Infrasound and the Avian Navigational Map

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Birds can accurately navigate over hundreds to thousands of kilometres, and use celestial and magnetic compass senses to orient their flight. How birds determine their location in order to select the correct homeward bearing (map sense) remains controversial, and has been attributed to their olfactory or magnetic senses. Pigeons can hear infrasound down to 0·05 Hz, and an acoustic avian map is proposed consisting of infrasonic cues radiated from steep-sided topographic features. The source of these infrasonic signals is microseisms continuously generated by interfering oceanic waves. Atmospheric processes affecting the infrasonic map cues can explain perplexing experimental results from pigeon releases. Moreover, four recent disrupted pigeon races in Europe and the north-eastern USA intersected infrasonic shock waves from the Concorde supersonic transport. Having an acoustic map might also allow clock-shifted birds to test their homeward progress and select between their magnetic and solar compasses.

KEY WORDS

1. Animal Navigation. 2. Birds. 3. Homing.

1. INTRODUCTION. Kramer (1953) first suggested that birds must have both map and compass senses to traverse great distances (hundreds to thousands of km), and demonstrated that their usual daytime compass is the sun. Homing pigeons whose circadian rhythm has been shifted by 6 hours (quarter day) will depart 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 having magnets and control birds having brass bars attached to them, 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 Wiltschko, 1976).

The elusive map sense, on the other hand, has been tested at one time or another against most of the homing pigeon's senses (Gould, 1982). Sight has been ruled out because birds fitted with frosted contact lenses can return to within < 500 metres 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 having 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 airflows 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).

2. MICROSEISMS AND TOPOGRAPHY. Griffin (1969) first raised the possibility that atmospheric infrasound provides directional cues 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 <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 of these sources might serve as acoustic beacons. No perennial geographic sources, other than waterfalls and geothermal activity, have been identified. Seismically-generated movements of the ground, however, can produce infrasound.

Microseisms are low-frequency seismic waves constantly generated by interfering oceanic waves, and are background noise in seismic records (Bullen and Bolt, 1985). They have regular periods of 5 to 8 or more seconds, and peak at periods around 6 seconds (Bullen and Bolt, 1985; Aki and Richards, 1980). The 6-second 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 $\sim 10^{-3}$ cm in coastal regions and $\sim 10^{-4}$ cm in continental interiors like central Asia (Bullen and Bolt, 1985). The frequency of the 6-second microseism peak is $\sim 0{\cdot}14$ Hz, and the surface vertical displacement velocity is $\sim 10^{-3}$ cm/sec (Bullen and Bolt, 1985; Aki and Richards, 1980). In order to be useful to the avian navigational system, 6-second microseismic waves must be transformed into audible (to birds), horizontally propagating infrasonic signals with geographic significance.

Seismic surface waves radiate infrasound into the atmosphere, and because surface waves travel at much faster speeds than air waves ($\sim$ 10x) the infrasound generated propagates upward 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's location. The second signal detected, if it occurs, is from intermediate sources with non-horizontal surfaces, like mountains, acting as large acoustical radiators (Cook, 1971). Young and Greene (1982) analysed records from Boulder, Colorado, Boston, Massachusetts, and Washington, DC, associated with the 1964 Alaskan earthquake ($M_W = 9{\cdot}2$), and identified an acoustic source that moved down the Rocky Mountains concurrently with passage of the surface waves (Figure 1). 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).

