Combining spatial modelling and radar to identify and protect avian migratory hot-spots

Mark DESHOLM1,2*, Rashpal GILL3, Thomas BØVITH3, Anthony D. FOX1
1 Department of Bioscience, Aarhus University, Kala, Grenåvej 14, 8410 Rønde, Denmark
2 BirdLife Denmark, Vesterbrogade 140, 1620 Copenhagen V, Denmark
3 Research Department, Danish Meteorological Institute, Lyngbyvej 100, 2100 Copenhagen Ø, Denmark

Abstract
Migrating landbirds are known to follow coast lines and concentrate on peninsulas prior to crossing water bodies, especially during daylight but also at night, creating enhanced potential collision hazards with man-made objects. Knowing where these avian migration “hot-spots” occur in time and space is vital to improve flight safety and inform the spatial planning process (e.g. environmental assessments for offshore windfarms). We developed a simple spatial model to identify avian migration hot-spots in coastal areas based on prevailing migration orientation and coastline features known, from visual and radar observations, to concentrate migrating landbirds around land masses. Regional scale model validation was achieved by combining nocturnal passerine movement data gathered from two tier radar coverage (long-range dual-polarization Doppler weather radar and short-range marine surveillance radar) and standardised bird ringing. Applied on a national scale, the model correctly identified the ten most important Danish coastal hot-spots for spring migrants and predicted the relative numbers of birds that concentrated at each site. These bird numbers corresponded well with historical observational data. Here, we provide a potential framework for the establishment of the first three-dimensional avian airspace sanctuaries, which could contribute to more effective conservation of long-distance migratory birds [Current Zoology 60(5): 680–691, 2014].

Keywords
Radar ornithology, Migration, Orientation, Conservation, Spatial model

Long-distance migrant songbirds seem to be declining worldwide (Sanderson et al., 2006; Heldbjerg and Fox, 2008; Wilcove and Wikelski, 2008), despite international protective legislation (e.g. the Bonn-Convention and the Migratory Bird Treaty Act in the USA) and site safeguard on breeding and winter quarters (Perlut et al., 2006). Many birds migrate nocturnally (Alerstam, 1990), transcending national boundaries, making study on passage difficult, yet mapping migration corridors is increasingly important, as flying migrants face greater sources of anthropogenic collision mortality from wind turbines, bridges, power lines, antenna masts, aircraft, tall buildings and other illuminated structures (Bevanger, 1998; Harden, 2002; Desholm and Kahlert, 2005; Drewitt and Langston, 2008; Loss et al., 2012). This is especially important if we are to avoid creating exceptional hazards to avian migrants in areas where birds are highly concentrated both on the ground (such as constructing lighthouses and other large illuminated objects in migration “hot-spots” i.e. areas with high concentration of migrating birds; Avery et al., 1978; Jones and Francis, 2003) and in the airspace immediately surrounding migration hot-spots because of the density of bird traffic dispersing from such concentrations. Migrant landbird orientation is seasonally determined, but shaped by local wind strength and direction, as well as by the preference to remain over land rather than cross water (Alerstam, 1990; Bruderer and Liechti, 1998), features lending themselves to spatial modelling. It is generally believed that nocturnal landbirds migrate along broad fronts responding less to the presence of coastlines (Lack, 1962; Casement, 1966; Eastwood, 1967; Zehnder et al., 2001), in contrast to landbird migration by day, which very often is shaped by geography and ground topography (Alerstam, 1990). However, other studies suggest that nocturnal migrating passerines may also use coastlines for guidance (Lowery and Newman, 1966; Åkesson, 1993) for example to help compensate for wind drift (Drury and Nisbet, 1964; Richardson, 1978) although infrared camera studies along French and Spanish Mediterranean coasts showed considerable variation in the direction of migration (Bruderer and Liechti, 1998; Rivera and Bruderer, 1998). It has also been shown that nocturnal avian migrants per-
form reverse movement after initiating a sea barrier crossing (Bruderer and Liechti, 1998; Zehnder et al., 2002; Buler and Moore, 2011), which indicate that the migrating birds can see the coastline.

Modern long-range weather radars now enable three-dimensional regional mapping of migrating birds (Konrad et al., 1968; Gauthreaux et al., 2008; Schmaljohann et al., 2008; Van Gasteren et al., 2008). Spatial models to predict the distribution of avian migration hot-spots can therefore now be objectively verified using large scale observational radar data (Gauthreaux et al., 2003; Gauthreaux and Belser, 2003; Bonter et al., 2009).

We hypothesise that spatial movement patterns of migrating landbirds can be effectively modelled, based on two simple premises, namely that: a) birds migrate in a preferred direction in a given season under given wind conditions and b) they migrate over land for as long as possible (i.e. until the angle between the preferred migration direction and the flight direction along the coast exceeds some unknown threshold) before crossing a water body. Assuming these two premises hold, it would be simple to predict relative aggregations of landbirds along coastlines to contribute to e.g. the strategic planning process in areas where bird migration densities were likely to be a major element contributing to environmental assessment or flight safety.

