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DIRECTION OF THE PRECEDING RELEASE AND INITIAL ORIENTATION OF HOMING PIGEONS

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PRATT and Thouless (1955) and later Wallraff (1959) suggested that single homing flights of pigeons (*Columba livia*) may establish directional training. The home direction of the preceding release was to produce a measurable bias on the initial orientation of the next homing flight. The few incidental data published by Wallraff (1959, 1967) in support of this notion have been questioned owing to inadequate controls and small sample sizes (for detailed discussion see Schmidt-Koenig 1965, Alexander and Keeton 1972). Specifically designed series of releases were subsequently carried out by Graue (1965) and by Alexander and Keeton (1972). Graue's results presented support inasmuch as the means of all groups were biased in the direction predicted from the home direction of the preceding release. The deviations were, however, numerically mostly small and frequently not significant. Alexander and Keeton (1972) found no evidence of an effect by the preceding release. Wallraff (1974), reanalyzing the data of Alexander and Keeton (1972), did not entirely agree with their conclusions. He also selected 14 releases from his older records, including those from Wallraff (1959, 1967), and again claimed support for the notion that the direction of the preceding release has a predictable effect on initial orientation of the next. Thus, no final answer seems yet to have been reached.

Here I contribute to the discussion a rather large batch of data that qualify by experimental design, not by selection. I also chose a novel approach to assess the proposed bias.

MATERIAL AND METHODS

Two series of 64 releases each (Durham and Frankfurt) were carried out and their results were, so far, published only with respect to the effect of the distance on initial orientation, vanishing time, and homing (Schmidt-Koenig 1966, 1970).

Each series involved two releases of 20 (exceptionally 19) experienced homing

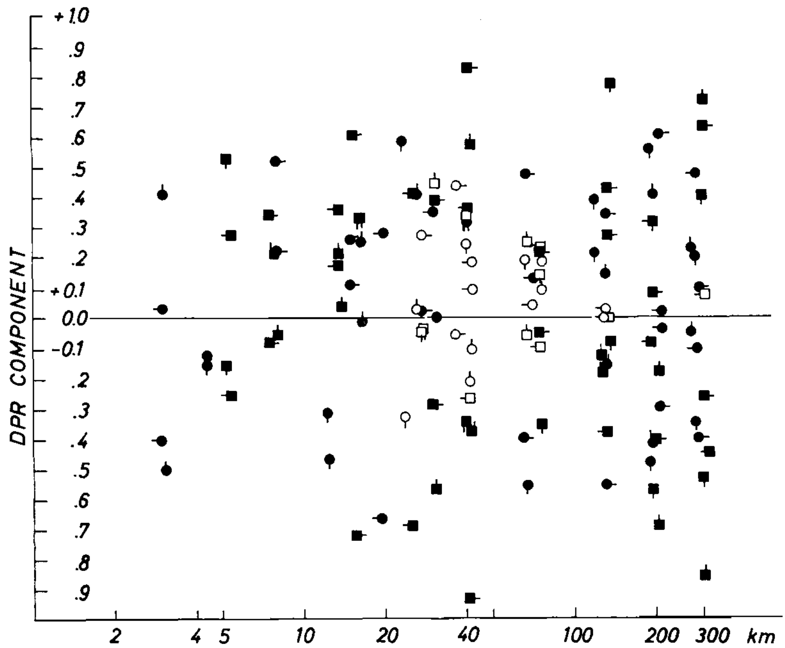

Fig. 1. The component of the direction of the preceding release (ordinate) as a function of the distance of release (abscissa, logarithmic scale) of 128 releases of veterans. For the calculation of C_{DPR}, see text. Circles show 64 scores from the Durham releases; squares show 64 scores from the Frankfurt releases. Bristles indicate the direction of the release (from north, etc.). White scores identify releases that were random (1% level, Rayleigh test).

pigeons (veterans) from each of 32 release sites symmetrically centered on the Durham and the Frankfurt lofts, i.e. a total of 128 releases from 64 release sites involving 2544 individual vanishing bearings. In order to average out a possible effect of the preceding release the sequences of releases had been designed so that in the two releases per release site the home direction of the previous release always was about 90° to the right for one release and about 90° to the left for the other. The releases were made on different days in the course of 9 months in Durham and of 4 years in Frankfurt (for more details see Schmidt-Koenig 1966, 1970).