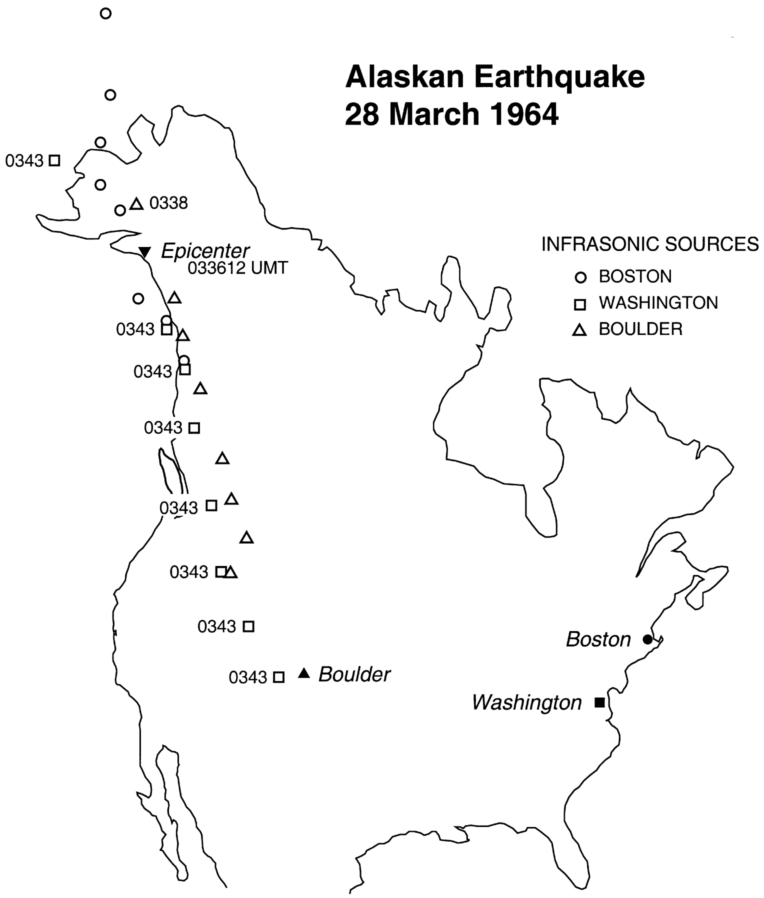

Figure 1. Calculated positions and times of seismic-to-air wave conversions after the Alaskan earthquake of 28 March 1964 (after Figure 6 of Young and Greene, 1982).

The relationship between velocity of vertical ground motion and perturbation air pressure at ground level is $p = \rho c v$, where p is the perturbation pressure, ρ the air density, c the sound velocity in air, and v the vertical ground velocity (Donn and Posmentier, 1964). Inserting values for average conditions ($\rho = 1{\cdot}19 \times 10^{-3}$ g/cm^3, $c = 330$ m/sec), the equation becomes $p = 247a/t$, where p is the peak-to-peak pressure in μbars, a the double amplitude of ground motion in 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-second microseisms is $\sim 0{\cdot}08$ μbar (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). On the other hand, a coplanar source with dimensions much greater than the infrasound wavelength ($\sim$ 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 kilometres act as point sources, and could be useful as local map cues; signals from linear point sources would also constructively interfere at long range (Figure 2). Beacons with rich near-infrasonic frequencies (1 to 20 Hz) might also provide unique identification characteristics of the signal (A. J. Bedard, Jr., writ. comm., 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).

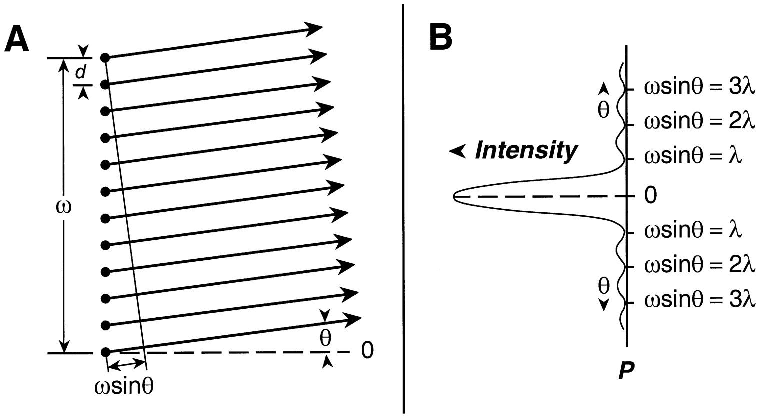

Figure 2. Radiation from an idealized row of point sources (e.g., 12 flatirons along a mountain range front) oscillating in phase with λ being the wavelength, d the distance between points ($d \ll \lambda$), ω the length of the array, and θ the angle between the normal to the line of sources and the line joining any of the sources to a point P a large (infinite) distance away. The relative intensity is greatest when $\theta = 0$, and has minima when the path difference between sources is a factor of λ.

