermediate sizes. In support of the first assumption, large individuals are known (Burley 1981b, Johnston and Johnson 1989) to be preferred mates, and large individuals of both sexes probably have high reproductive fitness (Johnston and Johnson 1990). In support of the second, crosses between pigeon varieties of different sizes inevitably produce offspring of intermediate sizes (Wexelsen 1937). There is, how-

ever, no satisfactory demonstration of above average fitness for small pigeons under feral conditions.

(2) Under an assumption that some very large or small birds in feral colonies are of low fitness, they may not survive to time of reproduction, they may not be able to form a pairbond if they survive, or they may be inadequate parents if they manage to pair. In support of the assumption, small individuals are least preferred at the time of mate choice (Burley 1981b) and they evidently compete poorly with larger pigeons for food (Murton et al. 1972). Very large size may be disadvantageous under conditions of food scarcity, owing to absolutely high maintenance costs and leading to inadequate nutrition of the individual or its offspring (cf Ricklefs 1974). Large individuals of heavy wing-loading fly under metabolically costly conditions (Pennycuick 1968, Rayner 1988), leading them to make heavier demands on food resources than smaller birds (Norberg 1981).

Accordingly, it appears likely that feral pigeon populations are subjected to stabilizing selection on body size. Only in colonies regularly infiltrated by racing homers would distribution of body sizes be positively skewed, as is found in Ontario, Canada.

Sexual dimorphism in size occurs along conventional lines except for the suggestion that SSD may decrease on latitude. Sexual dimorphism in shape is unlikely to be found in *C. livia*.

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HAWK MOUNTAIN-ZEISS RAPTOR RESEARCH AWARD

The HAWK MOUNTAIN SANCTUARY ASSOCIATION jointly awarded the 1990 Hawk Mountain-Zeiss Raptor Research Award to Eduardo E. Iñigo Elias at the University of Florida and Karen L. Wiebe at the University of Saskatchewan. Iñigo's project is entitled "Effects of forest fragmentation on a tropical raptor community in the biosphere reserve of "Montes Azules" in the Lacandona region of Chiapas, Mexico" and Wiebe is studying "The effect of food supply on reproductive decisions and success in the American Kestrel."

The Hawk Mountain Sanctuary Association is now accepting applications for its fourteenth annual award to support student research on birds of prey. Support for this award is provided by Carl Zeiss Optical, Inc. Up to \$2000 in funds are available and will be awarded to one or two recipients. To apply, a student applicant should submit a brief description of his or her research program (five pages maximum), a *curriculum vitae*, a budget summary including other funding anticipated, and two letters of recommendation to Dr. James C. Bednarz, Hawk Mountain Sanctuary Association, Rte. 2, Kempton, Pennsylvania 19529, USA. The deadline for applications is 15 November 1990. The Association's board of directors will make a final decision in February 1991. Only undergraduate and graduate students in degree-granting institutions are eligible to apply. The awards will be granted on the basis of the project's potential to improve understanding of raptor biology and its ultimate relevance to the conservation of raptor populations. Applications from anywhere in the world will be considered.