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Are flight paths of nocturnal songbird migrants influenced by local coastlines at a peninsula?

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Abstract By recording nocturnally migrating passerines with tracking radar we have investigated how coastlines affect the migrants' flight paths. Birds could use coastlines as an orientation aid or as a reference cue to compensate for wind drift while migrating. However, on the small scale of Falsterbo Peninsula in southern Sweden, we found very little effect of coastlines on migrants flight paths, irrespective of altitude. We tracked 2 930 migrants in three autumn and two spring seasons, at altitudes from 60 up to 3 000 meters. We compared tracks of migrants flying in three different areas, which correspond to the three main coastlines, and can demonstrate that the orientation of the tracks did not differ in a way consistent with the coastlines between the areas in autumn, and showed only a slight effect in spring. This is in accordance with earlier infrared device monitoring in Falsterbo, but contrary to earlier visual observations. It supports the view of nocturnally migrating passerines as mainly broad-front migrants. Even though the coastlines on the scale of the peninsula affected the flight paths very little, it is possible that the coastline has an effect on a larger regional scale, by migrants avoiding long sea crossings and thereby being funneled towards the peninsula, but this remains to be investigated [*Current Zoology* 60 (5): 660–669, 2014].

Keywords Bird migration, Passerines, Coastlines, Leading lines, Flight paths

Migration is a complex set of behaviors where the birds are constantly faced with different options on how to act. One important “decision” they make is the choice of flight path, where navigation, wind drift and safety are some of the factors that need to be taken into account. It is unclear to what extent landmarks and topography play a part when migrating birds determine the path that will lead them as quickly and safely as possible to their goal. By supplying a fixed reference cue, leading lines in the landscape could benefit migrants in their orientation, and perhaps also in their ability to avoid wind drift. Land birds could also follow leading lines in the form of coastlines, to, as far as possible, avoid hazardous water crossings. If birds are more vulnerable to drift over sea than over land, they would benefit from following coastlines that do not deviate too far from their migratory direction, especially in high wind speeds and strong opposed side winds or crosswinds (Alerstam and Pettersson, 1977). Leading lines are predicted to be of greater importance at low than at high flight altitudes, partly because of the proximity to the visual cues and partly because birds tend to fly at lower altitudes, where the wind speed is lower, in head and opposing side winds, which is also when they would benefit the most from following the coast (Alerstam

and Pettersson, 1977). Some studies have found a greater tendency to follow coastlines later in the night than earlier, probably due to an increased reluctance to embark on water crossings towards the end of the night (Bruderer and Liechti, 1998; Fortin et al., 1999).

Whether, and to what degree, leading lines, and especially coastlines, affect the flight paths of migrating birds has been subject to some debate. There is much evidence of important coastline effects in diurnal migrants, especially in strong winds (Rudebeck, 1950; Snow, 1953; Svårdson, 1953; van Dobben, 1953; Gruys-Casimir, 1965; Meyer et al., 2000), but for nocturnal migration there is conflicting evidence (Åkesson, 1993; Bruderer and Liechti, 1998; Fortin et al., 1999; Gagnon et al., 2011). Falsterbo is a migration hotspot at the south western tip of Sweden, where thousands of migrating birds pass every season (Fig. 1). A long-term ringing regime collects data on species composition, abundance and movements. In previous studies done in Falsterbo, coastline effects have been shown by visual observations of low flying nocturnal migrants (Åkesson, 1993) but in a study of nocturnal passerines at higher altitudes (up to 3,000 m) using infrared recording there was no coastline effect (Zehnder et al., 2001). By using tracking radar we can plot exact flight paths of passing

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migrants over the peninsula and evaluate to what degree flight directions of nocturnally migrating passerines in Falsterbo are affected by the coastlines. In this study we will evaluate how the coastlines affect the mean track directions, the mean heading directions and the scatter in directions. We will do this for both spring and autumn migration and in several different altitude categories.



Fig. 1 Satellite image of the region around Falsterbo peninsula with a close up of Falsterbo peninsula (yellow box) Satellite image from Google Earth; Landsat.

1 Materials and Methods

We have tracked nocturnal migrants at Falsterbo peninsula (55.41°N, 12.87°E, 5 m above sea level) by use of tracking radar (200 kW peak power, 0.25 μ s pulse duration, 504 Hz pulse repetition frequency, 1.5° pencil beam width, X-band) during the autumn of 2009, and during both spring and autumn 2010 and 2011. During 53 nights of sampling we have collected 2,930 high quality tracks of free flying nocturnal passerines using bounding flight. The tracking radar tracks one individual target at a time, but it is not possible to identify the species of the target. Bounding flight of passerines is however easily recognizable from the wing beat signature of the radar echo (Bäckman and Alerstam, 2003; Bruderer et al., 2010) and only targets classified by the operator of the radar as flying with bounding flight have been used in this analysis. Therefore we are confident that the targets included in our analysis are passerines. All tracks were recorded during the night from around sunset until around 3 hours after midnight (local summertime, GMT +2), except for a few (73) tracks recorded around sunrise. Based on data from the ringing station on the peninsula, Falsterbo Bird Observatory,

some of the most likely species in our data are European robin *Erithacus rubecula*, goldcrest *Regulus regulus*, chiffchaff *Phylloscopus collybita*, willow warbler *Phylloscopus trochilus*, redstart *Phoenicurus phoenicurus* and song thrush *Turdus philomelos* (Nilsson et al., in prep; Karlsson, 2009).