It has long been known that migrating birds follow major topographic features like coastlines and mountain range fronts. Migrants also tend to follow segmented routes with legs of different orientation, with some legs reaching up to several thousands of 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 like 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, 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 35 to 45 dB) tend to have more difficulty orienting and returning to their loft over greater distances (Schöps and Wiltschko, 1994). Overall, the results of this study are 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 likely 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

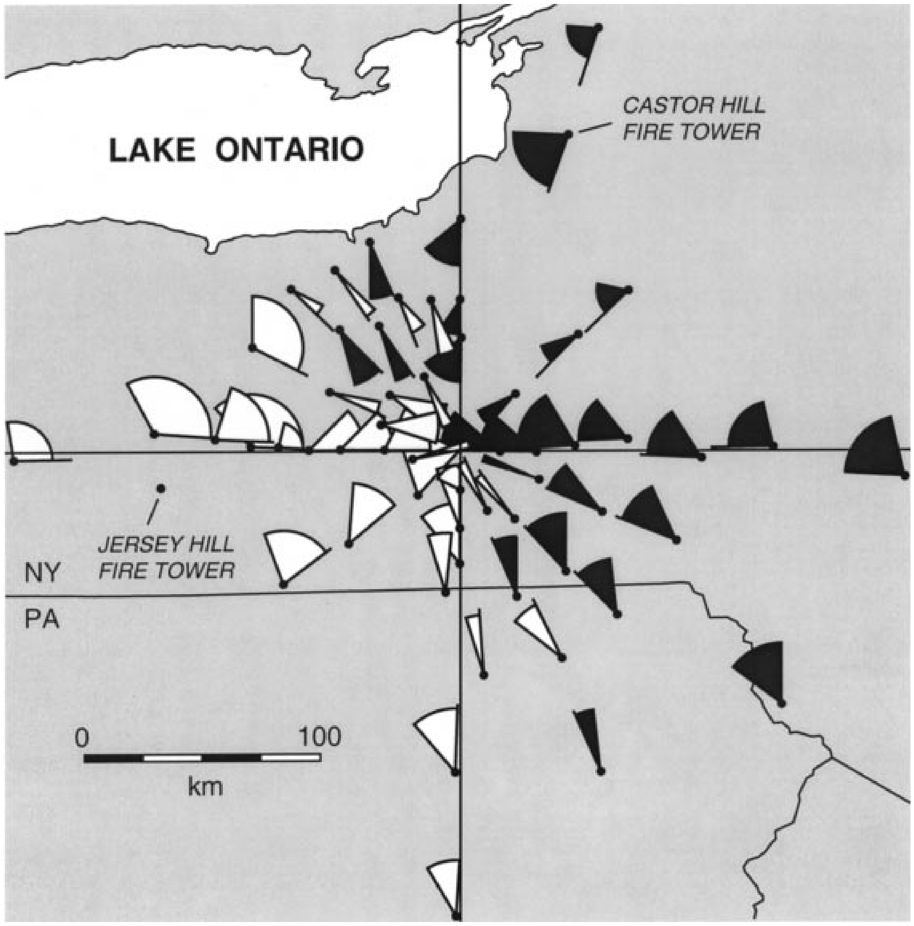

Figure 3. Map of central upstate New York (NY) and northern Pennsylvania (PA) showing mean vanishing vectors from radio-tracked homing pigeons at 56 of 68 different release sites. At each site, a unit vector points to the Cornell University lofts located 3 km east of Ithaca, NY (centre of map), and a 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 black (white) arc sections between the mean departure and homeward-pointing vectors (modified from Figure 3 of Windsor, 1975).

