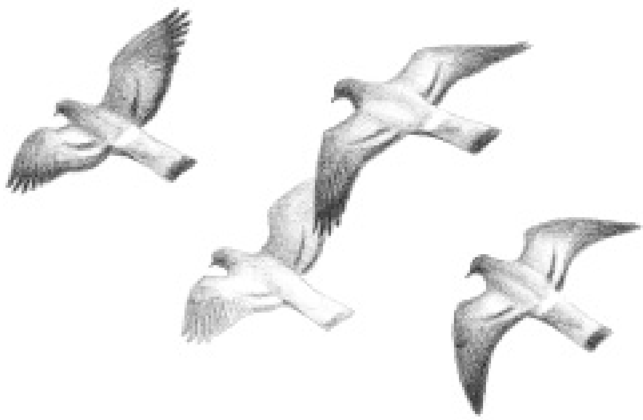
Do homing pigeons follow their noses?

JØRGEN RABØL



(Med et dansk resumé: Brevduer finder hjem ved at bruge næsen)

The system by which pigeons find their way home remains a mystery for the public because some researchers maintain that things are more obscure and multifactorial than they really are.

In this way, H.G. Wallraff castigates some of his colleagues, in particular the Wiltschkos in Frankfurt, who for many years have underrated the importance of a navigation system based on olfaction. The new development is that Wallraff – together with Italian researchers – is now supported by the Americans K.P. Able and C. Wallcott who formerly distrusted the role of olfaction in homing.

This development appears from a special issue of *Journal of Experimental Biology* (vol. 199, 1996). What is not told is that the story goes beyond pigeons and into the orientation system of migrant birds where the Wiltschkos and others maintain the dominant role of the magnetic inclination compass. Furthermore, in the scenario of the Wiltschkos, juvenile migrants never navigate, and if they did, the process would be based on the magnetic field of the Earth.

It appears that the underlying battle is about which orientation or navigation system is the one and only. Is it based on olfaction, magnetism or celestial cues? Three pigeon experts (Wallraff, Wallcott, Rosi Wiltschko) and a referee (Able) tell the story. Able – who is an expert on the orientation of migrant birds – never released a homing pigeon and therefore considers himself a neutral referee.

The pigeon fancier

Charles Wallcott not only studies homing in pigeons, he is also an enthusiastic observer of their astonishing abilities and the peculiarities of their behaviour. However, like Wiltschko and Able he resigns when it comes to explaining the sometimes chaotic pattern of departure directions. Wallcott maintains that the most important component in the homing process of pigeons is based on olfaction, but also that "perhaps they could use sources of sounds as acoustic guideposts". He disbelieves navigation based on the magnetic field, and the possibility of sun-arc navigation is not even mentioned.

Wallcott acknowledges "Kramer's idea that pigeon homing is a two-step process: a 'map' to determine the directions towards home and a compass to guide the birds in that direction (Kramer 1953)". However, this dissociation of the 'map' and the compass may be misleading, which becomes obvious when Wallcott observes that "clock-shift experiments ... introduced an error into the sun compass system, but since the pigeon flies off at an angle with respect to the home direction, the bird still obviously knows the direction towards home". In my opinion this is not so; the 'map' or the navigatory axes are tightly locked to one or several compasses, and following a clock-shift the whole system turns temporarily because of the dominant sun compass. Consequently, for example, a 6 hour fast clock makes departing pigeons believe that home is 90° degrees to the left of the true home direction. However, fairly soon they recognise their error and compensate, perhaps because they also have a magnetic compass which is not altered by the clock-shift. Furthermore, they may be guided by the visual landscape (sensu Wallraff) in familiar areas. When consulting the old paper of Kramer I found it rather difficult to understand what he really meant, although common practice has been to interpret him in the same way Wallcott did. This interpretation, unfortunately, prevents an operational understanding of the system involved.

Wallcott renders inexplicable the release-site biases which fascinates him so much because he fails to take into consideration the zones-of-uncertainty and zero-axes navigation system introduced by Wallraff (1974). Wallcott emphasizes that the release-site biases in departure directions are independent of stock; they are a function of the geographic, or relative, positions of the loft and the release site. He shows an interesting map of departure direction distributions from about 80 release-sites centered around his loft at Cornell. In Fig. 1, I have summarized and elaborated somewhat on the main directional tendencies in the different zones. The principles behind Figs 2-3, which are based on the zones-of-uncertainty system of Wallraff (1974, see also Rabøl 1985, 1988, 1997), offer part of an explanation of the pattern in Fig. 1.