Wind measurements were made by releasing helium balloons that were tracked by the radar, and heading vectors were calculated from the measured wind vectors and the track vectors of the birds. Heading directions were not calculated if there was more than 2 hours or 150 meters in altitude between the tracking of the bird and the wind measurement, so the number of track directions is larger than the number of heading directions. For more details on operating the radar see Karlsson et al. (2012) and on data processing see Bäckman and Alerstam (2003).

In this analysis we divided our sample into three areas (Fig. 2), corresponding to the three main coastlines of the Falsterbo Peninsula, and investigated whether the track and heading directions of the birds differed between the areas. The areas were defined as sectors around the radar, area A is 350°–105°, area B 105°–225° and area C 225°–350° (see Fig. 2). Individual tracks were assigned to the area containing the longest part of the recorded flight trajectory. Three tracks were excluded as they had exactly half of their trajectory in two areas. We roughly estimated the directions of the coastlines to be 70°/250° in area B and 25°/205° in area C. Area A covers the bay Höllviken and it has a curving coastline in several directions. Therefore we will not discuss it directly in the comparison of mean directions and coastline directions. To test if the mean directions in the areas differed from the coastlines in those areas we investigated if the direction of the coastline was included in the confidence intervals for the mean direction. The scatter in directions was estimated by mean vector length, r . If the directions are uniformly distributed r is 0 and if they are unidirectional r is 1.

To investigate the effect of altitude we divided the sample into three altitude intervals, below 300 meters, 300–800 meters and above 800 meters. Targets below 100 meters are difficult to track with radar, but there were also few targets at the lowest altitudes indicating that only a small minority of migrants fly very low (Zehnder et al., 2001). Altitude intervals with less than 15 tracks were not included (Table 1). The track with the highest altitude was 3,058 m in autumn and 2,581 m in spring. All heights are above the level of the radar antenna (5 meters above sea level).

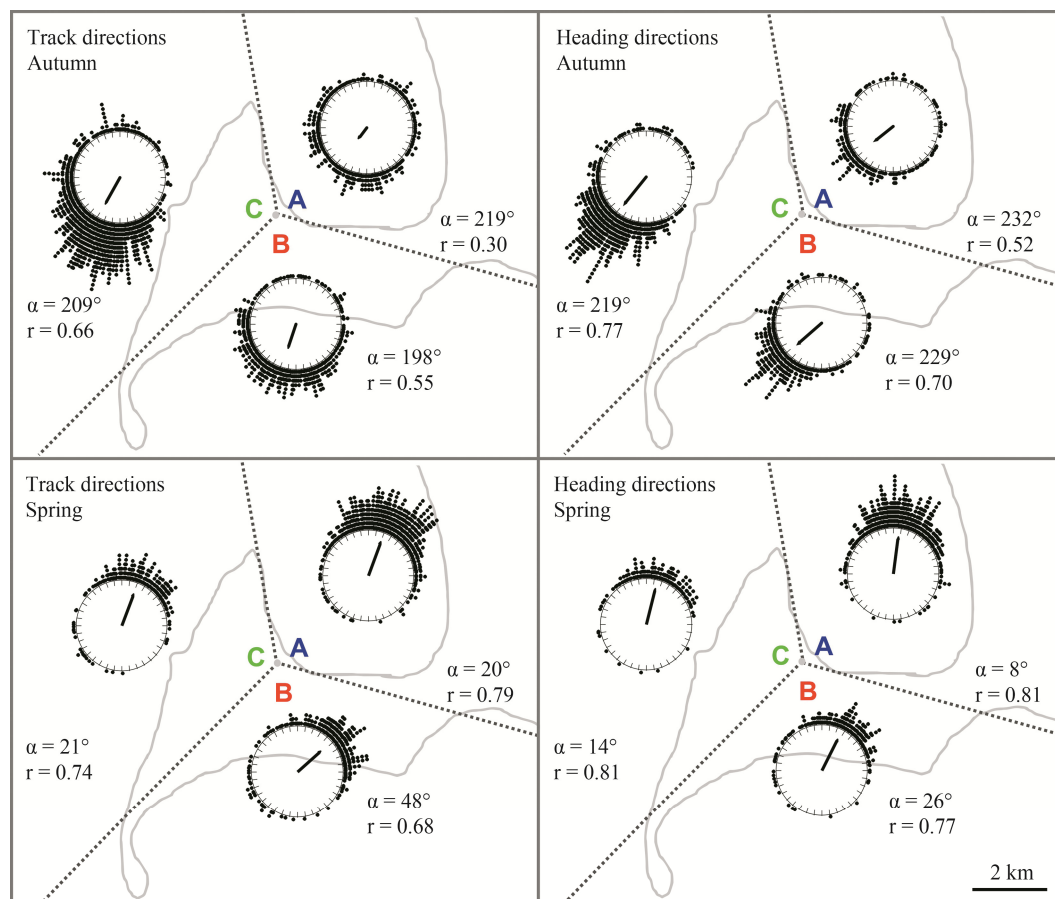


Fig. 2 Mean track and heading directions in the three different areas of Falsterbo peninsula plotted on top of a map of the peninsula

The areas are defined as sectors around the radar, area A is 350°–105°, area B 105°–225° and area C 225°–350°. Within each area the mean direction (α) and r is given. All mean directions are significant, Rayleigh uniformity test, $P < 0.001$ for all cases. See Table 1 for n -values.