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, sense and correct for deviations, or have hearing and breathing ports that evolved to minimize such dynamic effects (A. J. Bedard, Jr., writ. comm., 1999).

As with the magnetic compass sense (Wiltschko and Wiltschko, 1996), birds' hearing abilities are likely 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 < 80 metres. 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 on the other hand, 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) allows them to also distinguish between higher-frequency natural infrasounds in the atmosphere and those generated by 6-second microseisms and surface topography.

3. RELEASE-SITE BIASES. Experimenters releasing birds individually or in groups determine the release-site 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 Cornell University's lofts in upstate New York (Winsor, 1975; Figure 3). 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 north-east of Ithaca had departures biased clockwise, whereas those to the south-west showed anticlockwise biases. It appears that the pigeons were homing to a virtual loft displaced northward. Walraff also observed a similar pattern from release sites around his loft at Wilhelmshaven, Germany (Wallraff, 1967). These observations are consistent with deflection of infrasonic map cues during their transit by prevailing southerly winds. At larger 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 $\sim 90°$; minimal deflections occur with or against the winds.

Because of the relatively short release distances from Ithaca (< 200 km), rays for most infrasonic waves used as map cues likely did not reach the stratosphere (Donn, 1978; Figure 4) and probably stayed in the lower troposphere. Atmospheric data for the 1971 release dates, available from Buffalo daily at 7:00 and 19:00 hrs EST, show that winds with southerly directions occurred within one kilometre of the surface at some time on 90% of the days, and that wind direction fluctuated as much as 180° during the 12 hour period between observations. At medium latitudes (30° to 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.

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 kilometres north of their loft in Göttingen, Germany (Figure 5). Homing performance reached a minimum in February and March and a maximum in July for veteran birds or July to September for naive birds. Although similar in relative performance, the absolute performance of veteran birds was generally much greater than that for naive birds. Assuming 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

