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OLFACTORY NAVIGATION IN HOMING PIGEONS: ARE THE CURRENT MODELS ATMOSPHERICALLY REALISTIC?

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ABSTRACT.—True olfactory navigation necessitates that homing pigeons (*Columba livia*) employ an odor "map" when determining their position relative to the home loft. Two models exist currently to explain the nature of this olfactory map. The "mosaic" map model suggests that pigeons learn a patchwork of olfactory cues by direct experience with local odors and determine displacement from the home loft by recognizing these familiar odors upon release. The "gradient" map model postulates the existence of stable odor gradients that extend over distances of up to 1,000 km. Pigeons learn the home value of an olfactory gradient while growing up, and then determine their positions with respect to home by comparing this learned value with the gradient value detected at the point of release.

I analyzed both the mosaic and gradient olfactory map models in light of new data on the long-range transport of atmospheric aerosols. These data, obtained in 1983 as part of the Cross-Appalachian Tracer Experiment (CAPTEX '83), cover the region of New York state where extensive experiments on pigeon homing have been conducted from the Cornell University pigeon loft during the past 18 yr. The CAPTEX '83 data provide the first opportunity to assess accurately the atmospheric plausibility of an odor-based navigation system for homing pigeons flown in the northeastern United States. I conclude that the observed patterns of long-range aerosol transport place important limits on the type of olfactory navigation system potentially utilized by homing pigeons. Moreover, a comparison of the CAPTEX '83 data with meteorological information relevant to atmospheric conditions in other geographic locations suggests that regionally specific atmospheric patterns may dictate whether pigeons can reliably employ odors during navigation. This regional specificity is proposed as an explanation for the observed discrepancy between results obtained in olfactory navigation tests conducted in Italy and those performed in the northeastern United States. Received 29 September 1986, accepted 30 January 1987.

OLFACTORY sensitivity in birds has traditionally been considered inferior to that of most other vertebrates (early work reviewed by Bang and Wenzel 1985). Recent evidence, however, indicates that several avian species possess highly functional olfactory systems. Studies of avian olfactory anatomy (Bang and Cobb 1968, Bang 1971), physiology (Wenzel and Sieck 1972, Macadar et al. 1980, Smith and Paselk 1986), and behavior (Stager 1964; Wenzel 1968, 1971; Goldsmith and Goldsmith 1982; Buitron and Nuechterlein 1985) support the possibility that

odors play a significant role in the life of at least some bird species.

With the exception of work on the Turkey Vulture (*Cathartes aura*; Stager 1964), most demonstrations of olfactory orientation in birds involve studies of foraging at short distances, usually a few meters or less. Recently, Sooty Shearwaters (*Puffinus griseus*), Pink-footed Shearwaters (*P. creatopus*), Northern Fulmars (*Fulmarus glacialis*), Black-footed Albatrosses (*Diomedea nigripes*), and Ashy Storm-Petrels (*Oceanodroma homochroa*) have been observed to

make downwind approaches toward experimental releasing wicks scented with the odors of fish oils, squid, or krill (Hutchison and Wenzel 1980, Hutchison et al. 1984). Although the range over which these odors were effective in attracting procellariid species was not determined precisely, distances of at least a few hundred meters probably were involved.

The most impressive claim for long-range olfactory orientation in birds has been made in an effort to explain the homing of pigeons (*Columba livia*; Papi 1976). Questions about the validity of this theory have generated considerable debate (e.g. see Papi et al. 1978, Gould 1982), and research groups in Italy and Germany continue to report results that support the possibility of olfactory navigation in pigeons. Despite the fact that similar tests conducted from other lofts in Germany and the United States generally do not support the olfactory theory (reviewed by Able 1980), some investigators suggest that the bulk of the evidence permits the conclusion that olfaction forms an essential component of the pigeon's navigation system (Wallraff 1980, 1984; Papi 1982).

Unlike the simple olfactory orientation response observed in procellariids (where the birds orient directly upwind toward the source of an odor), pigeons are thought to develop a two-dimensional odor "map" of the area surrounding their home loft. This map allows navigation from any direction with respect to home without having to detect odors emanating from the loft itself. An olfactory map can thus potentially be used over tens or hundreds of kilometers to determine the correct homeward direction from any given release point. Wallraff (1981) discussed two forms that this navigational odor map may take. The first model, the "mosaic" map, is based on the original model proposed by Papi et al. (1972). The mosaic map is learned by young pigeons while growing up at their home loft, and develops from direct experience with the odors encountered during exercise and training flights. More distant odors brought to the loft by prevailing winds also may be incorporated into the mosaic map. While the mosaic map is thought to operate at distances of up to 200 km, its use is necessarily limited to areas where the bird has had direct experience with local or wind-borne odors. A second model, the "gradient" map, overcomes this distance limitation by assuming the existence of

very long-range atmospheric odor gradients that are stable in space and time. Pigeons would use such gradients to fix their positions at distances well beyond their previous flight experience by comparing the observed odorant concentration at the release point with the remembered value of the gradient at the home loft. The concept of a gradient map helps to explain the rapid homing of pigeons from release points up to 1,000 km from their loft (Wallraff 1981).