2 Results

2.1 Track directions

We compared the mean track directions between the areas at different altitudes but found no effect of the coastline in the sense that differences in directions between the areas did not coincide with directions of coastlines in those areas (Table 1, Fig. 2 and 3). In most cases the rough direction of the coastline was not included in the confidence interval of the mean direction in that area, showing that most birds were not flying in parallel with the coastline (Fig. 3). There were some exceptions in spring, in area B and area C. In area C the direction of the coastline was included in the confidence interval of the mean direction in the area, however the direction of the coastline in that area (25°) is very close to the total mean track direction in spring (26.9°). In area B the mean track direction (48.0°) was shifted away from the total mean direction of the season (26.9°) towards the direction of the coastline in area B (70°), as

seen in Fig. 3. This could be an indication that at least some of the birds tracked in that area were flying in parallel to the coastline, even though the majority were not.

In autumn the mean track directions differed more between the three areas in the lower altitude span than at the higher altitudes, but the differences were not clearly associated with the configuration of the coastlines (Fig. 3, Table S1). At high altitudes the mean track directions in the three areas converge close to the direction of coastline C. Mean track directions in the different sectors were quite consistent during the night, and did not differ in any consistent way between areas before and after local midnight either in spring or autumn (Fig. 4).

We also investigated the effect of wind (winds from east and west) on mean track directions without seeing any clear differences in alignment of the birds' tracks with the different coastline directions in the three areas (Fig. 5). However it is seen in figure 5 that the birds

Table 1 Track directions (A) and heading directions (B) in the different sectors at three different altitude intervals in autumn and spring

		Sector A				Sector B				Sector C			
Altitude	<i>n</i>	Track dir.	95% CI	<i>r</i>	<i>n</i>	Track dir.	95% CI	<i>r</i>	<i>n</i>	Track dir.	95% CI	<i>r</i>	<i>n</i>
		Autumn											
All	1792	219.2	205.3–233.1	0.30	349	197.8	191.9–203.8	0.55	492	208.5	205.2–211.9	0.66	951
64–300m	211	254.9	224.0–285.8	0.40	37	187.8	168.3–204.4	0.47	66	226.1	212.2–240.1	0.51	108
300–800m	872	224.4	197.4–251.4	0.22	174	195.8	187.0–204.7	0.53	237	214.1	209.0–219.2	0.63	461
800–3058m	709	206.4	190.2–222.6	0.40	138	202.8	194.2–211.4	0.60	189	199.5	195.3–203.8	0.76	382
Spring													
All	1138	20.3	17.2–23.4	0.79	600	48.0	42.3–53.8	0.68	299	20.8	15.2–26.4	0.74	239
122–300m	24	18.8	0.9–36.8	0.79	18	–	–	–	5	–	–	–	1
300–800m	521	22.0	17.5–26.6	0.79	284	48.3	38.4–58.2	0.61	134	17.9	8.1–27.8	0.68	103
800–2581	593	18.7	14.2–23.1	0.79	298	47.2	40.1–54.2	0.73	160	23.1	16.6–29.5	0.80	135
B. Heading													
Altitude	<i>n</i>	Head. dir.	95% CI	<i>r</i>	<i>n</i>	Head. dir.	95% CI	<i>r</i>	<i>n</i>	Head. dir.	95% CI	<i>r</i>	<i>n</i>
		Autumn											
All	1256	231.7	222.5–240.9	0.52	242	228.7	223.7–233.7	0.70	357	218.6	215.5–221.8	0.77	657
64–300m	98	237.8	204.1–271.5	0.59	14	217.6	194.7–240.6	0.54	35	228.8	212.6–245.0	0.62	49
300–800m	619	234.9	220.3–249.6	0.46	123	234.1	227.2–241.0	0.72	170	222.6	217.9–227.3	0.75	326
800–3058m	539	227.9	215.7–240.1	0.57	105	224.5	217.2–231.8	0.72	152	213.1	208.9–217.3	0.82	282
Spring													
All	875	8.2	4.9–11.5	0.81	479	26.3	20.9–31.8	0.77	223	14.2	8.7–19.7	0.81	173
122–300m	13	–	–	–	11	–	–	–	2	–	–	–	0
300–800m	395	8.9	3.8–14.0	0.79	229	27.0	17.5–36.4	0.72	94	19.7	9.9–29.4	0.76	72
800–2581	467	8.0	3.8–12.1	0.85	239	25.8	19.2–32.4	0.80	127	10.7	4.3–17.1	0.85	101

Mean track direction (Track dir.) or mean heading direction (Head. dir.) is given together with 95% confidence intervals for the mean (95% CI), concentration parameter (*r*) and number of tracks. We have not calculated mean directions, confidence intervals or *r* for cases with less than 15 tracks. See table S1 for pairwise tests of mean directions.

showed a clear tendency of being drifted by wind, in a similar way in all three areas. The distribution of tracks between the areas differed between easterly and westerly winds (autumn: $\chi^2=42.39$, $P < 0.001$, spring $\chi^2=10.29$, $P < 0.005$, Fig. 5), which could explain some of the differences in mean directions between areas.