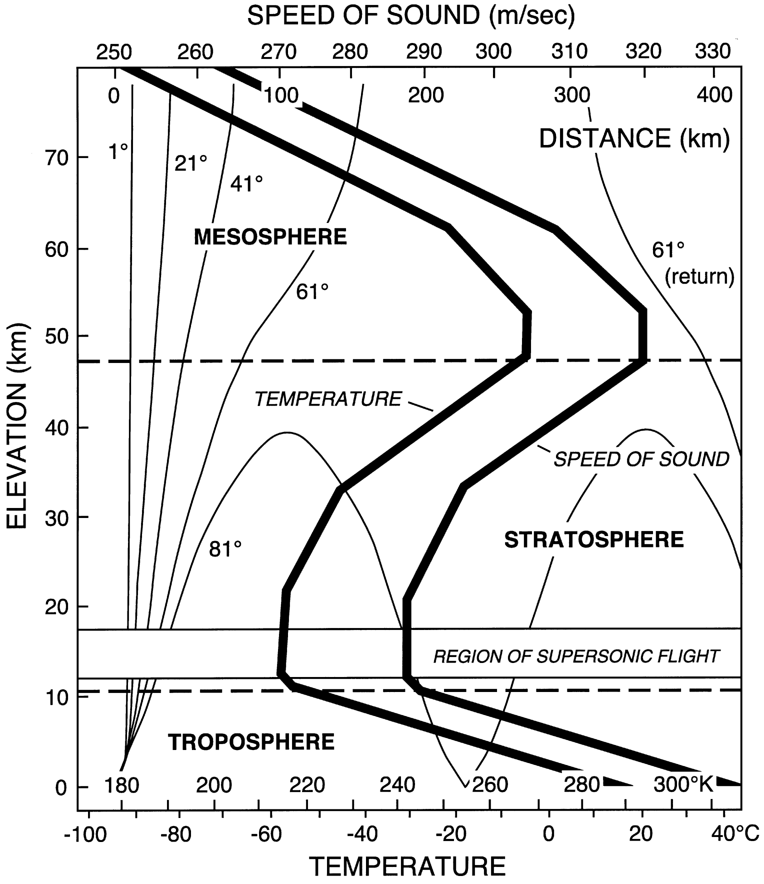

Figure 4. Cross section of the troposphere, stratosphere, and mesosphere of the Earth's atmosphere. The thermosphere above the mesosphere (80 to 110 km) has increasing upward temperatures (180° to 260° K) and is not shown. Temperature and speed of sound are plotted against elevation (heavy lines), and 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 of the ray's initial upward path (modified from Figures 5 and 7 of Donn, 1978).

thermosphere and surface (Donn, 1978; Figure 4). Because the sea is more active in winter than in summer, the atmospheric background noise is much stronger during 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 therefore would be best observed east of the Atlantic Ocean in Europe.

Keeton (1974) often referred to two sites where he believed that the release-site biases had particular significance in understanding the pigeon's map sense. They are the Jersey Hill fire tower 132 kilometres to the west, and the Castor Hill fire tower 160 kilometres to the north-north-east of Ithaca (Figure 3). Many releases of different configurations were made from these two sites to characterise the biases. The 50° to

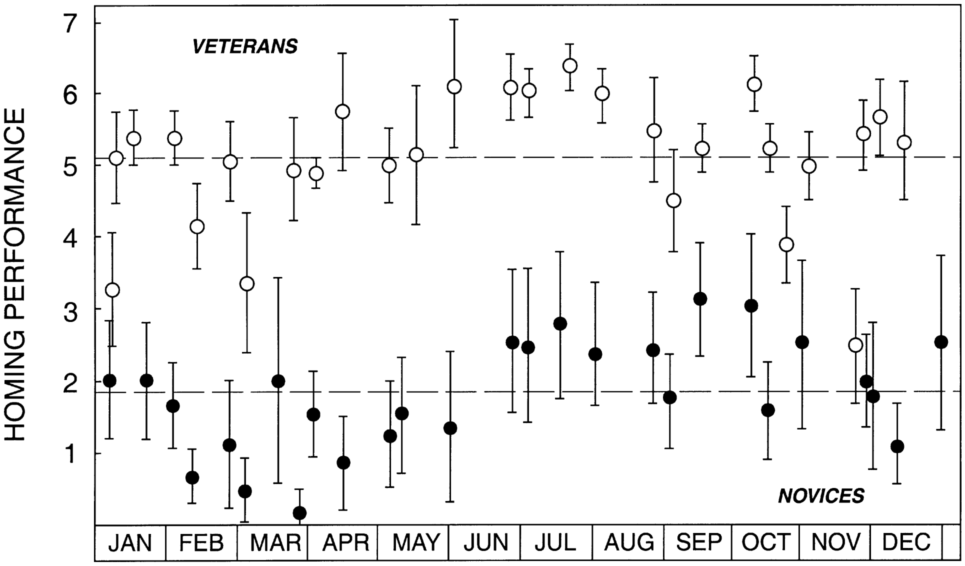

Figure 5. Mean relative homing performance of veteran and novice birds. The 99% confidence interval is given for each symbol of $n = 20$. The horizontal dashed lines show the overall mean of the veterans and novice birds. Relative homing performance: 0 = no bird homed, 7 = all birds homed at > 60 km/h (after Figure 1 of Gronau and Schmidt-Koenig, 1970).