Numerous examples exist that document olfactory homing to the source of an odor by means of upstream orientation in a well-defined directional medium (e.g. the river phase of adult salmon migration and the attraction of male insects to female sex pheromones). Yet the use of an odor map for true navigation has never been demonstrated conclusively for any species. A major problem for airborne olfactory navigation is that odors that contribute to the formation of a map are subject to spatial and temporal distortions created by atmospheric turbulence and changes in synoptic flow patterns. Modifications of wind flow due to orographic (terrain) features are also important factors in determining odor directionality. Orographic features are particularly important for the pigeon, which generally flies at altitudes of <30 m (i.e. treetop level). Thus, the relative influence of several atmospheric mixing parameters that contribute to wind and odor directionality ultimately determine the usefulness of olfaction as a basis for true navigation in any low-flying animal.

The phenomena of dispersion and long-range transport of particulate and aerosol matter in the upper atmosphere has been well documented and discussed (references cited by Darzi and Winchester 1982, Parrington et al. 1983, Ottar et al. 1984, Robinson 1984). Such upper-air transport probably is not important to avian navigation because of the substantial altitudes involved (generally several thousand meters or more). To date, however, only one attempt has been made to address formally the influence of lower atmospheric dynamics on odor navigation in birds. Becker and van Raden (1986) concluded that the concept of avian olfactory navigation has important shortcomings based on the European meteorological examples they analyzed, primarily because of differences between observed air currents and mean wind directions for a given locality; temporal and

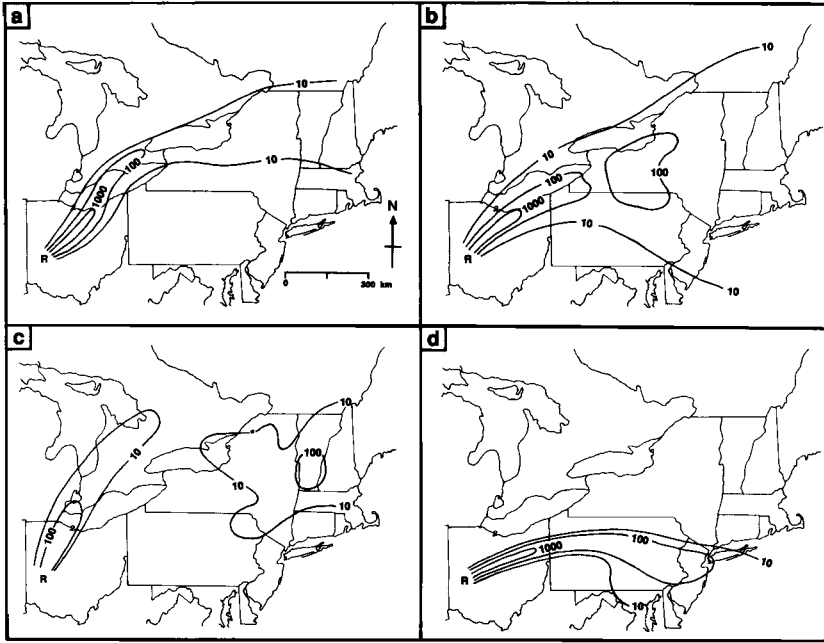


Fig. 1. Maximum observed tracer concentrations measured in femtoliters per liter (fl/l) for each of the CAPTEX '83 releases from Dayton, Ohio (labeled R). Each panel (a-d) represents the results of one 3-h release. Tracer concentrations were measured over the 52 h following each release. Isolines of equal concentration indicate the shape and trajectory of each tracer plume. (Redrawn from Ferber et al. 1986.)

spatial instability of different odor sources; and lack of evidence for long-lived, strong, and stable olfactory gradients in the lower atmosphere.

A similar analysis of lower atmospheric dynamics has not been possible for the area surrounding the Cornell University pigeon loft (Ithaca, New York), where detailed observations of homing pigeon behavior have been made during the past 18 yr. This was due primarily to the lack of adequate information on long-range, lower atmospheric flow patterns over the North American continent. Recently, data collected in a study of long-range atmospheric transport in the northeastern United States (the Cross-Appalachian Tracer Experiment; CAPTEX '83) have become available, and provide the first comprehensive analysis of surface-level flow patterns in regions where Cornell pigeons are flown regularly. This combination of atmospheric and navigation data presents a unique opportunity to determine empirically whether observed atmospheric transport patterns support the use of odors in the homing pigeon's navigational map as suggested by the mosaic and gradient map models.

