

# NONRANDOM MATING IN FERAL PIGEONS<sup>1</sup>

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*Abstract.* Feral pigeons (*Columba livia*) showed two sorts of nonrandom mating: size-based assortative mating and plumage-based disassortative mating. Size-based mating was evident in that individuals of like sizes were paired; such mating was presumably based on perception of size or a size-correlated variable, such as social dominance rank, by both sexes. Plumage-based pairing was evident in that individuals of unlike plumages were bonded; this was based on perception of unlike plumage patterns, probably by females. Both size-based and plumage-based pairing influenced reproductive output.

*Key words:* Nonrandom mating; plumage; body size; reproductive output; feral pigeon; *Columba livia*.

## INTRODUCTION

Nonrandom mating is distinct from nonrandom mate choice, which is a behavioral phenomenon that can provide nonrandom mating as its consequence. Nonrandom mating in a population implies that certain combinations of genotypes or phenotypes occur more often than expected by chance alone. One form of nonrandom mating, assortative mating, has important evolutionary consequences (Crow and Felsenstein 1968). Although gene frequencies do not change under assortative mating, average homozygosity increases, assuming genotypes are accurately reflected by phenotypes. Disassortative mating, however, should increase average heterozygosity. Additionally, gene frequencies will inevitably change if differences in fitness occur among such nonrandomly mated pairs. Thus, nonrandom mating can have important evolutionary consequences.

Study of nonrandom mating is most often undertaken on organisms amenable to experimental study, but larger and free-living organisms have nevertheless provided critical information on nonrandom mating. Some studies have concerned the feral pigeon, *Columba livia* (Goodwin 1958, Warriner et al. 1963, Kerfoot 1964, Murton et al. 1974, Davis and O'Donald 1976, Burley and Moran 1979, Obukhova and Kreslavskii 1982); these have provided contradictory results, to which we return later.

Our concern is with the nature of nonrandom mating based on two character suites in a population of feral pigeons in eastern Kansas: assortative mating based on variation in body size, and disassortative mating based on a range of discrete plumage pattern polymorphs. Many genetic models for the evolution of preferential mating require some specific selective advantage to result from the expression of preference (Fisher 1930; O'Donald 1980, 1983), so an additional aim of this paper is to examine possible reproductive or survival consequences of nonrandom mating based on either body size or plumage.

## METHODS

### SUBJECTS

The pigeons studied were feral birds living on the outer faces of the Museum of Natural History at the University of Kansas (KU). Approximately 50 nest sites were monitored and the birds marked with unique combinations of numbered and colored aluminum leg bands. The colony was studied from January 1983 to January 1986. Body sizes were measured from April 1984 to September 1985.

Feral pigeon populations are polymorphic in plumage for both color and pattern (see Dunmore 1968, Cole 1969, Levi 1974). The color locus is sex-linked; the blue allele is extremely common, and at Kansas more than 99% of the birds were in blue plumage. "Blues" regularly show four patterns: "Blue Bar," "Blue Checker," "T-pattern," and "Spread." The plumage of wild Rock Doves and of a significant proportion of feral pigeons is Blue Bar—a bird's mantle is pearl

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TABLE 1. Variation in frequencies of plumage phenotypes in feral pigeons at Lawrence, Kansas, 1983–1985.<sup>a</sup>

| Plumages     | Time period   |              |               |                |
|--------------|---------------|--------------|---------------|----------------|
|              | November 1983 | October 1984 | November 1985 | All: 1983–1985 |
| <i>N</i>     | 273           | 219          | 304           | 796            |
| Blue Bar     | 38.1          | 31.0         | 39.5          | 36.6           |
| Blue Checker | 22.7          | 53.0         | 39.1          | 37.6           |
| T-pattern    | 30.7          | 12.0         | 17.8          | 20.6           |
| Spread       | 4.0           | 3.0          | 2.6           | 3.2            |
| Other        | 4.3           | —            | 1.0           | 1.8            |

<sup>a</sup> Counts of birds sunning on a south-facing rooftop; 20× telescope used at approximately 50 m.

