FEDUCCIA, J. A. 1967. A new swallow from the Fox Canyon local fauna (Upper Pliocene) of Kansas. Condor, 69: 526–527.

FEDUCCIA, J. A. 1968. The Pliocene rails of North America. Auk, 85: 441–453.

FORD, N. L. 1966. Fossil owls from the Rexroad fauna of the Upper Pliocene of Kansas. Condor, 68: 472–475.

HIBBARD, C. W. 1950. Mammals of the Rexroad formation from Fox Canyon, Meade County, Kansas. Contrib. Mus. Paleontol., Univ. Michigan, 8: 113–192.

HIBBARD, C. W. 1967. New rodents from the late Cenozoic of Kansas. Pap. Michigan Acad. Sci., Arts, and Letters, 52(1966): 115–131.

MURRAY, B. G., JR. 1967. Grebes from the late Pliocene of North America. Condor, 69: 277–288.

TORDOFF, H. B. 1951. Osteology of *Colinus hibbardi*, a Pliocene quail. Condor, 53: 23–30.

TORDOFF, H. B. 1959. A condor from the Upper Pliocene of Kansas. Condor, 61: 338–343.

WETMORE, A. 1944. Remains of birds from the Rexroad fauna of the Upper Pliocene of Kansas. Univ. Kansas Sci. Bull., 30: 89–105.

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Comparative orientational and homing performances of single pigeons and small flocks.—It has long been a question in pigeon orientation studies whether data obtained from flocks (e.g. Griffin, 1952; Hitchcock, 1952) and data obtained from single birds (e.g. Michener and Walcott, 1967a, 1967b) are comparable. Homing pigeons have been selected for many years for their performance in races, but in these races the birds are released in a flock; when the birds are released individually in orientation experiments, their behavior might possibly be significantly different. Indeed, Hamilton (1967) has recently suggested, concerning birds generally, that "The orientation of groups of animals is more accurate than that of individuals." He draws a series of curves that predict decreasing deviation from the goal direction as the flock size increases, the decrease being most rapid as flock size rises from 1 to 5.

In an attempt to answer some of the questions concerning possible behavioral differences between single birds and flocks, and to evaluate Hamilton's ideas, I made a series of test releases designed to compare the performance of single pigeons with that of small flocks. All the pigeons used in these tests were of similar age and training (up to 8 miles in all directions), were housed together in the same loft pen, and were fed and exercised at the same time. It was hoped that this procedure would minimize differences in physical condition or in motivation.

For each test, some birds were randomly selected to be released singly, and others were randomly grouped to form flocks of four birds each. The singles (S) and flocks (F) were then randomly paired, and the tosses followed the sequence S,F,S,F, etc.; this minimized differences in exposure of the two treatments to changes in the weather during the day, or to other temporally varying parameters. The direction in which the birds were pointed at the toss was randomized. Each single bird or flock was watched with 10 × 50 binoculars until it vanished from sight, and a compass bearing for the vanishing point was recorded to the nearest 5 degrees. The interval between toss and disappearance was timed with a stop watch. We waited at least 8 minutes after each bird or flock vanished before making the next release, to ensure that neither influenced the other's choice of direction. An associate at the loft recorded the arrival times so that homing speeds could be calculated.

A total of 16 tests were performed, all from sites where the birds had never previously been released, and all at distances as great as, or greater than, those at which Hamilton (1967) obtained the data on starlings used in his paper. Eleven of the tests were at distances of approximately 20 miles from eight release sites located N, NE, E, SE, S, SW, W, and NW of the loft. Two tests were conducted from a site 30 miles N of the loft. Three tests were at distances of approximately 60 miles, using sites N, NE, and E of the loft. All release sites were high points with good visibility for a long distance in all directions. A total of 102 matched pairs (single vs. flock) were used in these 16 tests.

For each test the circular means of the bearings of the singles, the flocks, and the two treatments combined were calculated by vector analysis, following the procedure outlined by Batschelet (1965). The mean bearings for the two treatments were compared by means of an F test for circular distributions proposed by Watson and Williams (1956) and discussed by Batschelet (1965). The differences in the scatter of the bearings of the two treatments were evaluated using a test proposed by Watson and described by Emlen and Penney (1964). Vanishing intervals and homing speeds of the two treatments in each test were compared by the Wilcoxon matched-pairs signed-ranks test (see Siegel, 1956).

