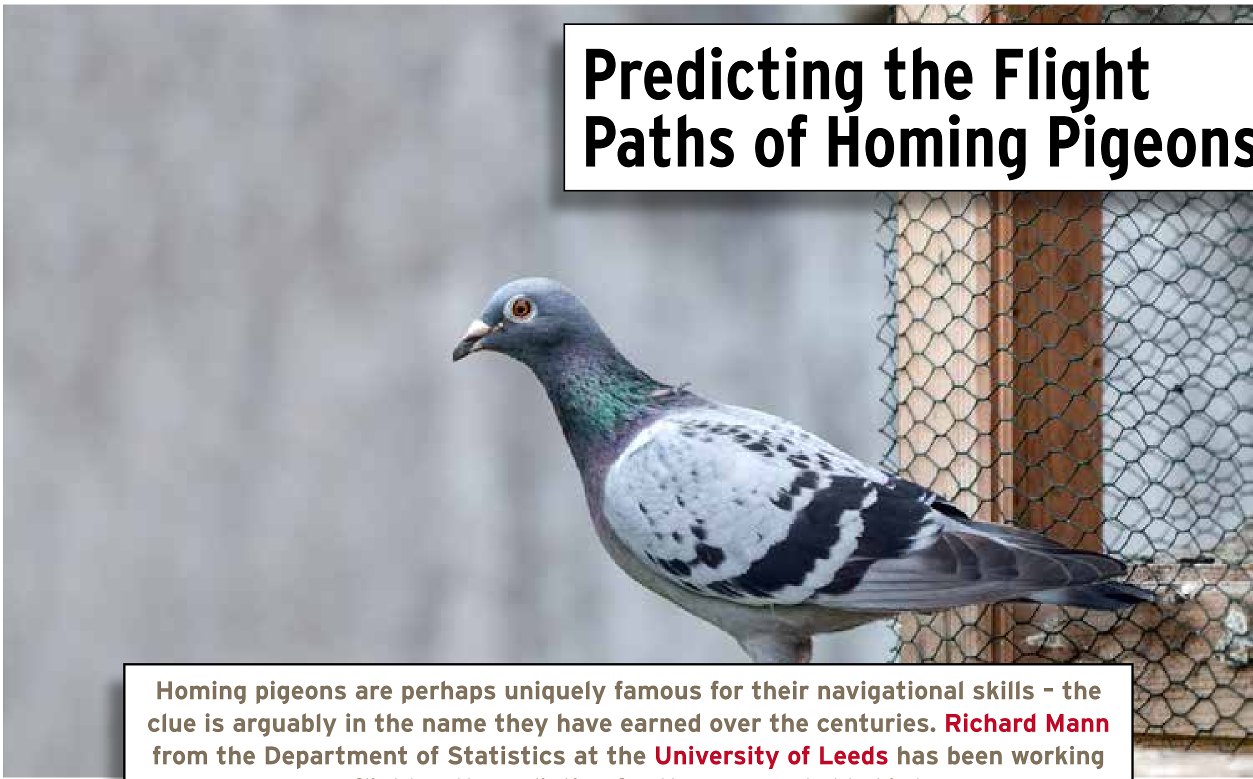

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Predicting the Flight Paths of Homing Pigeons

Homing pigeons are perhaps uniquely famous for their navigational skills – the clue is arguably in the name they have earned over the centuries. Richard Mann from the Department of Statistics at the University of Leeds has been working on flight path prediction for these remarkable birds.

Many animals exhibit extraordinary powers of navigation that have long astounded human observers. From the migration of wildebeest across the savannah to the worldwide seasonal movements of whales in the ocean, these journeys impress us not just in scale but in precision. Some of the most readily observed and impressive of these feats are performed by birds. For example, the Manx Shearwater travels each year between the British Isles and Argentina and back, a journey of some 6000 miles each way. But perhaps more impressive than the distance covered, each bird will find its way back to the exact nest site it used the year before, in a patch of ground less than a square metre on the other side of the world.

It has long been known that birds can sense and respond to compass directions, using either the Earth's magnetic field or the position of the sun. The instinct to migrate is a powerful, innate force in many species. A caged migratory bird in the northern hemisphere will repeatedly push against the southern wall of its cage as winter approaches, driven to migrate to more southerly latitudes. What is less well understood is exactly how these birds find their way to such small targets so accurately. In particular, how do they navigate when close to the target to pinpoint the exact location required?

My colleagues and I are fascinated by this question - how do birds navigate so precisely when closing in on their target? What information are they using to remember their route back? And how can we design experiments and analyse the data we collect to solve this puzzle?

Technological Transformation

In just over a decade the study of avian navigation has been transformed. Smaller and more powerful microprocessors and batteries have enabled engineers to produce GPS trackers that are small enough for many birds to carry unobtrusively as they move around (Figure 1). This tracking technology has done more to revolutionise navigational research than any other development in the

Figure 1: Mr Grizzle, a pigeon from the Oxford Field Station, wearing a miniature GPS tracking device on its back. These devices, which can record an animal's movements in high spatiotemporal precision, and which are light enough to be carried in flight, have revolutionised the study of avian navigation. Image credit: © Dr Dora Biro, University of Oxford. Reproduced with permission.