70° clockwise bias at Castor Hill has previously been explained by southerly winds in the lower troposphere deflecting the infrasonic map cues northward. 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 of them were later found in central Canada. There is one exception; on August 13, 1969, birds from Cornell and Fredonia to the west were released at Jersey Hill. The Cornell birds vanished in a tight group to the north-east and the Fredonia birds vanished well-oriented to the west, and all of 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. Atmospheric data recorded at 7:00 hrs EST at Buffalo (218 m elevation) for 30 release days between 1968 and 1979 (C. Walcott, writ. comm., 1999) show steady southerly to southwesterly winds at the surface that 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 August 13, 1969, the wind speeds throughout the troposphere were exceptionally low (4–6 m/sec). Thus, the calm conditions above western New York State that day likely allowed infrasonic waves from distant eastern landmarks to reach Jersey Hill at an intensity the birds could hear and use to return home.

4. PIGEON RACES AND SONIC BOOMS.

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

On Sunday, June 29, 1997, a race of more than 60000 homing pigeons, celebrating the centenary of the Royal Pigeon Racing Association (RPRA), was begun at 6:30 hrs from Nantes, France, to lofts all over England (Figure 6a). Normally ~ 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 hrs 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/hr, a bird leaving Nantes at 6:30 hrs would have been over the Channel (~ 300 km distance) by ~ 11:30 hrs. The SST departing Paris goes supersonic after crossing the French coastline, between intersections EVX and TESGO, and was passing over the Channel between ~ 11:20 and ~ 11:35 hrs (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 Centre (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 cone's sides at the ambient speed of sound (Figure 7a). Because atmospheric temperatures and sound velocities increase below the SST (Figure 4), ray paths of the downward shock waves are refracted upward with lateral distance from the aeroplane (Figure 7b). The distance from directly beneath the SST's flight path to points on either side at which the rays just graze the surface before heading upward 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, $x = 2\,(T_0 h/g)^{1/2}$, 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; Donn, 1978). Inserting the average values given, the width of the boom carpet on the ground ($2x$) would be ~ 100 km.

Birds within the boom carpet on Sunday, June 29, 1997, were probably affected. Most of the birds that arrived at their lofts that day had average velocities between 30 and 50 km/hr (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 ~ 0·23 seconds within the boom carpet and an overpressure of ~ 1 100 μbars (128 dB SPL; Donn, 1978); the loudest sounds human ears can tolerate without temporary or permanent hearing changes have amplitudes of ~ 280 μbars (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 pigeons' extremely sensitive low-frequency hearing. 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, July 31, 1998, two pigeon races were started in southern France, one