Following analysis of the data for each test separately, the data from the 16 tests were combined and the deviations from the home direction, deviations from the mean direction, vanishing intervals, and homing speeds of the two treatments were compared by means of the matched-pairs sign test (the signed-ranks test could not be used because of large differences between the variances of the different tests).

None of the 16 tests showed a significant difference between the mean bearings of single birds and flocks, and in only one test (60 miles from the north) was the difference in scatter significant, the bearings of the flocks being more scattered.

Although the mean vanishing interval of the flocks was slightly longer than that of the single birds in 12 of the 16 tests, the difference was significant ($P = 0.03$) in only one test (20 miles from the northeast).

The homing speeds of the two treatments were comparable in most tests, although in one (60 miles from the east) the flocks were faster ($P = 0.02$).

Analysis of the combined data from the 16 tests (Table 1) shows no significant dif-

TABLE 1

SUMMARY OF DATA FROM RELEASES OF MATCHED PAIRS[1]

Variable[2]	Number of times singles had greater value	Number of times flocks had greater value	Binomial *P* (two-tailed)
Deviation from home	45	52	0.54
Deviation from mean	48	49	1.00
Vanishing interval	35	65	0.004
Homing speed	30	42	0.19

[1] Single pigeons vs. small flocks.

[2] Omitted from the comparison for each variable are pairs in which the singles and flocks had the same value. Also omitted from the analysis of homing speeds are pairs in which the flocks broke up or the single bird returned with another bird.

ferences between single birds and flocks in deviation from the home direction, deviation from the mean direction, or homing speed, but the vanishing intervals of the flocks were significantly longer than those of the single birds.

The significant difference in vanishing intervals probably reflects the fact that flocks are easier to follow visually than are single birds, and can thus be kept in view longer. It is thus probably an artifact of the procedures used in the tests rather than an indication of a true behavioral difference. If this is so, then these tests indicate that in the parameters here investigated no important differences exist between single birds and small flocks.

The complete absence of any indication that the bearings of flocks are more accurate than those of single birds casts serious doubt on Hamilton's (1967) hypothesis. Hamilton assumes that a flock will choose a direction that is determined by the simple vectorial sum of the separate directions preferred by the individuals comprising the flocks, i.e. "the orientation of the flock represents a compromise by each individual to the directional preference of the other individuals of the flock." Such an assumption and Hamilton's curves, which are derived from equations that depend on this assumption, consider the influence of each bird to be equivalent to that of every other bird in the flock. But in almost all other aspects of the social behavior of birds that have been studied, dominance relationships have been found to be important. It seems reasonable to expect, therefore, that some birds may play a much more important role than others in selecting the direction a flock flies. If this is so, and if the qualities that make a bird a leader in a flock are not necessarily correlated with orientational ability, then there is no reason to expect flocks to orient more accurately than single birds. The data here presented, which show that small pigeon flocks orient no more accurately than single birds, tend to support this model rather than that of Hamilton.

Literature Cited

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. Washington, D. C., Amer. Inst. Biol. Sci.

Emlen, J. T., and R. L. Penney. 1964. Distance navigation in the Adelie Penguin. Ibis, 106: 417–431.

Griffin, D. R. 1952. Airplane observations of homing pigeons. Bull. Mus. Comp. Zool., 107: 411–440.

Hamilton, W. J. 1967. Social aspects of bird orientation mechanisms. Pp. 57–71 *in* Animal orientation and navigation (R. M. Storm, Ed.). Corvallis, Oregon State Univ. Press.

Hitchcock, H. B. 1952. Airplane observations of homing pigeons. Proc. Amer. Phil. Soc., 96: 270–289.

Mitchener, M. C., and C. Walcott. 1967a. Navigation of single homing pigeons: airplane observations by radio tracking. Science, 154: 410–413.

Mitchener, M. C., and C. Walcott. 1967b. Homing of single pigeons—an analysis of tracks. J. Exp. Biol., 47: 99–131.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.

Watson, G. S., and E. J. Williams. 1956. On the construction of significance tests on the circle and the sphere. Biometrika, 43: 344–352.

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