THE CAPTEX '83 STUDY

Objectives and methods.—CAPTEX '83 was a major field study designed to simulate the long-range transport of pollutants in the atmosphere (Ferber et al. 1986). The study was directed by the National Oceanic and Atmospheric Administration, in cooperation with several other federal and private agencies in the United States and Canada. From the perspective of research on olfactory navigation in pigeons, CAPTEX '83 was ideal for three reasons. First, it monitored ground-level concentrations of a tracer gas, rather than concentrations at high altitudes. This more accurately represents the odor concentrations a pigeon would encounter at its typical flight altitude. Second, the tracer used in the study was released in aerosol form, which closely resembled the aerosol nature of most biologically important odorants. Last, the tracer gas plume was monitored for 50 h after release, providing extensive temporal and spatial resolution of the plume path.

The study was conducted from mid-September through the end of October in 1983. Individual tests consisted of the release of a harmless perfluorocarbon tracer [perfluoro-monomethyl-cyclohexane (PMCH): C_7F_{14}]. The subsequent tracking of this gas was performed over a 1,000-km array of ground stations located in 100-km arcs from the two release points in

Dayton, Ohio, and Sudbury, Ontario. This array configuration effectively covered the entire northeastern United States and parts of southeastern Canada. In all, 7 tracer releases were conducted during the study period, 5 from Dayton and 2 from Sudbury. Releases were planned for the early afternoon to assure good vertical mixing of the tracer. Both Sudbury releases, however, took place after midnight behind cold fronts (also with good vertical mixing) that provided the northwesterly winds required to carry the plumes over the sampling array. All releases were made at ground level by vaporizing the tracer with a stream of nitrogen gas and passing this mixture through a tube furnace heated to 105°C. Quantities of tracer released varied from 180 to 208 kg over 3 h (except the fifth release from Dayton, which lasted only 30 min and therefore was not included in my analysis). The ground stations that formed the sampling array were equipped with automatic sequential samplers capable of chemically capturing and storing the perfluorocarbon tracer for later analysis. Sampling rates were variable, but usually consisted of 6 consecutive 6-h samples at each site. Sites closest to the release point generally took 3-h samples (total duration 18 h) for better resolution of the plume. Additional information on the release, sampling, and analysis techniques used in the CAPTEX '83 study are given by Ferber et al. (1986), including specific information on the location and altitude of each site in the sampling array.

Measurements of PMCH concentration were made in units of femtoliters per liter (fl/l; equivalent to one part in 10^{15}). The ambient background concentration of PMCH, as determined by the Brookhaven National Laboratory, is constant at 3.0 fl/l across the sampling array. (Transformed to units of grams per cubic meter, the background concentration of PMCH equals 4.68×10^{-11} g/m³). To remove background and most of the "noise" inherent in sampling near the background level, a value of 3.4 fl/l was subtracted from all measured PMCH concentrations before plotting.

Results.—Isolines of maximum measured tracer concentrations obtained after each 3-h release from Dayton are shown in Fig. 1. In all cases the tracer was detected above background levels at least 800 km from the release point. Concentrations varied from over 1,000 fl/l at the closest sampling stations to just above background levels at the most distant sites. Plume paths and shapes varied from well-defined, narrow plumes (Fig. 1a, d) to widely dispersed, irregular plumes (Fig. 1b) to scattered and broken plumes (Fig. 1c). Some plumes covered cross-sectional areas of less than 300 km at the far end of the sampling array, while others spanned areas nearly 800 km wide at the same distance. Substantial concentration gradients (1,000 to 100 fl/l) were observed over the first few hundred kilometers in most releases, but these steep gradients disappeared rapidly beyond about 400 km. In one release, a maximum concentration equal to that observed near the source was measured nearly

1,000 km away from the release point (Fig. 1c). This pattern resulted from upward mixing of the plume during the afternoon following release of the tracer. The air mass was subsequently cut off from the surface layer that evening by the stable atmosphere below and then mixed down to the surface again the next morning after having traveled downwind several hundred kilometers. Such complex mixing and transport patterns apparently are not uncommon features of synoptic flow patterns in the northeastern United States.