For the purpose of the present paper, the component of the home direction of the previous release (DPR component) for each vanishing diagram of 20 (19) birds was calculated as $C_{DPR} = a \cdot \cos(\alpha - \phi)$ where a represents the length and α the direction of the mean vector of each vanishing diagram and ϕ represents the home direction of the preceding release. If all birds headed precisely into the home direction of the preceding release (i.e. 90° left or right of the actual home direction) C_{DPR} would be +1.0. Values $+1.0 \geqslant C_{DPR} > 0$ represent various degrees of mean headings in the semicircle of the home direction of the preceding release. Values $0 > C_{DPR} \geqslant -1.0$ would indicate mean headings in the semicircle opposite the home direction of the preceding release. If the home direction of the preceding release had an effect

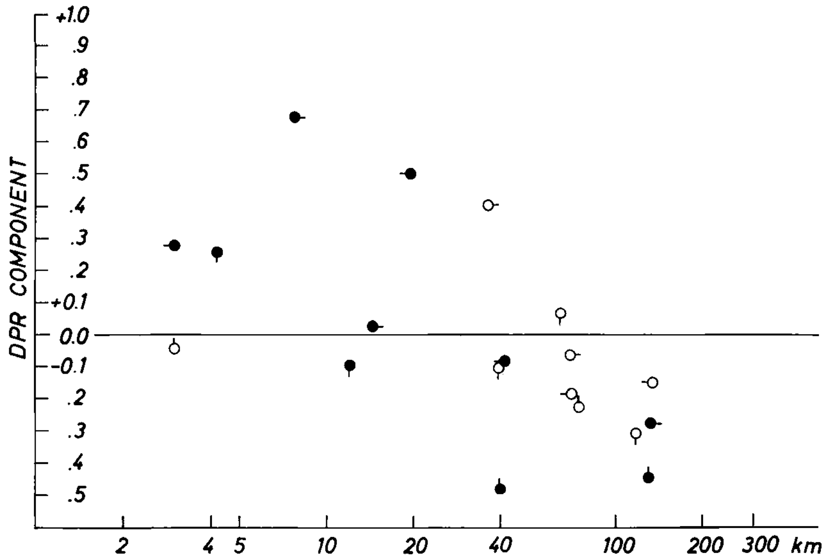

Fig. 2. The C_{DPR} (ordinate) as function of the distance (abscissa, logarithmic scale) of 19 releases of juniors at Durham. Symbols as in Fig. 1.

on the initial orientation of the next release, it should produce a mean value of C_{DPR} significantly larger than zero or a significant majority of values of C_{DPR} larger than zero.

Results

Fig. 1 presents the 128 scores of veterans from the Durham and the Frankfurt series plotted against distance. Different symbols identify scores from the Durham and from the Frankfurt series and the direction of release. It should be noted here that 28 of the 128 vanishing diagrams were random (1% level, Rayleigh test) and that of the 64 pairs of releases, although performed on different days, only 8 pairs were at all different at $P \leqslant 0.01$ (Watson test). In four of these the difference is in the expected direction; in four it is opposite. The arithmetic mean of C_{DPR} $\bar{x} = 0.030$, the 99% confidence interval $C_{99\%} = \pm\ 0.086$, and thus shows no significant difference from zero. Another second order analysis would consider that 56 scores are smaller and 72 scores are larger than zero. A χ^2 test yields $P > 0.10$, again no significance. The pattern of C_{DPR} given in Fig. 1 represents a chance fluctuation (quite in contrast to that of the homeward component). There is no correlation of C_{DPR} with distance. Thus large samples of well-experienced birds show no trace of an effect of the direction of the preceding release.