gray with two blue-black bars crossing the secondaries and greater secondary coverts. Owing to a set of at least three alleles at the autosomal pattern locus, Checker (dominant to patternless) and T-pattern (dominant to Checker and patternless), are found in feral populations (e.g., Murton et al. 1974). The bars are controlled at another locus, with recessive “Barless” being very rare. The Spread locus is autosomal and epistatic to “Red” and “Blue,” resulting in a melanic (Spread) plumage. Other genetic loci govern schizochromism and partial and complete albinism. Most of the breeding pigeons on the KU campus were referred to the four common plumages (Table 1) as were birds in the overall population as determined by telescopic censuses of plumages of resting or sunning individuals on the roof of Spooner Hall, 50 m east of the Museum of Natural History.

Assigning pigeons to plumage categories was ordinarily straightforward except for birds having white or bronze feathers in an otherwise recognizable plumage, which we classified as “Other.” Pairs in essentially identical plumages were considered to have mated *homotypically*; those in unlike plumages mated *heterotypically*. If we could detect a plumage variant, we assumed a pigeon also could detect it, so when a Checker female paired with a Checker male having, for instance, white primaries, we considered this to be a heterotypic mating, Checker × Other.

#### ANALYTIC PROCEDURES

Principal components of variation in size were extracted from size variables (cube root of body weight, ninth primary length, tarsus length, length of culmen, and width of culmen at the nostril).

TABLE 2. Variation in adult body weight over sets of feral pigeons at Lawrence, Kansas, 1983–1985.<sup>a</sup>

| Sample ( <i>n</i> )    | $\bar{x}$ (g) | SD   |
|------------------------|---------------|------|
| Total sample (126)     | 346.9         | 38.0 |
| Nonbreeding birds (48) | 333.5         | 32.0 |
| Breeding birds (78)    | 355.1         | 39.3 |
| Breeding females (37)  | 340.1         | 34.7 |
| Breeding males (41)    | 368.7         | 38.6 |

<sup>a</sup> For individuals weighed more than once as adults, mean weights were entered into the basic data matrix.

Owing to skewed distributions, the data were log-transformed, and components were computed using the correlation matrix from data for adult specimens of both sexes.

Nonrandom pairing by plumages was analyzed by contingency tables. Parametric correlation coefficients were used to assess relationships between body size, nesting frequency, and other variables.

## RESULTS

### RANGE OF BODY SIZES

Feral pigeons are sexually dimorphic in size, but sufficient size overlap exists so that birds cannot consistently be sexed by weight or linear dimensions (Burley 1981a). At Lawrence, 37 breeding females averaged 340.1 g, significantly less than 41 males averaging 368.7 g ( $F = 11.75$ ,  $df = 1$ ,  $76$ ,  $P < 0.001$ ; Table 2). A major fraction of the population did not mate, presumably owing to scarcity of nest sites. The nonbreeding birds consisted of individuals of all sizes, but had a larger proportion of smaller birds than the breeders—48 unsexed and nonbreeding birds averaged 333.5 g, indistinguishable from the breeding females ( $F = 0.82$ ,  $df = 1$ ,  $83$ ,  $P > 0.75$ ) but significantly less than the aggregate of breeding males and females which averaged 355.1 g ( $F = 10.32$ ,  $df = 1$ ,  $124$ ,  $P < 0.01$ ).

### BODY SIZE AND MATE CHOICE

We assessed correlations between each morphological variable of mated pairs; no unitary variable showed significant intersex correlation (Table 3). However, principal component (PC) analysis of the five variables provided a PC I summarizing 60% of the variance in the data, with weight, tarsus length and bill length having significant positive loadings: the PC I body sizes of the pairs show significant positive correlation ( $r = 0.37$ ,  $0.05 > P > 0.01$ ,  $n = 32$ ; Table 3).

