

Supplemental Material to:

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Pigeon homing from unfamiliar areas: an alternative to olfactory navigation is not in sight

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Do pigeons use infrasound to find their way home?

Hagstrum (2000, 2001, 2007, 2013a, 2013b) pursues the idea that pigeons might use the perception of infrasonic signals to find their way home. Without clearly explaining how a navigation system based on infrasonic 'map' cues might hypothetically function, he immediately focuses on the supposed causes of some peculiarities and imperfections of its output.

In his first publications (2000, 2001), Hagstrum describes a few cases where pigeon races were disrupted concurrently with the occurrence of infrasonic shock waves produced by *Concorde* supersonic aircraft and he speculates about a possible causal connection between the two events, yet without giving any evidence of such a connection (see Wallraff 2001, p. 40).

In his more recent publications (2013a,b), Hagstrum focuses on three sites at which the research group of W.T. Keeton conducted hundreds of release experiments with pigeons from a loft at Cornell University in Ithaca, N.Y., between 1968 and 1987. At each of these three sites (distance from home 74, 120 and 143 km), the initial bearings of singly departing pigeons showed a site-specific 'release-site bias', i.e., a typical deviation to the left or right from the direct direction towards home and a typical degree of angular scatter among the individual bearings. (The existence of such release-site biases per se does not imply any hint on their causation. Hardly any animal 'map' system can be expected to function geometrically fully accurate, and models using real atmospheric trace gases as navigational cues do in fact produce release-site biases; see ref. 1, Fig. 7.32, and ref. 7, Fig.2.) Hagstrum tries to explain the release-site biases observed at his three selected sites by modeling atmospheric propagation conditions for infrasound using an acoustic ray-tracing program based on daily meteorological data. In a number of graphs, he shows the calculated propagation conditions for the range between the home site and the release site on a given day. These conditions are variable depending on the weather, but they also depend on the orographic profile between the two sites.

More remarkable than Hagstrum's speculative deductions from these modeling results is the surprising premise on which the 2013 approach is based. In the following, I describe Hagstrum's hypothesis, as I understand it, and discuss a number of arising consequences and problems.

- (1) Upon release at one of the three sites, the pigeons are thought to respond "to infrasonic signals originating from the Cornell loft's vicinity" (2013a, Summary p. 687) by striving to fly home along the (often deflected) infrasonic waves arriving from an "acoustic source area surrounding the loft" (2013a, p. 696). We can take it for granted that neither the Cornell loft nor any other pigeon loft has been installed based on considerations about microseisms / microbaroms that might generate infrasound in its vicinity. Thus, as a pigeon loft can be established successfully almost anywhere, continuously operating sources of infrasound must be densely distributed almost everywhere. Much louder infrasonic noise than that coming from >100 km away must originate around each site where the pigeons are released, and superimposed waves must arrive there from all directions and distances. I consider it physically impossible that the birds can filter out the spectrum of wavelengths to which they were accustomed at home and which itself must consist of a mixture of locally generated infrasound and waves arriving from all directions. Moreover, the local non-attenuated release-site noise should largely mask signals coming from far away.
- (2) An additional difficulty arises from the premise that the pigeons need to determine the direction from which the home-site infrasonic signals (frequency ca. 10–0.1 Hz, wavelengths ca. 30–3000 m) arrive at the release site. Theoretically, this could be achieved, if at all, only by exploiting the Doppler shift during flight in various directions (see ref. 27, Quine and Kreithen 1981, and Hagstrum) and must also be performed within the chaos of waves arriving from eve-

rywhere. Furthermore, not all pigeons circle around for a while upon release; quite a number of birds fly away fairly straight; as early as 20 sec after take-off pigeons are, on average, homeward oriented (see ref. 1, Figs 2.3 and 2.4). From experiments with pigeons breathing air sucked through a container before release, we can even conclude that the birds know where they are before they start flying (see ref. 1, Figs 7.7 and 7.8).

- (3) If it were true that the whole earth is covered by a dense infrasonic grid, and if this ubiquitous noise were loud enough to be heard by birds over distances >100 km, it should not be difficult to record it by technical means. Hence, it should be a well-known worldwide phenomenon. Instead, Hagstrum's discussions appear to indicate that variably scattered infrasonic emissions can be found here and there and that not all sources are continuously activated, e.g. when caused by earthquakes (e.g. 2013a, p. 695). In the context of pigeon homing results, Hagstrum never deals with really existing and measured infrasound, but merely with fictitious sources at or around Ithaca and with modeled atmospheric and orographic *conditions* for infrasound propagation.
- (4) Hagstrum (2013a,b) discusses in great detail the pigeons' initial orientation at the three release sites and interprets these data based on the concurrent propagation conditions for infrasound. Given his focus on selected days with exceptional pigeon behavior, however, he never exceeds the level of case studies that cannot prove any causal connections or, at least, correlations. He does not extract biological and atmospheric parameters that might be suitable for a correlation analysis of the complete set of Cornell experiments, and hence he does not present any results that are testable to determine statistical significance.
- (5) If pigeons would actually identify infrasonic signatures coming from the home site and would follow their trajectories, they would need neither a map nor a compass. They would fly directly toward a directionally localized source of an acoustic signal without requiring any previous knowledge of spatial configurations and compass alignments. Consequently, they should not be deflected from the infrasonic trail by a clock shift. (The birds could, nevertheless, use the sun as a directional reference to stay on course while continuous determination of infrasound direction is difficult; see also my comment on the gravity hypothesis.)

Having enumerated a sufficient set of direct objections to Hagstrum's recent (2013) publications, I refrain from discussing the incompatibility of his infrasound hypothesis with the statistically well-substantiated experimental findings that demonstrate the crucial role of atmospheric olfactory signals and home-site winds in pigeon navigation. I also refrain from commenting on Hagstrum's (2007) sketchy discussion of these experiments. His attempt (also 2007) to interpret the better initial bearings of deafened pigeons compared with untreated control birds (see ref. 28) based on their possible reliance on learned visual cues is absurd. None of the birds had ever been released before within a radius of 50 km of the actual release site (151–159 distant from home), and the controls had a similar background of preceding experience (under these conditions, anosmic pigeons would have been clearly disoriented and hardly anyone would have returned; ref. 1, Figs 7.2, 7.3, and 8.1). I see the statistically insignificant difference between deaf and intact birds as an indication that deafness did not even slightly reduce the homing ability of the pigeons.

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