Testing the role of sensory systems in the migratory heading of a songbird

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SUMMARY

The identification of the sensory cues and mechanisms by which migratory birds are able to reach the same breeding and wintering grounds year after year has eluded biologists despite more than 50 years of intensive study. While a number of environmental cues have been proposed to play a role in the navigation of birds, arguments still persist about which cues are essential for the experience based navigation shown by adult migrants. To date, few studies have tested the sensory basis of navigational cues used during actual migration in the wild: mainly laboratory based studies or homing during the non-migratory season have been used to investigate this behaviour. Here we tested the role of olfactory and magnetic cues in the migration of the catbird (*Dumetella carolinensis*) by radio tracking the migration of birds with sensory manipulations during their actual migratory flights. Our data suggest that adult birds treated with zinc sulphate to produce anosmia were unable to show the same orientation as control adults, and instead reverted to a direction similar to that shown by juveniles making their first migration. The magnetic manipulation had no effect on the orientation of either adults or juveniles. These results allow us to propose that the olfactory sense may play a role in experience based migration in adult catbirds. While the olfactory sense has been shown to play a role in the homing of pigeons and other birds, this is the first time it has been implicated in migratory orientation.

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INTRODUCTION

The spectacular transcontinental migration of animals is a subject that has fascinated humanity for millennia, but despite intensive study, many aspects of migration remain unresolved (Alerstam, 2006). In particular, migrating songbirds make journeys of thousands of miles, and often return to the same breeding and wintering grounds year after year (Newton, 2007), but the question of how they achieve this remarkable feat remains open to debate (Berthold, 2001; Wiltschko and Wiltschko, 2003; Wallraff, 2005). It has been demonstrated that some juvenile songbirds have an inherited species specific compass direction to reach their wintering grounds on their first journey (Berthold, 1991). However, this may result in a failure to reach their normal winter range if they are displaced large distances (Perdek, 1958). Adult migratory birds appear to be able to recognise and correct for such displacements, and head back to their normal winter range (Perdek, 1958; Thorup et al., 2007; Chernetsov et al., 2008). It has been argued that this ability to recognise their direction of displacement and correct over distances that outstrip their familiar range represents an example of true navigation (Bingman and Cheng, 2006), originally defined by Griffin (Griffin, 1952) as 'type III' navigation. This is the ability to find the way to a known goal across unfamiliar terrain, 'the ability to choose approximately the correct direction to its goal when carried in a new and unaccustomed direction'. True navigation has become the holy grail of research in orientation and navigation and more than 50 years of research effort have been expended on trying to

discern the sensory cues and mechanisms used by animals to locate their position to a known goal from an unfamiliar area (Wiltschko and Wiltschko, 2003; Wallraff, 2005; Phillips et al., 2006). It is thought to be achieved by referring to environmental cues which vary predictably in their intensity or concentration over a large, if not global, scale (Bingman and Cheng, 2006). While this has been the focus of much research on navigation ability in animals and is certainly the most spectacular feat they could achieve, in practice, return migrants have the opportunity to learn from their experience of the route travelled and may possess a hierarchy of cues which come into play at different spatial scales (Bingman and Cheng, 2006). Despite these theoretical constructs, in practice even the sensory cues necessary to achieve true navigation are still uncertain, let alone the mechanisms (Newton, 2007).

A number of cues have been proposed to play a role in the location of position by migrating birds: celestial cues, i.e. the sun (Matthews, 1953; Pennycuick, 1960) and the stars (Sauer and Sauer, 1960) have been proposed to allow the determination of both latitudinal and longitudinal position. Current evidence does not support their use in this way, however, but rather indicates they act as a compass (Wallraff, 2005). Infrasound has been proposed to play a role in the navigation of homing pigeons (Hagstrum, 2000; Hagstrum, 2001), but so far only correlative evidence based on disturbance of orientation exists. The intensity and/or inclination of the Earth's magnetic field could be used to determine latitude (Phillips, 1996), and it has also been argued that the difference between magnetic

