

us to think that the often described iron oxidation by fungi¹⁵ should intervene secondarily, in the subapical, mitochondrial zone of the hyphae. The known close redox interaction of Fe⁺³ and cysteine suggests that the strong Fe⁺³ to Fe⁺² reducing power of the hyphal tips is reflecting less the NADH production (revealed more specifically above with the PMS test) than the apical concentration of the sulfhydryl-rich enzymes (glyceraldehyde-phosphate dehydrogenase, hexokinase, ADH).

The cylindrical, polarized extension of the hyphal tips is maintained as long as pro-glycolytic conditions such as semi-anaerobiosis, high glucose in ammonium medium, excess of antioxidants (cysteine, diphenylamine, etc.) are maintained. Contrary effects such as oxidative starvation, inactivation of the -SH compounds (iodoacetate, Hg-compounds, quinones, etc.) lead to a premature disappearance of the apical reducing zone which is 'invaded' by mitochondria. Thus, in *Neurospora*, the conidiogenic transition is marked by a progressive enlargement of the hyphal tip accompanied by a loss of the PMS or Fe⁺³ reducing power and a generalization of the oxidative vital staining with neutral red (Figure 1, d) or Janus green¹⁶. In *Allomyces*, the club-like stage shows a generalized re-oxidation of the methylene blue and no reduction of phenazine methosulfate.

We can admit that glycolytic, apical dominance over the oxidative activity of the subapical mitochondrial population enforces and maintains an acropetally reductive gradient (tip redox value negative, averaging those of NADH and -SH). Such a redox gradient could provide the electrochemical power postulated by BARTNICKI-GARCIA¹⁷, to insure continuous polarized transportation to the growing apex of the wall precursors-containing vesicles. Conversely, the progressive (by ageing) or prematurely induced (see above) loss of the apical reducing power (through lifting of the glycolytic dominance), would then lead to a uniform distribution of the mitochondrial oxidative activity in the enlarging hyphal tip. The uniform 'oxidative climate' thus created would restrict vesicles transport and delay setting of the wall (plasticized for apical enlargement) while triggering transcription of the sporogenic genes in the apical nuclei.

¹⁵ F. G. MULDER, Rev. Ecol. Biol. Sol 9, 321 (1972).

¹⁶ G. TURIAN, N. OULEVEY and M. CORTAT, Ann. Microbiol. (Inst. Past. 124A, 443 (1973).

¹⁷ S. BARTNICKI-GARCIA, in *Microbial Differentiation* (Eds. J. M. ASHWORTH and J. E. SMITH; Symp. Soc. gen. Microbiol., 1973), vol. 23, p. 245.

Pigeons Homing: Some Experiments for Testing the Olfactory Hypothesis¹

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Summary. Homing experiments on Swiss pigeons show that the birds use olfactory cues for navigational purposes and that outward journey detours influence their initial orientation.

A few years ago, Italian researchers presented a new hypothesis of pigeon homing, according to which olfaction plays an important and specific role in the navigation mechanism of these birds². This hypothesis has been supported by the results of a long series of experiments performed in Tuscany and in the surrounding areas³. In addition to the olfactory cues detected while aloft, pigeons may also use those detected during the outward journey, while they are carried to the release site. Indeed, when 2 groups of pigeons were carried by different routes, with the first part of the 2 routes being very divergent, each group showed in most cases the tendency to fly in a direction which was roughly between the home direction and the direction opposite that of the first segment of its outward journey. Moreover, the orientation of one group was often at random, whereas that of the other was not (detour effect)⁴.

American authors confirmed that experimental pigeons whose olfactory nerves had been cut were much poorer at homing than the control birds, both in terms of speeds and of the number of birds lost⁵. However, their attempt to repeat two other experiments produced results which did not agree with those of the Italian workers^{6,7}. This fact gave rise to the idea that pigeons may use different navigational cues according to their strain, the region in which they live, or the way in which they are reared or trained⁸. It is commonly believed that birds may utilize cues some of them repetitive, for navigational purpose⁹. Therefore, the possibility that different strains may use different navigational cues, should be considered. How-

ever, other explanations for the discrepancies between the results of the two research teams are possible.

In this situation, it seemed appropriate to repeat 3 of the experiments of the Italian workers, using Swiss pigeons. The first 2 experiments had already been repeated in the States, but with different results.