Most of the plumes observed in the CAPTEX '83 study were symmetrically shaped, resulting in equal concentration gradients on either side of the plume center line and spanning distances of several tens or hundreds of kilometers. In one release (Fig. 1d), for example, the same general concentration gradient was observed directed both north and south over a large portion of eastern Pennsylvania. This same gradient also was directed east-southeast from Pennsylvania toward New Jersey and the Atlantic Ocean. While the directional ambiguity of concentration gradients was particularly obvious in cases where the plume was widespread (Fig. 1b), it was also true of the narrower plumes, even at sampling sites near the release point. In the release shown in Fig. 1a, for example, a gradient from 1,000 to 100 fl/l was observed in three different directions starting at the southern shore of Lake Erie (near Cleveland) and heading east, west, and northeast. For points located near the Cornell pigeon loft in central New York state the presence of tracer could be measured in only two of the four releases; all the tracer moved north of this area in one release and south of it in another.

Both of the plumes generated by the two releases from Sudbury were relatively narrow and well defined, and there was virtually no overlap in the area covered by the plume beyond 200 km downwind of the release point (Fig. 2). Thus, concentrations of 100 fl/l were found in several widely divergent areas at distances of only 400 km from the source. This directional ambiguity was magnified as the plume traveled farther across the sampling array. The comments made earlier regarding plume concentration patterns for the releases from Dayton are generally applicable to the Sudbury data as well.

Other aspects of atmospheric transport patterns in the northeastern United States became evident in a time-course analysis of the second release from Dayton (Fig. 3; this release is the same as that shown in Fig. 1b). These data showed that reasonably unambiguous concentration gradients existed for only 10–16 h after release of the tracer, and only at distances of less than 300 km from the release point. After 16 h the plume had spread over a large geographic area and had begun to form secondary high-concentration zones within the overall plume perimeter. Moreover, this time-course analysis made evident the directional changes that can occur 40–50 h after the release (600–

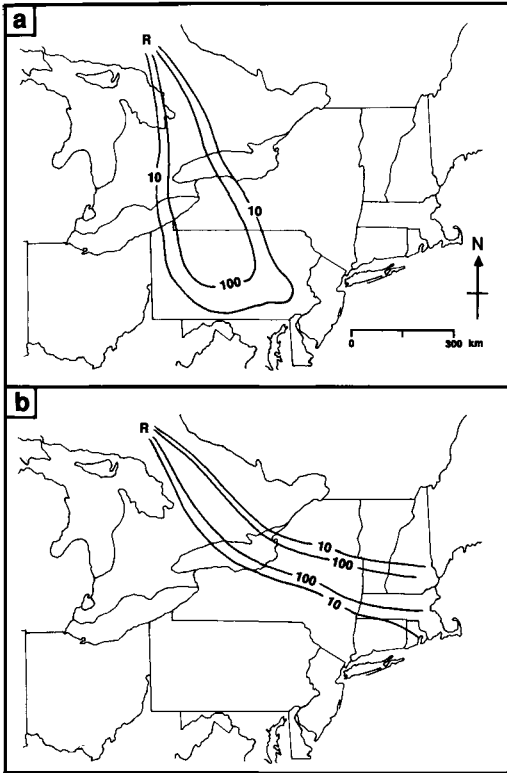


Fig. 2. Maximum observed tracer concentrations (fl/l) for the two CAPTEX '83 releases from Sudbury, Ontario (labeled R). All symbols and plotting conventions are the same as in Fig. 1. (Redrawn from Ferber et al. 1986.)

800 km downwind), when what was originally a northeasterly flow pattern became a strong southeasterly movement of the tracer.

DISCUSSION

Avian olfactory sensitivity and the concentration of natural odorants.—Pigeons have been tested for their olfactory sensitivity to only a handful of standard laboratory chemicals, all of which bear little or no resemblance to biological odorants (Henton 1969, Shumake et al. 1969). Absolute thresholds for the detection of substances such as heptane, hexane, pentane, and amyl acetate range from 0.1 to 39.7 ppm. These sensitivity thresholds are comparable to the absolute olfactory thresholds measured for the detection of carrion-associated odorants by the Turkey Vulture (Smith and Paselk 1986). If biologically accurate, these measurements of olfactory

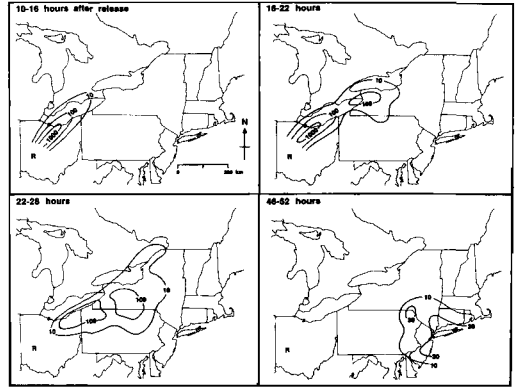


Fig. 3. Tracer concentrations (fl/l) measured at various times after the start of release 2 from Dayton, Ohio (labeled R), showing the detailed path of the tracer plume. This release is the same one depicted as a maximum concentration plot in Fig. 1b. (Redrawn from Ferber et al. 1986.)

thresholds mean birds like the pigeon and the vulture are 10^5 times less sensitive than is necessary to detect the strongest concentrations of tracer gas observed in the CAPTEX '83 study. This suggests that, for olfaction to be an important factor in long-range avian orientation, natural odor sources must either emit enormous quantities of odorants or do so at much higher rates than the 1 kg/h rate of release used in the CAPTEX '83 study. Furthermore, such emissions would have to occur on a virtually continuous basis for long-range gradients to persist at concentrations within the known range of avian olfactory sensitivity.

