PERSPECTIVE

INFRASOUND AND THE AVIAN NAVIGATIONAL MAP

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Summary

Birds can navigate accurately over hundreds to thousands of kilometres, and this ability of homing pigeons is the basis for a worldwide sport. Compass senses orient avian flight, but how birds determine their location in order to select the correct homeward bearing (map sense) remains a mystery. Also mysterious are rare disruptions of pigeon races in which most birds are substantially delayed and large numbers are lost. Here, it is shown that in four recent pigeon races in Europe and the northeastern USA the birds encountered infrasonic (low-frequency acoustic) shock waves from the Concorde supersonic transport. An acoustic avian map is proposed that consists of infrasonic cues radiated from steep-sided topographic features; the source of these signals is microseisms continuously generated by interfering oceanic waves. Atmospheric processes affecting these infrasonic map cues can explain perplexing experimental results from pigeon releases.

Key words: navigation, map, homing, pigeon, infrasound, shock wave, topography, microseism.

Introduction

Homing or carrier pigeons (*Columba livia*) have been used by humans throughout history as aerial messengers because they will regularly return to their home loft when released from distant and unfamiliar locations. More recently, this ability has become the basis of an international sport for which birds are selectively bred and trained. Pigeons can home whether the sun is visible or not, in both head and tail winds, and at night with training, but they will land in heavy rain (Walcott, 1996). Homing pigeons rather than migratory birds are the preferred subject of avian orientation and navigational studies because they will home on demand instead of seasonally. This remarkable ability of birds raises the question of what sensory cues they use to determine their location relative to their destination (map sense) and to select and maintain that direction in flight (compass sense). The compass senses are fundamentally understood but, although experimental birds react to a number of different sensory cues, the nature of the long-range map sense remains unknown.

Kramer (1953) first suggested that birds must have both map and compass senses to traverse great distances (hundreds to thousands of kilometres), and he demonstrated that their usual daytime compass is the sun. Homing pigeons whose circadian rhythm has been shifted by 6 h (quarter day) will depart from release sites 90 ° off the homeward bearing (quarter circle) under clear skies (Schmidt-Koenig, 1961). Keeton (1971) found that clock-shifted pigeons, however, oriented and homed normally on cloudy days. He experimented with birds fitted

with magnets and control birds fitted with brass bars, and concluded that pigeons also have a magnetic sense, used as a directional compass. Further experiments have shown that young birds carrying magnets cannot orient in full view of the sun, and that the sun compass must first be calibrated to the innate magnetic compass (Wiltschko et al., 1981). A similar pattern of orientation and calibration to an innate magnetic compass has also been demonstrated for nocturnal migrants, which use the stars as their celestial compass (Wiltschko and Wilstchko, 1976).

The elusive map sense, in contrast, has been tested at one time or another against most of the senses of the homing pigeon (Gould, 1982). Sight has been ruled out because birds fitted with frosted contact lenses can return to within less than 500 m of their home loft (Schmidt-Koenig and Schlichte, 1972). Laboratory experiments show that pigeons have extraordinary low-frequency hearing and can detect sounds as low as 0.05 Hz (Kreithen and Quine, 1979; Klinke, 1990; Schermuly and Klinke, 1990). Birds with some homing experience that have had their cochleae and lagenae removed still orient and return home (Wallraff, 1972). Olfactory cues are considered important to the homing process because birds with severed olfactory nerves sometimes cannot orient or home from unfamiliar sites (Papi, 1989). In addition, birds raised in lofts with deflected natural air flows show similar homeward-bearing deflections at release sites (Papi et al., 1971). Variations in the direction and intensity of the geomagnetic field have also been suggested as potential map cues (e.g.

Gould, 1982). Neither the proposed olfactory nor geomagnetic map, however, can explain why pigeons leave some release sites at consistent directions off the homeward bearing (site-release bias), are almost always lost at other sites, or are infrequently delayed or lost in large numbers during pigeon races.

Pigeon races and sonic booms

In 1997 and 1998, four pigeon races in Europe and the northeastern USA were disrupted, and no scientific explanation for these occurrences has been proposed. There is one circumstance, however, that is common to all these races: the intersection of the racecourses, when the birds were present, with shock waves generated by the Concorde supersonic transport (SST).

On Sunday 29 June 1997, a race of more than 60 000 homing pigeons, celebrating the centenary of the Royal Pigeon Racing Association (RPRA), was begun at 06:30 h from Nantes, France, to lofts all over England (Fig. 1A). Normally, approximately 95 % of the birds in a race return home to their lofts, but few birds returned as expected on this particular Sunday. Although the RPRA's official inquiry blamed poor weather conditions for the calamity, the majority of racing pigeons were crossing the Channel at the time the 11:00 h SST from Paris (LFPG) was flying along the Channel on its way to New York.