Materials and methods. The pigeons came from the loft of one of us (G. W.) at Grächwill and from the Swiss Army loft at Sand. Both localities are near Berne. The birds were different in age and experience. The pigeons for the 2 groups used in the 1st and 2nd experiments were chosen by lot, and for the 3rd experiment so that age differences were minimized. α -pinene was used in a mixture of 10 ml with 50 g of pure vasoline. This mixture was spread just before the release onto the beak of each experimental bird; pure vasoline was applied to the

¹ This work was supported by the Consiglio Nazionale delle Ricerche and by the Swiss National Foundation for Scientific Research.

² F. PAPI, V. FIASCHI, L. FIORE and S. BENVENUTI, *Monitore zool. ital.* (N.S.) 6, 85 (1972).

³ References in N. E. BALDACCINI, S. BENVENUTI, V. FIASCHI and F. PAPI, *J. comp. Physiol.* 99, 177 (1975).

⁴ F. PAPI, V. FIASCHI, S. BENVENUTI and N. E. BALDACCINI, *Monitore zool. ital.* (N.S.) 7, 129 (1973), and unpublished data.

⁵ W. T. KEETON, personal communication (November 6, 1974).

⁶ W. T. KEETON, *Monitore zool. ital.* (N.S.) 8, 227 (1974).

⁷ W. T. KEETON and A. IRENE BROWN, in press.

⁸ Round table at the 14th International Ethological Conference, Parma 1975, see also J. R. KREBS, *Nature*, Lond. 257, 358 (1975).

⁹ W. T. KEETON, *Adv. Study Behav.* 5, 47 (1974).

control birds. All the pigeons used in the 3rd experiment were subjected to a sectioning of the right olfactory nerve under Equithesin anesthesia on August 7 or 8, 1975. One nostril of each of these birds (the right one for the controls, the left one for the experimentals) was plugged at the loft in the afternoon before the day of the release by means of a dental silicon paste.

In all the experiments, the birds were taken to the release site in baskets which let in plenty of air and some light. However, they could not see outside. Test releases were performed at 2 sites, Birrfeld and Avully. The area between the home loft and the former site was familiar to the birds, but they had to cross an unfamiliar region when flying home from the latter site. Birds were released with

the sun's disk visible, except for a part of those used in the 2nd experiment. The pigeons were tossed singly by hand, except, for the experiment 1b, in which 10 out of the 11 birds of each group were released in couples. Bearings of the birds released in couples and vanishing together were considered, for statistical treatment, as single points. The mean vector for each group in each experiment was calculated by vector analysis. Bearings were tested for randomness by the Rayleigh test and their clustering around the home direction by the V test¹⁰. The 2 bearing sets of each experiment were compared by the MARDIA, WATSON and WHEELER test¹¹. Homing performances were compared by the Mann-Whitney U test¹².

Results. 1st experiment. Experimental birds were released after application of α -pinene. Two test releases were made, the first with birds of the Grächwill loft (Exp. 1a), and the 2nd with birds of the Sand loft (Exp. 1b).

Experiment 1a. August 9, 1975. Release site Birrfeld. Home direction 233°, home distance 81 km. 12 experimentals, and 11 controls were released, but only 11 and 10 vanishing points respectively were recorded (Figure 1a). Bearing distribution was not random both for the experimentals ($z = 5.165$, $p < 0.01$) and for the controls ($z = 4.853$, $p < 0.01$). The controls were homeward oriented ($u = 2.973$, $p < 0.001$), whereas the experimentals were not ($u = 0.055$, $p > 0.10$). The difference between the 2 sets of bearings was significant ($u = 10.103$, $p < 0.01$). All birds homed.

Experiment 1b. Same date and release site as in exp. 1a. Home direction 229°, home distance 72 km. The 5 couples and 1 single bird which composed each group were released. Among the experimentals, the bearings of 1 couple and of the singly released bird could not be recorded, but 1 couple furnished 2 bearings as the birds flew in different directions (Figure 1b). Bearing distribution was not random for the controls ($z = 4.791$, $p < 0.01$), but was for the experimentals ($z = 1.946$, $p > 0.10$). The controls were homeward oriented ($u = 2.774$, $p < 0.005$), while the experimentals were not ($u = -0.439$, $p > 0.10$). The difference between the 2 sets of bearings was significant ($B = 12.343$, $p < 0.025$). All birds homed.

