

An overview on how birds utilize smell in navigation.

Bachelorthesis

Wicher Vos

University of Groningen

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Supervised by dr. M.W. Dietz

## Contents

Abstract .....	2
Introduction.....	2
First evidence: homing pigeons.....	2
Excluding non-specific effects .....	3
Olfactory navigation is learned .....	3
Manipulating the map.....	4
Creating a mirrored map .....	4
Using artificial odours results in an artificial map .....	5
Simulating an existing area.....	6
Limits on range .....	6
Minimum range .....	6
Maximum range .....	7
Procellariiformes: evidence in an ideal subject.....	7
Evidence in a migratory species .....	9
Maps, plumes and patches.....	9
Discussion .....	10
Plausibility of the olfactory navigation hypothesis .....	10
A patchy map for familiar terrain .....	11
A guiding odourous plume .....	11
If you can smell it then use it .....	11
Is olfactory navigation alone sufficient for navigation? .....	11
An evolutionary urge to learn .....	12
Olfactory navigation: does it exist in nature? .....	13
References.....	13

## Abstract

About 50 years ago the first evidence that birds use odours in navigation was found. Afterward evidence has mounted for this olfactory navigation hypothesis. The precise way birds utilize olfactory information for navigation and orientation is not fully known but several ideas have been postulated and tested. Most evidence has been found through experiments with homing pigeons, *Columba livia domestica*, but convincing evidence has also been found in procellariiformes and some migratory birds.

These three sampled species/orders navigate through vastly different circumstances and as such need different navigational information which odours could provide. Because odours consist of easily dispersed gasses olfactory navigation is not without limits. It is, however, complemented and supported by other navigational mechanisms like landmarks. When taken together these mechanisms form a steady and reliable navigational system that is versatile enough to potentially serve different species with different needs.

## Introduction

Since Perdeck formulated the idea of true navigation (Perdeck, 1958) this has been the holy grail of bird navigation research. Birds were thought to have a “map” and a “compass” element. A bird would use its map to determine the location of its goal (orientation) and then use the compass to determine the direction towards its goal (navigation). True navigation incorporates both the map and the compass in one strategy. When discussing bird navigation the first mechanisms that are mentioned are geomagnetism and the positions of celestial bodies. Odours are seldom considered as a possible means to provide spatial information because, at first glance it seems improbable that odours are useful in navigation as they are easily dispersed. That being said displacement experiments with olfactory manipulated pigeons have been conducted since the early seventies. Unfortunately the more established theories could not illustrate true navigation in birds. Much evidence has accumulated that prove a role for geomagnetism in orientation/navigation but mostly as a supporting mechanism (REF). The same goes for using visual cues from the celestial bodies (REF). but olfactory navigation showed huge promise as a discrete strategy that functions completely on its own. We are now almost 50 years later and the early findings of olfactory navigation have been placed in context with additive research and findings.

This review organizes these findings since the first clues of the existence of olfactory navigation in birds arose and provides insight into the possibilities and limits of olfactory navigation and its plausibility.

## First evidence: homing pigeons

The first indication that odours affect navigation in birds emerged in 1970 (Wallraff, 1970). From 1966 to 1970 Wallraff had been testing if the view of the horizon has an effect on homing capabilities of homing pigeons, *Columba livia domestica*. Every year aviaries with different specific features were set up. An aviary would for example be surrounded by glass or nettle-cloth to deprive the birds a view of the horizon to a certain degree. When Wallraff combined the four years of data he came upon something peculiar. Some groups of pigeons were significantly worse at homing than others, though the view of the horizon was not the determining factor. Instead it turned out that homing capabilities were diminished when birds were held in an aviary that did not allow free flow of air. Birds held in an aviary allowing a free flow of air showed normal homing capabilities. Wallraff

theorized that an atmospheric factor was probably key in pigeon homing though it could also be attributed to disturbance of an elaborate coordination system, infrasound or non-specific effects. Around that same time Floriano Papi conducted a homing experiment in which he dissected the nasal nerves of ten pigeons turning them anosmic (deprived of the sense of smell) (Papi et al. 1971). He did so because smelling was the only sense not yet addressed in a bird navigation experiment. In contrast to the control group none of the anosmic birds returned to the home loft.

### *Excluding non-specific effects*

Papi himself suggested that dissection of the nasal nerves have had an effect on lower physiological processes other than olfactory by damaging other tissues than the intended nerves or by causing a general demotivation to home.

To further test the effects of odours on homing capabilities Papi conducted an experiment in which control and experimental pigeons experienced the same interference with breathing and nervous system. Both groups received a nasal wash with a 4% zinc-sulphate solution. A 4% zinc-sulphate solution applied to the olfactory mucosa reversibly degenerates the nerve tissue of the olfactory cells in the catfish, *Ictalurus punctatus* (Cancalon, 1982). The experimental group then received a nasal plug contra-laterally and the control group ipsi-laterally. The results were clear: only if the plug was placed contra-laterally the pigeons would show dramatically impeded homing capabilities (Papi et al. 1972).