TABLE 3. Product-moment correlation coefficients for body size variables among mated pairs of feral pigeons in Kansas, 1984-1985.

| Size variable            | Correlation coefficient <sup>a</sup> |
|--------------------------|--------------------------------------|
| Cube root of body weight | 0.16                                 |
| Tarsus length            | 0.17                                 |
| 9th primary length       | 0.19                                 |
| Bill length              | -0.08                                |
| Bill width               | 0.26                                 |
| Principal component I    | 0.37 <sup>b</sup>                    |

<sup>a</sup> Sample size = 32.  
<sup>b</sup>  $P < 0.05$ .

FEMALE BODY SIZE AND REPRODUCTIVE OUTPUT

In Kansas pigeons, large females (PC I scores) have shorter interclutch intervals than smaller ones (Fig. 1; see also Johnson 1986), and produce more flying young than small females during the time of year most favorable for reproduction. A long breeding season in large females also contributes to significantly higher reproductive output than seen in smaller birds (Johnston and Johnson 1989).

Additional information on reproductive output of 23 females for which only body weight was measured, and for which we therefore lack PC scores, supports this conclusion (Table 4). Larger-than-average breeding females have more successful nesting attempts (fledging one or two young) and fewer unsuccessful nests (fledging zero) than smaller breeding females ( $\chi^2 = 12.9$ ,  $df = 1$ ,  $P < 0.0001$ ).

PLUMAGES AND MATE CHOICE

The proportions of the plumage polymorphs in our population varied through time (Table 1; see also Murton et al. 1973), but all common plum-

TABLE 4. Productivity of size classes of female feral pigeons in Kansas, 1984-1985.

|                                    | Number of instances <sup>a</sup> |                                   |
|------------------------------------|----------------------------------|-----------------------------------|
|                                    | Zero productivity                | Productivity<br>1 or 2 fledglings |
| Female body weight more than 340 g | 27<br>(40.1)                     | 62<br>(48.9)                      |
| Female body weight less than 340 g | 74<br>(60.9)                     | 61<br>(74.1)                      |

$\chi^2 = 12.9$ ,  $df = 1$ ,  $P < 0.0001$

<sup>a</sup> Expected values (in parentheses) are for a model assuming independence between number of flying young and body weight; observed values appear above the expected.

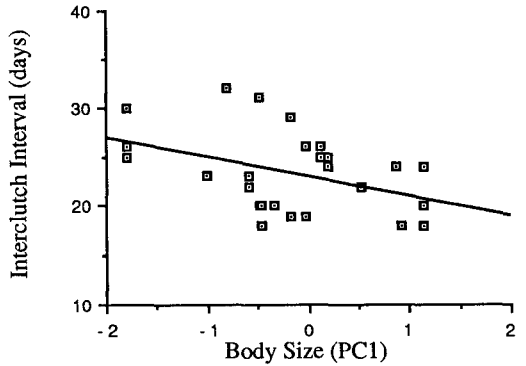


FIGURE 1. Variation in length of interclutch interval as a function of body size in female feral pigeons at Lawrence, Kansas, summer, 1985. The equation is  $II = 23.04 - 1.94(FBS)$ ;  $F = 4.7$  ( $df = 1, 24$ ),  $P < 0.05$ .

ages were represented in both the breeding and nonbreeding segments of the population. Spread was absent from our records for breeding females, and Other was absent from the breeding males for the period in question, although not subsequently.

To examine how mate choice might have occurred we generated expected frequencies of plumages of the breeding pairs; we used the observed frequencies of plumages in both sexes and then computed the expected frequencies of plumages that would have been found in mated pairs, had they mated at random (Table 5). Three yearly samples show more heterotypic, and fewer homotypic, pairs than expected, consistent with disassortative mating.