The aims of this paper are four-fold:

1) to construct a simple generic spatial migration model to predict the geographical distributions of migratory landbird concentrations (“hot-spots”) at multiple spatial scales,

2) to confirm the location of hot-spots predicted by the model at two different geographical scales using two tier radar surveillance and standardized bird ringing to identify departure points for nocturnal passerine migration at a regional scale,

3) to confirm the relative concentration of diurnal passerine and raptor migration at hot-spots by comparison with observations from amateur ornithologists at the national scale (in this case Denmark) to validate the relative numbers of migrants concentrated at each of the predicted hot-spots and

4) to provide a generic framework for the future designation of networks of three-dimensional avian airspace sanctuaries that can identify and protect the most important migratory hot-spots, in terms of bird densities, at national and international scales. Although developed for application within the relatively restricted territory of Denmark, the use of weather radar networks to validate migration models and provide real-time model/simulation input data to future avian airspace sanctuaries, dynamic in time and space, potentially supports its wider applicability throughout the world.

1 Materials and Methods

1.1 The spatial migration model

An intuitive, simple graphic spatial migration model was developed to identify the most important migratory hot-spots for landbirds encountering coastline features known to concentrate migrants (e.g. peninsulas and headlands on the edges of landmasses) under different prevailing migration directions. The model assumes that, because of an aversion to cross water any more than is absolutely necessary, a migrating landbird will hit and follow a coastline in the orientation that is closest to its prevalent migration direction, until it encounters a point where the coastline swings away more than 90° from the preferred direction. We have arbitrarily set this deviation threshold at 90° in the absence of empirical data and accept that this threshold could be species, age and stage specific. This point represents its ultimate point of departure and this simple mechanism is sufficient to explain why migrant landbirds concentrate at promontories orientated in the direction of migration. We make the assumption that over even, homogenous terrain, with flat topography landbird species undertake broad front migration along a specific heading when traversing landmasses. This means that the leading front of the migration is a line perpendicular to the orientation of travel. In the case of Denmark, the orientation of migration is on a NE heading for most raptors and passerines in spring based on ringing recoveries (Bønløkke et al., 2006). In reality, every small peninsula penetrating out into the water in the general direction of the prevailing migration orientation will potentially gather migrants and qualify as a migration hot-spot, but depending on relative proximity to each other, not all will function as such. To identify only the most important of these, the base topographical map can be replaced by a “grid-map” (see Fig. 1 using all of Denmark as an example overlaid with a 10 km square grid lattice), effectively removing smaller appendages of land (and therefore potentially less important sites) and the smallest bodies of water (i.e. those least perceived to be genuine barriers to migrating landbirds). Given the predominantly northeast orientation of bird migration in that season (indicated by the arrows in Fig. 1), the model simply comprises drawing a line perpendicular to the migration orientation which was progressively moved on-shore from the northeast until it first hits land, which repre-
sents the point of the first hot-spot (in this case Skagen, hot-spot a in the extreme northeast end of Jutland; Fig. 1). Continuing to move the perpendicular line onshore against the direction of migration generates more discrete new points of contact with land, each of which constitutes a potential hot-spot. Grid-cell size selection can be determined by the number of highest ranking hot-spots required, but using 10 km grid squares across Denmark results in the identification of 10 “peninsulas” with a north easterly orientation that will be expected to function as hot-spots (marked a to j in Fig 1).

On the basis of their geographical orientation alone, these northeast-pointing “peninsulas” will be expected to funnel migrant birds at their extremities, but we would further predict the degree to which each site concentrates migrants would vary in proportion with the extent of the catchment “up-stream” from which it draws. We define this hinterland catchment for each hot-spot by the major embayment features (orientated 180° to that of the direction of migration, in this case to the southwest) that separate each hot-spot from the adjacent one, since these represent the divisions about which migrants will stream to the north and east as they move northeast. Assuming that the broad front migration is consistently moving northeast (see above), we therefore consider lines drawn (shown as arrows in Fig.1) through the major embayment features extended back on the same heading as the dominant axis of migration and these lines would divide and define the stream of birds in the “catchment” that ultimately gather at each of the hot-spots. The broader the catchment landmass, the more migrants will potentially be funnelled into a coastal hot-spot. This enables an assessment of the relative importance of each hot-spot (on the basis of the relative concentration of birds gathered at each hot-spot), ranking the identified hot-spots on the basis of the breadth of each “catchment” area that lies inland (see below; Fig. 1).

