Short communication

Migrating ducks in inland North America ignore major rivers as leading lines
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A recently developed radar-based technique permitted empirical re-evaluation of the established but poorly supported theory that migrating North American waterfowl (Anatidae) use landscape features such as rivers as leading lines. Ducks departing the Illinois River Valley in the autumn of each of 15 years travelled SSE with a mean track that was 68° different from the 220° course of the Illinois River (P < 0.001). We conclude that leading lines were unimportant navigation aids for ducks leaving this major stopover site in autumn and suggest that rivers have less effect on the spatial course of duck migration than previously thought. Timing of departures was examined in a representative subset of 8 years and found to be consistent, with a mean start time of 44 min after civil sunset.

Keywords: migration, navigation, radar, waterfowl.

Waterfowl (Anatidae) use a variety of environmental cues to orient and navigate during migration, as evidenced by direct study (Bellrose 1958, 1963, 1967) and extrapolation of results from related taxa (Kramer 1950, Matthews 1951, 1963, Sauer 1958, Merkel & Wiltschko 1965, Emlen 1967, Walcott & Green 1974). Early in the study of migration, explanations of avian navigation were based largely on vision and landscape features. Reports of major flights along rivers, dunes and coastlines in Europe and North America provided meaningful evidence for the use of visual-based navigation by several avian taxa including ducks (Lincoln 1935, van Dobben 1953, Svardson 1953, Hochbaum 1955, Bellrose 1957, 1968, Bellrose & Sieh 1960, Bergman & Donner 1964; Fig. 1, Supporting Information Fig. S1). ‘Leading lines’, which were originally defined as linear landscape features with characteristics that induce migrating birds to follow them (Geyer Von Schweppenburg 1963), became a prominent and long-standing explanation for the mechanism by which birds navigated during migration.

When the magnitude of nocturnal migration became apparent in the mid-20th century, researchers recognized that visual mechanisms could not fully explain the accurate navigation by birds that occurred at night because cues from the ground and sky were often obscured by darkness and clouds (Griffin 1973, Richardson 1978). Sophisticated mechanisms involving geomagnetic cues were later documented experimentally in Passeriformes and Columbiformes and observationally in other taxa including Anseriformes (Able & Able 1995, Wiltschko & Wiltschko 2009). There is still uncertainty regarding the particular mechanism(s) by which birds perceive geomagnetic cues (e.g. retinal, Möller et al. 2004; beak, Cadiou & McNaughton 2010; and inner ear receptors, Wu & Dickman 2011); nevertheless, considerable evidence supports the presence of a geomagnetic compass that enables birds to orient over great distances without visual cues from the landscape or sky (Wiltschko et al. 2011, Deutschlander & Beason 2014). Therefore, visual cues are probably redundant and perhaps unnecessary for many nocturnally migrating birds such as ducks (Cochran et al. 2004, Rozhok 2008, Wiltschko & Wiltschko 2009). However, direct documentation of migratory events and their dependence or independence of leading lines is lacking with respect to duck migration at night, which is now known to account for most duck migration. The spatial scope of migration and the obscurity of nocturnal movements present serious logistical challenges. We used a recently developed radar-based technique (O’Neal 2010, O’Neal et al. 2010, 2012) to study the large-scale, nocturnal movements of migratory ducks relative to a key landscape feature. Specifically, we examined departure tracks of ducks migrating from a major stopover site along the Illinois River in central Illinois over 15 years (1995–2009); average autumn turnover of 140 260 ducks from 2005 to 2009; O’Neal et al. 2012). We examined the same area as that studied by Bellrose in earlier studies of the spatial characteristics of migration (Bellrose & Sieh 1968).
1960, Bellrose 1968). By comparing departure directions of all major nocturnal movements (and diurnal, if present) with the leading line of the Illinois River, we were able to test the expectation that migrating ducks relied on rivers as landscape cues during and after migratory departure.