TABLE 5. Observed and expected pairing in feral pigeons in Kansas, 1983-1985.

|                                | Homotypic pairs | Heterotypic pairs |
|--------------------------------|-----------------|-------------------|
| 1983                           |                 |                   |
| Observed                       | 2               | 35                |
| Expected                       | 11              | 26                |
| $\chi^2 = 10.44$ , $P = 0.005$ |                 |                   |
| 1984                           |                 |                   |
| Observed                       | 4               | 33                |
| Expected                       | 11              | 26                |
| $\chi^2 = 6.33$ , $P = 0.02$   |                 |                   |
| 1985                           |                 |                   |
| Observed                       | 6               | 46                |
| Expected                       | 14              | 38                |
| $\chi^2 = 6.25$ , $P = 0.02$   |                 |                   |

TABLE 6. Contingency table analysis of number of nests by sex and plumage for feral pigeons in Kansas, 1984–1985.<sup>a</sup>

|                 | Plumages       |              |                | Totals |
|-----------------|----------------|--------------|----------------|--------|
|                 | Blue bar       | Checker      | T-pattern      |        |
| Number of nests |                |              |                |        |
| Males           | 70<br>(90.3)   | 43<br>(53.6) | 131<br>(100.1) | 244    |
| Females         | 122<br>(101.7) | 71<br>(60.4) | 82<br>(112.9)  | 275    |
| Totals          | 192            | 114          | 213            | 519    |

<sup>a</sup> Expected values (in parentheses) are from a model assuming independence between number of nests and plumage class; observed values lack parentheses;  $\chi^2 = 32.6$ ,  $P < 0.005$ .

#### PLUMAGE AND REPRODUCTIVE OUTPUT

We found a difference in number of nesting attempts in the Kansas pigeons: among the three common plumages, T-pattern males and Blue Bar females tended to have more nesting attempts than expected, while Blue Bar and Checker males and Checker and T-pattern females had fewer than expected (Table 6). Number of times nested reflects number of flying young produced. Birds nesting more times per year produced more flying young than birds nesting fewer times. T-pattern males produced 45% of all flying young, Blue Bar 28%, Checker 14%, and Spread 13%; among females, Blue Bar produced 40% of all young, T-pattern 34%, and Checker 26%. These frequencies are related neither to the frequencies of the plumage morphs in the general population nor to differences in their body weights.

#### DISCUSSION

##### BODY SIZE AND MATE CHOICE

When both sexes make parental investment, both should not only show selectivity in mate choice, but the degree of selectivity should be proportional to parental investment in each sex (Burley 1981b). Investments of each sex are close to parity in pigeons, and we therefore expected to see selectivity in both females and males. We have no evidence that either sex ignores size in pair formation, and the significant positive correlation of overall body size for mated pairs could well be a result of positive assortative mating.

Nevertheless, the correlation could be a consequence of mate choice based wholly on selection of large size (Burley 1983). If large birds are preferred by both sexes, many large birds will

pair with another; the largest remaining would then be preferred over smaller ones and chosen before the latter. Additionally, individuals ready to form a pair bond do not necessarily (or hardly ever) examine the entire unmated population subsample for potential mates. Under these circumstances, small birds probably have a choice of taking generally small mates or perhaps not mating at all. The pattern would be indistinguishable from one generated by size-based assortative mating. These points also emphasize a frequency-dependent aspect of assortative mating, that is, the disappearance of a preferred class may elevate preference for a class that was earlier of lower preference.

Sexually mature, nonbreeding birds of both sexes averaged significantly less in body weight than breeders, and were in fact slightly smaller than the average breeding female (Table 2). We think this means a significant fraction of smaller birds did not or could not mate. However, we do not know if the unmated sample simply included more females than males, an imbalance in sex ratio that could account for the disparity in weights (and which is of course absent in any sample of breeding pairs).

Feral pigeons may not assess body sizes directly, because pigeons are also known to prefer mates of relatively high social dominance (Burley 1981b). Large individuals tend to have higher dominance rank than smaller ones (Murton et al. 1972), and mate choice could be based on a trait correlated with body size. Whether preference is based on body size or some positively covarying trait, nonrandom mating on size occurs.

The pattern of size-based positive assortative mating could be realized by either possibility just noted. The sexes probably use different techniques to make their respective choices. The differences in the alternatives are important, since a number of factors influences how an individual bird achieves any position in a peck-dominance hierarchy. Moreover, in some cases one sex may have little choice based on size, as when a female pairs with a male that has lost its mate: she may bond irrespective of male size; such a male perhaps has greater choice, as when more than one female visits his domain.