1.2 Model validation at local and regional scales

The model can be applied at any spatial scale and in response to variable migration orientation, as long as there is good evidence of a dominant heading to avian movement. In our first worked example, we analysed the island of Bornholm (55°08′N, 14°54′E) using our spatial model for autumn migration. In the present study, migrating birds (almost exclusively small passerines) migrated in different directions in response to wind conditions, so three different hot-spot model exercises were undertaken under contrasting wind (and therefore migration) directions within the same autumn season (Fig. 2).

The capability of the spatial model to identify the geographic position of the hot-spots was validated on the local and regional scale over the central part of the Baltic Sea (Fig. 2A) using standardized bird mist-netting for ringing and a surveillance radar at the small rocky island of Christiansø (55°19′N, 15°11′E; Fig. 2A), and a dual-polarization Doppler weather radar on the island of Bornholm (55°06′N, 14°53′E; Fig. 2A) and covering the island of Bornholm and the south-eastern coastal part of Sweden. The field campaign reported here was conducted from 18 August to 1 September 2008 during the peak autumn migration period for trans-Saharan passerine migrants and combines data gathered by weather radar and surveillance radar with systematic bird capture data to track migration in the air and on the ground.

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Fig. 1 Topographical map of Denmark and the super-imposed 10 km grid map excluding the smaller water bodies and peninsulas

The geographical distribution of the ten landbird spring migration hot-spots identified by the spatial migration model are depicted as double circles and numbered with individual letters. Widths of catchment areas, defined as the distance between two neighbouring arrows (acting as migratory dividers on each side of each headland and is situated in the deepest intervening landward embayment) are used as a relative measure of importance. Hot-spot “a” is associated with the catchment area between arrow 1 and 2 (numbered sequentially from the top downwards starting with 1 and ending with 11), b between 2 and 3, c between 3 and 4, d between 4 and 5, e between 5 and 6, f between 6 and 7, g between 7 and 8, h between 8 and 9, i between 9 and 10 and j between 10 and 11.
Fig. 2  A. Map showing the study area in the Baltic Sea, the star marks the position of the Bornholm weather radar, the solid arrow (panel A) indicates the prevailing migration direction used for modelling in panel b and the broken line (panel a) the sliding tool described in Materials and Methods. The inset map of Denmark shows the location of the study area. (B), (C) and (D) show the nights under which the weather radar detected the prevailing migration direction towards the northeast, southwest and southeast, respectively. The related sample sizes are 5, 3, and 3 and the northwest-quartile was omitted because it was only represented by one night.

Inserted circular histograms (top right) show the relative frequency of track directions taken by individual birds (each dot is a single bird and the line indicate mean direction) observed and mapped with a short range radar situated on the island Christiansø, position arrowed in (a). Inserted circular histograms (bottom left) show wind directions for each 15-minute interval during the period of radar data collection (the line indicates the overall mean direction). Double circles are centred on avian migration hot-spots identified by the spatial migration model. Colours indicate frequency of occupancy of 1 × 1 km grid cells with migrating birds as measured by weather radar (darker colours indicate more nights with presence of avian migrants) where migrating birds were leaving land. Grid cells with black borders represent squares with intense and significant \( p < 0.001 \) clustering of high Z-values (significant hot-spot cells).

One potential bias associated with the use of radar for ornithological studies is the contamination of data on avian flight patterns with reflections from insects (Schmaljohann et al., 2008). Several well described and widely used procedures can overcome this potential bias (Gauthreaux et al., 2008; Schmaljohann et al., 2008). However, for various reasons we did not have radar information on wing beat frequency, object airspeeds, or the results of Doppler radar products on radial velocity and dual pol data at our disposal.

Instead, to ensure that we were in fact tracking migrating birds, not insects, with the weather radar we developed and applied a novel three tier study approach. First, we used standardized bird catching and ringing to document and demonstrate that passerines were departing from Christiansø on specific nights during this period, known to be the most intense migration period for trans-Sahara avian migrants (Bønløkke et al., 2006). Because of its size and position, Christiansø is famous for accumulating the highest concentrations of passerine migrants staging between the nightly migration episodes anywhere in Denmark. Second, passerine migrants taking off from Christiansø were mapped using a horizontal scanning surveillance radar located on the island. This equipment has been successful in tracking small passerines at distances of up to 2km based on a number of daytime ornithological studies verified by visual observations (own unpublished data). Furthermore, the timing of echo departures tracked by this radar correspond very well with local and general observations of
nocturnal avian migrants normally starting their migration 1–2 hours after sunset (Alerstam, 1990; Newton, 2008). During the day, hundreds of individual small passerines identified visually to species were also detected by the radar, whereas not a single one of the c. 30 individual butterflies passing the radar antenna was ever detected by the radar. Third, the well-known “blooming” pattern (Gauthreaux et al., 2003) characteristically originating from the mass exodus of departing nocturnal avian migrants was observed on every night by the weather radar. On the basis of these three tiers of evidence, we are confident that the tracks mapped using surveillance radar and weather Doppler radar were migrating birds. Whilst we cannot dismiss the possibility that some insects may have contributed to our data, if this were the case, they seem to react to wind in the same manner as small songbirds (see Results below), and hence, are unlikely to bias our findings (Fig. 2).