Several years later Papi repeated this experiment but, instead of using a nasal wash he dissected the nasal nerves. Regardless of the treatment (nasal wash or dissection) the results were the same (Papi et al. 1980). Because all birds were completely anosmic but had the nerves of one nostril intact it meant that it couldn't be a non-specific effect caused by dissection of the nerves. Also subjects were motivated to home albeit navigating in the wrong direction.

### *Olfactory navigation is learned*

Based on these findings the author posed the olfactory navigation hypothesis: Pigeons, in the first months after hatching, learn to recognize the odours at the home loft and learn to associate foreign odours carried on the wind with the direction the wind is coming from (Papi et al. 1972).

This means that, according to this hypothesis, pigeons create a map based on the odours of the areas surrounding the home-loft and to do this they need ample time to experience wind from any wind-direction for an extended amount of time.

To prove this theory Papi designed a release experiment in which the nervous system was blocked but kept intact. 2 aviaries were build. An open and a closed aviary (O-aviary or C-aviary). The O-aviary was a simple aviary surrounded by wire netting and allowed pigeons to leave the aviary. The C-aviary was constructed the same way except it was surrounded with semi-transparent plastic and did not allow pigeons to leave. Inside this aviary it was impossible to discern the wind direction. When held in the O-aviary, experimental birds were outfitted with masks that impeded breathing and when held in the C-aviary the masks were removed. The control group wore masks in the C-aviary and not in the O-aviary. Every three days the birds were relocated to the other aviary and got one extra day for preparations at the end of the experiment. This treatment lasted for over 40 days. Ultimately the birds were released without their masks at 160 kilometers from the loft. The results were clear compared to control birds less experimental birds arrived back at the loft and they also took longer to do so. Hence pigeons not only need their sense of smell while navigating this also supports Papi's theory that birds need experience of the wind directions and the odours these winds carry with them

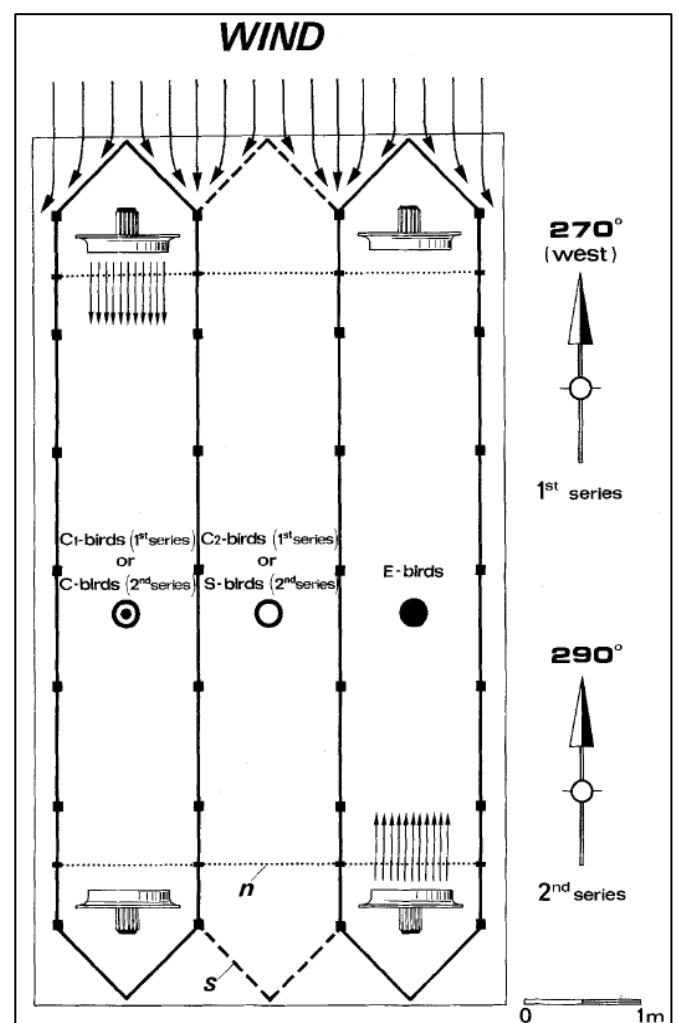
over a period of time. According to Papi the reason many experimental birds made it back to the loft might be through a process of trial and error. Pigeons, after a failed homing attempt, would return to the release point and try another direction until they encountered the odour of the home-loft (with which the pigeons were familiar) on the wind and were able to home properly. (Papi et al. 1973)