The discussion of Wallcott is concentrated around two release-sites: Castor Hill (160 km NNE of the loft) and Jersey Hill Fire Tower (132 km to the W), see Fig. 1. Fig. 4 shows the distribution of departure direction vectors based on releases of many groups of pigeons at these two sites and at a site close to Jersey Hill. According to Wallcott, most pigeons released at Jersey Hill are randomly oriented and few birds actually home. At Castor

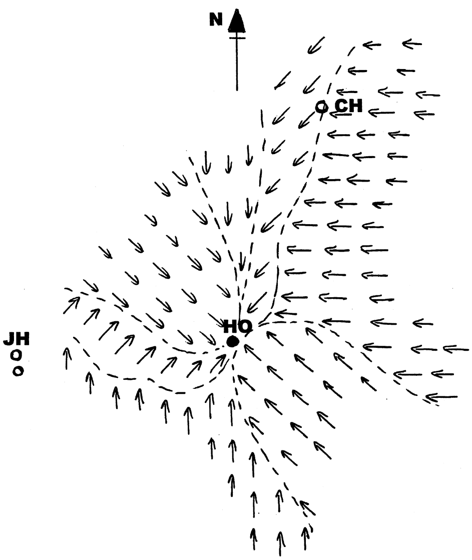


Fig. 1. The general pattern of departure directions of pigeons released at about 80 sites around a loft at Cornell (HO, black dot). The three white dots to the NNE (CH) and W (JH) designate Castor Hill, Jersey Hill, and a release site close to Jersey Hill. Compilated on basis of Fig. 1 in Wallcott (1996).
Mønstret af bortflyvningsretninger af Cornell-duer fra Castor Hill (CH) og Jersey Hill (JH). Cornell er markeret med HO.

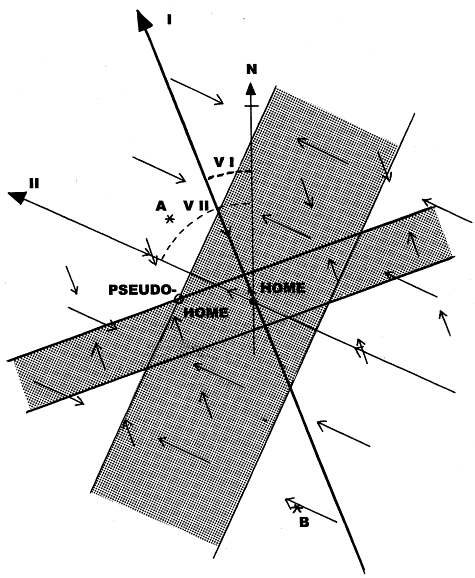


Fig. 2. A bicoordinate navigation system with the two axes oriented towards 340° and 290° relative to compass N. At right angles to the two axes are denoted two zones-of-uncertainty (grey). When displaced outside a zone-of-uncertainty, the bird orients in parallel to the axis in the direction towards the home: in A towards 160° and 110° in relation to coordinates I and II, respectively, and in B in the two opposite directions. If these directions are considered as vectors with equal strength the resultant directions will be SE (135°) and NW (315°) at A and B, respectively. Within the zones-of-uncertainty, the orientation is polarized in one of the two opposite directions, here 340° (I) and 290° (II). As shown in Fig. 3, the resultant directions in the four quadrants converge towards a pseudo-home.
Princippet i koordinatnavigation med tilhørende usikkerhedszoner (gråtonede). De to koordinatakser peger mod NNV (340°) og WNW (290°). Uden for usikkerhedszonerne orienterer fuglene sig parallelt med koordinatakserne og i den retning, der er mest rettet mod hjemmet (home). Inden for usikkerhedszonerne er orienteringen NNV og WNW, og ikke nødvendigvis i den retning, der er mest hjemrettet.

Hill the pigeons depart within a directional sector clockwise to the home-direction, but these birds home well. Comparisons between Fig. 1 and Fig. 4 show that the orientation at Castor Hill fits into the general pattern. If the orientations at Jersey Hill are considered in concert with the orientations at the nearby site, directional modi in a cross NE-SE and SW-NW are rather prominent. A reasonable explanation of this pattern could be that Jersey Hill is close to the pseudo-goal of Cornell (Figs 2-3) and is perceived by the pigeons as being situated sometimes in the NE-quadrant and sometimes in one of the three other quadrants.