Nocturnal migrating songbirds were caught on a daily basis in 10 to 25 mist-nets (mesh size 16 × 16 mm) open for 5 to 10 hours after sunrise on Christiansø to demonstrate that birds came and left the island every night. Only 3, 6 and 12 metre long mist-nets were used with a mean of 462.9 (SD: 457.2; Range: 27–1992) net-metre-hours per day. For each pair of consecutive dates a chi-squared test for each of the four most common species (i.e. four tests per night and hence no correction for multiple testing was necessary) was conducted to test if the effort-normalized daily catching numbers (i.e. number of caught birds per 100 net-metre-hours) differed significantly, implying that avian migrants had arrived or left the island in significant numbers. Catches at time $t$ were used as the observed values and catches at time $t + 1$ as the expected values. Due to extremely low recapture rates daily turnover rate could not be estimated (e.g. Frederiksen et al., 2001), hence, significant numbers may also have arrived and/or departed the island on nights when the capture of specific species did not differ significantly. Daily species composition in the catches is assumed to reflect a random sample of those resting on this small remote island by day between intervening nocturnal migration episodes and, thus, those migrating over the island during the night.

Departures of migrating passerines were tracked every evening just after sunset, as individual birds took off from Christiansø (normally starting 1–2 hours after sunset), using a surveillance radar (Furuno FR2125, X-band, peak power 25 kW, variable pulse length/volume 0.3–1.2 µs, antenna rotating speed 144°/sec, transmitted frequency 9,410±30 MHz, vertical beam width 20°) situated on the top of the island at 23 metres a.s.l., scanning horizontally (360°) to a range of 0.5 km. For each night 30 randomly chosen migration tracks of individual birds were digitized and extracted with regard to migration direction using ArcGIS.

Finally, the exodus of migrating passerines just after sunset, on the regional scale (with a maximum range of c. 80 km at nights when the birds were flying at relatively high altitudes of ~ 900 – 1,500 m), was observed using a dual-polarization Doppler weather radar (C-band, peak transmitted power of 275 kW, 0.8 µs pulse length, antenna rotating speed 20°/sec, pulse repetition frequency 625 Hz, radar beam width ~ 1°). The weather radar makes 9 elevation scans ranging from 0.5°–15° once every 10 minutes, but only the lowest elevation scan was used in the present study. The radar is operated in dual-polarization mode, where radar pulses are transmitted and received simultaneously in horizontal and vertical polarisations. Only the normal radar reflectivity data, Z, were analysed for bird detection, using manual interpretation of the gif-videos made up by the individual frames (one per 10 minutes), which display the time series of the low radar reflectance data (maximum 10 dBZ to 15 dBZ). These time series data were analysed manually by identifying the exodus of nocturnal migrants, up to an hour after sunset, as a large coalesced echo around the radar growing in size as the birds enter the upper part of the radar beam (i.e. furthest away from the radar source). Normally, reflection intensity levels depend on distance, shading and clutter distribution when attempting to quantify the intensity of avian migration in different areas using weather radar. However, the weather radar used in this study was situated almost exactly in the middle of the relatively small island of Bornholm, so distance related bias on the birds departing the island was not an issue. Furthermore, we did not compile quantitative data on bird densities, but based our analyses only on presence-absence data for the various nights which also further limited the risk of distance related bias. Finally, the radar was situated on top of the island and therefore did not suffer from any shading, land- or significant sea-clutter effects. Under normal circumstances, the direction of movement would be estimated by analysing the radial velocity product of the weather radar. However, as stated above this parameter was not at our disposal due to the preliminary installation state of the radar. For each night the first 10 minute-scan, represented by one frame in the radar movie sequence, was used to estimate the general migration direction for that particular migration event.
These night-specific pictures showing the echoes of the first 10 minutes of migration always showed a non-even circular shape enabling the general migration direction to be assessed by visual inspection.

On each night, the first 10-minute period (coinciding with the observed take off time from Christiansø) when birds were observed leaving Bornholm and the Swedish coast after sunset was stored as a screenshot and digitized for later analyses using the geographic information system ArcGis 9.3. Data on the migration directions taken by passerines departing the island on each night were divided into four groups dependent upon the predominant direction of observed departures, based on the weather radar data and the four quarters of the compass rose (northeast, southeast, southwest and northwest). For each 90°-quartile, the digitized exodus of birds taking off into the atmosphere was superimposed on a map showing the occupancy of each 1 × 1 km grid cell around Bornholm and southern Sweden which identified, by the cumulative density of departures over the sea, the migration hot-spots from which birds had left Bornholm on most nights (Fig. 2). The same dates as were used to group the migration nights for the weather radar data were used to group data from the surveillance radar data on Christiansø and the migration directions were presented as circular histograms. The general migration directions derived from the two different radar systems could then be compared visually to confirm, in combination with the bird catches, that it really was bird movements that we mapped using the long range weather Doppler radar (see argumentation above).