**METHODS**

**Identification of departure movements**

Weather surveillance radar (WSR) offers a unique method of observing the nocturnal movements of groups of birds over large spatial extents (Gauthreaux 1970, 1992, Gauthreaux & Belser 1998, Koistinen 2000, Diehl et al. 2003, Larkin 2005) and has recently been validated as a technique for the study of taxon-specific movements from discrete migratory stopovers (O’Neal et al. 2010, 2012). By examining a series of echoes captured on sequential scans, and comparing the characteristics of these movements with the natural history of organisms present in a region during the period of interest (e.g. autumn migration), the source of echoes can sometimes be attributed to a specific taxon (Russell & Wilson 1996, Koistinen 2000, Larkin 2005). Specifically, migratory ducks can be separated from insects, songbirds and other waterfowl based on particular criteria: (i) the unique way in which an animal reflects radar waves (radar cross-section), which is a function of the size and shape of the study subject’s body relative to the wavelength of the study radar (10 cm); (ii) spatial distribution of ducks throughout the region and within a wetland (wetlands rather than uplands and non-hunted refuges rather than hunted areas); (iii) timing of movements at the daily and annual scale (following sunset in October–December); (iv) distance flown (greater than local movements); (v) environmental conditions associated with movements (e.g. following winds, high pressure); (vi) abundance of ducks at the source wetland relative to other species; and (vii) spatial patterns (i.e. spatially discrete echo associated with temporally clustered departures). In a separate study during 2007 and 2008, we empirically validated these classification criteria for the same weather radar data using portable radar and thermal infrared ground-truthing techniques (O’Neal et al. 2010). Portable radar also enabled us to determine the average height at which ducks in our study region consistently migrated (500 m ± 159 sd, n = 110). Given these data on migratory heights and the distance between our study site and the weather radar unit used in this study (‘KILX’; 60 km), we were confident that most ducks departing from our study site would fly within the range of altitudes surveyed by the weather radar (282–1333 m above ground level).

We focused our study on ducks departing from a 14 431-ha complex of wetlands and backwater lakes along the Illinois River in central Illinois (Fig. 2). The Illinois River is a continentally significant region for migrant waterfowl, and representative of other major rivers in the Midwestern USA (i.e. Mississippi, Missouri, Ohio and Wabash). According to aerial surveys of waterfowl on the study area, dabbling ducks (Anatini) accounted for 90% of waterfowl use during the autumns of 1995–2009 (M. M. Horath, Illinois Natural History Survey unpubl. data; Havera 1999). According to these data and our classification of radar data, our study
species were predominantly dabbling ducks, namely Mallard *Anas platyrhynchos*, American Black Duck *Anas rubripes*, Northern Pintail *Anas acuta*, Green-winged Teal *Anas (crecca) carolinensis*, American Wigeon *Anas americana*, Gadwall *Anas strepera* and Northern Shoveler *Anas clypeata*. Potential wintering destinations for these birds include the major reservoirs of southern Illinois, western Kentucky and western Tennessee (e.g. Carlyle, Shelbyville, Rend, Reelfoot and Kentucky Lakes), the Wabash River, major wetland complexes in the Lower Mississippi Alluvial Valley and wetlands in the southeastern USA (e.g. Florida and South Carolina; Bellrose 1968, 1980, Kremenz et al. 2012).

**Acquisition of weather service radar data**

We downloaded level II KILX data for autumn (defined as 15 October–31 December) 1995–2009 from the National Environmental Satellite, Data, and Information Service (http://has.ncdc.noaa.gov/pls/plhas/plhas.dsselect). We screened all reflectivity scans (24 h/day; ≥ 144 scans/day) from 1996–1998, 2003 and 2006–2009 and identified duck departures based on the previously defined criteria (GRLEVEL2; Gibson Ridge Software 2005, Integrated Data Viewer 2.6; Murray et al. 2003, O’Neal et al. 2010). All departure events we detected in those 8 years occurred near dusk, appearing on radar an average of 44 ± 6 (sd) minutes after civil sunset. For the remaining 7 years, we screened a 2-h period surrounding sunset (1700–1900 Central Standard Time (CST)/1800–2000 Central Daylight Time (CDT)/2300–0100 Greenwich Mean Time (GMT)) each night. Our starting date (15 October) was based on the initiation of aerial inventories (Havera 1999), which were used to help verify WSR targets. We terminated analyses on the date when wetlands in our study area were estimated to have

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**Figure 2.** An estimated 20,485 ducks emigrating from our Illinois River study area (black area; 40°21’18"N, 90°2’57"W declination = 1°21’W) captured on the KILX weather surveillance radar reflectivity scan (0.5° elevation) at the time of departure (1740 CST) and 40 km into migration (1800 CST) on 8 November 2008. Bounding boxes surrounding the migrant mass and the leader lines dividing them vertically and horizontally demonstrate the bounding box method used for quantification of this 143° track.
frozen, based on field observations and daily mean temperatures below 0 °C (A. P. Yetter, Illinois Natural History Survey unpubl. data). We excluded from analysis 11 nights when radar data were unavailable and another 11 nights when weather systems obstructed the radar (Gauthreaux & Belser 2005); thus, we included data from 851 nights in analyses.