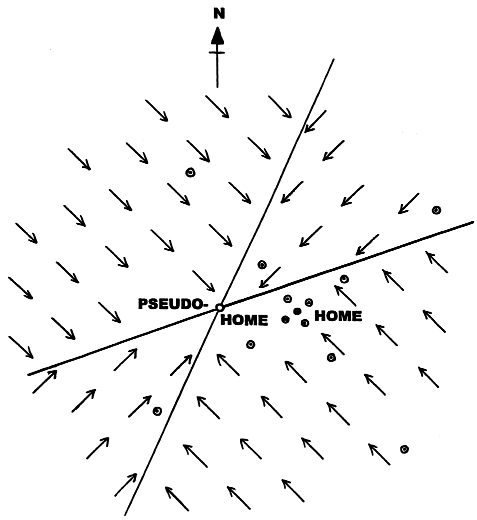


Fig. 3. Consequences of Fig. 2. The resultant NE-, SE-, SW-, and NW-orientations within the four quadrants around the pseudo-home. Also shown are three quartets of symmetrical release points along the axes 53°/233° and 143°/323° through home. The combined mean departure directions of pigeons released at the four inner sites is 315° (concentration 1.00) in relation to compass N (0°), whereas the combined mean vector in relation to the direction towards home has a concentration of 0. In the four outer sites combined, the concentration in relation to the compass is 0, whereas in relation to the home direction the mean vector is -8° (1.00; homeward component 0.99). Combining the four middle sites yields a mean compass vector of 297° (0.79), whereas the homeward vector is -37° (0.35; homeward component 0.28). As an average for many symmetrical releases there will be a general tendency for W-orientation corresponding to the direction from home towards pseudo-home, and this may be considered as the mean preferred compass direction (PCD).

Denne figur bygger videre på Fig. 2. Indenfor hver af de fire kvadranter – afgrænset af de to usikkerhedsgrænser, der går gennem det såkaldte pseudohjem (pseudo-home) – forestiller man sig, at de to retninger (opfattet som to lige store vektorer) parallelt med koordinatakserne er lagt sammen til vektorer i retning mod hhv. NØ-, SØ-, SV- og NV. Duer sluppet i en af de fire nærmeste positioner (prikkede prikker) omkring hjemmet (home, sort prik) orienterer sig således alle mod NV, mens de i de fire fjerneste positioner er orienterede mod henholdsvis NØ, SØ, SV og NV. Som gennemsnit for mange positioner beliggende symmetrisk omkring hjemmet vil duerne være nogenlunde hjemorienterede, men udvise en vis tendens til V-orientering svarende til retningen fra home mod pseudo-home.

The neutral referee

With few reservations Kenneth Able recognizes the importance of olfactory navigation in pigeons ("... olfaction plays a major, sometimes primary, and sometimes perhaps even exclusive, role in what we call the 'map' component of homing").

Able observes that anosmic pigeons perform poor departure orientation and homing compared with non-manipulated controls. However, the

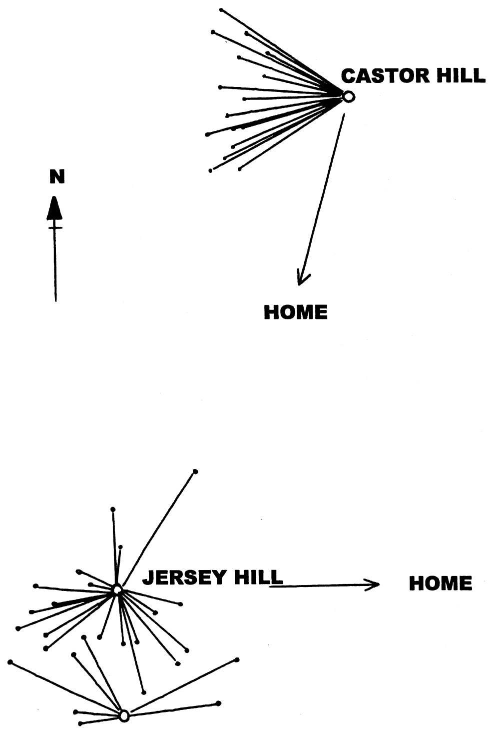


Fig. 4. Sample mean vectors from many releases from Castor Hill (upper figure) and Jersey Hill and a nearby release site (lower figure) shown in relation to the compass reference (N) and the home-direction. Drawn on the basis of Fig. 1 in Wallcott (1996).

Resultaterne af mange frislipninger fra Castor Hill og Jersey Hill (se Fig. 1). Hver streg viser retning og koncentration af gennemsitsvektoren for en gruppe duer. En kort streg signalerer stor uenighed i retningsvalg.

crucial evidence for Able is that manipulations of the olfactory 'map' "provide strong tests of the hypothesis because one can manipulate the putative orientation cue, and the predicted effects are usually a change in direction rather than the more problematical disorientation".