2nd experiment. August 11, 1975. For this detour experiment, birds of the Sand loft were used. Release site, home distance and direction as in exp. 1b. The outward journey of group N went first towards the NW, that of group S towards the SSE (Figure 2c). 20 N- and 20 S-birds were released. 17 vanishing points were recorded for each group. Due to a change in the weather, a part of each group had to be released under totally overcast skies. However, their behaviour was similar to that of the birds released while the sun was visible (Figure 2a-b). The N-birds were oriented not randomly ($z = 11.999$, $p < 0.001$) towards the SE, deviating as predicted from the home direction. In contrast, S-birds oriented themselves randomly ($z = 1.111$, $p > 0.10$). The difference between the 2 sets of bearings was significant ($u = 10.329$, $p < 0.01$).

3rd experiment. 2 test releases were performed with the birds of the Grächwill loft subjected to an unilateral sectioning of the olfactory nerve and the occlusion of one nostril.

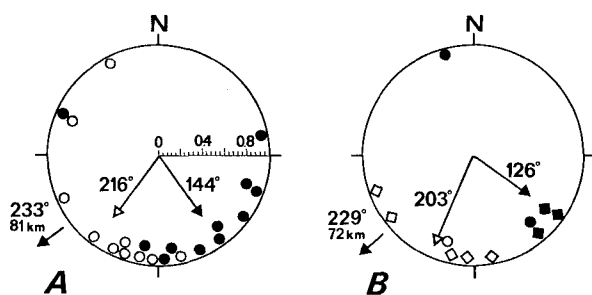


Fig. 1. Initial orientation in the α -pinene experiment. A) Birds of the Grächwill loft (exp. 1a), B) Birds of the Sand loft (exp. 1b). Each symbol on the periphery of the 2 circle indicates the bearing of 1 bird (circles) or of a couple of birds released and vanished together (diamonds). Open symbols for the controls, filled for the experimentals. The outer arrows indicate the loft site, the direction and distance of which are given; the inner arrows represent the mean vectors, the length of which can be read using the scale in the first diagram.

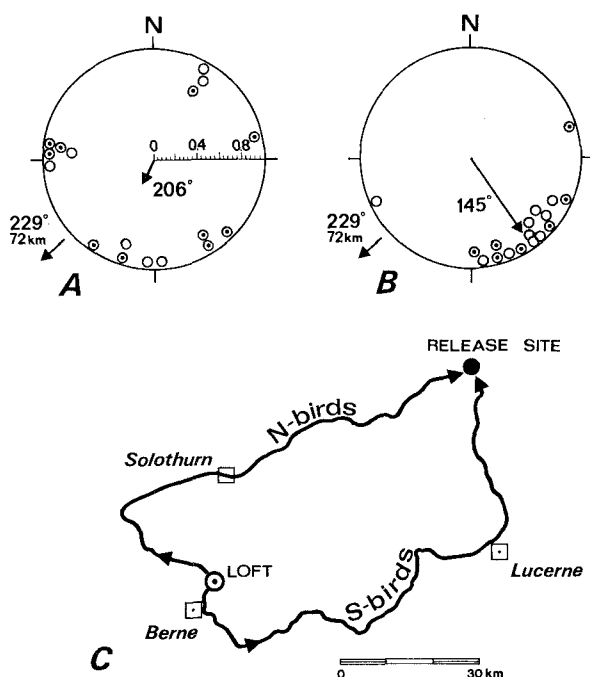


Fig. 2. Initial orientation in the detour experiment. A) S-birds, B) N-birds. Dotted symbols refer to birds released under total overcast skies, C) Map showing the routes from the loft to the release site. Other explanation as for Figure 1.

¹⁰ E. BATSCHELET, in *Animal Orientation and Navigation* (U.S. Government Printing Office, Washington, D.C. 1972).

¹¹ K. V. MARDIA, *J. R. statist. Soc. B31*, 98 (1967).

¹² S. SIEGEL, *Nonparametric Statistics for the Behavioral Sciences* (McGraw-Hill, New York 1956).

Experiment 3a. August 14, 1975. Release site, home direction and distance as in exp. 1a. Both groups consisted of 13 birds, but the vanishing point of 1 experimental pigeon could not be recorded (Figure 3a). Control birds were oriented not randomly ($z = 3.717$, $p < 0.05$) and flew home ($u = 2.545$, $p < 0.005$), whereas the experimental birds were oriented at random ($z = 1.649$, $p > 0.10$) and did not show homeward tendencies ($u = -1.347$, $p > 0.10$). The difference between the 2