To identify those grid cells that represented statistically significant aggregates (i.e. observed hot-spots, in contrast to a random distribution) of departing birds on different nights, the Getis-Ord Gi hot spot analysis test was applied to the spatial data derived from the weather radar mapping (ArcGis 9.3). If these observed hot-spots coincided with the predicted hot-spots from the spatial migration model we conclude that the model has been validated as a means of identifying hot-spots based on evidence from weather radar data. Given a set of grid cells with values representing the number of nights where birds departed Bornholm from a given location, the Getis-Ord Gi statistic identifies those clusters of cells with values of higher magnitude than would be expected by chance. The tool works by looking at the value (in this case, the number of nights when nocturnal migrants started to leave the Bornholm coast through a specific grid cell) of each grid cell within the context of the neighbouring grid cells. A grid cell with a high value is interesting, but may not represent a statistically significant hot-spot. To attain statistical significance, a cell must achieve both a high value and be surrounded by other cells with high values as well. The local sum for a cell and its neighbour cells is compared proportionally to the sum of all cells. When the local sum differs from the expected local sum, and that difference is too large to be the result of random chance, a statistically significant Z score is generated from the Gitis-Ord local statistic. The critical value of P was set to 0.001 to reduce the risk of falsely accepting a random spatial pattern as a significant hot-spot and the P-values for each grid cell can then be mapped.

Data on average wind direction for each 15-minute interval during the period of radar data collection to compile data on avian departures (the first part of the night) were collected using a Vantage Pro2 weather station (Davis Instruments Corp. 3465 Diablo Ave., Hayward, CA 94545) placed on the top of Christiansø at 26 metres a.s.l. and were presented in circular histogram form.

1.3 Model validation at national scale

The spatial migration model was also run on a larger, national scale for Denmark (using the grid map, cell size 10 × 10 km, excluding Bornholm shown in Fig. 1) to identify and especially assess the relative significance of the 10 most important Danish spring migration hot-spots. No islands were included in this analysis, as off-shore islands tend to attract migrants over large distances in a way that is different to birds moving across a landmass being concentrated along mainland shorelines. In the Danish case, the number of hot-spots was arbitrarily limited to the 10 most important sites and the grid cell size was selected to meet this criteria. The measure of relative importance of sites, inferred from the width of the catchment area, was validated using the numbers of observations of birds seen migrating through these sites over a 14–20 year observation period reported to “DOF-basen” (the Danish national online “citizen science” database of bird watcher observations from Denmark, where observers report on a site-specific basis the observed species and numbers). Only observations labelled as “migrating birds” and which could be assigned to one of the ten hot-spots were incorporated into the database. Six migrant species were chosen, three common species (buzzard Buteo buteo, swift Apus apus and chaffinch Fringilla coelebs) and three relatively rare species (red-throated pipit Anthus cervinus, golden oriole Oriolus oriolus and serin Serinus serinus) as being representative of different groups of avian mi-
grants. To overcome the potential observer bias associated with the three common species (where only unusually high numbers or early spring observations are likely to be reported to the database) we calculated a mean annual peak count for each site and expressed this as a percentage of the total for all ten sites. We then correlated these percentages with the width of the sites’ respective catchment areas as identified by the spatial model. Because of the very low numbers reported for the three rarer species, we simply used the proportions of all records from the sites over the multi-year observation period to correlate with catchment size. Only sites with at least one of the three species reported as migrating were included in the two analyses.

2 Results

2.1 Model validation at local and regional scales

The spatial model predicted the locations of eight migration departure hot-spots; a) three on Bornholm during northeast migration, b) one on Bornholm and one on the Swedish coast during southwest migration and c) two on Bornholm and one in Sweden during southeast migration (Fig. 2). Since we experienced only one night with migration directions in the northwest-quartile (i.e. birds orientated towards northwest) these data were excluded, together with the three nights when birds migrated eastwards (and which therefore did not fit into our analysis which was divided into quartiles of the compass rose), from the analysis. The number and position of all but one of the hot-spots predicted by the spatial model matched perfectly with the statistical significant spatial clustering (i.e. observed hot-spots identified by the GIS analysis) of grid cells with high Z-scores (i.e. hot-spot cells) observed using Bornholm weather radar observations from 11 nights (i.e. those of the 15 nights where birds migrated either towards northeast, southeast or southwest as observed by the weather radar) under different weather conditions (Fig. 2; see video S1 in Supporting Information for an example of nocturnal exodus of avian migrants).