north and geographic north (i.e. declination) could allow birds to distinguish longitude, at least over distances where there are large discrepancies between the two (Phillips et al., 2006). In migratory birds, the results of a simulated magnetic displacement experiment suggest that magnetic cues may play a role in the determination of latitude (Fischer et al., 2003). A second line of evidence that magnetic cues play a role in migratory navigation comes from treatments involving strong, brief magnetic pulses. These are thought to disrupt magnetite based magnetoreception (Kirschvink et al., 2001). When a pulse perpendicular to the normal geomagnetic field is applied to adult birds, reorientation results when their migratory restlessness is measured (Wiltschko et al., 1994; Beason et al., 1995; Wiltschko and Wiltschko, 1995; Beason and Semm, 1996; Wiltschko et al., 1998). While the direction of the response is not always predictable from the direction of application of the pulse (Wiltschko et al., 1994; Wiltschko et al., 1998), the effect relative to controls is always clear. The pulse has no effect on juvenile migratory birds (Munro et al., 1997b) and does not appear to prevent compass orientation (Wiltschko et al., 2006).

Another environmental cue which has been proposed to play a role in navigation are environmental odours and it has received extensive experimental testing in the homing pigeon (Benvenuti et al., 1973; Papi et al., 1973; Papi, 2001; Wallraff, 2005). The data indicate that olfactory cues are required for successful homing in pigeons. The olfactory navigation hypothesis argues that homing pigeons build up a navigational map by associating the olfactory information carried by the winds to the home area with the direction from which they come. Once at the release site pigeons are able to determine the direction of displacement by recognising the prevalent local odours. If they detect the odour that is normally associated with a north wind, for example, they assume they have been displaced north and fly south. While two migrant bird species have been shown to be unable to home to their nest during the breeding season if their olfactory sense is removed (Fiaschi et al., 1974; Wallraff et al., 1995), the question of whether olfactory cues play a role in the navigation of birds during migration has not been tested. Indeed, it is thought that navigation over thousands of kilometres is unlikely to be based on olfactory cues, given atmospheric constraints (Bingman and Cheng, 2006). Wallraff, however, has proposed that it may play an intermediate role in conjunction with the inherited migratory programme (Wallraff, 2005).

One of the problems with investigating the sensory cues used in bird migration has been the difficulty of testing small songbirds in a natural setting (Wikelski et al., 2007). Development of the technique of fitting migratory birds with radio transmitters and following them for approximately 100 km as they continue to migrate, however, finally allows for the study of the sensory cues used by migrating birds during migration (Thorup et al., 2007). The aim of this study was to address this unresolved issue by observing the behaviour of a migratory songbird after sensory manipulation to provide the first test of the cues used for migration in the wild.

MATERIALS AND METHODS
Experimental animals
New Jersey
Catbirds (*Dumetella carolinensis* L.) were caught by mist netting at Stony Ford field station, Princeton, NJ, USA, during autumn migration from 16/9/07 to 29/9/07. Birds were separated into adults and juveniles and then into one of three groups with 8 individuals in each group: olfactory manipulated, magnetic manipulated, or controls. Thus a total of 48 birds (24 adults and 24 juveniles) were used in this part of the experiment.

Illinois
A total of 19 adult catbirds were caught in Illinois between 22/9/07 and 26/9/07. This allowed for the displacement by car of 6 controls, 8 olfactory manipulated and 5 magnetic manipulated adult birds to New Jersey (a distance of 1095 km), where the birds were released. Only 2 juveniles could be caught during the period of netting in Illinois and so no juvenile birds were displaced.

Experimental treatments
Olfactory manipulated birds received an intranasal treatment with 2–2.5 ml of 4% $ZnSO_4 \cdot 7H_2O$ solution. It has been demonstrated that comparable solutions briefly applied on the olfactory mucosa induce degeneration of the olfactory cells without affecting the basal cell layer in the catfish *Ictalurus punctatus* (Cancalon, 1982). Moreover it has been shown that a nasal wash with even a 2% zinc sulphate solution is able to suppress or diminish a cardiac response to a strong odour stimulation in pigeons (Benvenuti et al., 1992). By using a combination of intranasal zinc sulphate treatment and either contralateral or ipsilateral nasal plugging, Benvenuti and Gagliardo (Benvenuti and Gagliardo, 1996) demonstrated that zinc sulphate treatment specifically produced a navigational impairment due to the lack of access to olfactory information in homing pigeons. Only those birds with zinc sulphate treatment in one nostril and the contralateral nostril plugged were impaired in homing.