21st century.

Historically, experimental navigational research relied on a few key indicators. The simplest of these was success - whether a bird reached its target at all. If the bird returned then the researcher could measure its speed - how *quickly* it returned. A third measure, much more difficult to obtain, was the 'vanishing bearing,' the direction the bird was last seen flying in after release. This required the experimenter to release the bird and then attempt to follow it with binoculars until it was seen to disappear over the horizon. It was not unknown for researchers in the field to disagree on exactly when the bird had disappeared from view, and in which direction it was going - clearly not the best basis for a scientific study!

By contrast, modern tracking technology can give us exquisitely accurate records of where a bird flies (Figure 2). The power to see exactly what the birds do with such accuracy allows us to probe much more deeply into how they achieve such navigational precision.

Pigeons: A Navigational 'Laboratory Rat'

Studying how birds navigate, scientists often turn to the humble pigeon as a test specimen. Pigeons are fantastic animals to experiment with. They exhibit powerful navigational skills, as evidenced by their use to carry messages in previous centuries and in the continuing popularity of pigeon racing. Originally domesticated for food, there is a large body of knowledge on the rearing and keeping of pigeons. They can be kept in relatively large numbers in simple lofts. They display an urge to return to the home loft throughout the year.

As such, pigeons have become the workhorses of experimental research. Groups across the globe have established programs of research into the mechanisms of pigeon navigation. Many have become strongly associated with research into a specific sensory system: The Italian group in Pisa is famous for its research into the olfactory system, Frankfurt is more synonymous with research into the magnetic sensory abilities. My own work has been in collaboration with the team based in Oxford, led by Tim Guilford and Dora Biro, who have done more than any other group to decipher the pigeon's visual navigation system.

New Insights

Prior to the use of GPS trackers, substantial evidence existed that vision was an important factor in pigeon navigation close to the home loft. Pigeons would navigate more successfully, faster and more directly when allowed to view familiar landscapes prior to release. But the use of trackers completely transformed the picture of visual landmark use. When the full flight paths of individual birds were revealed for the first time, scientists could immediately see that the pigeons were not flying directly home, following their inbuilt compass bearings. Instead they were learning, and then repeating, highly complex, idiosyncratic homeward routes. These routes often deviated far from the straight path home, but the birds would follow them faithfully, time after time.

What was more, these routes seemed strongly linked to the underlying landscapes. Some birds visited the same church tower again and again. Others repeatedly made their way carefully around the edge of a forest in the same way on every flight. Perhaps the most astonishing finding was the high propensity of pigeons to follow roads in the general direction of home. So strong was this tendency that birds were even observed leaving the highway at designated exits, and swerving around roundabouts!

The observation of idiosyncratic route formation, and the subsequent recapitulation of learned routes by pigeons released from new locations, was heavily suggestive of visual navigation. No other information source seemed sufficient to provide the level of detail necessary to follow a route so closely: often within a corridor of a few metres. But if pigeons were using visual landmarks, how could we identify them? Most routes were not confined to roads, so what else could the birds be using?

When these questions were coming to the fore, I was starting my PhD and looking for a thesis topic. Having finished my undergraduate studies in physics, I was playing around with bioinformatics when I fortuitously attended a seminar by Robin Freeman, then finishing his PhD. He outlined his work applying mathematical models to study avian navigation, and I concluded that this sounded much more fun than analysing gene sequences. Within weeks I'd started work with Robin's supervisor, Stephen Roberts, in the Engineering Science Department at Oxford.

> A serious limitation in studying the role of visual landmarks in pigeon homing has been the inability of researchers to experimentally manipulate the landscape on large scales.

Predicting A Flight Path

Playing around with existing data from pigeon navigation experiments, I concluded that a new approach would be useful. Previous work extracted properties from the pigeons' flight paths: Did they get nearer to each other? How 'wiggly' were they? How efficient was the route? I decided instead that a good test of any navigational theory was whether it could predict the flight paths *themselves*.

What does this mean? Primarily, that one should be able to take a flight path, the raw series of recorded positions over time of a navigating bird, and ask how probable those data were, based on a biological hypothesis. If we can do that then we can use powerful statistical techniques to decide which theories are more likely to be true than others, using the data we collect.