## Manipulating the map

### *Creating a mirrored map*

After these results were published it was hard to reject the notion that odours and the olfactory system have a meaningful impact on coordination in pigeons. Researchers had succeeded in disturbing orientation by disrupting the olfactory system of pigeons. The nature of the information that olfactory cues provide were still obscured. To further investigate the idea of olfactory navigation experiments in intact birds were necessary. It should be possible to manipulate the olfactory cues in

such a way that unmanipulated birds would navigate in a predictable erroneous direction. Ialé took a straightforward approach in this and adapted an aviary such that wind directions were reversed (Papi et al. 1974). He hypothesized that pigeons, when adjusted over time to reversed wind directions, would create a mirrored olfactory map and, when subjected to a displacement experiment, would try to home in the opposite direction from actual home. He did this by placing two fans at opposite sides of the aviary. Experimental birds (E-birds) were kept in a screened aviary. Wind would be blocked from the side it arrived on while a fan on the opposite side blew air into the aviary. This effectively reversed the side from which the wind came in. 2 groups of control birds were used. C1-birds had the same set-up as the experimental birds except the fan on the sides corresponded with the actual wind directions, thus effectively changing nothing. C2-birds were exposed to natural winds in an unscreened aviary. A last group, S-birds (screened birds) were kept in a screened aviary with no exposure to wind at all (picture 1). When the pigeons were subjected to a displacement experiment on unfamiliar terrain the control birds' initial bearings were aimed home while the experimental birds chose the opposite direction. The S-birds initial bearings were completely random, supposedly because they could not rely on any spatial information procured from the wind. These results corresponded with Ialé's prediction and gave some very concrete insights into the spatial information the wind can convey. Although this



Picture 1 (reprinted from Ialé et al. 1978): The situation when wind came from the west. Control birds (left) received an artificial wind from the corresponding direction whilst experimental bird (right) would receive a reversed wind. In the middle resided either Control2-birds which were exposed to the actual wind or screened birds that received no wind at all.

experiment itself does not prove the effect of odours it does clearly demonstrate that cues carried on the wind are used by birds to create a map of unvisited areas around the home loft and that an artificial air current can convey these cues. In the light of previous research it is very plausible that the nature of these cues are of an olfactory nature.

The researchers did note something unexpected. The experimental birds' initial bearings were more scattered compared to controls and they took more time to choose their initial bearings. This is interesting as experimental birds were expected to be just as confident about the direction the home loft should be in as the control birds.

### *Using artificial odours results in an artificial map*

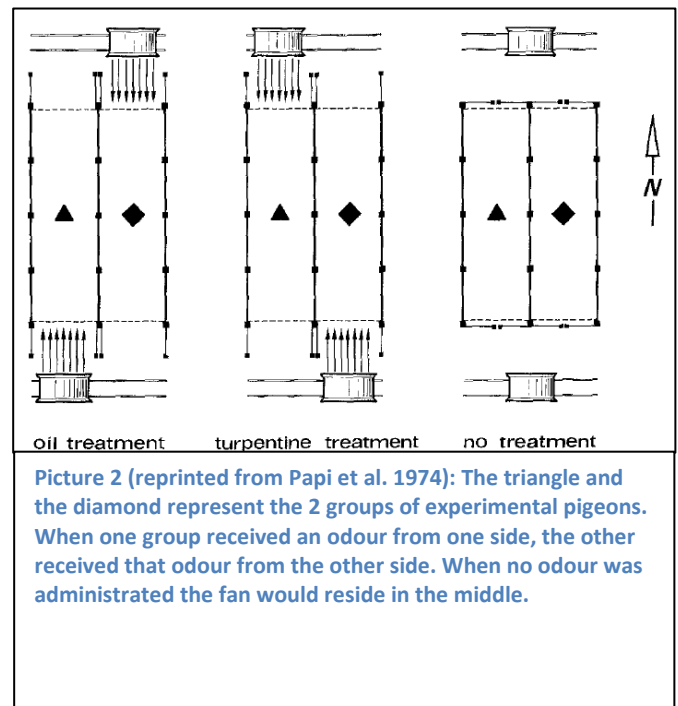
Prove that cues carried by air used by pigeons to create a map are of olfactory nature was given several years earlier by Floriano Papi. He used a similar set-up as laolé, using fans to present pigeons with a manipulated air current, but rather than redirecting the existing winds odours were added to an artificial wind. As the olfactory navigation hypothesis states, birds are expected to incorporate “foreign” odours into their olfactory map. Hence it should be possible to use artificial odours to manipulate the olfactory map. On the other hand it is possible that pigeons use a number of very specific natural odours to create this map.

2 groups of experimental fledgling pigeons were created. These groups were exposed to artificial winds from the north & south. For one group the southern air current contained olive oil and the northern air current contained turpentine and for the other group these were reversed. The birds were excluded as much as possible from natural winds. Pigeons were expected to create an olfactory map based only on the artificial air currents, consequently associating the odours with the direction they are presented from and choosing a homing course accordingly (picture 2).

After 48 days of this treatment the pigeons were subjected to several displacement experiments over unfamiliar terrain. Before release the birds were treated with either olive oil or turpentine on the beak and in the nostrils fooling them into thinking they were in the wind direction they perceived the odour from at the loft.

For example: birds that were treated with olive oil and had learned to associate olive oil with northern winds headed south because they assumed they were displaced north. Regardless the odour, wind direction or direction of displacement all birds chose their course based on the odour they were treated with. Furthermore, these results were consistent on subsequent releases (Papi et al. 1974)

Researchers managed to manipulate pigeons into creating an adapted map, however this map was not a distortion of the real map but an entirely artificial map and based on odourous cues on a wind current.