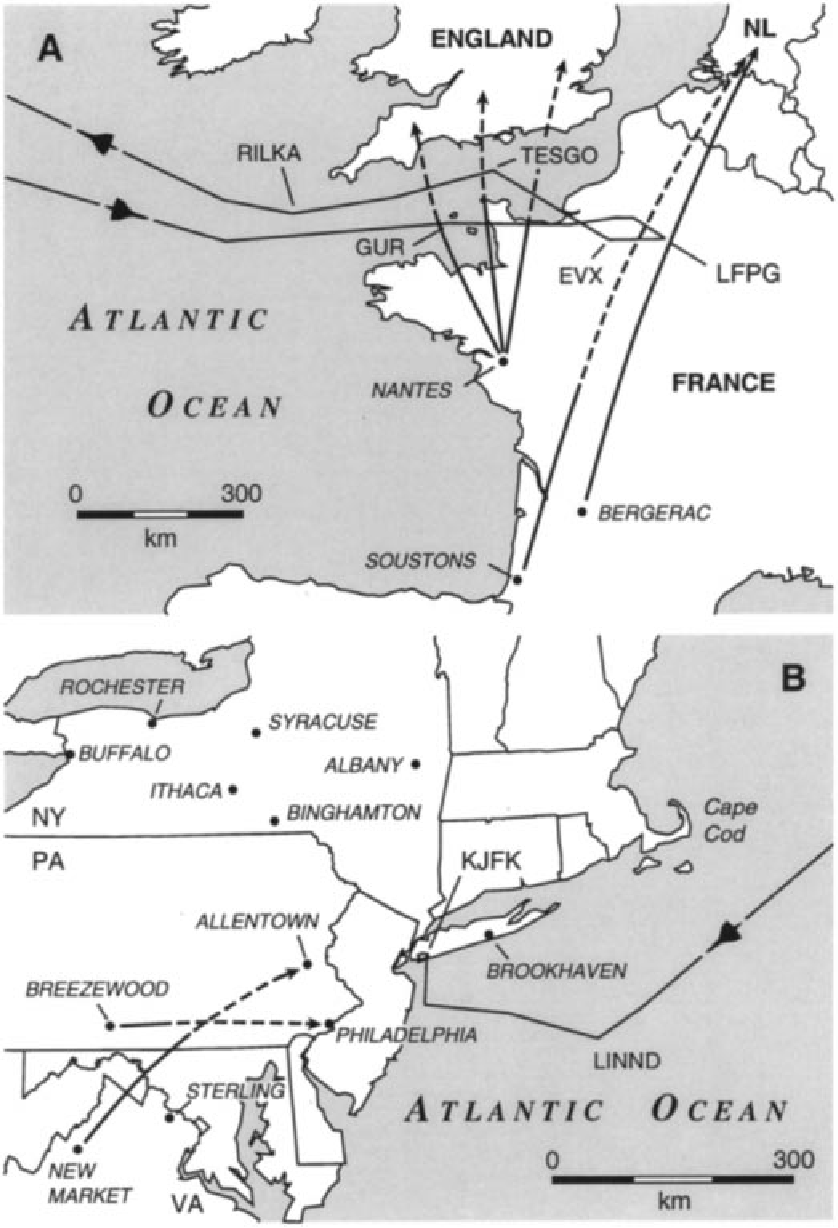

Figure 6. Flight paths of the Concorde supersonic transport (SST) in (a) Europe arriving and departing Paris (LFPG) and (b) the north-eastern USA arriving New York (KJFK). Labelled points along the flight paths (e.g. RILKA) indicate some of the intersections near where the SST changes course. Dashed 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 ~ 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 km most likely under favourable atmospheric conditions.