During the study period, 1,293 individuals of 32 species were mist-netted and ringed at Christiansø (15 km northeast of Bornholm, Fig. 2A), 90.7% of which were trans-Saharan long-distance migrants. The four commonest species (willow warbler *Phylloscopus trochilus*, lesser whitethroat *Sylvia curruca*, garden warbler *Sylvia borin* and pied flycatcher *Ficedula hypoleuca*) accounted for 77.6% of these (Fig. 3). Daily catch data indicated that individuals of these species must have departed Christiansø on at least nine (21–26, 28–29, and 31 August) out of the 14 nights ($\chi^2 > 3.84, df = 1, P < 0.05$; Fig. 3) where significant changes in numbers caught on successive days were observed at least for one of the four species. For example, the mass arrival of very large numbers of willow warblers on the island during the night between 22–23 August 2008 had virtually all gone on 24 August, confirming large numbers departed that night and were represented amongst the many echoes tracked by the radar on Christiansø on the night between 23–24 August. However, turnover rates could not be taken into account and, since the short range radar tracked birds leaving the island on every night, it was clear that avian migration took place during every night of the study period. Short range radar on Christiansø provided migration directions and departure timing of individual birds leaving the island. Wind direction heavily influenced the directions taken by the 10–25 gram songbirds which, depending on wind speed, were more or less forced to fly with the wind (Fig. 2). A thorough analysis of the degree to which the trans-Saharan migrants were constrained by wind in their ability to determine their migration direction is beyond the scope of this paper. As expected for African migrants, most left in southerly directions during northerly winds.

Long range weather Doppler radar provided general migratory directions of birds (for a video example see S1 in the online Supporting Information) departing Bornholm and Southern Swedish coasts 30 minutes either side of the initial takeoff times recorded by radar on Christiansø. In general, the migratory directions re-
corded by the two radars corresponded well on individual nights (Fig. 2B–D). Bird banding and two tier radar coverage confirmed that the weather radar reflections were birds, not insects or sea clutter (radar backscatter from the sea surface).

2.2 Model validation at national scale

The model identified the ten most important Danish coastal hot-spots for the predominantly northeast orientated spring landbird diurnal migration (Fig. 1) and most of them are well-known to ornithologists as sites which are good migration watch points because of their spring concentrations of avian migrants (unpublished information). For both groups of species, the predicted relative numbers of migrants concentrated at each of these sites (based on the breadth of the landward catchment area behind each of the hot-spots) correlated significantly with the proportions of birds observed in the historical data distributed between the sites, both showing $P$-values of less than 0.02 for the rare and common species (Spearman Rank tests; Fig. 4).

3 Discussion

3.1 The spatial migration model

It is well known that migrating landbirds concentrate at key features in the landscape (e.g. peninsulas, mountain passes and rivers) where they tend to aggregate as a result of physical impediments to sustaining their favoured migration direction (Alerstam, 1990; Berthold, 2002). At small scales these movements can be documented visually by observers and nocturnally by the use of marine surveillance radars. However, until recently, aero-ecologists have been heavily constrained by the spatial distribution of existing long range radars operated by meteorologists, the military or air traffic controllers, which are not necessarily available for application to avian migration studies. Despite all the limitations associated with identifying the precise source of echoes, radar offers a unique data source for validation of spatial migration models, and increasingly now provides insights at large spatial scales. The use of the present migration model, validated by large scale radar observations, offers exciting possibilities to support the cost-effective identification of migratory hot-spots at large spatial scales and identify their relative importance. This provides a tool for guiding spatial planning (e.g. establishing constraints on the construction of hazardous objects) or air traffic control risk assessment in areas where large numbers of migrant birds aggregate. It also offers the novel opportunity for new forms of protection of migratory hot-spots, under spatial planning mechanisms or nature reserve designation, in the same way as the very “best” wetlands are protected in recognition of their numerical importance for staging migratory birds under the EU Birds Directive and the Ramsar Convention on Wetlands (e.g. Miljø- og Energiministeriet, 1995; Stroud et al., 2001). Using these methods, such an assessment can now be achieved without the laborious work of collecting and analysing extensive data sets from ground truthing and data collation. The model developed here is very simple, which represents

Fig. 4  A. Relationship between the relative importance of migration sites, as estimated by the spatial migration model (width of catchment area), and the percentage at each site of the total (for the six sites where at least one of the three species have been observed during the study period) number of spring observations over the period 1987–2006 (except for red-throated pipit for which data were only available for 1993–2006 ) for three relatively rare avian migrant species. B. As in “A” but showing the percentage at each site of the mean annual day-maximum on the y-axis for three common avian migrant species over the period 1987–2006.
a great strength, since this offers greater potential for being extensively used in the future, especially in areas with less information on migrating bird concentrations than elsewhere in the world. However, the present radar study was carried out over a two weeks period only, and hence, has focused solely on small nocturnal trans-Saharan migrating songbirds. In the future, studies following up on the present findings will need to cover other time periods, and thereby species (such as autumn thrush migration), before general conclusions can be drawn.