Magnetic manipulated birds received a strong brief pulse from an SCR-fired capacitive discharge unit (a SOTA[TM] magnetic pulser, Sota Instruments, Penticton, BC, Canada) modified by the addition of a double-wrapped, 10 cm diameter Lee Whittling coil (Kirschvink, 1992). The coil system produced a unidirectional magnetic pulse of ~0.1 ms duration, with peak amplitude slightly over 0.1 T, and a rise time of ~100 ns. The pulse was administered from a solenoid aligned perpendicular to the Earth's magnetic field, applied 'south anterior' as defined by Beason and colleagues (Beason et al., 1995). A pulse of this strength is sufficiently large to overcome the coercivity of all known biogenic magnetite and thus re-magnetise it in the direction of the applied pulse (Dunlop, 1981; Kirschvink, 1983). Control birds were left untreated. New Jersey birds were treated immediately upon capture. Illinois birds were treated in Illinois and then transported by car overnight to New Jersey.

Tracking procedure
After being treated, each bird was fitted with a 0.9 g, 164 MHz radio transmitter (Holohil Systems, Carp, Ontario, Canada) placed on its back 3 cm from the head, and immediately released at the Princeton University Field station, NJ, USA. Upon release birds were monitored from a ground based tracking vehicle until they could not be located at the field station, at which point they were located from a Cessna 152 or 172 aircraft as many times as possible over the duration of the experiment using the same technique as in Thorup et al. (Thorup et al., 2007). From this, a final bearing at which the animal was last located before being lost was obtained.

Analysis
GPS locations obtained from the aerial survey were plotted in Google Maps©. From this the bearing from the capture site was calculated and mean bearings, vector lengths and statistical differences between groups were calculated using Oriana 3.0© (Kovach Computing services, Anglesey, UK). Significant orientation was tested by the Rayleigh test as a baseline for further analysis and all groups showed orientation significantly different from random (Rayleigh test, $P<0.01$ all cases, Table 1). Statistical differences between groups were calculated using the Watson–Williams test, which is a

parametric test for angular differences between samples, and the Mardia–Watson–Wheeler test for differences in distribution of the samples (Batschelet, 1981).

Approval
This work was approved by Princeton University Institutional Animal Care and Use Committee, New Jersey Fish and Wildlife Services and the Illinois Natural History Survey.

RESULTS
New Jersey birds
Adult migrating catbirds flew southwest during their autumn migration through New Jersey. This direction differed from the more southern direction displayed by the juveniles (Fig. 1A,B; New Jersey control adults $N=6$ vs control juveniles $N=5$; Watson–Williams test, $F_{1,9}=15.163$, $P=0.004$).

Adult anosmic birds captured while migrating through New Jersey migrated in a southern direction different from the south-western one shown by both adult magnetic treated and control birds and similar to the one shown by juveniles. There was a significant difference between adult anosmic birds and adult control and magnetic birds (Fig. 2A,B; Watson–Williams test; anosmic $N=5$ vs control $N=6$, $F_{1,9}=7.426$, $P=0.023$; anosmic $N=5$ vs magnetic $N=8$, $F_{1,11}=6.655$, $P=0.026$). There was no significant difference between adult control birds and adult magnetic treated birds (Fig. 2A,B; Watson–Williams test, $F_{1,12}=0.047$, $P=0.831$). There was also no significant difference between adult anosmic birds and juvenile controls (Watson–Williams test, $N=10$, $F_{1,8}=0.551$, $P=0.479$). There was no significant difference between New Jersey juveniles in any comparisons among the three groups of juveniles (Fig. 3A,B; Watson–Williams test; anosmic $N=8$ vs control $N=5$, $F_{1,11}=2.204$, $P=0.166$; control $N=5$ vs magnetic $N=5$, $F_{1,8}=0.814$, $P=0.393$; anosmic vs magnetic, $F_{1,11}=0.649$, $P=0.438$).