There are at present very few data available on what constitute normal emission rates for biogenic sources of odorants. These odorants include some of the volatile secondary compounds emitted by plants (particularly the terpenes), natural sources of sulfur and ammonium compounds as well as those produced by the biological action of microbes, and the inorganic aerosols created by wave action in large lakes or seas. Although large quantities of these chemicals are released worldwide on an annual basis (e.g. the yearly sulfur output from natural sources located between 30° and 50° N alone is estimated at 17×10^6 metric tons; Eriksson 1963), measurements of specific emission rates for localized geographic areas are rare in the literature. The few that exist estimate sulfur and ammonia emissions as being less than $10 \text{ kg} \cdot \text{ha}^{-1}$.

day⁻¹, which results in ambient atmospheric concentrations of 1–5 ppb (Graedel 1978). Estimates of emission rates for plant terpenes (e.g. alpha-pinene) emanating from the pine-oak forests of the United States yield daily values of about 1–5 kg/km² of woods, depending on the depth of foliage used in the calculation (Rasmussen 1972). This rate of emission would produce ambient air concentrations directly above the wooded area of 10–100 ppb, which is considerably below the known detection threshold of avian olfactory sensitivity. It is important to emphasize, however, that the exact concentrations and daily emission rates of these substances are not well established empirically, especially when one considers that they are subject to daily and seasonal fluctuations that could significantly affect calculations by one or more orders of magnitude. These emission rates and concentration values thus should be taken only as rough approximations. Nevertheless, the emission rates employed in CAPTEX '83 were considerably greater than would be the case for most biogenic point sources of odorants.

Only one field test has been conducted with homing pigeons to determine the physical characteristics of odors relevant to navigation. Wallraff and Foa (1981) used fiberglass and charcoal filters to trap airborne particles ranging in size from 0.04 to 2.0 μm before this air was pumped into containers used to transport pigeons. In tests conducted 24–155 km from the home loft in Germany, they reported significantly poorer orientation in the birds transported with filtered air when compared with unfiltered controls. This result is suggestive of olfactory involvement in homing, although whether the odors are used as a direct cue for navigation or serve as a motivational factor remains unclear. Similar tests should be carried out in other parts of the world at longer distances from the home loft and with more specialized filters or aerosol traps to determine precisely the types of odorants that might be of use to pigeons in navigation.

Evaluation of the olfactory map models.—The CAPTEX '83 data provide valuable information on the nature of atmospheric odor transport at distances of 300–1,000 km, and are well suited for an analysis of the gradient map model. They do not, however, allow detailed analysis of short-range transport mechanisms because of the lack of sampling sites less than 300 km from the two release points. Nevertheless, previous work on

atmospheric transport suggests that some of the important mechanisms involved in odor dispersion operate at both short and long ranges (reviewed by Chatigny et al. 1979, Elkinton and Carde 1984), and general conclusions may still be drawn about the atmospheric plausibility of the mosaic model.

If, as suggested by the mosaic model, pigeons derive their olfactory map information by sensing specific odors during low-altitude flight over the source of these odors, then the mixing properties of the lower atmosphere will not interfere severely with the detection process. This is especially true early in the day, before significant warming of surface air masses begins and convective mixing activity becomes vigorous. Such benign atmospheric conditions often do not persist past midmorning, however, and may not exist at all given certain synoptic influences (Becker and van Raden 1986). The mosaic map is therefore a potentially viable navigational tool only under the most favorable of atmospheric regimes. In addition, even under favorable circumstances the mosaic map has distinct limitations on the range over which it can be used as a navigational tool. Unless a bird has been transported passively through or has flown actively over an area of olfactory "importance" (a term that is difficult to define both physiologically and atmospherically), the only way it can have any familiarity with the appropriate local olfactory cues is if those odors are carried to its home loft by prevailing winds. Once an odor is carried aloft by winds, even at relatively low altitudes, it becomes subject to numerous atmospheric mixing processes. This mixing, coupled with orographic influences specific to local topography, can substantially reduce concentrations and alter the apparent directional origin of airborne odorants in a few tens of kilometers or less (Colacino and Dell'Osso 1980). Thus, in most topographic configurations the mosaic map apparently has a usefulness that is limited to much less than 100 km, and only then if stable sources of strong odors are present. Because pigeons routinely home from distances far beyond this range, despite having no direct olfactory experience with the area of release, the mosaic map at best can be one component of a more extensive navigational system.