Able explicitely states that there is no need of a very precise 'map'. A distance-component may not exist and direction alone suffices. In other words, the birds are permitted to repeat the navigatory process many times during the home flight, thereby fitting Wallcott's reflection that a group of 6-hour clock-shifted pigeons recomputed "the direction towards home roughly every 15-30 min". Able recommends that the most important pro-olfaction experiments by the Italians and Wallraff be repeated by other researchers.

Able mentions the preferred compass direction (PCD) of Wallraff and the release-site-biases of Wallcott, but offers no explanation of these phenomena ("Whatever the case, it is not clear how or if the biases are directly related to homing").

Considering the widespread resistance against accepting an olfactory 'map' in homing pigeons, Able follows Wallraff by stressing that "Hypotheses can only be rejected through the results of empirical tests, not on the basis of theoretical considerations" and concludes that "In the case of olfactory navigation, I think the burden of proof clearly rests with those who still believe that odours play no role in homing".

Obviously this pro-olfactory attitude of the "neutral referee" puts strong pressure on Wiltschko, who does not accept any prominent role of olfactory navigation in the homing process of pigeons.

Die magnetische Frau Dr.

The main points in Rosi Wiltschko's critique of olfactory navigation are the following: 1) There is no meteorological or atmospheric basis for olfactory navigation. The atmosphere is too turbulent and unpredictable. Therefore useful olfactory gradients do not exist in the real world. 2) The orientational patterns in many experiments manipulating olfaction one way or another are not compatible with expectations or predictions involving olfaction. 3) Olfactory manipulations (above all olfactory nerve sections) significantly influence the general condition of the pigeon and in some way lowers its motivation, intelligence or ability to integrate information, so that the orientation deteriorates and the homing performance becomes poor.

As emphasized by Able (and Wallraff), 1) is not a strong and perhaps not even a valid point. 3) is a weak point too, as the general flight behaviour of pigeons seems not to be influenced by olfactory manipulations. Furthermore, the departure orientation and homing performance of olfactorily manipulated pigeons released from familiar sites are not influenced by the treatment.

Concerning 2), Wiltschko finds evidence against olfactory navigation in a few cases only, and the argumentation is not convincing. In her discussion of the important true home/false home experiments of Benvenuti & Wallraff (1985; see below), Wiltschko states that "when pooled none of the groups was homeward-oriented". This is at best misleading, because the 'false open' birds were significantly oriented towards false home, and significantly oriented away from true home. Wiltschko also underlines the positive coupling between 'false open' and 'false filt', but this is not a strong point against olfactory navigation in the experiment as a whole. Certainly, she may be right that something else than olfaction influences the departure directions, and in fact this something else was reported by Benvenuti & Wallraff: a strong SW-tendency of Italian (but not German) pigeons, irrespective of treatment, in the year of experimentation. I therefore calculated the couplings between the four mean directions of 'false open' and the corresponding 10, 9, 7 and 8 individual departure directions of 'false filt' – and the couplings between the four mean directions of 'false filt' and the corresponding 11, 10, 8 and 5 individual departure directions of 'false open' – in the German releases separately. The two comparisons showed opposite tendencies and neither came close to statistical significance. In conclusion, the experiments by Benvenuti & Wallraff should be interpreted as pro- and not contra-olfactory.

For readers unfamiliar with the experiment of Benvenuti & Wallraff: Three groups of pigeons were considered. 'True open' was transported directly to the release site where they were allowed to smell the ambient air for three hours before being released under local anaesthesia of their olfactory mucosae. 'False open' was first transported to a site ('false site') in a direction approximately opposite to that of the release site and about the same distance from home. Here they were allowed to smell the ambient air for three hours. Afterwards they were transported to the same release site as 'true open', but they were not allowed to smell the ambient air here before

Homing pigeons are – probably – able to use olfactory clues in their navigation. Photo: Lone Eg Nissen.
Brevduer kan tilsyneladende bruge dufte til at navigere efter.

they were anaesthetized and released. During transport 'true open' and 'false open' were prevented from smelling outside odours by filtration of the air. The third group, 'false filt', was transported together with 'false open' and treated in the same way, except that they never smelled the ambient air at 'false site'. This third group was included in order to find out whether the route of transportation had any influence on the departure orientation. If so there should be a positive correlation between the orientation of 'false open' and 'false filt'.

It is not clear to me why Wiltschko on the one hand advocates a redundant, multi-factorial homing system and on the other hand totally refutes any influence of olfaction ("At the moment, no experiment unequivocally proves the use of odours as navigational cues. Hence, it does not appear justified to accept that they provide navigational information"). Wiltschko may refute olfactory navigation because of her strong conviction that magnetism plays the major role in animal orientation and navigation, and that compass-based route reversal, not position-dependent navigation, is the more important homing system, at least in young inexperienced pigeons.