3.2 Model validation at local and regional scales

Given knowledge of the predominant migration direction of small (10–25 gram) songbirds, the simple model presented here was highly successful at a regional level (central Baltic Sea) in predicting departure hot-spots from southern Sweden and Bornholm under highly contrasting wind directions, as validated by departure of birds detected by the Bornholm meteorological Doppler radar. We conclude that the two simple premises, i.e. (i) dominant migration direction and (ii) the constraints imposed by coastlines, seem to describe the spatial pattern of assortment of landbirds aggregated between coastal migration hot-spots. Birds are known to migrate in a predominant direction and when encountering the sea, do seem to simply follow the coastline until the angle between the coast and the preferred direction of flight exceed a so far unknown threshold where they start their trans-sea flight. We applied a subjective 90º threshold which seems to match reality.

There may be alternative hypotheses to explain why migrating landbirds tend to concentrate at peninsulas, and we here present some of these even though we could not test them in the present study. First, nocturnal migrants may concentrate in coastal features as they forage as they move between trees and bushes in their preferred migration direction. Second, nocturnal migrating passerines are known to reorient at dawn; if this happens over open water, they will be drawn back to the coast from where they set out during darkness. Under these circumstances, peninsulas will be more obvious from the air and may therefore concentrate more birds (Diehl et al., 2003). However, several studies have shown that both night- and day-migrating birds follow leading lines in the landscape which eventually will funnel birds into coastal features (Alerstam, 1977; Åkesson, 1993). Thus, to what degree these additional explanations interact and which (if any) of them play a more dominant role in determining the spatial pattern of migration is at present unknown and will most probably vary between situations.

This study also demonstrated (confirming other studies e.g. Åkesson et al., 1996; Deutschlander and Muheim, 2009) that reverse migration is a regular and widespread phenomenon among nocturnal avian migrants at least in coastal sites. Our data indicate that wind direction and speed may explain short term anomalies in migration orientation, but this topic will be dealt with in a future, more thorough analysis.

Nocturnal migration is often considered to take place on a broader front compared to more geographically and topographically mediated avian migration by day (Drury and Nisbet, 1964; Lowery and Newman, 1966; Richardson, 1978; Alerstam, 1990; Åkesson, 1993; Bruderer and Liechti, 1998; Berthold, 2002). It could therefore be argued that we should have used weather radar to track day-time migrants. Nevertheless, we used data on the exodus of nocturnal migrants because daytime migration often is defuse and difficult to track by long-range weather radars (Gauthreaux et al., 2003), probably due to generally lower flight altitudes and very much reduced migration volumes. In conclusion, we found funneling effects from the coast lines also for nocturnal migrants, at least in the beginning of a migratory episode just after take-off when there most properly is sufficient light for the birds to see the coastline.

Daily early morning capture of birds on Christiansø identified the nocturnally migrating species that had departed during each previous evening. For example, the mass arrival of willow warblers on 23 August 2008 and their equally dramatic departure the following evening confirmed that many of the departing echoes tracked by radar involved this species on that date (Fig. 3). Although individually ringed passerines were recaptured on the island, these data were too sparse to enable capture-mark-recapture analysis to estimate specific daily turnover rates (based on local daily “survival” estimates, e.g. Frederiksen et al., 2001). Nevertheless, the almost complete absence of recaptures amongst willow warblers, compared with multiple recaptures of individual lesser whitethroats confirmed the species-specific nature of the turnover of arriving and departing individuals to and from the island every night during the study period.

National weather radar networks offer increasing potential for studying large-scale avian migration patterns (Van Gasteren et al., 2008), with the caveat that researchers are aware of the limitations of the different types of radars, especially in discriminating between birds and insects (Schmaljohann et al., 2008). However,
we are confident here that the combination of two radar data collection methods, combined with intensive catching and marking of birds on Christiansø enabled confirmation that the Bornholm Doppler radar reflectivity patterns were indeed songbird echoes from large movements of night time migrants.