The CAPTEX '83 data are better suited for an analysis of long-range olfactory gradients and their potential usefulness in pigeon homing. Several features of long-range atmospheric

transport in the northeastern United States are clear from the CAPTEX '83 data:

- (1) Plume paths are variable in both space and time, and are highly dependent on the wind patterns present at the time of odorant release.
- (2) Concentration gradients within the plume, while often substantial for 300–400 km downwind from the source, are nevertheless highly variable in space and time.
- (3) Significant dilution of the substance being transported occurs, so that enormous quantities of an odorant must be released continuously for substantial concentration gradients to persist hundreds of kilometers downwind from the source.
- (4) Depending on the nature of the plume path, the same odorant concentration can be found at more than one location downwind, with these locations often separated by tens or even hundreds of kilometers. This produces a problem of directional ambiguity within the gradient field.
- (5) Plume paths are subject to properties of atmospheric mixing, which can result in "leap-frogging" of the plume over large geographic areas. Such irregular mixing action is a frequent atmospheric phenomenon and occurs in association with the proper combinations of convective instability and upper-air steering winds. It can easily generate secondary high-concentration zones within the plume similar to those found near the source but displaced by hundreds of kilometers downwind.

These empirical observations raise doubts about the usefulness of olfactory gradients as a navigational aid to pigeons flying in the northeastern United States. For example, recall that the gradient model suggests a pigeon can determine its displacement by comparing the gradient value detected at the point of release with the value remembered from home. Based on the observed concentration gradients in CAPTEX '83, this strategy is flawed in situations where the same odorant concentration exists at widely divergent locations within the odor plume. Faced with the problem of determining the direction of a nonregular gradient, pigeons might be expected to exhibit an irregular flight path similar to that observed for procellariids as they

fly upwind toward an odor source (Hutchison et al. 1984), or for insects as they localize a pheromone source. Pigeons are rarely observed to make such zig-zag flight movements as they vanish from view after release, but rather tend to fly overhead in close circles with diameters not exceeding a few tens or hundreds of meters before heading off in an essentially straight path. Circles of such diameter cannot provide adequate directional information about odor gradients at distances of hundreds or even tens of kilometers from their source. Moreover, airplane tracking reveals that the flight paths of experienced pigeons are essentially straight and generally directed toward the home loft shortly after leaving the release point (Walcott and Michener 1967).

Even in areas of the odor plume where gradients are well defined and reasonably stable, problems of directional ambiguity can exist. Because odorant concentrations are usually symmetric with respect to a line drawn through the long (downwind) axis of the plume, equal concentrations are often present on either side of this center line. Positional errors of several tens of kilometers therefore can result from these ambiguities in the gradient field, even at distances of <300 km from the odor source. Such errors are magnified considerably as the bird is displaced further downwind in the odor gradient.

Direct observations of initial orientation and homing success in Cornell pigeons released from different directions within a presumed odor gradient also argue against the likelihood of olfactory navigation. In areas of well-defined odor gradients and stable prevailing winds, one would predict that upwind displacement should make determining its position easier for a pigeon than would downwind displacement. This is because an upwind displacement takes the bird toward higher (and therefore more easily detected) concentrations of the relevant odor. In Cornell pigeons, which experience primarily southwesterly to northwesterly prevailing winds during the summer months, releases from the western parts of New York state do not result in better orientation when compared with releases from the east. Indeed, for most release sites to the west of home, Cornell birds exhibit statistically poorer homeward orientation and slightly reduced homing success when compared with eastern release sites at equivalent distances from the loft (Windsor 1972).