Der olfaktorische Dr. Brieftaube

The kernel in the 7 theses of Hans Wallraff is that only olfactory and visual landscape navigation are proven facts and that no indications exist of e.g. magnetic, sound, or celestial navigation in homing pigeons. It is not clear whether Wallraff believes in a magnetic compass in pigeons, but he does consider the significance of the sun compass.

A central point is that a navigation system or 'map' based on location-dependent signals is much more important in home-related orientation than is reverse path integration based on a compass system. The signals are detected not only on the release site but also en route during the displacement, meaning that the route by which the pigeon was displaced affects the departure direction, although not – as formerly hypothesized – as a reverse path integration.

The three first theses of Wallraff are: 1) "passively displaced pigeons find their way home by using location-dependent signals and not by path integration based on recording of movements", 2) "Home-related orientation of pigeons in unfamiliar areas requires positional information aquired olfactorily from atmospheric trace gases", and 3) "In familiar areas, known from previous flights, the visual landscape is used additionally to find the way home".

When released in unfamiliar areas, anosmic pigeons are disoriented and the homing speed and performance is no better than chance would permit. The reason is "specific navigational deficits" and not "general disturbances" as maintained by Wiltschko.

According to Wallraff, the departure direction of released pigeons are not solely the outcome of a "home-related navigation but includes components independent of the position with respect to home". He explains that the departure directions can be considered as originating from four different sources: 1) visual piloting (releases from familiar sites); 2) olfactory navigation; 3) a preferred compass direction (PCD); and 4) distracting topographical features. The establishment and maintenance of direction connected with 1) and 2) are considered to be unimodal and largely unbiased in relation to the home direction, and the PCD is a constant direction unrelated to the olfactory navigation system. In fact, Wallraff (1996) never mentions his zones-of-uncertainty/zero-axes navigation system (Wallraff 1974) from which the PCD is a logical outcome (at least in the extension of Rabøl 1985, 1988, 1997; see also Figs 2-3). Thus, at present Wallraff seems to recognize no zones of uncertainty.

Clearly, Wallraff considers the navigation system as based on at least two and probably more olfactory gradients. The system is founded at the home loft by by the smell of different odours from different directions. More precisely, his sub-thesis 2.1 says that "Knowledge needed to make appropriate use of airborne information at distant sites is acquired at the home site by associating olfactory inputs with wind direction (creation of an olfactory 'map')".

Sub-thesis 2.2, "Directional information, associated with olfactory map information at home and abroad, is derived from the sun's azimuth taking current time into consideration", does not refer to any Kramerian 'map' or compass (sensu Wallcott); the 'map' has no meaning without, and cannot be separated from, the compass.

The central conclusion of Thesis 2 is that "Positional information is deduced from a spectrum of atmospheric trace substances whose proportional composition varies with a fairly regular gradient in any horizontal direction over fairly long distances". Later Wallraff writes that "empirical findings ... strongly suggest the existence of sufficiently monotonic olfactory gradients over geographically varying ranges".

Conclusions (JR)

Wallraff considers neither the navigation system nor the preferred compass direction (PCD) in any detail. His navigation system seems to have no zones-of-uncertainty, and the PCD no declared function. However, the PCD may be an inevitable outcome of a zones-of-uncertainty system (Fig. 3).

Clearly, Wallraff operates with at least two olfactory gradients, but several types of navigation systems are possible.

At one extreme is a simple, qualitative system based on several to many different olfactory sources around the home loft (Fig. 5), so that e.g. smell D from SW is imprinted and associated with winds from the compass direction of SW. When released in an unfamiliar area and experiencing smell D, the pigeons depart towards NE. Other smells are associated with winds from other compass directions.

The system hypothesized by Rabøl (1988, see Fig. 2) represents the other extreme. All relevant smells merge into a single gradient, while a second navigatory gradient could be, for example, an E/W-coordinate based on the biological clock so that the pigeon determines whether it is released E or W of home on the basis of observed and