**Measuring departure tracks**

When ducks migrated out of our study area they typically appeared on WSR as a single, discrete, oval echo (Fig. 2). As these echoes moved away from the source wellt they grew in size, but remained spatially distinct throughout much of the radar domain. Capture of a departure movement on multiple radar scans enabled us to estimate the direction relative to the ground (track) of each migratory movement that originated from our study area. We quantified departure tracks by measuring the bearing (degrees) from the location of a migrant mass on the radar scan when it first emerged to the location on the scan when it was last evident as a cohesive mass on radar (ARCMAP 9.3; Environmental Systems Research Institute 2008). In all cases, the distance between these two locations was >20 km (41.0 ± 1.1 (se) km).

This method required estimation of the two-dimensional centre of the migrant group. We examined techniques for this task, centroids and bounding box centres. We randomly selected a sub-sample of five departure events from 2006, computed the centre of the migrant mass for initial and final locations using both methods, and estimated the resulting track. Centroids were derived from the two-dimensional mean of all pixels (pulse volumes) weighted according to echo strength (i.e. reflectivity). Bounding box centres were based on the median x- and y-values for a box bounded by the maximum two-dimensional extent of the migrant mass (Fig. 2). We excluded all KILX reflectivity pixels below a volumetric density of 1 duck-sized point echo per km^3 (6 dBZ) prior to delineation of the migrant mass for either method (O’Neal et al. 2010). Both computations were made using a geographical coordinate system (latitude–longitude). The differences in resulting tracks ranged from 0° to 6° with a mean of 3° ± 2° (sd). We used the bounding box technique because results from the two methods were not significantly different ($t_{8} = 0.065$, $P = 0.950$) and calculating bounding box centres took less time.

**Data analysis**

We used circular statistics for all analyses due to the directional nature of the data (ORIANA 2.0; Kovach Computing Services 2004). We estimated the mean direction for all departures and quantified variation in departure direction within and among years (Fisher 1993). To test for circular normality (von Mises distribution), we conducted a Kuiper’s test for each year and all years combined (Batschelet 1981, Fisher 1993, Mardia & Jupp 2000). We tested for a preferred direction of departure by conducting Rayleigh’s uniformity test for each year and all years combined (Fisher 1993, Zar 1999, Mardia & Jupp 2000). Using a V-test (Fisher 1993, Zar 1999), we tested whether ducks migrated along a track that differed statistically from the track of the Illinois River (220°). Leading line analysis was restricted to the Illinois River because no other leading lines with significance to migratory ducks were present in the region (e.g. other major rivers, mountain ranges or coastlines).

**RESULTS**

Ducks departed from our study site on 281 of 851 nights (33%), with no more than one departure on any given night (Table 1). Ducks departing our study site travelled SSE in each of the 15 years we analysed (1995–2009; Table 1; Supporting Information Fig. S2). Variation about the mean track (151.8°) was small within and among years (Table 1, Fig. 3; 95% CI = 150.4–153.2°; all 15 years). Based on the results of the Kuiper’s tests, tracks were normally distributed (i.e. had a von Mises distribution) about the intra-annual mean in each year except 2006.

The uniformity of tracks indicated migrant ducks had a strong directional preference in each year and in all years combined ($Z = 269.1$, $P < 0.001$; Table 1). Throughout the entire study period, departure tracks differed significantly from the course of the Illinois River (220°; mean difference = 68.2 ± 4.5° sd; $V = 0.363$, $P < 0.001$; Table 1, Fig. S2, Fig. 3).

**DISCUSSION**

The use of leading lines for migratory navigation has been documented many times in numerous avian taxa, and remains as a common contemporary paradigm in waterfowl science and conservation (Gill 2007). Contrary to this idea, ducks departing from our study site consistently travelled to the SSE, a direction that was nearly perpendicular to (i.e. independent of) the SSW course of the Illinois River. Some ducks could have migrated down the Illinois River at altitudes not scanned by the radar (>282 m); however, the magnitude of movements captured on radar relative to the abundances of ducks documented in formal surveys (O’Neal et al. 2012) suggests the vast majority of individuals were indeed captured by our study radar. In addition, the spatial scope of our study radar relative to the course of the Illinois River gave us confidence that ducks were not returning to other portions of the Illinois River within...
the same migratory leg. Therefore, we conclude that riparian leading lines were unimportant for the navigation of ducks departing from this heavily used North American site during 1995–2009.