### 3.3 Model validation at national scale

Scaling up from a regional analysis of migration hot-spots in autumn under differing prevailing wind directions, the model proved successful at identifying similar features throughout all of Denmark. The application of the model predicted the location and relative importance (in terms of numbers of migrants concentrated at each) of the ten most important land-bird spring migratory hot-spots in Denmark, most of which were already well-known to birdwatchers for their funnelling effects on, for example, migratory raptors. However, predictive migration models also have the potential to identify lesser well-known hot-spots, such as hot-spot b (Frederikshavn) and c (Als Odde) in Fig. 1, which would reward extra observational attention in future. Furthermore, such migration models have the potential to overcome the inherent bias associated with data collection by birdwatchers who volunteer their observation to citizen science portals (Bildstein, 1998), which results from the tendency for observers to concentrate at previously well-known birding sites. Fig. 4 suggests that both for rare and more common migrant species, the relationship between catchment size and frequency of observations may be non-linear, which may in itself be due to the concentration of bird-watchers at (and therefore over representation of records from) the very best sites, i.e. those with the greatest catchment and therefore greatest potential to concentrate species, both rare and commonplace. Modelling therefore offers a potentially more objective approach than pure observation, since this model identified hot-spots currently less well known as good bird migration observation locations. Such objectivity is essential if the results of migration models are to inform strategic spatial planning mechanisms (e.g. in risk management of avian collisions with man-made obstacles such as power lines and bridges or contributing to environmental assessments for offshore windfarms) and air flight safety systems (e.g. zoning of low level air force fighter training). Basing this validation procedure on only six avian migrant species risks that the model describes the spatial migration pattern for these species only. However, the six landbird species selected for study were very different in size and ecology, and we see no reason to believe that they are not representative of all landbirds migrating through Europe twice a year.

Our national scale analysis was based on a 10×10 km grid map of Denmark and excluded all smaller islands, and thus, all smaller peninsulas and islands were not explicitly considered in this paper since we focussed on defining the ten theoretically most important coastal hot-spots of Denmark. Likewise we chose our grid cell size subjectively to identify only the most important ten spring hot-spots of Denmark. In reality, the numbers of hot-spots identified will vary considerably with grid size selection and the species involved – too small grid cell sizes will erroneously identify small peninsulas as migration hot-spots. However, it is beyond the scope of this study to identify how to establish minimum cell sizes, since we aimed to develop a tool to simply identify the most important hot-spots on a national level for Denmark.

Intervening peninsulas will also concentrate migrant birds, but to a far lesser extent than the major ones considered here. Furthermore, the spatial migration patterns resulting in high densities of migrating landbirds on islands is very different from what can be observed at coastal sites, because they also draw migrants from a large catchment of airspace relative to their size when birds seek refuge crossing the ocean and hence, need special attention in a separate, dedicated island analysis in a different process. Likewise, the applicability of the present model for landbird migration over land is likely very poor, however, models can also be developed for this kind of habitat where for example rivers and forests could influence the flight pattern.

### 3.4 Modelling at multiple scales

The use of the model at regional and national scales proved highly effective at predicting both where migratory hot spots should occur and the relative numbers of migrants concentrated at each, confirming its utility at different geographical scales. Wind farms (Langston and Pullan, 2003; Fox et al., 2006) are not the only source of anthropogenic mortality affecting migrating bird populations at coastal hot-spots; lighthouses, military and communication towers, tall buildings, local

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1 Langston RHW, Pullan JD, 2003. Windfarms and birds: An analysis of the effects of wind farms on birds, and guidance on environmental assessment criteria and site selection issues. – Report written by BirdLife International on behalf of the Bern Convention.
habitat degradation and aircraft are all known to take their toll on migrant birds where they concentrate in such areas. Beyond conservation issues, avoidance of bird strikes with aircraft bring savings in human lives and financial costs (e.g. the recent Airbus emergency landing on the Hudson River in New York after a bird collision; Marra et al., 2009).

3.5 Avian airspace sanctuaries

Finally, knowledge about avian staging patterns and migration corridors offers up the intriguing possibility to inform efforts to conserve migrant bird species along their migration corridors at the continental scale, including the prospect of establishing three dimensional avian airspace sanctuaries, contributing to more effective conservation of long-distance migratory birds. We have now developed a spatial migration model for identifying the avian coastal hot-spots and the next step will be to provide a framework for defining the form and the three dimensional extent of dispersal cones away from such land-based migration hot-spots and other avian migration corridors over the oceans. To do this, data on the altitudinal behaviour of the migrating landbirds needs to be collected and analysed in the light of avian responses to wind. A large proportion of the avian migrants will fly higher than most buildings, bridges and wind turbines. However, in coastal staging areas birds will take off and land, and hence, fly at relatively low altitudes at least temporally over water. Furthermore, birds already engaged in migration flights might be forced downwards by e.g. bad weather. Defining these avian migration corridors could form the basis for the designation of future 3D avian airspace sanctuaries. Such guidance would need to be based on spatial modelling and radar as well as other data sources, incorporating theory about how birds distribute themselves in time and space after leaving coasts and are the subject of our present research.

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SUPPORTING INFORMATION

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

Video S1. Video example showing the exodus of passerine nocturnal migrants taking off from the Bornholm and Swedish coasts as recorded on the night of 24 August 2008 by the Bornholm weather Doppler radar.