Only 19 scores, each comprising 20 (exceptionally 19) vanishing bearings of juniors, are available from a series of releases supplementary to that of veterans at Durham (Schmidt-Koenig 1966). There was only one release at each release site. The juniors had performed up to five previous releases with a 90° change of home direction between releases. Their 19 DPR components are given in Fig. 2. The arithmetic mean $\bar{x} = -0.01$. Seven scores are > 0 and 12 scores are < 0; $P\ \chi^2 \gg 0.1$ for a difference. Again, there is no indication of an effect of the direction of the preceding release, not even in juniors.

CONCLUSION

While the homeward component of the Durham and Frankfurt veterans (Schmidt-Koenig 1966, 1970) demonstrated an unequivocal bias of initial orientation toward home (lower or higher values depending upon distance), the DPR component (Fig. 1) reveals no such bias toward the home direction of the preceding release. In accordance with earlier statements (Schmidt-Koenig 1965) I agree with Alexander and Keeton (1972) that the effect advocated by Wallraff is not a general phenomenon, if it is at all real. The approach used in the present paper does not compare pairs of releases as does that of most other authors. Thus a discussion of the validity of pairing, pooling, and plotting is irrelevant here. Likewise attempts to explain results that seem to have too little or too much of the expected effect by additional assumptions (Wallraff 1974: 30–32) are superfluous. It should be emphasized that of the 64 pairs of releases, although performed on different days, only 8 pairs were different at $P \leqslant 0.01$ (Watson test). Of the 62 pairs qualifying for the following analysis, in 30 the difference between pairs was in the expected direction, in 32 it was opposite. This analysis disregards the numerical magnitude (ranging from 2° to 177°) and the (lack of) first order significance; however, it is added here to offer values comparable to those of the other authors.

One could, of course, include this (insignificant) proportion of 30:32 into Wallraff's (1974: 33) third order split, which would then read 6:1 with a binomial probability of $P = 0.062$ (or 7:1 with $P = 0.035$ if Durham and Frankfurt would enter as two separate series), i.e. back to insignificance also on this level. The data of the present paper and their lack of significance may illuminate how relevant and how important for practical purposes such a third order analysis is.

Finally the results presented here and those obtained by Alexander and Keeton (1972) once more support the view expressed earlier i.e. Schmidt-Koenig 1963, 1966; Sonnberg and Schmidt-Koenig 1970) that experimenting with well-experienced birds has a number of advantages over experimenting with little-experienced birds. Experienced birds represent a more homogenous group in many respects and variables that may increase scatter or mask results are eliminated. Sonnberg and Schmidt-Koenig (1970) also presented evidence that large numbers of short distance flights are not equivalent to and cannot replace long distance flights to produce what we call experienced birds. At least some of Wallraff's birds were also much less experienced than our birds, and Graue's had mostly short distance experience. Less experienced pigeons may, as part of their learning process, be more inclined to follow the direction that was successful in the previous release. This may explain at least part of the apparently diverging results. Although the rather small sample of 19 scores of little-experienced birds on the average supports Wallraff's effect as little as do the scores of the veterans, I would be more inclined to expect its manifestation in the initial orientation of very little experienced birds as part of their learning process. But the scores of Fig. 2 do not confirm even that.

I do not consider Wallraff's effect an important factor nor emphasizing it very helpful to answer the question how pigeons navigate. The direction of the preceding release can be neglected for all practical purposes, certainly in experiments with experienced birds. The bias in initial orientation frequently observed must have largely other causes.

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Summary

The component of the home direction of the preceding release (C_{DPR}) was calculated for two series of 64 releases of 20 (19) experienced birds with a 90° change of home direction between releases. If the home direction of the preceding release caused a systematic bias on the initial orientation of the next release as proposed by Wallraff (1959, 1967, 1974), C_{DPR} would be mostly positive. This was clearly not so. Other statistical analysis comparable to those of Wallraff (loc. cit.) and Alexander and Keeton (1972) likewise do not support the notion of a predictable bias.

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