Assuming a velocity for the average pigeon of 60 km h^{-1}, a bird leaving Nantes at 06:30 h would have been over the Channel (approximately 300 km distance) by 11:30 h. The SST departing from Paris goes supersonic after crossing the French coastline, between intersections EVX and TESGO, and was passing over the Channel between approximately 11:20 h and 11:35 h. Information on the flight path, intersection locations and departure and arrival times of the Concorde SST was obtained from Air France and British Airways, the Federal Aviation Administration (FAA) and the Air Route Traffic Control Center (Tra-Con) in New York.

In flight, the SST generates a cone-shaped shock wave (Mach cone) which travels with the aeroplane's bow at supersonic speeds and moves away from the sides of the cone at the ambient speed of sound. Because atmospheric temperatures and sound velocities increase below the SST (Fig. 2), the ray paths of the downward shock waves are refracted upwards with lateral distance from the aeroplane. The distance from directly beneath the SST's flight path to points on either side at which the rays just graze the Earth's surface before heading upwards defines the boom 'carpet' where direct shock waves reach the ground. The half-width of the boom carpet (x), considering only temperature, can be calculated using the formula:

$$x = 2(T_0 h/g)^{1/2}, \tag{1}$$

where T_0 is the surface temperature (296 K), h is the elevation of the aeroplane (12 km), and g is the vertical temperature gradient (6 K km^{-1}; Donn, 1978). Inserting the average values
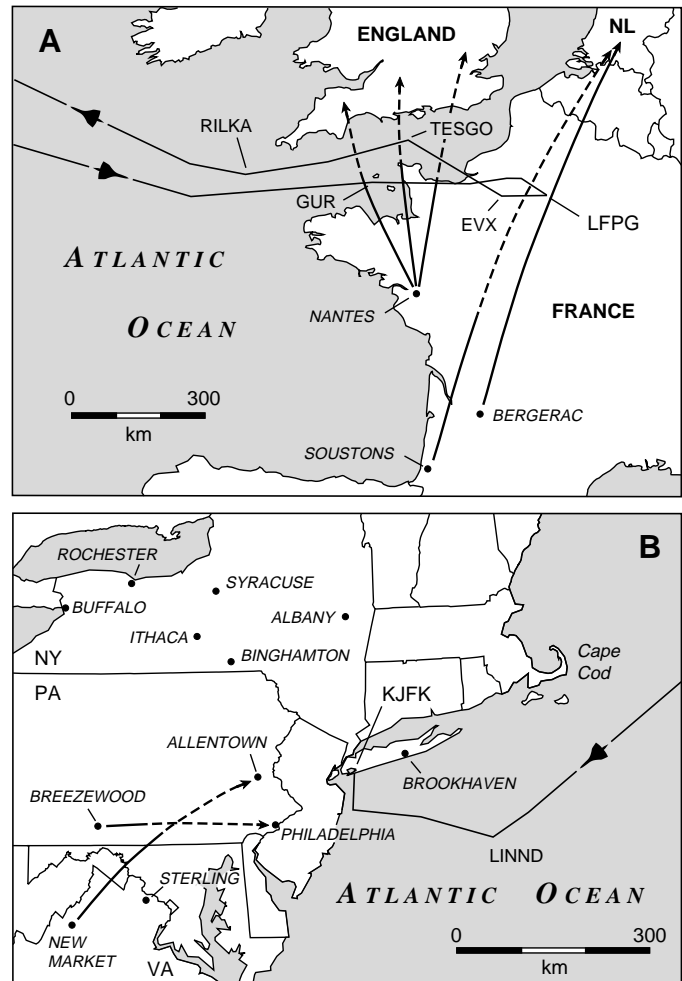

Fig. 1. Flight paths of the Concorde supersonic transport (SST) in (A) Europe arriving at and departing from Paris (LFPG) and (B) the northeastern USA arriving at New York (NY; KJFK). Labelled points along the flight paths (EVX, GUR, TESGO, LINND and RILKA) indicate some of the intersections near where the SST changes course. Dashed parts of the pigeon racecourses are beyond the approximate point where most of the participants encountered the SST's shock wave. For the race from Nantes, France, to England, most birds were caught within the approximately 100 km wide boom 'carpet' beneath the SST flying over the English Channel. For the race from Soustons, France, to the Netherlands (NL), and the two races in Virginia (VA) and Pennsylvania (PA), USA, the birds encountered shock waves from the sides of the SST's Mach cone propagating hundreds of kilometres, most probably under favourable atmospheric conditions.

given, the width of the boom carpet on the ground ($2x$) would be approximately 100 km.