### *Simulating an existing area*

These experiments have all shown a distinct influence of olfaction in pigeon navigation yet in every experiment either the pigeon or the smellable air was manipulated in exaggerated ways. Because these exaggerated cues do not reflect natural conditions they do not rule out a possible, until now unnoticed site specific information of another nature. An attempt to find and/or rule out this potential influence, a homing release experiment was performed in which pigeons were supplied with natural air from another, existing, location whilst they were deprived from smelling the actual present air on location. This experiment was unsuccessful as transporting sufficient amounts of air was too complex (Baldaccini et al. 1982).

Another experiment was more successful. Pigeons were transported first to a sham release site and exposed to the air for three hours after which the birds were put in charcoal filtered containers and transported to the actual true release site. Charcoal filters are a general means to purify air and water and thus filter odours from air. 1 group of controls were treated in the same way except they were not transported to a second release site. Another group of controls was treated as the experimental birds except they got to breath unfiltered air for three hours. At first glance the results from this experiment was not as convincing as some of the earlier experiments in olfactory navigation yet statistical analysis were decisive by showing a significant effect. Experimental birds did home, but did at a much slower pace than either group of controls birds. Difficulties in this experiment are mainly how to deprive pigeons of natural air during transport and handling. These difficulties may have clouded the results somewhat. (Benvenuti & Wallraff, 1985) The author however concluded that despite this, the experiment did prove that olfactory information alone is sufficient for a navigational effect because solely the location the air came from was altered and thus a secondary physiological effect or exaggerated absence or presence of odours could not be of the influence.

## **Limits on range**

### *Minimum range*

In several experiments anosmic pigeons showed normal homing capabilities at low range even when homing was disrupted at higher range (Papi et al. 1973, Papi et al. 1974, Ialé et al. 1978). One theory is when birds are lost they fly around randomly until they pick up the familiar scent of the home loft. This does not explain why in some experiments anosmic birds were able to home from as far as 30 kilometer from the home-loft as they were not able to smell the home-loft at all. This happened only if the bird in question was an experienced flyer and familiar with the landscape (Papi et al. 1972). Generally it is assumed that any animal with visual capabilities will use landmarks for orientation (Collet & Zeil, 1998) and it has been proven that pigeons try to find familiar landmarks when released from nearby unfamiliar locations and show route loyalty when they do so (Biro, Meade & Guilford 2004). This means that pigeons would rather take familiar routes than faster routes. These findings suggest that anosmic pigeons specifically and pigeons in general are able to use landmarks to home when they are on familiar terrain. Hence visual orientation can be a substitute for olfactory navigation, especially when a bird is released near the home loft. Experiments in other bird species have shown that at least some birdspecies use visual cues for finding and entering their nest, home, food-storage or any special purpose location (Sherry et al. 1996).



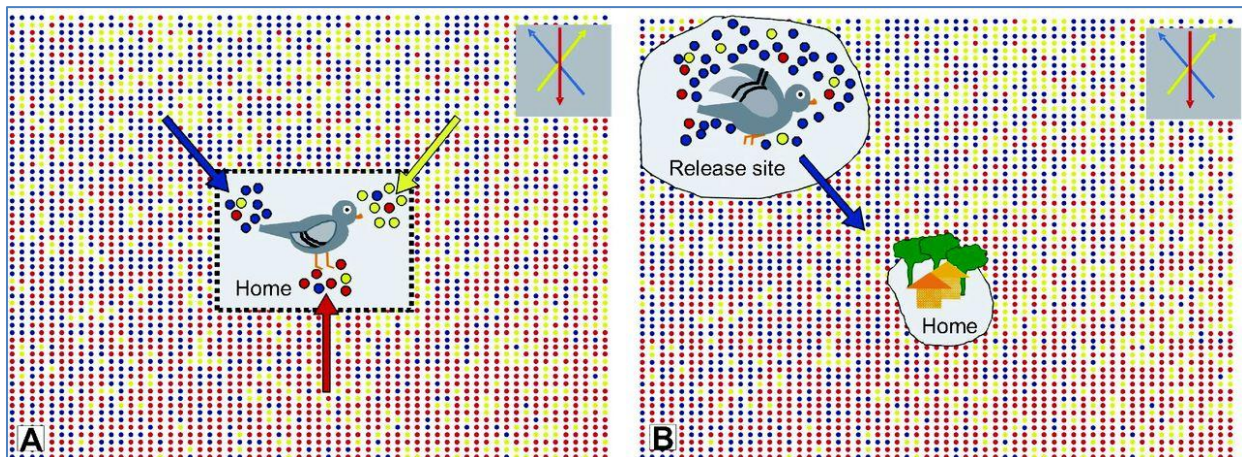
An experiment was conducted in which pigeons were outfitted with opaque lenses (experimental birds) or clear lenses (controls). Most birds were able to home quite well, yet had to be recovered from bushes and fields very close to the actual home loft. These results seem to indicate that visual stimuli are not of explicit importance in pigeons (Schmidt-Koenig & Schlichte, 1972). In another experiment pigeons were either anosmic or not and kept in either: a loft with a view of the surroundings or without such a view. Only pigeons that were both anosmic and deprived of a view were unable to home. When either olfactory cues or visual cues were allowed the pigeons were able to home unimpeded as were the control birds (Gagliardo et al. 2001).