2.2 Heading directions

Heading directions were more concentrated than track directions and also differed less between areas (Fig. 2). They were also quite consistent between different altitude intervals (Fig. 3). The heading directions in area B in spring were not skewed towards the coastline as the tracks were; instead they were quite close to the total mean heading direction. We found similar gen-

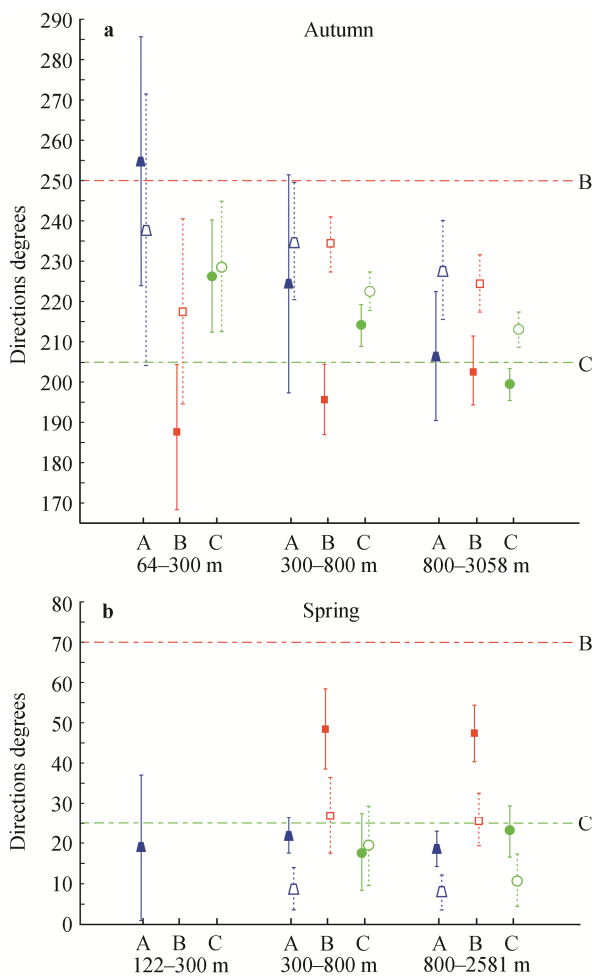


Fig. 3 Mean directions with confidence intervals for the different areas in different height intervals in A) autumn and B) spring

Blue is area A, red area B and green area C. Filled symbols and lines are mean track directions with 95% confidence intervals, open symbols and dotted lines are mean heading directions with 95% confidence intervals. Dotted horizontal lines show the approximate direction of the coastlines in area B (red) and area C (green). See Table 1 for n -values and table S1 for pairwise tests of mean direction.

eral results when considering heading directions in relation to coastlines as with track directions (i.e. no important influence of the local coastlines). We have therefore focused our presentation mainly on the results for the track directions. This is also reasonable in view of the main prediction that any influence of coastlines would primarily be expected to affect track directions if the birds align their track direction (rather than heading) to follow coastlines.

2.3 Scatter

There was more scatter in track directions at lower altitudes than at higher altitudes in areas B and C in both autumn and spring (Table 1). Tests of concentration parameter between highest and lowest altitude interval showed statistically significant differences in three of the four cases (area C in autumn, $F_{107,381} = 2.06$, $P <$

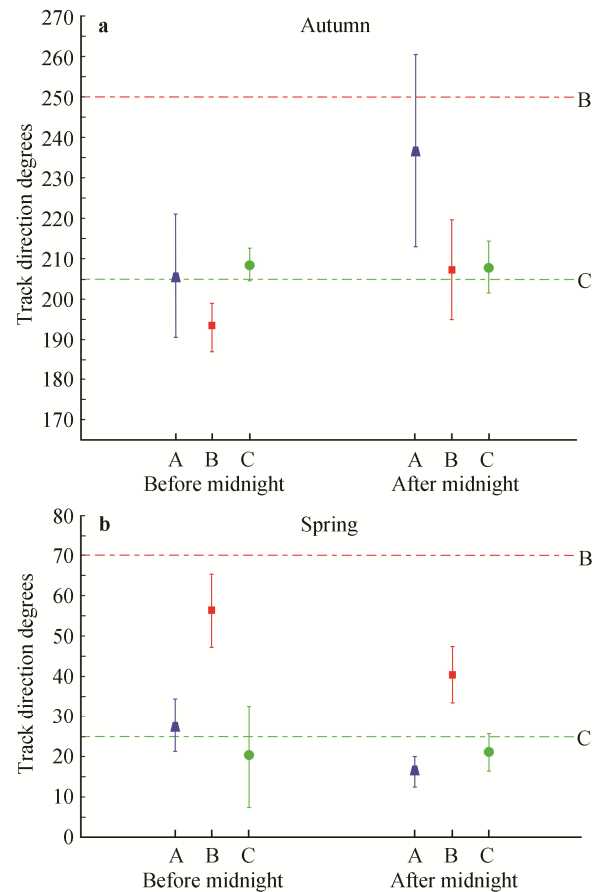


Fig. 4 Mean track directions with confidence intervals (95%) for the different areas before and after midnight (GMT +2) in a) autumn and b) spring

Blue is area A, red area B and green area C. Dotted horizontal lines show the approximate direction of the coastlines in area B (red) and area C (green). n -values, autumn before midnight: A: 148, B: 278, C: 547, autumn after midnight: A: 201, B: 214, C: 404, spring before midnight: A: 222, B: 162, C: 106, spring after midnight: A: 378, B: 137, C: 133. See table S1 for pairwise tests of the mean directions.