Birds within the boom carpet on Sunday 29 June 1997 were probably affected. Most of the birds that arrived at their lofts that day had average velocities of between 30 and 50 km h^{-1} (Glover, 1997) and were still south of the Channel when the SST passed over ahead of them. At the surface, the SST's shock wave has a duration of approximately 0.23 s within the boom carpet and an overpressure of approximately 110 Pa (128
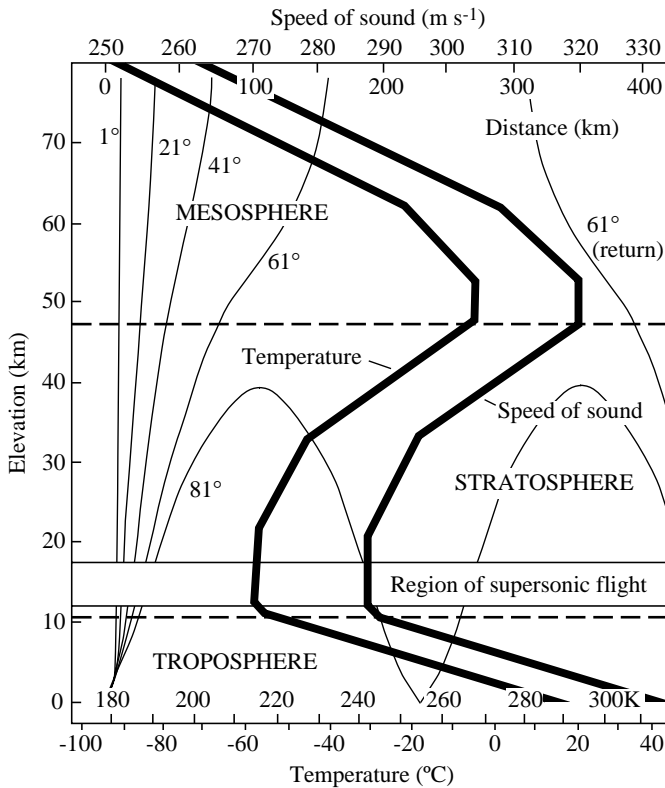
Fig. 2. Cross section of the troposphere, stratosphere and mesosphere of the Earth's atmosphere. The thermosphere above the mesosphere (80–110 km) has increasing upward temperatures (180–260 K) and is not shown. Temperature and the speed of sound are plotted against elevation (heavy lines), and the region of supersonic flight is shown in the lower stratosphere. Computed ray paths of sound waves (fine lines) to Palisades, New York, from a source to the east are also shown and have both stratospheric and thermospheric reflections. Values by the ray paths indicate the hade (the inclination from the vertical) of the ray's initial upward path (modified from Figs 5 and 7 in Donn, 1978).

dB SPL; Donn, 1978); the loudest sounds human ears can tolerate without temporary or permanent hearing changes have amplitudes of approximately 28 Pa (123 dB SPL). If infrasonic map cues are a major factor in pigeon navigation, strong shock waves from the SST could have disrupted the RPRA race by adversely affecting the extremely sensitive low-frequency hearing of the pigeons. A temporary threshold shift could explain why the majority of birds returned late, while a permanent threshold shift could explain why some birds did not return at all.

On Friday 31 July 1998, two pigeon races were started in southern France, one of 42 845 birds from Bergerac and the second of 13 610 birds from Soustons, to lofts throughout the Netherlands (Fig. 1A). Birds in both races were released at 13:00 h for flights of approximately 1110 km from Soustons and approximately 930 km from Bergerac (Anonymous, 1998; website at http://www.pww.nl/openingscherm.html). Although the Bergerac race was completed by Saturday afternoon with average speeds for some birds exceeding 100 km h^{-1}, by that

evening less than 10 % of the Soustons pigeons had returned. By Wednesday evening, approximately 60 % of the birds from Soustons were still missing.

During these two races, the SST from New York to Paris was approaching the western coast of France with an expected arrival time of 17:45 h. Forty minutes prior to landing, the aeroplane customarily begins its deceleration from Mach 2. The angle (θ) between the Mach cone and flight path is determined by the formula:

$$\sin\theta = 1/M, \qquad (2)$$

where M is the Mach number representing the aeroplane's velocity (Donn, 1978). The angle θ, therefore, changes from 30 to 90 ° as the aeroplane decelerates from Mach 2 to Mach 1. The SST arriving at LFPG (Paris) decelerates to subsonic speeds prior to the GUR intersection (Fig. 1A). The intersection of shock waves with the Soustons racecourse therefore depended on the angle at which the waves departed from the SST, the local sound velocity, the wind speed and the distance travelled. Assuming 70 km h^{-1} for the average bird's velocity (faster race) and 1100 km h^{-1} for the velocity of sound, the intersection would have occurred approximately 320 km north of Soustons.

On Monday 5 October 1998, two pigeon races were started in the eastern United States, the first of more than 1200 birds from New Market, Virginia, on a course of 322 km to Allentown, Pennsylvania, and the second of approximately 700 birds from Breezewood, Pennsylvania, on a course of 241 km to the outskirts of Philadelphia (Fig. 1B). Because of bad weather, the release of birds to Philadelphia was postponed until 10:00 h (Gary Moore, race coordinator, personal communication, 1999). The expected duration of this race was approximately 3 h, but the first birds returned after over 8 h had passed. Only five birds returned on Monday, and by Saturday only 300 birds had returned. Both this course and the course from New Market to Allentown had been flown successfully many times before.