Illinois birds
Birds displaced from Illinois to New Jersey (a displacement of 1095 km) showed a very similar pattern to that found in the birds captured locally in New Jersey. As found in non-displaced birds, adult birds captured in Illinois and transported to New Jersey showed a significant difference between the mean direction of migration in adult anosmic and adult control and magnetic treated birds (Fig. 4A,B; Watson–Williams test; anosmic $N=6$ vs control $N=5$, $F_{1,9}=7.784$, $P=0.021$; anosmic $N=6$ vs magnetic $N=5$, $F_{1,9}=14.108$, $P=0.005$; control vs magnetic, $F_{1,8}=0.00004$, $P=0.977$). Because there was no difference between New Jersey and Illinois adult magnetic treated and control birds, they were combined for further analysis. There was a significant difference between New Jersey magnetic/control birds and Illinois magnetic/control birds (Fig. 5; Mardia–Watson–Wheeler test, $N=24$, $W=8.19$, $P=0.017$; only marginal significance was present in the parametric Watson–Williams test, $N=24$, $F_{1,22}=3.326$, $P=0.082$). Our data on catbirds indicate the possibility that the effect of the zinc sulphate lasts as long as 24 days. Only two birds in total did not show orientation that appeared to be like that of the juveniles in either Illinois or New Jersey birds at the final bearing (supplementary material Table S1).

Migration timing and speed
There was no significant difference between the number of days from capture to the start of migration in the adult treatment groups (ANOVA: $N=43$, $F_{2,42}=2.269$, $P=0.117$) or juvenile treatment groups (ANOVA: $N=24$, $F_{2,23}=1.258$, $P=0.305$), indicating that no treatment differentially affected the motivation of the birds to start migrating.

There was no significant difference in migration speed between treatments in any group (Fig. 6; Illinois, $F_{2,13}=2.773$, $P=0.099$; New Jersey adults, $F_{2,16}=0.072$, $P=0.931$; New Jersey juveniles, $F_{2,16}=0.369$, $P=0.698$).

DISCUSSION
Our study reveals a number of important findings. Firstly, adult migrating catbirds displayed a different heading to juveniles during their autumn migration through New Jersey. The direction taken by control adults results in their avoiding crossing the Delaware bay, whereas juveniles fly south into Cape May, which means they must make a crossing over the sea, or head back north to cross the river at a narrower point. This may be the result of adults having learned from previous experience to avoid the sea crossing. Secondly, the data indicate that zinc sulphate anosmia impairs the ability of adult migratory catbirds to take up the same migratory heading displayed
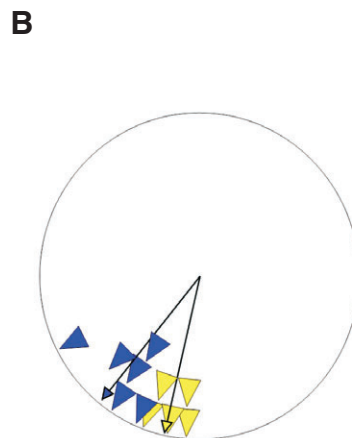

Fig. 1. (A) Tracks and (B) circular diagram of orientation of adult and juvenile catbirds captured in New Jersey. Blue, adults; yellow, juveniles. Arrows in B and all subsequent circular diagrams represent mean bearing and vector length (with the edge of the circle as $r=1$).
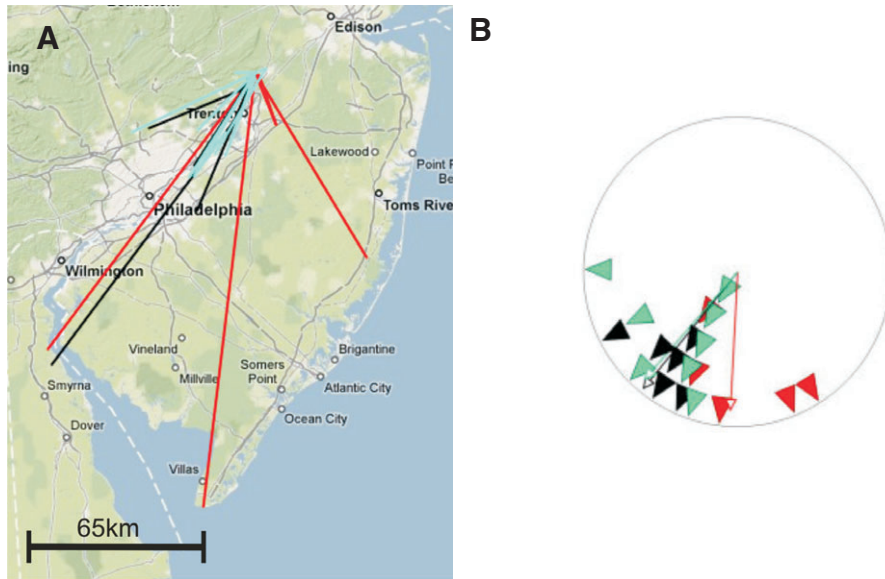
Fig. 2. (A) Tracks and (B) circular diagram of adult birds captured in New Jersey. Black, control; green, magnetic treatment; red, anosmic treatment.