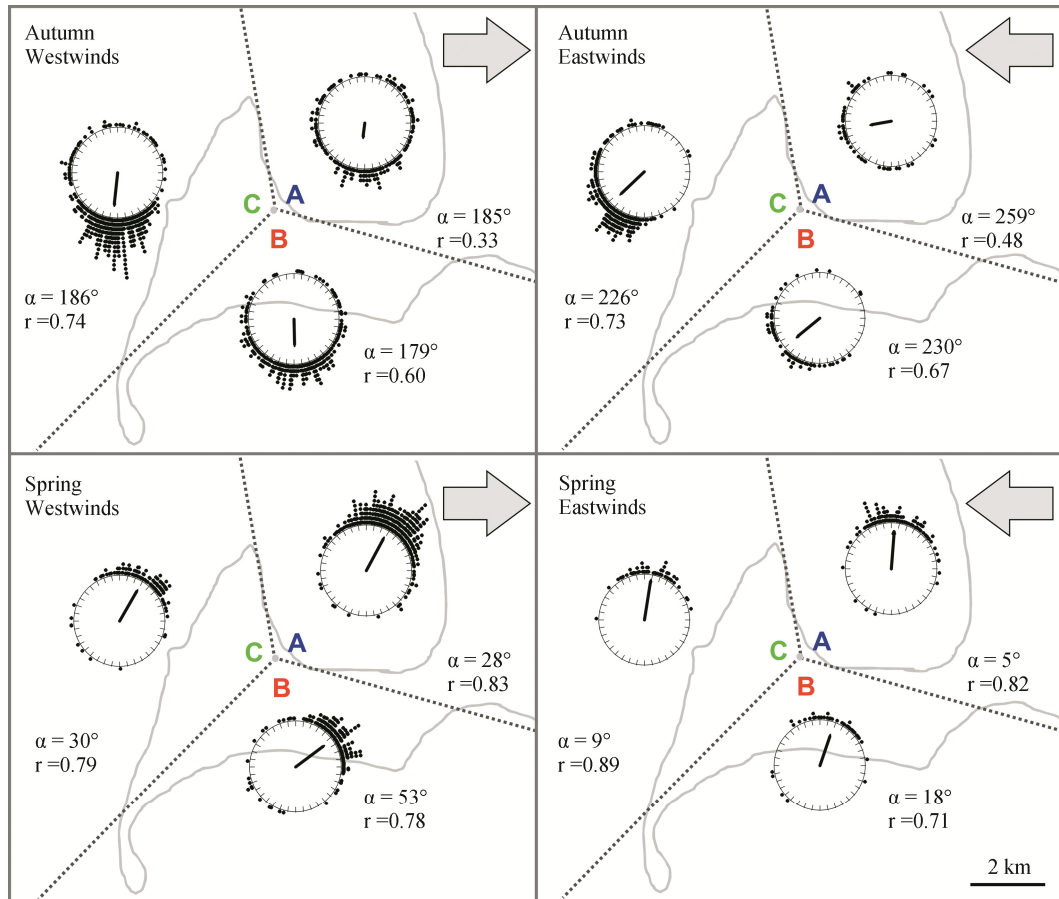


Fig. 5 Mean track directions in the three different areas of Falsterbo peninsula under different wind situations (grey arrows) plotted on top of a map of the peninsula

The areas are defined as sectors around the radar, area A is 350°–105°, area B 105°–225° and area C 225°–350°. West winds are defined as winds blowing towards 0°–180° and east winds blowing towards 180°–360°. Within each area the mean direction (α) and r is given. Autumn, west winds, $n = A: 185, B: 288, C: 410$. Autumn, east winds, $n = A: 57, B: 69, C: 247$. Spring, west winds, $n = A: 361, B: 182, C: 117$. Spring, east winds, $n = A: 118, B: 41, C: 56$.

0.001, area C in spring, $F_{102,135}=1.61$, $P < 0.01$, area B in autumn, $t_{253} = 1.64$, N.S., area B in spring, $t_{292}= 2.31$, $P < 0.05$; Batschelet, 1981; Mardia and Jupp, 2009). In area A there was no significant difference in either season. In autumn there was more scatter after midnight than before (Area A before: $r = 0.41$, after: $r = 0.23$, $t_{347} = 2.28$, $P < 0.05$, Area B before: $r = 0.66$, after: $r = 0.41$, $t_{490} = 5.06$, $P < 0.001$, Area C before: $r = 0.72$, after: $r = 0.58$, $t_{949} = 4.70$, $P < 0.001$; Mardia and Jupp, 2009).

2.4 Flight paths with the same alignment as the coastlines

In order to see to what degree birds migrating with track directions coinciding with the directions of the two main coastlines may have been under actual influence to follow these coastlines, we plotted the flight paths with these orientations in Fig. 6. The concentration of SSW trajectories at or closely offshore coastline C, as seen in Fig. 6B, may indicate that some of these migrants may have been flying under influence of this

coastline. However, there was no tendency of association of WSW tracks with the coastline B having this alignment; instead the flight paths with this orientation seemed to be rather uniformly distributed over the peninsula independently of the coastal configurations. In spring there was no concentration to coastline C among the tracks with a similar direction, rather there was a concentration to the other part of the peninsula (Fig. 6D). However, there was some concentration of spring tracks to coastline B among the tracks with a similar direction as this coastline, although many of these tracks crossed coastline B rather than adhering to it (Fig. 6C).