### Maximum range

When thinking of odours as a navigational tool one can quickly deduce that the maximum range at which it is effective is limited. Odours will dilute the further they are carried and as such there is a maximum range at which an odour is reasonably detectable moreover the reason the sense of smell was not considered a possible candidate in bird navigation earlier was because, intuitively, odours do not seem constant enough over even a few miles.

To solve this elementary problem in the olfactory navigation debate, an experiment was set-up in which 96 sites within 200 kilometers of the home-loft were sampled multiple times over a course of three years. Analysis of data showed that a handful of odours existed over a fairly stable gradient over these three years (Wallraff & Andrea, 2000). Next a simulation was created in which virtual pigeons were to navigate using comparable gradients. It was shown that these virtual pigeons were able to home with access to as little as three stable gradients (Picture 3) (Wallraff, 2000).

### Procellariiformes: evidence in an ideal subject



Picture 3 (reprinted from Gagliardo et al. 2012): Visualisation of how an odorous landscape consisting of 3 odours might look. The bird in A learns the ratios at which different odours reach the home-loft. Consequently when it is released away from the home-loft this information is, in theory, sufficient to guide it home.

Under normal circumstances wild-type pigeons, once settled, do not tend to travel fast distances from their home and thus have no need for highly developed homing abilities. These abilities were enhanced through breeding by humans. That means that a genetic basis for olfactory navigation was probably already established in the species genome. In fact navigational traits seem to be easily obtained and lost through evolution by a myriad of bird species and post glacial changes in travel patterns show high evolutionary flexibility in navigational traits. Some species even have migratory as well as non-migratory populations (Mila, Smith & Wayne, 2006). Taking this evolutionary plasticity



into account it is fair to assume that navigation traits in general and olfactory navigation traits specifically are not exclusive to domesticated pigeons but are present in some wild bird species as well.

A good candidate for possession of olfactory navigation abilities are birds in the order of procellariiformes. This order consists of, among others, albatrosses, petrels and shearwaters. Species in this order have some of the best developed senses of smell of all bird species and make long trips between their nests and foraging sites. These foraging sites occur in the ocean which is very uniform both in regards to landmarks as well as odours (Gagliardo et al. 2013). It is plausible that such a fine tuned olfactory system is very versatile and it can be reasoned that if olfactory navigation exists in wild bird species this is the order to demonstrate it most clearly. Therefore Nevitt and Bonadonna (2005) conducted an experiment on antarctic prions, *Pachiptila desolata*. The aim of their research was to demonstrate three principles for investigating olfactory cues in bird navigation. Namely: (1) to identify a potential odorous cue that can provide spatial information that is useful for navigation, (2) to show a physiological reaction to said odour cue and (3) to demonstrate that this odour cue, when in a natural concentration range, can be used for orientation.

Dimethylsulfide (DMS) was identified as a biogenic cue that can potentially be useful for navigation on the open ocean as it is one of the most occurring odorous gasses on the ocean. DMS is produced by phytoplankton, is scented and its global distribution has been extensively researched and described in global climate regulation research. A physiological reaction by Antarctic prions to DMS was successfully demonstrated by monitoring heart rate while presenting DMS to birds. All ten subjects showed a significant rise in heart rate ( $p < 0.01$ ). To demonstrate the last principle Nevitt and Bonadonna placed birds in the end of a closed Y-shaped maze. Through one arm of the maze flowed air enriched with DMS. Through the other arm flowed air enriched with ethylene glycol. Birds were expected to navigate towards the air current with DMS because this is the familiar smell of the ocean whereas ethylene glycol is not. Ethylene glycol was used to make birds choose between two odours instead of choosing between DMS and odourless.

Twenty-five birds were tested in this setup of which 17 oriented towards the arm with DMS, three to the control and five failed to make a choice (Nevitt & Bonadonna, 2005).

This experiment as the authors put it: “provides the most comprehensive demonstration to date that an animal can detect a naturally occurring odourant potentially useful for orientation and navigation over oceans.” This research did not prove the existence of olfactory navigation in procellariiformes but it did lay a basis for further research on olfactory navigation in procellariiformes.

Another species in this order underwent further research. Twenty-four Cory's shearwaters, *Calonectris borealis*, were outfitted with gps-trackers and released 800 km away from their breeding location. Eight of these birds were made anosmic through a zinc-sulphate nasal wash, another eight were outfitted with small magnets to test the effect of the geomagnetic field and another eight acted as controls. All controls made it back in five days, as did the magnetically manipulated birds except for one. Of the anosmic birds only two returned home. These birds took around two weeks to do so (Gagliardo et al. 2013). This experiment demonstrated impaired homing through anosmia in wild birds and it also raised Wallraff's demonstrated potential range of 200 kilometer to 800 kilometers.