The racing pigeons starting from New Market, Virginia (Fig. 1B), were released at 08:00 h on Monday, and the expected duration of this race was approximately 4 h. The birds departed quickly northward following the Shenandoah Valley (see Fig. 4). They too were substantially delayed: the first bird came in at 19:00 h, and only 13 birds arrived at their lofts that day. Only 50 birds had returned by Tuesday evening (Ron Lish, participant, personal communication, 1999).

The SST from Paris normally arrives at KJFK at 08:45 h, and the aeroplane goes subsonic prior to reaching the LINND intersection (Fig. 1B). Because the birds from Breezewood were not released until 10:00 h, the pigeons in both races (assuming 60 km h^{-1} velocities) would not have approached the intersection point of the racecourses until approximately 11:00 h. The SST arriving on the morning of 5 October 1998 must, therefore, have been more than an hour late if its shock wave was to affect the pigeons of the Breezewood race. The aeroplane was delayed by an extraordinary 2.5 h that morning because of mechanical problems in Paris. Thus, a shock wave

originating from the incoming SST (approximately 500 km distant) at 10:40 h and travelling at 1100 km h⁻¹ would have passed through both racecourses at approximately 11:10 h.

The race from Soustons and those in the USA were not within the SST's boom carpet, as was the RPRA race, but were hundreds of kilometres away. Such long-distance propagation of sonic booms, causing audible vibrations of buildings in Tucson, Arizona, from military aircraft hundreds of kilometres away occurred during April 1975 and along the northeastern coast of the USA during late 1977 and early 1978, when the number of SST flights between Europe and the USA increased substantially (Kerr, 1979). Channelling of sound waves near the surface occurs by reflection from the surface and refraction from a zone of either higher temperatures (inversion) or of high winds in the same direction as sound propagation (Donn, 1978).

Atmospheric data from stations at Brookhaven, New York (20 m elevation), and Sterling, Virginia (85 m elevation; Dulles Airport; Fig. 1B), reported daily at 07:00 and 19:00 h eastern standard time (EST), indicate a north-northeast wind below 600 m on the morning of Monday 5 October 1998, with a velocity of approximately 205 km h⁻¹ at 600 m above Brookhaven, and a temperature inversion (10 °C at the surface to 13 °C at 110 m). Weather data were obtained from the Northeast Regional Climate Center in Ithaca, NY, the National Climatic Data Center in Asheville, NC, and the National Ocean and Atmospheric Administration (http://roab.fsl.noaa.gov).

Microseisms and topography

Griffin (1969) first raised the possibility that atmospheric infrasounds provide directional information for migrating birds. Sound attenuation in air is proportional to the square of the frequency, so infrasound can be detected hundreds to thousands of kilometres from its source. In addition, these sounds are usually loud (120 dB SPL for sounds less than 1 Hz; Kreithen, 1978). Thunderstorms produce infrasound and, in summer, generally follow a repeatable diurnal pattern within a region; winds over mountains also produce infrasounds that are essentially continuous during the winter months (Bedard, 1978); both these sources might serve as acoustic beacons. No perennial geographical sources, other than waterfalls and geothermal activity, have been identified. Seismically generated movements of the ground, however, can produce continuous infrasound.

Microseisms are low-frequency seismic waves constantly generated by interfering oceanic waves and are background noise in all seismic recordings (Bullen and Bolt, 1985). Such microseisms have regular periods of 5–8 s or more and peak at periods around 6 s (Bullen and Bolt, 1985; Aki and Richards, 1980). The 6 s microseisms generally have similar features recorded at seismic stations distributed over wide areas, and their maximum amplitudes occur nearly simultaneously. Maximum amplitudes for microseisms are approximately 10⁻³ cm in coastal regions and approximately 10⁻⁴ cm in continental interiors such as central Asia (Bullen and Bolt,

1985). The frequency of the 6 s microseism peak is approximately 0.14 Hz, and the surface vertical displacement velocity is approximately 10⁻³ cm s⁻¹ (Bullen and Bolt, 1985; Aki and Richards, 1980). To be useful to the avian navigational system, 6 s microseismic waves must be transformed into audible (to birds), horizontally propagating infrasonic signals with geographical significance.

Seismic surface waves radiate infrasound into the atmosphere and, because surface waves travel at much faster speeds than air waves (approximately 10 times faster), the infrasound generated propagates upwards in a direction almost perpendicular to the Earth's surface (Cook, 1971). Thus, after a strong earthquake, the first infrasound signal detected at a recording station is that radiated by surface waves arriving at the station. The second signal detected, if it occurs, is from intermediate sources with non-horizontal surfaces, such as mountains, acting as large acoustic radiators (Cook, 1971). Young and Greene (1982) analysed recordings from Boulder, Colorado, Boston, Massachusetts, and Washington, DC, associated with the 1964 Alaskan earthquake (M_w=9.2; Kanamori, 1977), and identified an acoustic source that moved down the Rocky Mountains concurrently with passage of the surface waves. The third type of infrasound signal detected at a recording station after a strong earthquake is that from the epicentral region caused by uplift and subsidence of the ground surface at the time of the earthquake (Cook, 1971; Young and Greene, 1982).