by control adults, in the case of both those migrating through New Jersey and those displaced from Illinois. Thirdly, the heading displayed by New Jersey anosmic adult catbirds is not different from that of juvenile catbirds, indicating that they may revert to a species specific inherited direction when treated with zinc sulphate. In the case of the Illinois birds it is difficult to draw the firm conclusion that the behaviour of adult controls in this group represents correction for displacement, especially given the convergence of angular direction with that of New Jersey adult control birds (although we note that the two groups are different by statistical analysis). Nor is it possible, therefore, to be sure that the reversion to a southerly heading in the Illinois anosmic group represents a reversion to an inherited compass direction, but the similarity in the pattern of response between New Jersey and Illinois birds indicates the possibility of a similar effect in the two groups.

These results thus indicate the possibility that olfactory cues may play a role in the experience based migratory direction of adult catbirds, although exactly what role olfactory cues play in the migration of catbirds cannot be determined from our experiments. Differential effects of sensory manipulations on adults and juveniles are generally assumed to affect a navigational map (Munro et al., 1997b; Munro et al., 1997a). We would urge caution in assuming a navigational effect of the removal of olfactory cues at this stage, because the demonstration of a navigational role for olfactory cues in the map of homing pigeons has required a 30 year research programme (Wallraff, 2005). We do note, however, that the lack of an effect of zinc sulphate anosmia on juvenile birds indicates that there is no non-specific effect of this treatment. The lack of a difference in migration speeds between groups also argues against an effect of motivational differences. Intra-nasal olfactory treatments have also been criticised as potentially affecting non-olfactory peripheral sensory structures, e.g. the ophthalmic branch of the trigeminal nerve. This nerve is located in the same region and has been postulated to be responsible for the detection of magnetic intensity (Beason and Semm, 1996; Mora et al., 2004) *via* its innervation of magnetite containing cells in the upper beak of
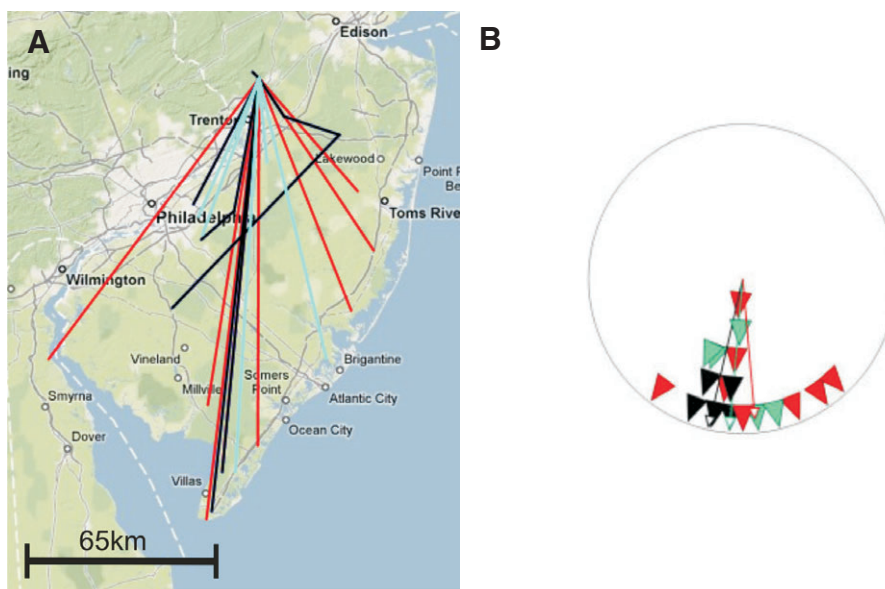