## Evidence in a migratory species

When talking about bird navigation in general one quickly and mainly thinks about migratory birds. Unfortunately relatively little research has been done on olfactory navigation in migratory birds. Three bird species have been addressed in this: swifts, *Apus apus*, starlings, *Sturnus vulgaris*, and catbirds, *Dumetella carolinensis* (Fiaschi, Farina & Ioalé, 1974, Wallraff et al. 1994, Holland et al. 2009).

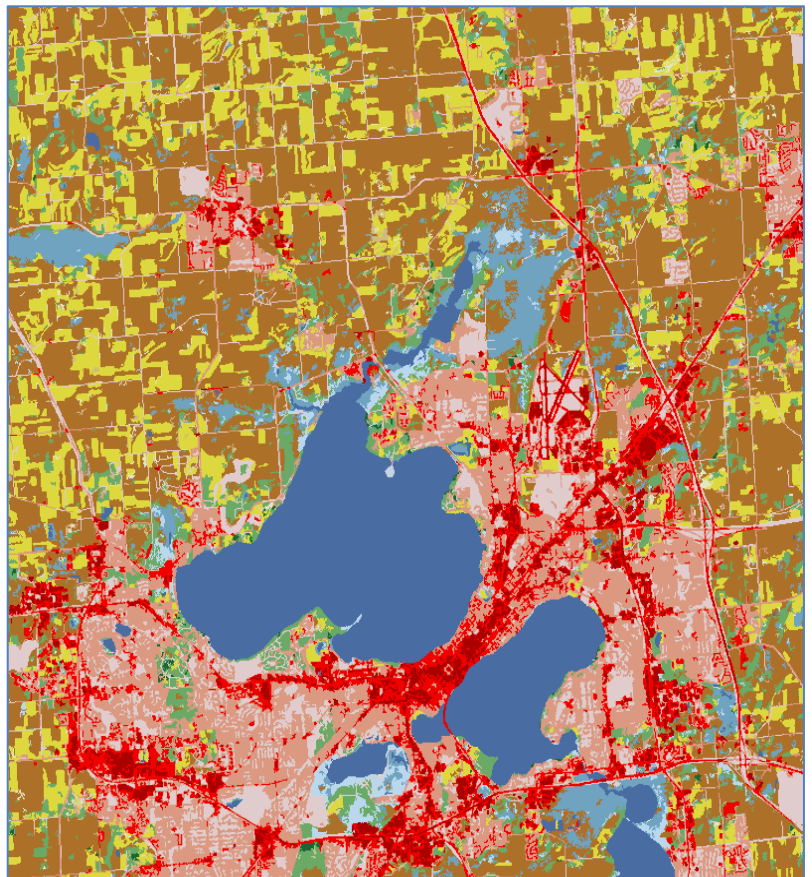
In all three experiments a number of anosmic and control birds were allowed to migrate. Navigation in migratory birds differs from that in the investigated homing pigeons or procellariiformes in that migration occurs during two specific moments in the year. That being said: in every experiment the results were comparable with those found in pigeons and procellariiformes. Anosmic birds were heavily impeded in their navigational capabilities.

In the experiment regarding starlings Wallraff interestingly notes that swifts apparently have a small olfactory apparatus (Bang, 1971), yet the control birds were able to migrate to the intentional location when displaced 240 kilometers away from their normal starting point, whereas anosmic birds could not. This suggests that they use this small olfactory apparatus for effective navigation (Wallraff et al. 1994).

In the migratory catbird experiment both naive birds on their first journey and experienced birds were outfitted with gps-trackers and were made anosmic, got magnetic interference, or acted as controls. Experienced magnetically manipulated and control birds all flew straight south-west. This normal migratory behaviour suggests that geomagnetism does not influence navigation in this species. Experienced anosmic birds and all naive birds flew south indicating that experienced birds deprived of smell turn to strategies used by naive birds. Because the ocean is due south from the normal starting point the author pointed out that olfactory navigation in this case might be as simple as trying to avoid the sea by smelling it ahead. (Holland et al. 2009)

## Maps, plumes and patches

Many speculations have been made about the nature of the olfactory map. The olfactory navigation hypothesis states that birds create an olfactory map based on the winds that arrive at the home loft and the odours they carry (Papi et al. 1972). Also proposed was a patchy map, see picture 4, also called a topographical map



Picture 4 (reprinted from author unknown, 2006): Visualisation of a patchy odorous landscape. Birds possibly identify their location by smelling the current patch they fly over and comparing that with subsequent patches they passed. Every colour in this example references a patch with a typical smell. Within these restrictive amount of colours subtle differences might be perceived by birds such that the actual patchy map might be a much more elaborate map than these colours can provide.

or mosaic map. Such a map would be learned during random flights over unfamiliar terrain. During these flights a bird would learn to associate different odours with different locations and create a patched maps on which each patch would have it's own distinct odour (Papi et al. 1972).

The odour plume (picture 5) is possibly the most basic explanation of olfactory navigation. It is based on how some male moths find female moths. These moths detect pheromones emanating from a female they follow a process of trial-and-error in which they zigzag until they can follow a gradient towards the female (Hansson, 1995). This method of navigation is perhaps translatable to bird navigational behaviour.