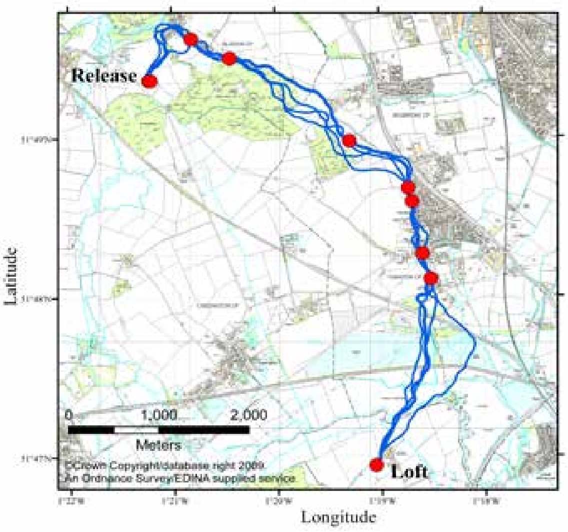

Figure 2: Flight paths of a pigeon navigating home to the Oxford loft when released from Bladon Heath to the north east. The red marks indicate where our research suggests the landmarks are most likely to be, based on the pigeon's movements. The Ordnance Survey map underneath shows that the forests near Bladon Heath and the village of Yarnton, including the church, are important visual features in these areas. Image credit: Mann et al. (2011). J. R. Soc. Interface. 8 210-219 CC-BY 4.0.

During my PhD I created a model that would predict where a pigeon would fly, based on seeing its previous flights home. Using this model one can isolate the points on its route that are most likely to be near landmarks, by virtue of how well they predict its future flights (Figure 2). For the first time this asked whether a specific hypothesis ('these are the landmarks') made the observed flight paths more or less likely.

How do we incorporate vision into this model? We believe that most landmarks are memorised using visual information. To understand how the landscape determines these points we need to uncover what it is about the landscape that makes them special. Sometimes we can see immediately what this is, eg, a road, a river, a church. But for general understanding we need a more systematic, algorithmic approach.

We investigated how potential landmark locations were related to an aerial image of the Oxford area. Specifically we looked at how complex parts of the landscape were, using a method from computer science called *edge-detection*. Edges are hard lines in an image where things change suddenly, like at the boundary of a field or the sides of a road. The number of edges in an area gives an indication of how much is 'going on' in the landscape. We found that pigeons were most faithful to their previous routes in areas where the number of edges was neither too low or too high, a sort of 'Goldilocks' approach to navigation, and that they seemed to memorise these areas more quickly (Figure 3).

Looking Forward

A serious limitation in studying the role of visual landmarks in pigeon homing has been the inability of researchers to experimentally mani–pulate the landscape on large scales. We cannot simply place a large new road between a release site and the home loft to test what influence it has, relative to some control group. Some ingenious strategies have been proposed to make use of natural experiments. For instance, my colleagues in Oxford once spent a winter waiting patiently for snowfall, hoping to test how a blanket of snow on the landscape would affect a previously learned homing route.

One thing that is clear is that the choice of a release site can create strong site-specific effects as a result of the particular landscape

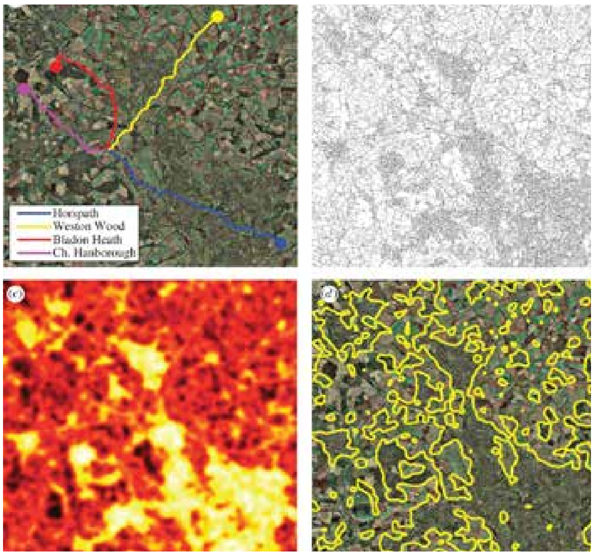

Figure 3: We analysed an aerial image of the landscape around Oxford (a). Using a computational algorithm we extracted features known as 'edges' from the image (b). The density of these edges (c) tells us how complex the landscape is. Pigeons learned their routes most quickly and accurately in areas where the complexity was neither too high or too low - the yellow contours in (d) indicate the preferred areas, which are often on the boundaries of towns and forests. Image credit: Mann et al. (2014). Biol. Lett. 10 20130885 CC-BY 4.0

features available. Not only do some sites seem more amenable to route learning that others, but different birds released from a single site often choose similar routes home. These characteristic 'corridors' suggest that certain features in the landscape are more salient than others, and that the routes pigeons learn may be predictable in advance. In other words, if we really understood how pigeons learn and use landscape features we could accurately predict, before any experiments are done, which routes those birds would memorise and repeat.

This year I will be speaking at the RIN Animal Navigation Conference on how we are going forward with this predictive approach, combining mathematical models for flight paths with our statistical analysis of the landscape. Only when we can make accurate, quantitative predictions will we be confident that we are truly getting to the heart of the visual navigation system. And based on the previous century of research, we expect that the birds have a lot of surprises in store for us yet.