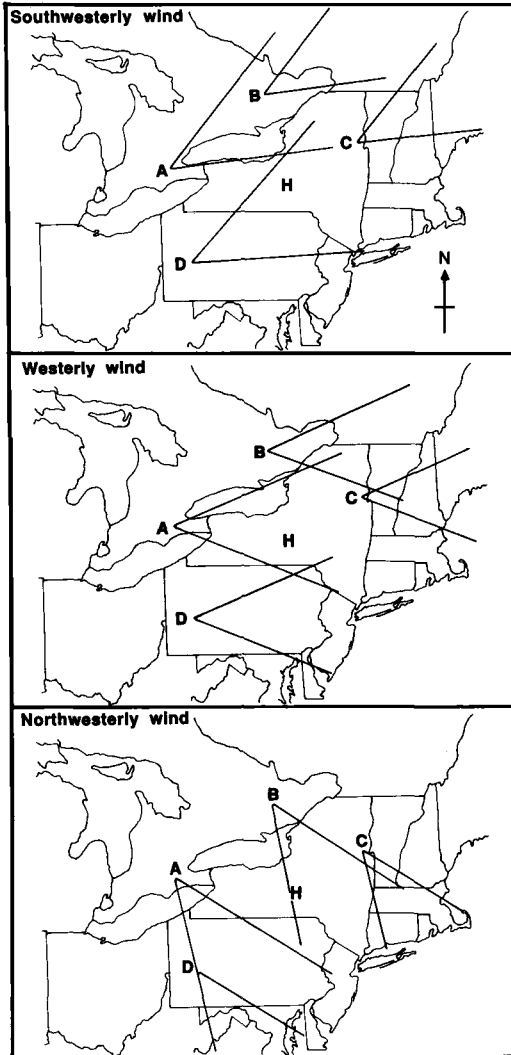


Fig. 4. The effect of wind direction on the overlap of four hypothetical odor gradients emanating from point sources A-D. Wind directions similar to those commonly observed in New York state during the summer months are depicted. H identifies the position of the Cornell University pigeon loft (Ithaca, New York).

Although not suggested in the original gradient map model, pigeons could use the intersection of orthogonal odor gradients to fix their position with respect to home, much as humans use lines of longitude and latitude in navigation. This is unlikely, however, because orthogonal winds cannot occur simultaneously at exactly the same altitude, which makes it difficult for odor gradients from sources located

in different directions to exist simultaneously. For a pigeon to assess orthogonal gradients simultaneously, it would need to adopt one of two strategies. The first is to remember the concentrations of two or more odors that normally occur independently on orthogonal winds and to compare these values with a mixture of the same odors that occurs on an "average" of the two orthogonal winds. For example, a bird would compare different odors that occur on north and west winds with a mixture of these same two odors on a northwest wind. This strategy presumably would be very difficult to employ because of the large combination of possible odors and winds the bird would need to remember to compensate correctly for all conceivable atmospheric mixing conditions. A second strategy is to take advantage of wind shear and sample odors at different altitudes over the same geographic location. This strategy also is unlikely because the vertical movement required to sample wind shear is rarely observed in pigeon flight, and when it occurs it involves a change in altitude of only a few tens of meters (Waldvogel unpubl. data). Such small changes in altitude are unlikely to provide sufficient comparative odor information. Moreover, in situations where gradient overlap can occur by either wind shear or odor averaging (e.g. a stable atmosphere with little or no horizontal flow), the geographic location of this overlap can vary widely depending on the direction of recent windflow. Thus, the same gradient overlap (e.g. the intersection of gradients A and D in Fig. 4) can occur anywhere from northern New York state to southern Pennsylvania and northeastern West Virginia, depending on the direction of recent horizontal wind flow. Without the aid of a reference system that is independent of wind direction, it would be impossible to determine the exact geographic location of the region of gradient overlap relative to the home loft. One possible reference system is the earth's magnetic field. While the combination of such independent map reference cues with olfactory map information is possible when developing a navigational strategy, proponents of the olfactory gradient and mosaic models have in the past rejected the necessity for nonolfactory components in pigeon navigation (e.g. Papi 1982).

Both the CAPTEX '83 study and the theoretical considerations discussed so far have dealt primarily with point sources of odors. Poten-

tially relevant navigational odors probably also emanate from line or patch sources such as seashores, lakes, or large expanses of relatively unbroken vegetation. Indeed, if the quantities of odorants apparently needed to create and maintain stable odor gradients that are within the known olfactory sensitivities of birds are to be achieved, line or patch sources are almost inevitable. Such a situation is modeled (Fig. 5) for the northeastern United States, and considers the downwind gradient of a hypothetical odor produced by Lake Ontario. This gradient might spread across New York state in the pattern shown if carried on a northwesterly wind. Because of the larger area over which emissions can occur, the gradient would be less conical in shape than for a point source. Nevertheless, as with point sources, equal concentrations of odorants would be present at widely divergent locations across New York and Pennsylvania. This gradient pattern could also be more complex than depicted in Fig. 5 depending on regional orographic features and the influence of terrain on convective mixing characteristics. The most useful function of such a line or patch gradient would be to provide directional information about displacement along an axis perpendicular to the source (i.e. to either the northwest or southeast of home in this case). Displacement perpendicular to this axis (i.e. southwest or northeast) would provide ambiguous information about the direction of travel, unless some independent source of information were also available. To this end it is interesting to note that two of the most orientationally anomalous release points so far documented for Cornell pigeons are located to the north-northeast (Castor Hill fire tower; Keeton 1974) and to the west-southwest (Jersey Hill fire tower; Brown and Walcott unpubl. data) of the home loft.