Because large females have a pronounced reproductive advantage over smaller ones, male pigeons would realize a selective advantage from any tendency toward choosing large (or domi-

TABLE 7. Studies of mate choice and associated variables in captive and feral pigeons.

| Author and date of study      | Kind of population | Available plumages                    | Mate choice <sup>a</sup> pattern |
|-------------------------------|--------------------|---------------------------------------|----------------------------------|
| Goodwin 1958                  | Free ferals        | All                                   | 1                                |
| Warriner et al. 1963          | Domestic           | Black, White                          | 2                                |
| Murton et al. 1973            | Free ferals        | All                                   | 3                                |
| Kerfoot 1964                  | Domestic           | Black, White, Red                     | 4                                |
| Burley and Moran 1979         | Captive ferals     | Blue Bar, Checker<br>Red Bar, Checker | 5                                |
| Obukhova and Krevlavskii 1982 | Free ferals        | "glaucous," "melanic"                 | 6                                |
| Present study                 | Free ferals        | All                                   | 7                                |

<sup>a</sup> 1: Blues chose Blues, Reds chose Reds, Others chose randomly; no pattern preference demonstrated. 2: Males chose mates with plumages like those of parents, but did not choose either homotypically or heterotypically; pattern preference not tested. Females chose at random. 3: Both sexes chose heterotypically. 4: Only White females tested; they chose either Black or Red males, consistent with color of female parents; pattern not tested. 5: Blues chosen over Reds; females chose Checker over Bar, with males having no preference. 6: Choice was either homotypic or random. 7: Blues apparently chosen over Reds; females chose heterotypically on pattern, and males probably had no pattern preference.

nant) females at the time of pair-bonding. Females probably are at some selective advantage in choosing large males as mates because large males are more successful at feeding sites than smaller ones (Murton et al. 1972), and probably also secure other important resources, such as nest sites.

#### PLUMAGE AND MATE CHOICE

Seven earlier studies of plumage-based mate choice or mating (Table 7) can be grouped into four types: (a) true choice experiments on captive birds; (b) observation of unmarked feral pigeons; (c) observation of color-banded ferals; and (d) a posteriori biometrical analysis of type c matings. Studies of the last three types infer the process of choice from the frequencies of plumages in the mated pairs.

Three experimental studies used banded birds, with a given male or female choosing between a homotypic and a heterotypic individual of the opposite sex. Tests between an inbred White strain and an inbred Black strain suggested that males chose mates in accord with color of the males' parents (Warriner et al. 1963). White females chose between Red and Black males in accord with color of the females' foster parents (Kerfoot 1964). Feral birds of both sexes and of Red and Blue color chose Blue mates, females preferred Checker to Bar pattern, and males had no pattern preference (Burley and Moran 1979).

Studies of free-living ferals are inconsistent. Goodwin (1958) found Blues mated with Blues, Reds with Reds, and "bluish-blacks" with Blues, but none showed any pattern preferences. Goodwin's samples are the largest of any here treated. Obukhova and Kreslavskii (1982) found two

populations in which "glaucous" (Blue Bar?) mated with glaucous, and "melanic" (Checker, T-pattern, and Spread?) mated with melanic, and one population in which no preference was detected. Murton et al. (1973) found their ferals to mate nonrandomly on color and pattern, but they did not specify sexes in their pairs.

The seventh study (Davis and O'Donald 1976) used the data from Murton et al. (1973) and concluded that the nonrandom assortment could have occurred as a result of female choice of color and pattern.

It is impossible to reconcile all differences between these studies and ours, but the work of Murton et al. (1973), Davis and O'Donald (1976), and Burley and Moran (1979) are consistent with what we found. Our birds mate most often with Blues, the patterned birds are more frequent in pairs than in the population as a whole, and the frequencies of plumage patterns of pairs could be a result of nonrandom, disassortative mating based on pattern preference by one or by both sexes.

Our analysis is based on the assumption that both sexes chose plumage patterns at mating (Table 5). The expected frequencies in Table 5 are generated by using observed frequencies in the mated sample, and assuming that mate choice is random. The differences in observed vs. expected frequencies are significant each year (but the samples are not combined, because some of the pairs are represented in two or more years) demonstrating the nonrandom nature of the pairing. However, we actually cannot do more than infer details of the pairing process because no experimental work was done.