Fig. 3. (A) Tracks and (B) circular diagram of juvenile birds captured in New Jersey. Black, control; green, magnetic treatment; red, anosmic treatment.
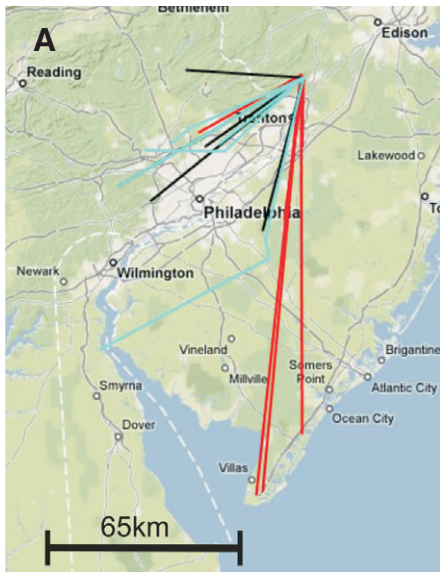
Fig. 4 (A) Tracks and (B) circular diagram showing directions of adult birds captured in Illinois and displaced to New Jersey. Black, control; green, magnetic treatment; red, anosmic treatment.

homing pigeons (Fleissner et al., 2003). This is an important consideration, although subsequent experiments on homing pigeons have indicated that only the olfactory nerve plays a role in the homing of pigeons, not the trigeminal nerve (Gagliardo et al., 2006; Gagliardo et al., 2008). It should be noted that we do not use Xylocaine, a local anaesthetic, as was used by Mora and colleagues (Mora et al., 2004), but zinc sulphate, which is a treatment targeted specifically at the olfactory mucosa, which destroys the olfactory epithelia while leaving the underlying nervous structure intact (Cancalon, 1982); and, unlike Xylocaine, it provides no evidence of systemic effects, as shown by Benvenuti and Gagliardo (Benvenuti and Gagliardo, 1996). These authors exposed homing pigeons to unilateral nasal treatment with zinc sulphate and either ipsilateral or contralateral nasal plugs. These procedures demonstrated that only those birds with contralateral plugs were impaired in homing. Of future importance if zinc sulphate is to continue to be used as a treatment for removing the olfactory sense in studies such as these would be captive studies of song birds to clarify the dose–response and time course of recovery, such as in the study of Cancalon (Cancalon, 1982) on catfish.

Two recent papers have indicated that in homing pigeons, olfaction may play a priming role rather than a direct navigational role in some circumstances, with the detection of 'non home' odours activating other cues for navigation (Jorge et al., 2009a; Jorge et

al., 2009b). Contrary to this, other experiments in which the olfactory information was manipulated by providing artificial odours and experiments in which the direction of the natural air flow was changed provide evidence for a specific role of olfactory cues in the navigational map (Wallraff, 2005 and references therein). However, in our experimental set up, it was not possible to distinguish between an activation and a navigational role for olfaction.

Other interpretations of the effects of zinc sulphate include the possibility that the birds use their sense of smell to avoid the sea coast, or that the adults use their sense of smell in some way to correct for wind drift. It is known that in some migrating birds adults, but not juveniles, correct for wind drift during migration (Thorup et al., 2003). Correction for wind drift is generally thought to be achieved by observing the flight path in relation to landmarks