3 Discussion

3.1 Track directions

In autumn we did not find any important effect of coastlines on the flight paths of nocturnal passerine migrants at Falsterbo peninsula, which is in agreement with many other studies showing that nocturnal passé-

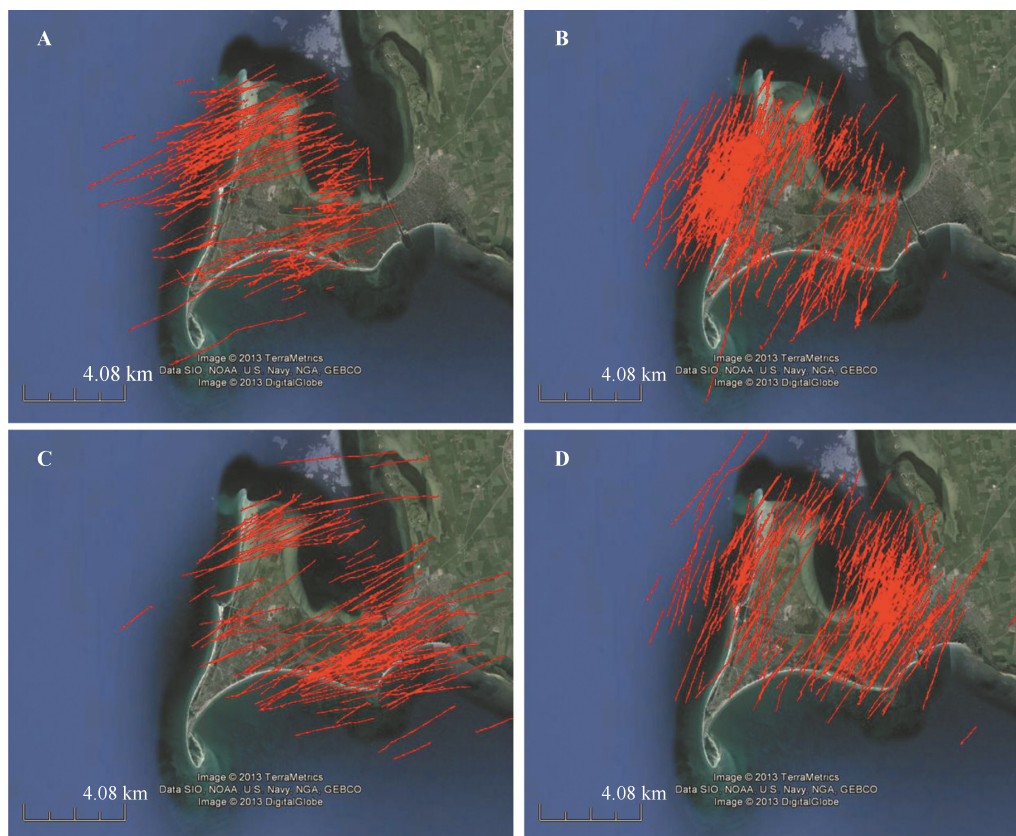


Fig. 6 Satellite image of Falsterbo peninsula with plotted flight paths in autumn (A, B) and spring (C, D)

Shown trajectories are those with track directions close to the directions of the east/west coastline (area B) (Panel A, C) and the north/south coastline (area C) (Panel B, D). A: Autumn, track directions between 235° – 265° (coastline 250°), $n = 215$. B: Autumn, track directions between 190° – 220° (coastline 205°), $n = 461$. C: Spring, track directions between 55° – 85° (coastline 70°), $n = 158$. D: Spring, track directions between 10° – 40° (coastline 25°), $n = 345$. There is an artificial lack of tracks very near and straight above the radar. Satellite images are from Google Earth; TerraMetrics and DigitalGlobe.

rine migration mainly takes place on a broad front (Bruderer, 1978; Richardson, 1978; Bruderer and Liechti, 1998; Zehnder et al., 2001). In spring we saw a very slight effect on the flight tracks in area B, but not on the headings in that area. This slight effect on track direction could be due to some of the birds in that area following the coastline, or it could be an effect of other factors, such as winds. It is also possible that the coastline is more important when reaching the peninsula from the south in spring, than it is when leaving the peninsula in autumn. The distributions of tracks over the peninsula change in different wind situations, which could explain some of the differences between areas in mean flight direction.

We did not see the same effect of time of night as some other studies (Bruderer and Liechti, 1998; Fortin et al., 1999) on mean track direction (Fig. 4). In these studies the increased tendency to follow coastlines late in the night is probably due to migrants' reluctance to cross the water increasing during the night and instead

they follow the coast to find suitable stopover habitat. Migrants reaching the Falsterbo peninsula late at night would have no reason to follow the coastlines of area B or C if they wanted to settle for the night. Instead they would need to turn inland, and we also see an increased scatter in track directions in the later part of the night.

This study clearly demonstrates that nocturnal songbird migrants generally pass Falsterbo Peninsula on a broad front without marked responses to the local coastal configurations. Some heterogeneity in the distribution of tracks over the peninsula suggests that somewhat enhanced concentrations of birds flying with a track direction similar to the alignment of the coastline may occur at (or offshore from) the west coast of the peninsula during autumn migration and at the south coastline of the peninsula during spring migration. However, these were weak tendencies of temporary possible flight alignments with the coastlines that do not significantly change the overall picture of a general broad-front migration pattern.