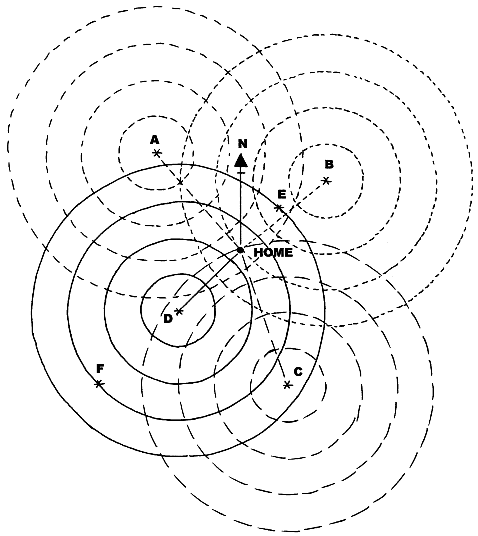


Fig. 5. Four sources of smell around the home loft in directions 319° (A), 49° (B), 160° (C), and 225° (D). Circular olfactory 'isobars' (of logarithmic strength 5 (inner circle), 4, 3, and 2) are denoted. The figure displays the situation under calm conditions.
Fire duftkilder i forskellige retninger og afstande fra hjemmet (home). Cirklerne viser aftagende duftstyrke udad fra kilderne under vindstille forhold.

remembered celestial cues. Such a coordinate was proposed for migrant birds navigating towards a moving goal area (Rabøl 1978, 1980), but seems much more obvious for the short-term process of homing in pigeons where a very precise clock is not so important (pigeons are normally released shortly after the displacement). Different systems intermediate between the two extremes are also possible.

To elaborate on the simple system consider again Fig. 5. The pigeons could have stored the average (or no-wind) olfactory values of the loft, in the shown example 2.4 (A), 2.9 (B), 2.1 (C), and 3.6 (D). If displaced to position E the pigeons will experience values of 2.3 (A), 4.5 (B), 1.0 (C), and 2.0 (D). All values except that of B have decreased, so a good strategy would be to depart towards SW, away from the source of B as experienced from home. Errors may arise in such a system, in particular if one of the smells dominates or if the pigeons are displaced outside the influence of the ABCD-system. At position F, the value of D is lower than at home, but a SW departure direction (towards the source of D as experienced from home) leads directly away from home.

Fig. 6 shows a more normal situation with windy conditions. In a southerly wind, the olfactory concentration zones around A, B, C, and D are displaced as shown. The home-values are about

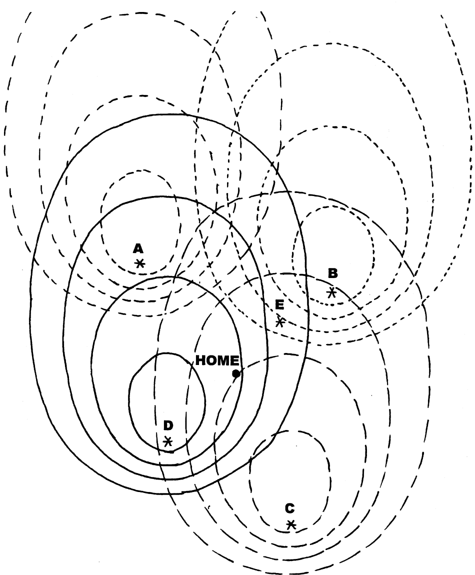


Fig. 6. With a southerly wind, the circular olfactory 'isobars' of Fig. 5 turn into ellipses.
Når det blæser, bliver cirklerne i Fig. 5 til ellipser.

0.1 (A), 0.5 (B), 3.9 (C), and 4.2 (D). In position E the following values are experienced: 0.8 (A), 2.8 (B), 3.5 (C), and 2.7 (D). If displaced pigeons compare these values with those last experienced at home, the significant increase in B and the significant decrease in D will both signal "go SW". Obviously, such an orientation leads towards home. If the pigeons, however, make use of the average home-values (Fig. 5), the weighted result of the increase in C and the decrease in A and D will lead to a departure direction of WNW-NW, roughly perpendicular to the home direction.

Summing up, there seems to be no reason to doubt the existence and primary importance of olfactory navigation in the homing process of pigeons, but as emphasized by Wallraff, we still do not know which trace gases are involved, nor do we know the details of the navigatory system. Navigation including zones-of-uncertainty may be the most simple and coherent system able to explain the release-site biases, but these may also arise from the systems outlined in Figs 5-6.

Olfactory navigation might also be involved (and at least partly on an inherited basis) when juvenile migrants head for important stop-over sites, narrow migratory flyways, or restricted wintering areas. Possible examples are the Red-backed Shrike in the northern part of Kruger National Park in South Africa, using the smell of the Mopane-trees, and the Pied Flycatcher in northern Portugal and Spain using the smell of oak-forests. As discussed by Thorup et al. (2000) and Thorup & Rabøl (in press), a simple clock-and-compass model cannot explain the observed concentration of ring recoveries of certain populations of migrant passerines, including juvenile birds. A navigatory system, based on the celestial sky, the magnetic field of the Earth, or olfaction, would seem to be a prerequisite for performing such a concentrated migratory progress.