Picture 5 (reprinted from author unknown, 2014): Example of an odourous plume. The intensity of the odour diminishes over distance. The most intense area being the red part which is near the source of the odour. The blue area is where the odour is diluted the most and therefore the least intense. Further out from the blue the odour is considered not perceivable.

Odourous plumes potentially used in olfactory navigation could be far larger than this example.

## Discussion

Given all accumulated evidence it is hard to deny the existence of a form of olfactory navigation. Birds deprived of discernible winds or the ability to smell birds show greatly diminished homing capabilities. The main objections given concern a possible secondary effect of certain treatments or a simple demotivation to fly in anosmic birds. These secondary effect have been invalidated numerous times through numerous ways and as such the likelihood of such secondary effects existing have grown increasingly unlikely. Likewise through modern tracking technology a possible demotivation to fly has been proven to be plainly non-existent.

### *Plausibility of the olfactory navigation hypothesis*

In the olfactory navigation hypothesis two basic principles are stated. 1- Homing pigeons create a “map” by picking up scents that are carried to the home loft by wind. This principle has been thoroughly tested by presenting false cues. Tested homing pigeons showed expected erroneous behavior. This gave strong evidence that the hypothesis is correct about how pigeons create their maps. Therefore I conclude that the existence of an olfactory map is proven 2- Homing pigeons need

time to create this map. Pigeons need over a month at the home-loft before they show sound homing abilities. This only follows reason as birds need a substantial amount of wind from all directions to be sure of the prevalently occurring odours.

In the case of the olive oil and turpentine experiment it may seem that birds use only one odour that is typical for that specific wind direction. This is an exaggerated response to exaggerated input. In a natural situation such situations are rare. Therefore it is plausible, but not without doubt, that pigeons pick up gradients of multiple odours to create a vector of the direction and distance the home-loft is in. This was demonstrated with virtual pigeons. Unfortunately when push comes to shove: nobody really knows how birds utilize olfactory spatial information.

### *A patchy map for familiar terrain*

The idea of a patchy map was formulated early in olfactory navigation research and does not account for many results obtained later (Papi et al. 1972). It certainly can not explain homing capabilities over unknown terrain because to create a patchy map the pigeon should have visited or passed over the patch to incorporate it in its map. The idea of a patchy map was mainly conceived to account for the effective (unlikely high) range of olfactory navigation. Wallraff specifically showed that this range is actually much higher than initially expected (wallraff & Andrea, 1999, Wallraff, 2000).

As a parallel existing strategy the patchy map can not be excluded. A pigeon could be able to use it on familiar terrain. A migratory bird might use it on subsequent flights to identify certain stages of the journey although visual cues, like landmarks, are likely more effective for such strategies.

### *A guiding odourous plume*

An odourous plume emanating from a specific source like a patch of food or home could direct a bird over unfamiliar terrain. This only works when the wind direction is coming directly from the goal and would not account for persistent correct initial bearings in most experiments. That means this explanation is not sufficient for olfactory navigation as a whole yet if a displaced pigeon picks up the well-known scent of the home-loft it could allow the pigeon to forgo more advanced navigational strategy's. The ability to follow an odourous plume could be a simplified component of olfactory navigation.

### *If you can smell it then use it*

Identifying potential useful odours for olfactory navigation is a recurring theme in many experiments. Up to this point almost every odour presented to birds has given an effect in olfactory navigation research (Gagliardo, 2012, Holland et al. 2009), This included anthropogenic odours. This makes sense when considering the plasticity of the odourous map (see below). When one has a navigational strategy based on odours, why not use any odour that provides spatial information?

### *Is olfactory navigation alone sufficient for navigation?*

Olfactory navigation does not seem to be sufficient for homing. Without visual stimuli pigeons can approach the home loft up to 50 meters. (Schmidt-Koenig & Schlichte, 1972). Without olfactory stimuli pigeons are consistently able to home from up to 30 kilometers.(Papi et al. 1972) This leaves an overlapping range at which both visual and olfactory stimuli are effective for homing (picture 6). It is possible that using landmarks for navigation is complementary rather than a substitute for olfactory navigation. Using wind-borne odours is a good way over higher range distances to give a