The SSE departure tracks we observed during 1995–2009 were considerably different from those reported in previous studies (Bellrose 1957, 1964, 1968). There are several possible reasons for these differences. First, we examined movements throughout the day and night, whereas early descriptions were largely derived from visual observations that occurred diurnally (Hawkins & Bellrose 1939, Bellrose 1957, Bellrose & Sieh 1960). Daytime migrations of dabbling ducks are in fact very rare (Beason 1978), with 14 years between occurrences in some areas (Bellrose 1980). We detected none in the 8 years examined comprehensively (i.e. all data within each 24-h period) on WSR. Although daytime movements constitute a minor portion of all migratory events (Berthold 2001), the visual spectacle of their appearance is likely to have led to the assumption that they were representative of local movement patterns and navigation strategies. Secondly, potential migratory corridors, such as the Illinois River valley, have been largely defined through the recovery of leg rings from hunter-harvested ducks (Bellrose 1968, Bellrose & Crompton 1970). Although early authors were aware that spatial bias was associated with the distribution of hunting effort, they nevertheless inferred migratory routes based on concentrations of recovered rings. Concentrated hunting pressure in riparian-associated habitats may have contributed to the notion that ducks primarily migrated along river courses (Havera 1999). Finally, changes in the distribution and quality of wetland habitat in the region could have also contributed to temporal differences in migratory direction.

In addition to their potential value for navigation, geographical features may serve as leading lines for other reasons, such as when land birds with aversions to water concentrate along coastlines (Mueller & Berger 1961), when soaring birds concentrate along mountain ranges due to the presence of updrafts that facilitate flight (Robbins 1956, Ulfstrand 1960) and when birds make multiple stops along a geographical feature to feed in certain habitats (Morrison & Harrington 1992). It is possible that the historical movements of ducks documented along rivers during the day (Bellrose 1957, 1964, 1968) could be attributed to a concentration of forage rather than migratory navigation.

Growing evidence of geomagnetic navigation suggests a sophisticated mechanism for navigation is present in many species (Wiltshko & Wiltshko 2009). Such advanced behaviour was perhaps best evidenced in our study by the fact that the migrant ducks we observed varied little from their SSE departure track over our 15-year study period, regardless of variable weather conditions such as cloud cover. The consistency of tracks may be evidence of the fidelity to migratory routes as reported by previous authors (Hochbaum 1955, Graber 1968) and could corroborate stopover fidelity documented through other methods (e.g. ring recoveries; Bellrose & Crompton 1970). In general, the strong uniformity of tracks we observed (95% CI difference = 2.8°) suggests the advanced navigation systems documented in other avian taxa may also be highly

Table 1. Number of duck departures detected on radar, mean direction, circular variance, standard error of the mean direction, 95% CI about mean direction, Rayleigh test of preferred direction (Z-statistic and associated probability), and V-test for difference between mean direction and direction of the Illinois River (V-statistic and associated probability) for each year (1995–2009) and all years combined.

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>Mean direction (°)</th>
<th>Circular variance (°)</th>
<th>se of mean (°)</th>
<th>95% CI minimum (°)</th>
<th>95% CI maximum (°)</th>
<th>Z-statistic</th>
<th>P-value</th>
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developed in ducks. In addition, the consistent temporal attributes of the observed departures (i.e. only one departure per night and a highly consistent time of departure with respect to sunset) provides evidence for a navigation mechanism that is precise and perhaps socially related.

Replication of our work taxonomically and spatially would help address the more general role of landscape features for avian navigation in other regions of North America (e.g. along the Mississippi, Columbia, Ohio, Missouri and White Rivers; along the Pacific and Atlantic coastlines). Similar studies of migratory waterfowl populations in the eastern hemisphere would also be useful for contrasting navigation behaviours among reproducitively isolated populations. In addition, research suggests many bird species differ substantially in the migratory strategies used during movements toward and away from breeding areas (Bellrose 1980, Berthold 2001). Spatial monitoring techniques, such as WSR and telemetry, could help elucidate differences and similarities in migratory behaviours between spring and autumn migration.

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REFERENCES


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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Map re-created from description of a major diurnal waterfowl migration through central North America from 31 October to 2 November, 1955 (note the flight directions that align with the course of the middle and lower Illinois River in the inset box) (Bellrose 1957).

Figure S2. Circular scatter plots of departure tracks of ducks observed emigrating from the Illinois River study area from 1995 to 2009 on weather surveillance radar (KILX; north at top; each triangular symbol (▼) represents a single emigration).