Postscript

Wallraff (in litt.) commented on a draft of this paper that "Curiously, you adhere even more faithfully to my old null-axis hypothesis than I do myself. I think that experimental evidence is now more against rather than in favour of it", and later on "Zones of uncertainty may well exist, particularly at shorter distances, but such zones do not enforce a null-axis explanation". Wallraff may of course be right, in particular when thinking in terms of olfaction and pigeons. At a more general level, however, and when including migrant birds and celestial or magnetic cues, null-axis/zones-of-uncertainty navigation still makes much sense and may well turn out to be necessary for a deeper understanding.

Another important comment of Wallraff was that "As regards your Figs 5-6, I consider it very unlikely that isolated point sources of smell (= single compounds or mixtures?) do exist whose products, together with their spatial gradients, remain distinguishable from those originating at other locations". Again Wallraff may be right, but my main objective was to demonstrate that a system based on odours could work in principle.

Recently, Wallraff (2000) published a paper where olfactory gradients were not just assumed to be present, but were calculated based on measurements of the concentrations of six different volatile hydrocarbons in the atmosphere of central Europe. Wallraff measured the concentrations of these compounds at 96 sites regularly spaced within an approximately circular area having a radius of 200 km. From the relative proportions of the six substances at the 96 sites the upward and downward directions of the six ratio-gradients were established. As an example, substance A had its maximal ratio increase (its upward direction) towards 310°. The ratio values at the center of the circular area (the 'home') were assumed to be the means for the 96 sites, and the model pigeons compared this ratio-set with the set of ratios at their actual position. If the ratio of substance A was smaller than at home, the model pigeons would go up the gradient towards 310°. In the same way, the model pigeons went up or down the other five gradients, the weight of each depending on the relative difference between actual and home ratio-values. In the great majority of cases the weighted mean vector was directed closely towards home.

This gradient-system work well for model pigeons and may work well also for real, free-flying pigeons. In all probability these should be able to establish up- and downward directions of olfactory gradients. The difficulty is whether aviary pigeons, i.e. pigeons spending all their time in an aviary prior to the first release, can establish the ratio-gradients (aviary pigeons generally have a significant homeward orientation when first released). Wallraff think they can; sitting in its aviary a pigeon may learn that the ratio of odour A is highest when the wind comes from 310°. The crucial question is whether the gradient-field of Wallraff is brought to the aviary with the winds to a sufficient degree.

Summing up, Wallraff (2000) makes a convincing case, and from now on no reasonable person can ignore or deny the possibility of olfactory homing in pigeons. In this connection it could be mentioned that, although many people (including Wallraff) have no confidence in stellar navigation in migrant birds (Rabøl 1998), no one denies that it is a possibility. However, homing in pigeons may rely on a more complex and redundant system than realized by Wallraff, with the olfactory component comprising only an important sub-system, but not the whole story.

Resumé

Brevduer finder hjem ved at bruge næsen

Man hører jævnligt om, hvordan trækfugle og andre skabninger (senest havskildpadder og monark-sommerfugle) finder vej ved hjælp af Jordens magnetfelt; hvorimod folket – og faktisk også de fleste orienteringsforskere – er meget dårligt eller slet ikke bekendte med brevduens brug af duft-navigation, skønt der faktisk er meget mere belæg for det sidste end for det første.

I *Journal of Experimental Biology* 1996 ridser tre specialister og en enkelt generalist linierne op: Hvad er det for et orienteringssystem, som brevduen bruger til at finde vej hjem? De tre af forskerne er meget enige: Duerne benytter sig af duft-navigation som det eneste eller i hvert fald langt det vigtigste. Kun Rosi Wiltschko er meget forbeholden og nærmest afvisende over for duft-navigation. Hun kommer dog ikke med andre konstruktive forslag, hvorimod hun andetsteds går kraftigt i brechen for magnetfeltets overlegenhed, når det gælder trækfuglenes orienteringssystem. Det kan være en vigtig del af baggrunden for hendes afvisning af duft-navigation hos brevduer.

Amerikaneren Charles Wallcott er meget optaget af mønstre i bortflyvningsretninger; disse er ofte uventede og virker iblandt kaotiske. Ved Castor Hill (Fig. 1 og 4) finder Wallcott en afvigende bortflyvning i forhold til hjemretningen, men ellers viser duerne fra hans slag i Cornell altid den stort set samme højreafvigelse. Fra Jersey Hill forsvinder duerne i alle retninger, og med stor variation fra gang til gang, og i modsætning til duerne fra Castor Hill vender duerne fra Jersey Hill kun sjældent hjem. Det fascinerer Wallcott, men han kan ikke forklare det, for han har ikke nogen hypotese at sætte det i relation til.