Geographic specificity in the use of olfactory navigation.—It would appear from the CAPTEX '83 data that the use of an olfactory gradient map cannot be an essential feature of pigeon navigation in the northeastern United States. Theoretical arguments about known levels of olfactory sensitivity in pigeons and the nature of atmospheric transport mechanisms also cast doubt on the importance of the mosaic map model (although the CAPTEX '83 data are not as clear on this point). Nevertheless, these conclusions do not explain the consistently positive results obtained in olfactory experiments per-

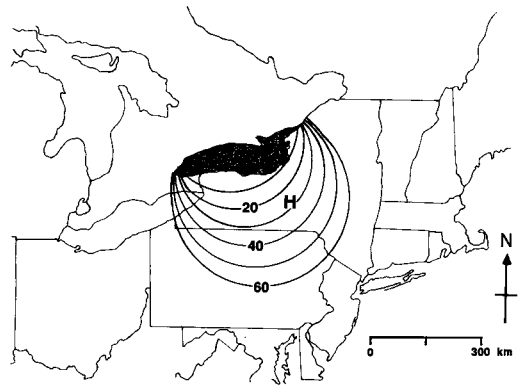


Fig. 5. Hypothetical odor gradient emanating from a line source such as Lake Ontario (shaded area). The isolines of odorant concentration are shown as they might appear if the gradient was created by a northwesterly wind. Several isolines are labeled with arbitrarily chosen concentration values for reference purposes. H is the position of the Cornell University pigeon loft.

formed with pigeons in Italy. It might be that the atmospheric conditions Italian pigeons experience are more conducive to making olfaction a prime component of their navigation system. If so, why is this the case? It should be noted that the pigeon lofts used by Papi's research group in Italy are located near a long, straight seacoast. A well-documented atmospheric phenomenon known as the sea breeze occurs predictably along such coastlines, and could provide a mechanism whereby olfactory cues are elevated in navigational importance for Italian pigeons.

Sea breezes are generated by the differential heating of land and water. Because of its higher capacity for heat storage and more efficient thermal mixing, water does not change temperature as rapidly during heating and cooling as does soil or rock. Land areas therefore heat faster than adjacent bodies of water, and the excess heat is transferred rapidly to the surface layer of air directly above. The warm air over the land rises relative to the cooler air over the water, and creates a decrease in surface pressure over the land. Because air always moves from high- to low-pressure areas, surface air over the water tends to move onshore as a result of this differential heating process, creating a "sea-breeze frontal zone." Along many coastlines sea-breeze fronts can penetrate 45–85 km inland, depending on the strength of the atmospheric

heating conditions and sea surface temperatures that drive them (Simpson et al. 1977). Such fronts carry with them odors associated with the sea, creating a strong odor gradient from "ocean" smells to "land" smells. In the case of the Italian peninsula this gradient would be oriented roughly west to east, theoretically providing an excellent olfactory indicator of displacement in those two directions and perhaps elevating the overall importance of directional odor information to pigeons living in the area. Indeed, some of the Italian researchers' most convincing evidence for olfactory influences on homing comes from experiments in which birds are trained to natural or manipulated odors along an east-west axis. When these birds are tested to the east or west of the loft, effects on orientation and homing are clear, but when they are tested to the north or south the effects are much reduced or missing altogether (e.g. Ioalé et al. 1978, Ioalé 1982).

The CAPTEX '83 analysis thus raises the likelihood that sufficient ambiguity exists in potential olfactory gradients formed across the northeastern United States to render them problematical as tools for navigation in Cornell pigeons. In the northeastern United States the use of odors therefore seems to be at best an ancillary component of the homing pigeon's long-range navigation system, but this does not preclude the possibility that pigeons, or other birds, can employ olfactory orientation given the proper atmospheric circumstances. Geographic variation in the apparent importance of olfaction to homing pigeons may be the result of local atmospheric and topographic interactions, which ultimately dictate the reliability of odors as a useful component of orientation systems. This possibility is consistent with previous claims by Keeton (1974) that avian navigation systems are comprised of redundant cues arranged in a hierarchy whose order is dictated by experience and environmental conditions. This idea is testable by means of an atmospheric analysis of the Italian peninsula similar to the CAPTEX '83 study in North America, or by conducting olfactory navigation experiments with American pigeons along the coastal areas of the Florida peninsula, where sea-breeze fronts also occur. Such comparative analyses, coupled with additional physiological and behavioral studies of olfactory sensitivity in birds, could resolve the current debate over the role of olfactory cues in avian navigation.

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