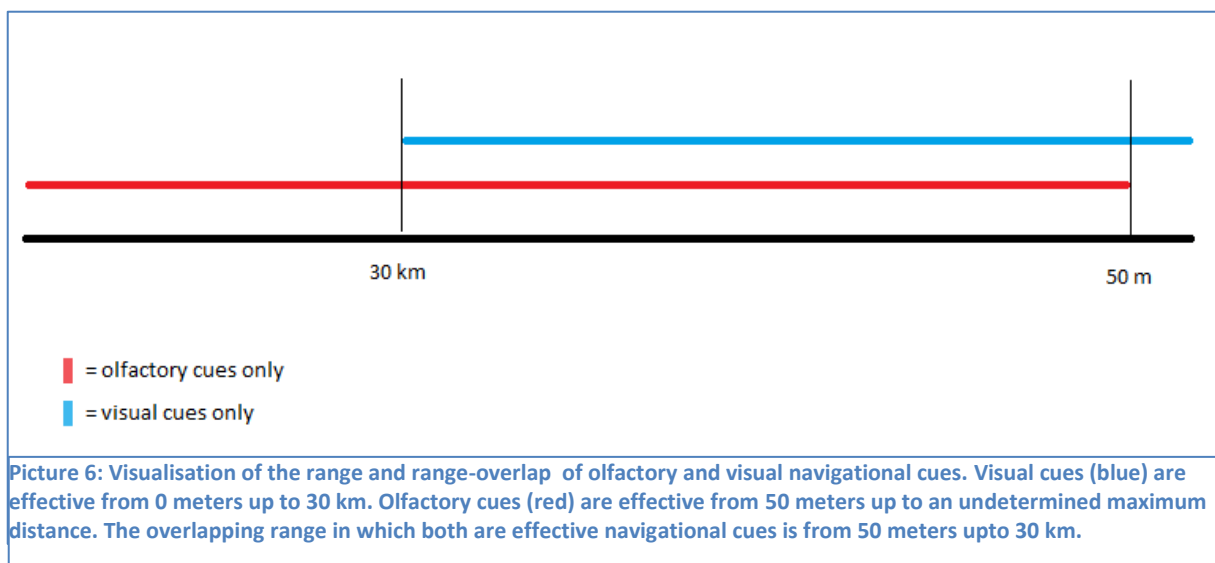
general direction of the home-loft. When approaching a goal, giving the gradual nature of odour intensity, it should become harder to choose the correct direction the goal is in. So when approaching the home loft pigeons should have a system besides olfactory navigation to find the home loft or else risk the possibility to fly around constantly following fluctuating gradients of odours. Within this possible range of 50 m to 30 km there exists an optimal suitable point at which to change from olfactory to visual navigation to minimize navigational stress. They might do this as soon as they recognize landmarks near the home-loft as pigeons show extensive route loyalty near the home-loft.

The maximum range at which olfactory cues are useful is unknown as this range has been proven to be higher than expected multiple times and no maximum range has yet been recorded in any discussed species. This maximum range might even be higher than the actual useful range turning a complementary navigational strategy for high range redundant.

One last thing that has not been touched upon is compass calibration. When pigeons have learned to associate a specific odour with north at the home-loft and are presented with this odour at a windless release point, then they need to determine what is south before they can navigate home.

Much has been discussed on this point and evidence suggests that both celestial and magnetic cues can be useful for this (Muheim, Phillips & Akesson, 2006, Wiltschko & Wiltschko, 2005).

In any case there are other navigational systems in place as in some experiments pigeons that were manipulated would hesitate in choosing their initial bearings where they should have been as decisive as control birds (laolé et al. 1978). This suggests something confused the birds when confronted with a mirrored olfactory map. The nature of these cues is unknown but it was secondary to the olfactory cues as, in the end, birds followed the olfactory cues.



### *An evolutionary urge to learn*

Clearly the endogeneous need to form an olfactory map has a genetic basis. We are still in the dark about the specifics of this urge but it is clearly present in most, if not all, individuals from tested populations. Note that only the urge is inherited. Theoretically speaking an olfactory map could be hereditary but pigeons need over a month to form a reliable olfactory map. Other evidence comes from catbird experiments, where experienced anosmic birds showed the same migratory headings as naive birds on their first flight. This suggests that anosmic experienced birds had to rely on strategies they utilized before they could incorporate experiences from former journeys.

Though it takes time to form a fully functional map, the map should keep a certain degree of plasticity. Odours and their long distances might be quite stable, but in the long run they do fluctuate. Be it between seasons, over the years, across generations or through sudden change: an inherited or young established olfactory map could very well be outdated within a generation. Birds should be able to correct for change in the olfactory landscape. On the other hand: one experiment with pigeons noted a persistence of the odourous map (Papi et al. 1974). This persistence occurred within a small time-frame of several weeks. A olfactory map as plastic that it can change within days would be of little use. The optimal olfactory map adjustment rate strikes the golden mean. The plasticity of the olfactory map can also account for the wide choice of usable odours.

### *Olfactory navigation: does it exist in nature?*

As has been said: pigeons be rapidly selected for olfactory navigational skills by breeders, and thus may not be the best model organism in this field, yet the same principles have been demonstrated in both procellariiformes and migratory birds. This suggests that even though skills of pigeons have been “man-bred” the same genetic basis is present as in wild birds. Even though the idea of olfactory navigation has met much skepticism it has grown to be a highly probable explanation for the bird navigation problem. Especially as the more traditional geomagnetism and celestial cues navigation theories have been more and more proven to be mere calibrating tools for actual navigational mechanisms (Holland et al. 2009, Nevitt & Bonadonna, 2005)

Unfortunately most research in this field has been conducted by a relatively small group of researchers. Without wanting to detract from their scientific prowess this does mean that they might show a predisposition to “their” theory. This does not mean their findings are incorrect attention should be given to reviewing these findings by outside scientists.

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