Kenneth Able er generalisten. Han har lavet mange forsøg med trækfugles orientering (især Savanna-spurven), men brevduer har han ikke beskæftiget sig med. Derfor er han en god og neutral dommer, siger han, og det er han også efter min bedømmelse. Ifølge Able bruger duerne duft-navigation, men som Wallcott er han ikke konstruktiv med hensyn til forslag om hvordan. Men det gør heller ikke så meget. Ables støtte betyder, at modstrømmen er vendt til medstrøm for anerkendelse af duft-navigation.

Rosi og Wolfgang Wiltschko fra Frankfurt står efterhånden isolerede i deres duft-modstand, og de har vist heller ikke lavet mange brevdueforsøg i de senere år. Kræfterne bruges nu mestendels på at konsolidere og

udbygge magnetismens førsteplads på top-fem-listen over trækfuglenes kompasser. Rosi Wiltschko kommer med en del indvendinger og "modbeviser", både af teoretisk og eksperimentel art, men disse er for lidt generelle, for lidt vægtige og delvis forkerte, så de rokker ikke afgørende ved betydningen af duft-navigation hos brevduer.

Hans Wallraff fra Seewiesen afskærmede allerede i 1960erne sit dueslag med diverse former for "palisader" og sandsyliggjorde, at der var "noget" i luften, der lod sig stoppe eller afbøje, og som havde betydning for duernes evne til at finde hjem. Dette "noget" kunne vanskeligt være synsindtryk eller lyde, da palisaderne bl.a. bestod af glas eller var opbygget som lameller, men Wallraff vovede ikke i første omgang at gætte på dufte. Som vi andre fra den tid havde han jo lært på universitetet, at fuglenes lugtesans var ringe udviklet. Det blev derfor nogle italienere med Floriano Papi i spidsen, der først påviste indflydelsen af dufte på hjem-navigationen. Wallraff sluttede sig snart til dem, mens alle andre var skeptiske. I mange år var duft-navigation – som også stjerne-navigation – den store vits i de bedre kredse. Men Wallraff og Papi m.fl. fortsatte og fortsætter med at ophobe dokumentation for duft-navigation, og nu er vi åbenbart ved at være ved vejs ende.

Fig. 2-3 resumerer min udvidelse af Wallraffs usikkerhedszone-model, som han ikke mere selv benytter sig af. Denne model forklarer meget godt diverse forsøgsresultater, såsom den skiftende orientering ved Jersey Hill og også Wallraffs PCD (preferred compass direction), hvormed Wallraff forstår en (altid tilstedeværende) tendens til bortflyvning i en bestemt kompasretning. Wallraff selv tror nu på et navigationssystem, der hviler på mindst tre duftgradienter. I deres hjem lærer duerne, at bestemte dufte kommer ind med vinde fra bestemte verdenshjørner, og herudfra kan de bedømme hjemretningen i fremmede omgivelser ud fra styrken af diverse dufte. Jeg har skitseret et sådant system i Fig. 5-6, og det kan bringes til at fungere godt, selv om duftkoncentrationer i den turbulente atmosfære på forhånd forekommer at være meget lidt egnede til opbygning af et navigationssystem. Dette er en anden vigtig grund til, at Rosi Wiltschko ikke kan tro på det.

Wallraff kender ikke de dufte, som duerne navigerer efter, men gennem filtreringsforsøg ved han, at de ikke bæres af støvpartikler eller aerosoler, men er på luftform. I sin seneste afhandling (2000) har Wallraff vist, at de indbyrdes forhold mellem seks virkeligt forekommende duftstoffer danner gradienter, der i hvert fald i princippet kan bruges til at navigere efter.

Mens vi venter på de nærmere detaljer vedrørende de stoffer, der udnyttes, og hvordan systemet er bygget op, kunne vi måske prøve at vende blikket en anden vej. Hvorfor skulle trækfugle ikke også kunne navigere i forhold til dufte? Hvordan kan alle Europas Brogede Fluesnappere finde vej til et 200 gange 300 km stort område i det nordlige Portugal og Spanien, inden de trækker videre til Afrika? Det kan næppe lade sig gøre ved simpel kompas-og-kalender orientering. Bruger de Nordstjernehøjden (breddegraden) i kombination med en bestemt duftkoncentration af korkeg eller en anden plante? Og kan de gøre det uden at have besøgt området før?

Der er stadig masser af ubesvarede spørgsmål, selv om vi nu ved, at brevduer duft-navigerer – på en eller anden måde.

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Jørgen Rabøl
Dept Terrestrial Ecology,
University of Copenhagen,
Universitetsparken 15, 2100
Copenhagen Ø, Denmark