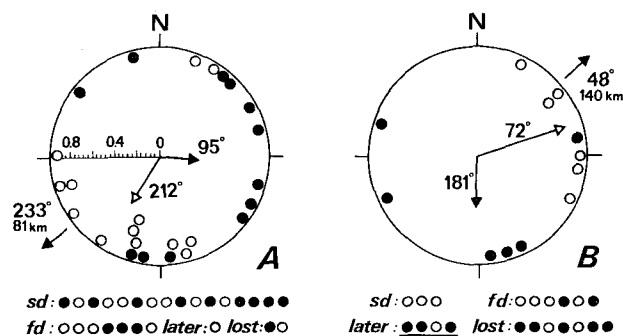


Fig. 3. Initial orientation and homing performances (bottom) in the 3rd experiment. A) Test release from Birrfield (exp. 1a), B) from Avully (exp. 1b). The open symbols refer to the controls, the filled to the experimentals. For the birds from Avully which homed after 3 days or more, the time of re-entry was not recorded and they were classified as having the same homing time (underlined symbols). sd, birds homed the same day as released; fd, birds homed the following day. Other explanations as in Figure 1.

sets of bearings was significant ($u = 6.59$, $p < 0.05$). All birds homed, except for 1 experimental and 1 control; no differences in homing performances resulted ($U = 83.5$, $p > 0.10$).

Experiment 3b. September 22, 1975. Release site Avully. Home direction 048° , home distance 140 km. The birds were a part of the group used in the exp. 3a; between the 2 tests they had been released from Courtelary (28 km NW). However, the rôles were inverted, the past controls being used as experimentals and viceversa (except for 1 bird, which was used as experimental in both releases). 10 experimentals and 10 controls were released, but only 6 vanishing points for each group were recorded (Figure 3b). As in the previous experiment control birds were not oriented randomly ($z = 4.418$, $p < 0.01$) and flew home ($u = 2.708$, $p < 0.005$), whereas experimental birds were oriented at random ($z = 1.292$, $p > 0.10$) and did not show homeward tendencies ($u = -1.095$, $p > 0.10$). However, the difference between the 2 sets of bearing was not significant ($B = 7.46$, $p > 0.10$). 5 experimentals and 2 controls did not home. In contrast with the exp. 3a, a difference in homing speeds resulted, the experimental birds homing slower ($U = 19.5$, $p < 0.025$).

The results of the present experiment add further evidence that homing pigeons use olfactory cues for navigational purposes and that outward journey detours influence their initial orientation. In our opinion, further experiments on American pigeons would be appropriate to ascertain whether pigeons from other strains or regions actually use or can switch to alternate cues without the loss of accuracy.

Variance to Mean Ratio and the Spatial Distribution of Animals

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Summary. Biological and statistical aspects of the application of variance to mean ratio to describe spatial distribution of animals are discussed. It is shown that the parameter b in TAYLOR's power law $s^2 = am^b$ shows intra-specific variation depending on the distribution of the constituent units of the population. a and b are only parameters of a very empirical way of describing the relation between variance and mean, which itself is an indicator for spatial distribution. Hence, a and b depend on the distribution behaviour of the animals, and not vice versa.

Variance (s^2) and mean (m) are the two statistical parameters commonly used to describe the spatial distribution of animals. In general, these two parameters are not independent, but tend to increase together. But, since a truly random distribution leads to a Poisson distribution, $s^2 = m$ becomes an indicator of randomness: every deviation from randomness indicates a deviation from this relationship. TAYLOR^{2,3} has shown that the variances and means of the sample counts can be empirically related by a power law, such that,

$$s^2 = am^b$$

when a is the sampling factor that affects the variance to mean ratio and b is the index of the spatial distribution characteristic of the species. a and b do not appear to have a known distribution function, and it is possible that b , instead of being specific, may show intra-specific variation depending on the distribution of the qualitative units of the population. This paper discusses this aspect with reference to the distribution of the Iulid diploped *Trigoniulus lumbricinus* (Gerst) in the soil.

Materials and methods. Details about the study area and sampling procedures are given elsewhere⁴. 21 sets of samples, each made up of 15 units of 1 square m , were examined. A metal frame was used to form the quadrat during sampling, and the diploped populations to a depth of 15 cm within these quadrats were sorted out according to their sex and developmental stages. Variances and means for each series were calculated and these were plotted on a $\log \times \log$ scale.

Results and discussions. Considered as a whole, i.e. without any distinction between sexes and developmental stages, $b = 1.35$ (Figure A) indicates *T. lumbricinus*

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² L. R. TAYLOR, *Nature*, Lond. **189**, 732 (1961).

³ L. R. TAYLOR, *Proc. 12th int. Congr. Ent.* (1965), p. 396.

⁴ B. BANERJEE, *Res. Popul. Ecol.* **16**, 132 (1974).