Fig. 5. Circular diagram of New Jersey and Illinois adult control and magnetic birds combined. New Jersey, black; Illinois, green.
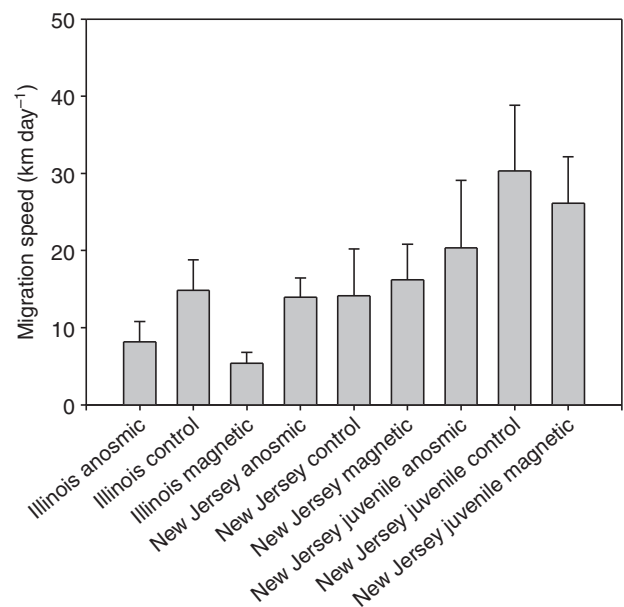

Fig. 6. Migration speeds of catbirds in each group. Means and standard errors are shown. Illinois adults, $N=14$, New Jersey adults, $N=17$, New Jersey juveniles, $N=17$.

Table 1. Mean bearing, vector length and significance for each group tested in the study

Group	Mean bearing	Vector length	Rayleigh test
Adult			
New Jersey control	218.912°	0.977	$P<0.0001$
New Jersey anosmic	182.678°	0.898	$P=0.009$
New Jersey magnetic	221.288°	0.924	$P<0.0001$
Illinois control	235.05°	0.907	$P=0.008$
Illinois anosmic	191.907°	0.932	$P=0.001$
illinois magnetic	235.446°	0.983	$P=0.002$
Juvenile			
New Jersey control	192.599°	0.994	$P=0.001$
New Jersey anosmic	175.006°	0.913	$P<0.0001$
New Jersey magnetic	185.392°	0.968	$P=0.003$

(Alerstam, 1979) and so the exact mechanism by which olfactory cues might achieve this is unknown. Because we could not locate each bird every day during the experimental period, an analysis of wind drift was not possible in this experiment, but further investigation is warranted. It would be of particular interest to know whether juvenile birds are affected during spring migration, which would be a further indication that the effect was based in some way on experience from the first migration.

The magnetic pulse treatment had no discernible effect on the orientation of either adult or juvenile birds. On the basis of previous experiments, no reaction would be expected from the juveniles (Munro et al., 1997b), but orientation cage experiments have indicated an effect on orientation in adults compared with controls. Only two experiments have tested the effect of pulses in the field: a homing pigeon study indicated a weak effect of magnetic pulses (Beason et al., 1997); and a study on homing bats indicated a clear difference between controls and the critical experimental group (Holland et al., 2008). A number of other field studies in birds have also failed to show an effect of magnetic treatments, which might raise the question of how important the magnetic field is to animals for long distance navigation (Benhamou et al., 2003; Mouritsen et al., 2003; Bonadonna et al., 2005; Gagliardo et al., 2006; Gagliardo et al., 2008). However, the fact that none of our birds migrated on the same day as the treatment was applied (supplementary material Table S1) suggests that in this case any effect might have been masked, as Emlen funnel experiments indicate a gradual return to normal orientation after about 13 days. We do not, therefore, argue that the lack of an effect of the pulse treatment represents evidence that magnetic cues play no role in experience based migration.

The migration speeds demonstrated by our birds were an order of magnitude smaller than those displayed by other North American songbirds tracked by geo-location (Stutchbury et al., 2009). This may represent a difference between the long distance migrants tracked in that study and a medium distance migrant such as the catbird.

Our data do not at this stage allow us to draw firm conclusions regarding the question of whether these olfactory cues are used to correct for large scale displacements as part of a true navigational map, but the technique used here provides a robust method for future study of the role of environmental cues in the navigation of migratory birds. To our knowledge, our data indicate for the first time the possibility that olfactory cues play a role in the migratory orientation behaviour of adult migratory birds. This finding suggests several directions for further investigation of the underlying mechanism(s), including the possibility that the cues may provide navigational information to allow a more efficient migratory route than the species specific inherited direction.

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