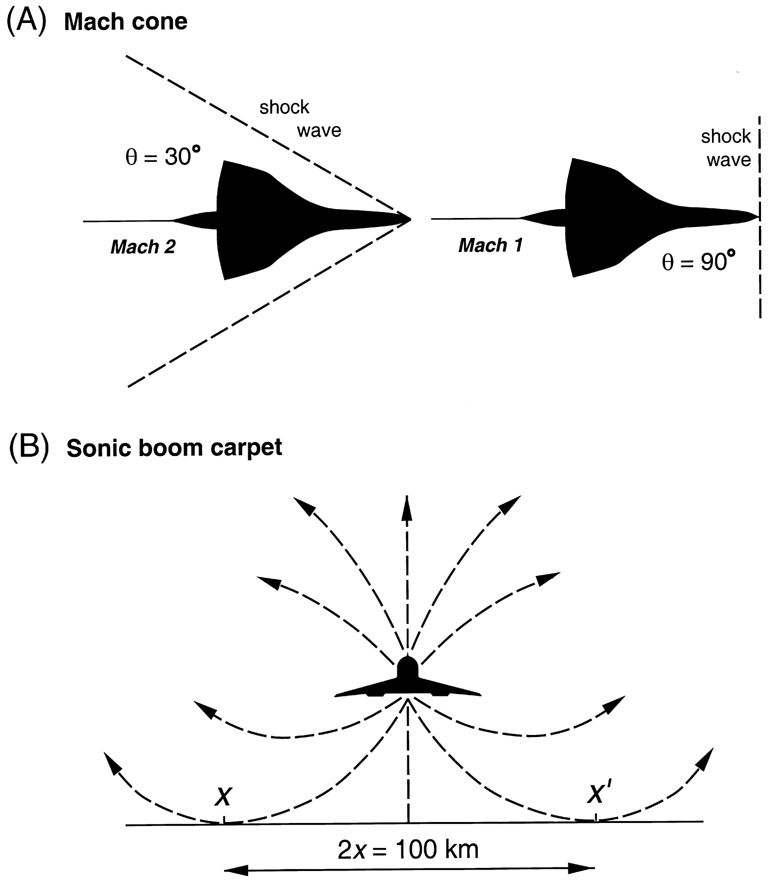

Figure 7. In flight, the SST generates a cone shaped shock wave (Mach cone, a) which travels with the airplane's bow at supersonic speeds and moves away from the cone's sides at the ambient speed of sound. Because atmospheric temperatures and sound velocities increase below the SST (Figure 4), ray paths of the downward shock waves (b) are refracted upward with lateral distance from the airplane. The distance from directly beneath the SST's flight path to points on either side at which the rays just graze the surface before heading upward defines the boom 'carpet' where direct shock waves reach the ground.

of 42845 birds from Bergerac and the second of 13610 birds from Soustons, to lofts throughout the Netherlands (Figure 6a). Birds in both races were released at 13:00 hrs for flights of ~ 1110 km from Soustons and ~ 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/hr, by that evening $< 10\%$ of the Soustons pigeons had returned. By Wednesday evening ~ 60% 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 hrs. 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, $\sin \theta = 1/\mathrm{M}$, 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 (Figure 6a). The intersection of shock waves with the Soustons racecourse therefore depended on the angle at which the waves departed the SST, the local sound velocity, wind speed, and the distance travelled. Assuming 70 km/hr for the average bird's velocity (faster race) and 1 100 km/hr for the velocity of sound, the intersection would have occurred ~ 320 km north of Soustons.

On Monday, October 5, 1998, two pigeon races were started in the eastern United States, the first of > 1 200 birds from New Market, Virginia, on a course of 322 km to Allentown, Pennsylvania, and the second of ~ 700 birds from Breezewood, Pennsylvania, on a course of 241 km to the outskirts of Philadelphia (Figure 6b). Due to bad weather, the release of birds to Philadelphia was postponed until 10:00 hrs (Gary Moore, race co-ordinator, pers. comm, 1999). The expected duration of this race was ~ 3 hours, but the first birds returned after over 8 hours had passed. Only 5 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 run successfully many times before.

The racing pigeons starting from New Market, Virginia (Figure 6b), were released at 8:00 hrs on Monday, and the expected duration of this race was ~ 4 hours. The birds departed quickly northward following the Shenandoah Valley. They too were substantially delayed: the first bird came in at 19:00 hrs and only 13 birds arrived at their lofts that day. Only fifty birds had returned by Tuesday evening (Ron Lish, participant, pers. comm., 1999).

The SST from Paris normally arrives New York (KJFK) at 8:45 hrs, and the aeroplane goes subsonic prior to reaching the LINND intersection (Figure 6b). Because the birds from Breezewood were not released until 10:00 hrs, the pigeons of both races (assuming 60 km/hr velocities) would not have approached the intersection point of the racecourses until ~ 11:00 hrs. The SST arriving on the morning of October 5, 1998, therefore must have been late more than an hour if its shock wave was to affect the pigeons of the Breezewood race. The aeroplane was delayed by an extraordinary ~ 2·5 hrs that morning due to mechanical problems in Paris. Thus, a shock wave originating from the incoming SST (~ 500 km distance) at ~ 10:40 hrs and travelling at ~ 1100 km/hr would have passed through both racecourses at ~ 11:10 hrs.

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 of 1975, and along the USA's north-eastern coast during late 1977 and early 1978 when the number of SST flights substantially increased between Europe and the USA (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).

5. CONCLUSIONS. 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 the loft. 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 likely use some form of triangulation on distant map cues to locate themselves.

An infrasound map 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 pigeon's hearing range (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 upward (A. J. Bedard, Jr., writ. comm., 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. Birds using infrasonic cues can also 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). Having an acoustic map might also allow clock-shifted birds to test their homeward progress and select between their magnetic and solar compasses.

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