Falsterbo is a migration hotspot for diurnal migrants during autumn because of a distinct coastal leading-line effect towards the peninsula in southwesternmost Sweden (Rudebeck, 1950; Karlsson, 2009, Malmiga et al., this issue). Without such important leading-line effects of the coastlines we would expect that Falsterbo would not be a particular autumn hotspot for nocturnal migrants. Still, large numbers of nocturnal migrants are captured at the Falsterbo Bird Observatory, and impressive concentrations of grounded nocturnal migrants may be observed on the peninsula (Karlsson, 2009). Given the present results, the concentrations of nocturnal migrants at the peninsula are likely to be caused mainly by the landing of large numbers of nocturnal migrants when confronted with the sea, rather than increased densities of migrants passing over the peninsula compared to over surrounding areas. However, there is the possibility that nocturnal songbird migrants, even if they do not follow local coastlines, still show more diffuse regional orientation responses to general topography (in a similar way as recorded for nocturnal shorebird migration; cf. Gudmundsson, 1994, Grönroos et al., 2012) that will lead to broad-front concentrations towards the Falsterbo Peninsula. If and to what extent this may occur is unknown.

3.2 Scatter

Scatter in track directions was consistently higher in autumn than in spring, perhaps due to the higher proportion of juveniles in autumn, or more local movements taking place as the birds hesitate to depart on the sea crossing. Scatter also increased in the later part of the night in autumn. In two of the areas the scatter in track directions was larger in the lower altitude intervals than in the higher (Table 1). If the passerines follow coastlines, one might expect them to do so to a higher degree at low altitudes rather than higher altitudes. Hence, if all passerines do so to the same extent we would expect less scatter at lower altitudes, but here we see the opposite. More scatter at lower altitudes could suggest that some birds at the lower altitudes followed coastlines but others did not, however there is no indication of mean directions being more skewed towards the coastlines at lower altitudes. We instead suggest that the higher scatter at low altitudes in area B and C is due to a higher degree of local movements and reverse migration taking place at lower altitudes, while migration in the seasonally appropriate direction takes place at higher altitudes.

Area A seems to differ from the other two areas in several ways. In spring it was the area containing most

tracks showing very little scatter at all altitudes, and in autumn it was the area with fewest tracks showing quite a lot of scatter at all altitudes. The peninsula is not a very good stop-over site, so birds arriving at the peninsula in autumn and deciding not to continue might very well choose to return inland, leading to increased scatter in area A in autumn (reverse migration; see Alerstam, 1978; Åkesson et al., 1996). The scatter in area A is also very large late in the night in autumn, which also is consistent with a high degree of reverse migration, particularly at low altitudes. It could however also be an effect of low-flying birds choosing different shortcuts over the bay, some perhaps aiming for the northern tip of the peninsula. In spring there will of course be very little reverse migration once the birds have reached the peninsula.

In conclusion, we could not see any clear and important local scale effects of the coastline on flight paths of nocturnally migrating passerines over the Falsterbo peninsula. There was some indication of an effect on flight paths in spring, and overall wind seems to be influencing the track directions more than the topography. We saw larger local differences in mean track direction and more scatter in directions at lower altitudes than at the higher altitudes, probably because some inclusion of local reverse migration, landing and take-off flights. There might however be a larger scale effect of coastline topography on the flight paths of the migrants. Radar tracking of diurnally migrating raptors at the same site as our study showed that the raptors often responded to the coastlines (Malmiga et al., this issue). Clearly, diurnal migrants have better opportunities to use landmarks and topography in their migration, even though the contrast between land and water could be one of few visible (and audible) cues available also during the night. The use of weather radar networks to study bird migration on larger regional scales offer exciting opportunities to shed further light on questions regarding how migrants react to the landscape (see for example Dokter et al., 2011).

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References

Åkesson S, 1993. Coastal migration and wind drift compensation in nocturnal passerine migrants. *Ornis Scandinavica* 24: 87–94.