Even so, if only females in our population were

TABLE 8. Frequencies of plumage phenotypes in each sex of breeding pairs in feral pigeons in Kansas, 1984–1985.

| Sexes  | Plumages*    |              |              |            |            |
|--------|--------------|--------------|--------------|------------|------------|
|        | Blue Bar     | Blue Checker | T-pattern    | Spread     | Other      |
| Female | 18<br>(19.0) | 19<br>(19.6) | 8<br>(10.7)  | 0<br>(1.7) | 7<br>(0.7) |
| Male   | 16<br>(19.0) | 6<br>(19.6)  | 25<br>(10.7) | 5<br>(1.7) | 0<br>(0.7) |

\* Expected frequencies (in parentheses) are those found in the population at large; observed values lack parentheses. We test the hypothesis that observed frequencies are dependent on those found in the population at large.  $\chi^2 = 44.03$ ,  $df = 8$ ,  $P < 0.001$ .

exercising choice based on a preference for melanic male plumages, we could expect to find proportionally more dark than light males among mated pairs than among the general population. Plumage frequencies of mated females, however, could be expected to reflect the frequencies of those plumages in the general population. Marginal support for occurrence of female preference for melanics is available (Table 8): if the frequencies of plumage phenotypes in the mated pairs are separated into female and male subsets, those of the females are statistically indistinguishable from the mean of the three rooftop censuses shown in Table 1. But males depart significantly from expectation, showing fewer Blue Checker, and more T-pattern and Spread, plumages than expected. As a consequence, we predict that intensive study of the process of pair formation in feral pigeons will show female choice of male pattern to be important, and that males do not exert any choice on pattern of females.

#### DISASSORTATIVE MATING AND REPRODUCTIVE PERFORMANCE

Murton's group thought that melanic males and Blue Bar females had reproductive advantages over other pigeons at the Manchester Docks, and that this could have provided an explanation for the pattern of disassortative mating they found among those pigeons (Murton et al. 1973). They assessed what they identified as negative assortative mate choice and used data undifferentiated to sex. They examined possible differences between productivity of homotypic and heterotypic pairs, and were able to show that homotypic pairs had a greater proportion of their eggs failing to hatch than did heterotypic pairs. We found no parallel—270 nests of heterotypic plumage pairs

TABLE 9. Productivity of plumage homotypic and heterotypic pairs of feral pigeons in Kansas, 1984–1985.<sup>a</sup>

| Number of fledglings/nest | Homotypic pairs | Heterotypic pairs |
|---------------------------|-----------------|-------------------|
| 0                         | 19<br>(22.5)    | 125<br>(121.5)    |
| 1                         | 13<br>(10.0)    | 51<br>(54.0)      |
| 2                         | 18<br>(17.5)    | 94<br>(94.5)      |
| Total nests               | 50              | 270               |

\* Expected values (in parentheses) are from a model assuming independence between number of fledglings and pairing type; observed values lack parentheses.  $\chi^2 = 0.59$ ,  $df = 4$ ,  $P > 0.90$ .

and 50 of homotypic pairs in 1984–1985 showed the former to average close to 0.9 fledgling per nest, not different from the latter at 1.0 (Table 9).

Our expectation that female choice of male plumage pattern influences pairing is supported by data on females mated to melanic males. Females mated with large male melanics (Ts and Spreads) have productivity superior to that of other females: with Blue Bar mates of any size they produced about 5.5 flying young per year, but with large melanics they produced about 8.5 flying young per year (Johnson and Johnston, unpubl.).