The relationship between the velocity of vertical ground motion and perturbation air pressure at ground level is:

$$p = \rho c v, \tag{3}$$

where p is the perturbation pressure, ρ is air density, c is the velocity of sound in air and v the vertical ground velocity (Donn and Posmentier, 1964). Inserting values for average conditions (ρ=1.19×10⁻³ g cm⁻³, c=330 m s⁻¹), the equation
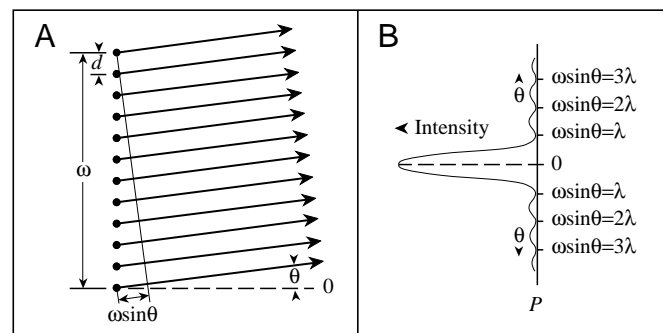

Fig. 3. Radiation from an idealized row of point sources (e.g. 12 flatirons along a mountain range front) oscillating in phase. λ is the wavelength, d is the distance between points ($d \ll \lambda$), ω is the length of the array and θ is the angle between the normal to the line of sources and the line joining any of the sources to a point P a large (infinite) distance away. The relative intensity is greatest when θ=0° and has minima when the path difference between sources ($\omega\sin\theta$) is a factor of λ.

becomes $p=247a/t$, where p is the peak-to-peak pressure (Pa), a is the double amplitude of ground motion (cm) and t the period of motion in seconds (Donn and Posmentier, 1964). The air pressure change at the Earth's surface related to 6 s microseisms is approximately 0.008 Pa (20 dB SPL), which is far below the 120 dB SPL amplitude at which pigeons detected a 0.14 Hz signal in the laboratory (Kreithen and Quine, 1979). In contrast, a coplanar source with dimensions much greater than the infrasound wavelength (approximately 2.4 km) generates waves interfering at long range. The in-phase signal is strongly amplified only along a line normal to the source area, thus providing a directional characteristic of the infrasonic signal. Sources with dimensions much smaller than 2.4 km act as point sources and could be useful as local map cues; signals from linear point sources would also constructively interfere at long range (Fig. 3).

Fig. 4 shows a shaded relief map of the eastern USA (western half of Fig. 1B) with the illumination from directly north at 45° elevation. The bright areas are basically coplanar and have orientations approximately normal to the illumination direction; the large steep-sided areas, such as those along the northern Appalachian Mountains, might generate infrasonic signals important to the regional avian map. Illumination from other directions would show a different set of bright areas indicating other possible infrasonic landmarks. Beacons with rich near-infrasonic frequencies (1–20 Hz) might also provide unique identification characteristics of the signal (A. J. Bedard, Jr., written communication, 1999). In addition, continuous constant-frequency sources at higher infrasonic frequencies could be exploited using Doppler shifts, and this might be what pigeons are doing while circling overhead prior to leaving release sites (Quine and Kreithen, 1981).

It has long been known that migrating birds follow major topographic features such as coastlines and mountain-range fronts. Migrants also tend to follow segmented routes with legs of different orientation, with some legs reaching up to several thousand kilometres in length and having endpoints registered to major topographic features (Alerstam, 1996). In Switzerland, Bruderer (1978) using radar and Wagner (1972) using helicopters showed that migrating passerines and waders followed topographic features such as valleys, passes and linear ridges in both lowland and Alpine regions. Remarkably, they followed these same features at night or under other conditions of extremely poor visibility. The direction of travel remained constant at all altitudes, although the ability to stay on course was reduced under windy conditions (Bruderer,
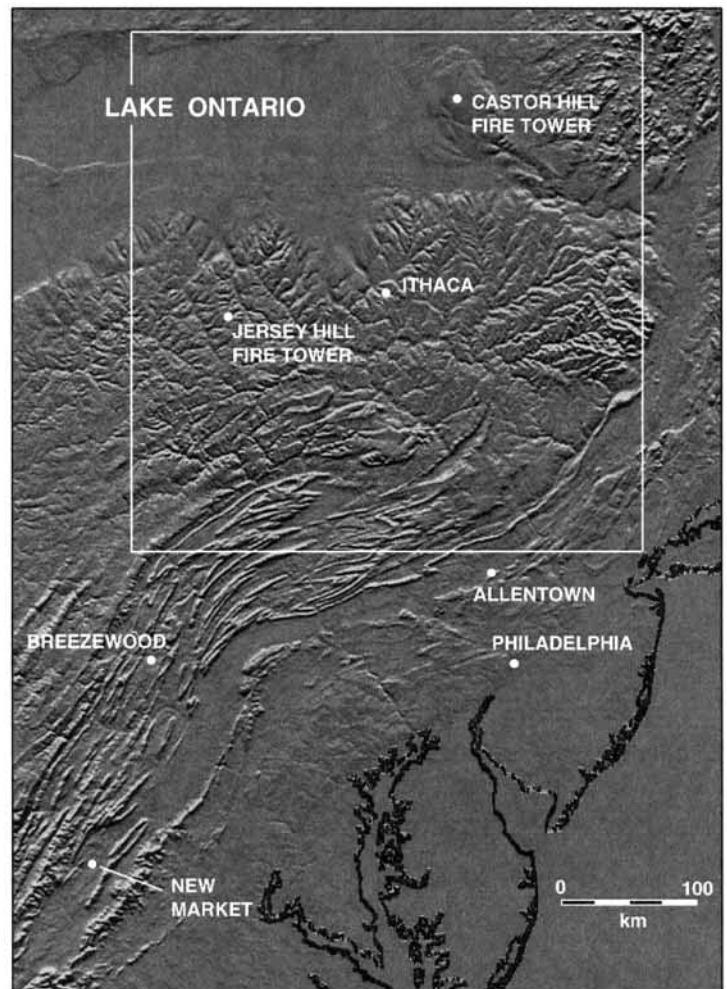

Fig. 4. Shaded relief map of the northeastern USA showing one view of its regional topographic pattern. In this example, the illumination is from directly north with 45° elevation. Bright areas generally have consistent slope and orientation with respect to the illumination direction. Such steep-sided areas might directionally amplify Earth's background microseismic signal at long range by constructive interference to an intensity that provides birds with navigational map cues (see Fig. 3). The boxed area appears in Fig. 5.

1978). Also using radar, Griffin (1973) was able to track well-oriented migrants flying between layers of opaque clouds. Moreover, satellite tracking has shown that albatrosses can pinpoint remote islands following straight-line courses (even in crosswinds) over thousands of kilometres of open ocean (Papi and Luschi, 1996).

Pigeons with their sensitivity to infrasound decreased by perforating both tympana (raising the threshold by 35–45 dB) tend to have more difficulty orienting and returning to their loft over greater distances (Schöps and Wiltschko, 1994). Overall, however, the results of this study were ambiguous because birds with perforated tympana, released south of their loft, were actually better oriented than unaltered control birds. The area south of the loft, however, is heavily industrialized and is probably filled with artificial infrasound that might have confused the control pigeons. To use infrasound cues in flight, birds must be able to distinguish navigational signals from pseudosounds caused by pressure variations due to local winds and turbulence and to variations in flight speed and altitude (Kriethen, 1978). To overcome these effects, birds might be able to maintain altitude and speed with high accuracy, might sense and correct for deviations or might have hearing and breathing ports that evolved to minimize such dynamic effects (A. J. Bedard, Jr., written communication, 1999).

As with the magnetic compass sense (Wiltschko and Wiltschko, 1996), the hearing abilities of birds are probably tuned to their acoustic environment so that they can respond to the available landmark sources. The ground directly below their flight path would not be a significant source because pigeons usually fly at altitudes of less than 80 m. However, Swiss pigeons initially cannot orient over large bodies of water and often avoid flying over them (Wagner, 1972), possibly because of loud noise generated by, or poor reflection of, infrasonic signals from the water's surface waves. Albatrosses, however, apparently have no difficulty in detecting an island's infrasonic signal while flying over open ocean. Sinusoidal or zigzag courses might indicate birds following a signal by continuously testing its frequency or directional intensity. The ability of pigeons to discriminate between small shifts in frequency (1 % at 20 Hz and 7 % at 1 Hz; Quine and Kreithen, 1981) also allows them to distinguish between higher-frequency natural infrasounds in the atmosphere and those generated by 6 s microseisms and surface topography.

Site-release biases

Experimenters releasing birds individually or in groups determine the site-release bias, if any, by recording the vanishing bearing at which the individual bird or group disappears from sight or radio contact. Such biases have been determined for birds from lofts at Cornell University in upstate New York (Windsor, 1975; Fig. 5). A single group of experienced pigeons was released and radio-tracked from a grid of sites centred on Ithaca between March and December 1971.

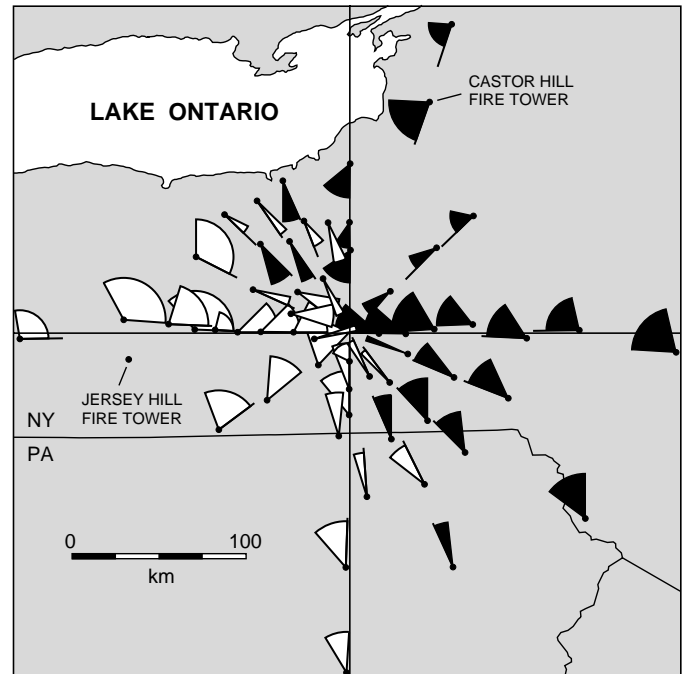A distinct pattern is readily apparent: release sites to the