#### EVOLUTIONARY ORIGIN OF PLUMAGE-BASED MATE CHOICE

The origin of nonrandom mating on male plumage pattern in feral pigeons has had to have occurred recently, because prior to the domestication of Rock Doves some 5,000 years ago (Sossinka 1982), variation in plumages of wild Rock Doves was probably restricted (Goodwin 1983, p. 57). We assume that in the absence of significant plumage variation, Rock Doves could not have shown plumage-based nonrandom assorting. The enormous qualitative variance in plumage color and pattern resulting from artificial selection would have been instrumental in allowing plumage-based mate choice to be feasible. Subsequently, if some of the plumages now commonly found in feral populations became indexes to high reproductive capability and multiple-locus genic heterozygosity, selection could have provided disproportionate rewards to females mating disassortatively.

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## LITERATURE CITED

- BURLEY, N. 1981a. The evolution of sexual indistinguishability, p. 121-137. *In* R. Alexander and D. Tinkle [eds.], *Natural selection and social behavior*. Chiron Press, New York.
- BURLEY, N. 1981b. Mate choice by multiple criteria in a monogamous species. *Am. Nat.* 117:515-528.
- BURLEY, N. 1983. The meaning of assortative mating. *Ethol. Sociobiol.* 4:191-203.
- BURLEY, N., AND M. MORAN 1979. The significance of age and reproductive experience in the mate preferences of feral pigeons *Columba livia*. *Anim. Behav.* 27:686-698.
- COLE, G. 1969. Plumage colors and patterns in the feral rock pigeons of central Arizona. *Am. Midl. Nat.* 82:613-618.
- CROW, J. F., AND J. FELSENSTEIN. 1968. The effect of assortative mating of the genetic composition of a population. *Eugen. Q.* 15:85-97.
- DAVIS, J., AND P. O'DONALD 1976. Territory size, breeding time and mating preference in the Arctic skua. *Nature* 260:774-755.
- DUNMORE, R. 1968. Plumage polymorphism in a feral population of the rock pigeon. *Am. Midl. Nat.* 79:1-7.
- FISHER, R. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford.
- GOODWIN, D. 1958. The existence and causation of colour preferences in the pairing of feral and domestic pigeons. *Bull. Br. Ornithol. Club* 78:136-139.
- GOODWIN, D. 1983. *Pigeons and doves of the world*. Cornell Univ. Press, Ithaca, NY.
- JOHNSON, S. 1986. *Quantitative genetics and life history in the Feral Pigeon*. M.A.thesis. Univ. of Kansas, Lawrence.
- JOHNSTON, R., AND S. JOHNSON. 1989. Reproductive ecology of feral pigeons. *In* J. Pinowski and D. Summers-Smith [eds.], *Granivorous birds in the ecological landscape*. Institute of Ecology, Polish Academy of Sciences, Warsaw.
- KERFOOT, E. 1964. *Some aspects of mate selection in domestic pigeons*. Ph.D.diss. Univ. of Oklahoma, Norman.
- LEVI, R. 1974. *The pigeon*. Levi, Sumter, SC.
- MURTON, R., C. COOMBS, AND R. THEARLE. 1972. Ecological studies of the feral pigeon *Columba livia* var. II. Flock behaviour and social organisation. *J. Appl. Ecol.* 9:875-889.
- MURTON, R., R. THEARLE, AND C. COOMBS. 1974. Ecological studies of the feral pigeon *Columba livia* var. III. Reproduction and plumage polymorphism. *J. Appl. Ecol.* 11:841-854.
- MURTON, R., N. WESTWOOD, AND R. THEARLE. 1973. Polymorphism and the evolution of continuous breeding season in the pigeon *Columba livia*. *J. Reprod. Fertil. Suppl.* 19:561-575.
- OBHUKOVA, N., AND A. KRESLAVSKII 1982. Structure of crosses in populations of rock doves *Columba livia*. *Zool. Zh.* 61:461-464.
- O'DONALD, P. 1980. *Genetic models of sexual selection*. Cambridge Univ. Press, Cambridge.
- O'DONALD, P. 1983. *The Arctic Skua*. Cambridge Univ. Press, Cambridge.
- SOSSINKA, R. 1982. Domestication in birds. *Avian Biol.* 6:373-403.
- WARRINER, C., W. LEMMON, AND T. RAY 1963. Early experience as a variable in mate selection. *Anim. Behav.* 11:221-224.