Fig. 5. Map of central upstate New York (NY) and northern Pennsylvania (PA), USA (see Fig. 4), showing mean vanishing vectors from radio-tracked homing pigeons at 56 of 68 different release sites. At each site, a unit vector points to the Cornell University lofts located 3 km east of Ithaca, NY (centre of map), and a mean vector indicates the actual mean vanishing bearing. The mean vector length is inversely proportional to the dispersion between individual departure bearings for birds within the group (1 is perfect agreement, 0 is random bearings). Clockwise (anticlockwise) mean vectors are indicated by filled (open) arc sections between the mean departure and homeward-pointing vectors (modified from Fig. 3 in Windsor, 1975).

northeast of Ithaca had departures biased clockwise, whereas those to the southwest showed anticlockwise biases. It appears that the pigeons were homing to a virtual loft displaced northwards. Walraff (1967) also observed a similar pattern from release sites around his loft at Wilhelmshaven, Germany. These observations are consistent with deflection of infrasonic map cues during their transit by prevailing southerly winds. At greater distances from the loft, an increasing northward velocity component is added to the infrasound signal in steady winds, and the greatest deflections occur along the east–west line where the winds cross the homeward direction at approximately 90°; minimal deflections occur with or against the winds.

Because of the relatively short release distances from Ithaca (<200 km), the rays of most infrasonic waves used as map cues probably did not reach the stratosphere (Donn, 1978; Fig. 2) and probably stayed in the lower troposphere. Atmospheric data for the 1971 release dates, available from Buffalo daily at 07:00 and 19:00 h EST, show that winds with southerly directions occurred within 1 km of the surface at some time on 90 % of the days, and that wind direction fluctuated by as much

as 180° during the 12 h period between observations. Daily averages of surface wind directions at Albany, Binghamton, Buffalo, Rochester and Syracuse (Fig. 1B) showed much greater variability on and between release days. The wind direction above Buffalo also changed with elevation and was usually northerly in the upper troposphere (>3–5 km, Fig. 2). The observations above Buffalo reflect the general pattern of circulation in the troposphere, driven by heat transfer from the equator, forming three cells in each hemisphere. At medium latitudes (30–60° N) the Ferrel cell has prevailing southerly winds in the lower troposphere (Ithaca, 42.3° N; Wilhelmshaven, 53.3° N) and northerly winds in the upper troposphere (Harvey, 1976).

Gronau and Schmidt-Koenig (1970) found an annual fluctuation in homing performance (consistency and speed) of both experienced and inexperienced pigeons released from a single site 15.3 km north of their loft in Göttingen, Germany. Homing performance reached a minimum in February and March and a maximum in July for veteran birds or in July–September for naive birds. Although similar in relative performance, the absolute performance of veteran birds was generally much better than that of naive birds. Assuming that the birds were responding to infrasonic homing cues, this annual fluctuation in performance is easily attributed to the annual variation in atmospheric background noise related to the generation of microbaroms.

Microbaroms are continuous infrasonic waves similar in form and origin to microseisms in the solid earth (Donn and Naini, 1973). These waves can travel great distances in the atmosphere by multiple reflections between either the stratosphere or thermosphere and the Earth's surface (Donn, 1978; Fig. 2). Because the sea is more active in winter than in summer, the atmospheric background noise is much stronger during the winter months. In addition, strong westerly winds prevail in the stratosphere during winter, so that effective sound velocities are enhanced for waves travelling east and are considerably reduced for those travelling west (Donn, 1978). The annual effect of atmospheric background noise on homing performance would therefore be best observed east of the Atlantic Ocean in Europe.

Keeton (1974) often referred to two sites where he believed that release-site biases had particular significance in understanding the pigeon's map sense. They are the Jersey Hill fire tower 132 km to the west, and the Castor Hill fire tower 160 km to the north-northeast, of Ithaca (Figs 4, 5). Many releases of different configurations were made from these two sites to characterise the biases. The 50–70° clockwise bias at Castor Hill has previously been explained by southerly winds in the lower troposphere deflecting the infrasonic map cues northwards. Something quite different, however, happens at Jersey Hill. Most birds released from this site departed in random directions and often did not return to the Cornell lofts at all; some were later found in central Canada. There is one exception: on 13 August 1969, birds from Cornell and Fredonia to the west were released at Jersey Hill. The Cornell birds vanished in a tight group to the northeast and the Fredonia

birds vanished well-oriented to the west, and all the birds returned to their lofts that day (Keeton, 1974).

Experiments at Jersey Hill (Walcott and Brown, 1989) show that, while Cornell pigeons generally leave in random directions, birds from other lofts, even those in the same direction as Ithaca (although closer), tend to home normally. Cornell birds randomly leaving to the north and flying west around Lake Ontario (to avoid flying over it; Wagner, 1972) would end up in central Canada (Fig. 4). Atmospheric data recorded at 07:00 h EST at Buffalo (218 m elevation) for 30 release days between 1968 and 1979 (C. Walcott, written communication, 1999) show steady southerly to southwesterly winds at the surface which progressively strengthened and became westerly to northwesterly towards the top of the troposphere (jet stream); such strong westerly winds would impede infrasound waves reaching the upper troposphere coming from greater distances to the east. On 13 August 1969, the wind speeds throughout the troposphere were exceptionally low (4–6 m s^{-1}). Thus, the calm conditions above western New York State that day probably allowed infrasonic waves from distant eastern landmarks to reach Jersey Hill at an intensity that the birds could hear and use to return home.

Concluding remarks

There is general agreement that homing pigeons use a wide variety of cues to navigate. Birds learn their navigational ability with experience, and captive pigeons are trained to home by releasing them at increasing distances in different directions from their loft. The relationship between migratory flight paths and topography (Alerstam, 1996; Bruderer, 1978; Wagner, 1972) suggests that the avian map is an inherent aspect of the features of the landscape. Sight and probably smell are useful for local orientation by pigeons, but not for long-distance travel. The accuracy with which pigeons can find their lofts, even when wearing frosted contact lenses (Schmidt-Koenig and Schlichte, 1972), indicates that birds probably use some form of triangulation on distant map cues to locate themselves.

Although wind-borne odours could be brought from afar, it is difficult to imagine how birds, especially in a tailwind, can navigate accurately using odours that are passively transported by variable winds (Wiltschko, 1996). There is no information about what odours birds might be using over great distances, and no evidence that pigeons have a highly developed sense of smell (Able, 1996). In addition, there is confusion about whether anosmic birds can orient (Papi et al., 1978). In those cases in which anosmic birds cannot home (Papi, 1989), surgery may also have affected the magnetic compass sense, which is based on single-domain magnetite crystals associated with the ophthalmic branch of the trigeminal nerve (Walker et al., 1997).

The magnetic sense of pigeons provides an excellent compass for orientation, but the geomagnetic field makes a poor map. How birds use only the local intensity and direction of the magnetic field to determine their position is unexplained.

Assuming that birds could detect minute gradients in the field, it would be seemingly impossible to distinguish these changes from those produced by magnetic anomalies, secular field variations and magnetic storms (Wiltschko and Wiltschko, 1996). Moreover, pigeons usually depart from the release site in the direction of their home loft and often follow nearly straight-line courses along the way that are inconsistent with the birds following magnetic field gradients. A magnetic map also cannot explain why pigeons have difficulty orienting over large bodies of water (Wagner, 1972) or why they can orient below but not above a temperature inversion (Wagner, 1978).

An infrasound map, however, appears to be the most feasible candidate for the long-range avian map. Pigeons and other birds have extremely sensitive low-frequency hearing (Kreithen and Quine, 1979; Klinke, 1990; Schermuly and Klinke, 1990). Infrasound waves can travel thousands of kilometres in the atmosphere with little attenuation, a distance comparable to the farthest range of pigeon homing. Significant levels of infrasound can be radiated from topographic features (Cook, 1971; Young and Greene, 1982) at frequencies within the hearing range of the pigeon (Kreithen and Quine, 1979), and atmospheric conditions affecting the infrasonic map cues can explain site-release biases and their more mysterious day-to-day variations (Keeton, 1974). Also, microbaroms in the atmosphere could interfere with avian map cues of similar frequency, adversely affecting homing performance (Gronau and Schmidt-Koenig, 1970). Microbaroms originating from terrain features have not been reported in the literature, but could be masked by the greater near-surface amplitudes of microbaroms originating from oceanic waves; near-terrain launch angles also tend to radiate the strongest energy upwards (A. J. Bedard, Jr., written communication, 1999). The infrasound model of the avian navigational map presented here should be tested by searches for atmospheric infrasound caused by microseisms.

Hearing as the map sense can also explain the major disruptions of pigeon races described above. Fortunately, these disruptions are rare, and shock waves, racing pigeons and often specific weather conditions (favouring long-distance propagation) must all coincide. Other implications of this study are that monarch butterflies might use a similar navigational system during migration, that significant changes in local infrasonic signals might be the cause of unusual animal (bird) behaviour prior to major earthquakes (Wallace and Teng, 1980) and that sea turtles (Papi and Luschi, 1996) and other marine animals might also use low-frequency acoustic signals in water to navigate accurately across great distances of open ocean.

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