- Åkesson S, Karlsson L, Walinder G, Alerstam T, 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south scandinavia. *Behavioral Ecology and Sociobiology* 38: 293–302.
- Alerstam T, 1978. Reoriented bird migration in coastal areas: Dispersal to suitable resting grounds? *Oikos* 30: 405–408.
- Alerstam T, Pettersson SG 1977. Why do migrating birds fly along coastlines? *Journal of Theoretical Biology* 65: 699–712.
- Batschelet E, 1981. *Circular Statistics in Biology*. London: Academic Press.
- Bruderer B, 1978. Effects of alpine topography and winds on migrating birds. In: Schmidt-Koenig K, Keeton WT ed. *Animal Migration, Navigation and Homing*. Berlin: Springer-Verlag, 252–265.
- Bruderer B, Liechti F, 1998. Flight behaviour of nocturnally migrating birds in coastal areas: Crossing or coasting. *Oikos* 29: 499–507.
- Bruderer B, Peter D, Boldt A, Liechti F, 2010. Wing-beat characteristics of birds recorded with tracking radar and cine camera. *Ibis* 152: 272–291.
- Bäckman J, Alerstam T, 2003. Orientation scatter of free-flying nocturnal passerine migrants: Components and causes. *Animal Behaviour* 65: 987–996.
- Dokter AM, Liechti F, Stark H, Delobbe L, Tabary P et al., 2011. Bird migration flight altitudes studied by a network of operational weather radars. *Journal of the Royal Society Interface* 8: 30–43.
- Fortin D, Liechti F, Bruderer B, 1999. Variation in the nocturnal flight behavior of migratory birds along the northwest coast of the mediterranean sea. *Ibis* 141: 480–488.
- Gagnon F, Ibarzabal J, Savard J-PL, Bélisle M, Vaillancourt P, 2011. Autumnal patterns of nocturnal passerine migration in the St. Lawrence estuary region, Quebec, Canada: A weather radar study. *Canadian Journal of Zoology* 89: 31–46.
- Gruys-Casimir E, 1965. On the influence of environmental factors on the autumn migration of Chaffinch and Starling: A field study. *Archives Néerlandaises de Zoologie* 175–279.
- Grönroos J, Green M, Alerstam T, 2012. Fine-scaled orientation changes in migrating shorebirds. *Ardea* 100: 45–53.
- Gudmundsson GA, 1994. Spring migration of the knot *Calidris c. canutus* over southern Scandinavia, as recorded by radar. *Journal of Avian Biology* 25: 15–26.
- Karlsson L, 2004. *Wings over Falsterbo*. Falsterbo: Falsterbo Fågelstation.
- Karlsson H, Nilsson C, Bäckman J, Alerstam T, 2012. Nocturnal passerine migrants fly faster in spring than in autumn: A test of the time minimization hypothesis. *Animal Behaviour* 83: 87–93.
- Malmiga G, Nilsson C, Bäckman J, Alerstam T, 2014. Interspecific comparison of the flight performance between sparrowhawks and common buzzards migrating at the Falsterbo peninsula: A radar study. *Current Zoology* 60: – .
- Mardia KV, Jupp PE, 2009. *Directional Statistics*. Hoboken: Wiley.
- Meyer SK, Spaar R, Bruderer B, 2000. To cross the sea or to follow the coast? Flight directions and behaviour of migrating raptors. *Behaviour* 137: 379–399.
- Richardson W, 1978. Reorientation of nocturnal landbird migrants over the Atlantic ocean near Nova Scotia in autumn. *The Auk* 95: 717–732.
- Rudebeck G, 1950. Studies on bird migration based on field studies in southern Sweden. *Vår Fågelvärd Suppl.* 1: 148.
- Snow D, 1953. Visible migration in the British isles: A review. *Ibis* 95: 242–270.
- Svårdson G, 1953. Visible migration within Fenno-Scandia. *Ibis* 95: 181–211.
- Van Dobben WH, 1953. Bird migration in the Netherlands. *Ibis* 95: 212–234.
- Zehnder S, Åkesson S, Liechti F, Bruderer B, 2001. Nocturnal autumn bird migration at Falsterbo, south Sweden. *Journal of Avian Biology* 32: 239–248.

Supplement

Table S1 Pairwise Watson-Williams tests of F the mean directions shown in Figures 3 and 4. In some cases the mean concentration parameter was too low to allow for the test to be performed (-) and for some (*) the n -values were too low (< 15, see Table 1)

Track			
Autumn	64–300m	300–800m	800–3058 m
Area A - Area B	-	-	$F_{1,325} = 0.20, P = \text{N.S.}$
Area B - Area C	$F_{1,172} = 11.37, P < 0.001$	$F_{1,696} = 14.00, P < 0.001$	$F_{1,569} = 0.52, P = \text{N.S.}$
Area A - Area C	$F_{1,143} = 3.73, P = \text{N.S.}$	$F_{1,633} = 1.48, P = \text{N.S.}$	$F_{1,518} = 1.18, P = \text{N.S.}$
Spring	122–300m	300–800m	800–2581m
Area A - Area B	*	$F_{1,416} = 27.41, P < 0.001$	$F_{1,456} = 46.81, P < 0.001$
Area B - Area C	*	$F_{1,235} = 17.79, P < 0.001$	$F_{1,293} = 23.39, P < 0.001$
Area A - Area C	*	$F_{1,385} = 0.66, P = \text{N.S.}$	$F_{1,431} = 1.18, P = \text{N.S.}$
Heading			
Autumn	64–300m	300–800m	800–3058m
Area A - Area B	$F_{1,47} = 0.96, P = \text{N.S.}$	$F_{1,291} = 0.01, P = \text{N.S.}$	$F_{1,255} = 0.24, P = \text{N.S.}$
Area B - Area C	$F_{1,82} = 0.65, P = \text{N.S.}$	$F_{1,494} = 7.37, P < 0.01$	$F_{1,432} = 7.72, P < 0.01$
Area A - Area C	$F_{1,61} = 0.25, P = \text{N.S.}$	$F_{1,447} = 3.85, P = 0.05$	$F_{1,385} = 7.35, P < 0.01$
Spring	122–300m	300–800m	800–2581m
Area A - Area B	*	$F_{1,321} = 11.78, P < 0.001$	$F_{1,364} = 21.22, P < 0.001$
Area B - Area C	*	$F_{1,164} = 1.06, P = \text{N.S.}$	$F_{1,226} = 9.88, P < 0.005$
Area A - Area C	*	$F_{1,299} = 3.77, P = \text{N.S.}$	$F_{1,388} = 0.49, P = \text{N.S.}$
Track			
Autumn	Before midnight	After midnight	
Area A - Area B	$F_{1,424} = 3.25, P = \text{N.S.}$	-	
Area B - Area C	$F_{1,823} = 18.10, P < 0.001$	$F_{1,616} = 0.01, P = \text{N.S.}$	
Area A - Area C	$F_{1,693} = 0.25, P = \text{N.S.}$	$F_{1,603} = 12.23, P < 0.001$	
Spring	Before midnight	After midnight	
Area A - Area B	$F_{1,382} = 26.06, P < 0.001$	$F_{1,513} = 44.07, P < 0.001$	
Area B - Area C	$F_{1,266} = 22.12, P < 0.001$	$F_{1,268} = 20.17, P < 0.001$	
Area A - Area C	$F_{1,326} = 1.29, P = \text{N.S.}$	$F_{1,509} = 1.98, P = \text{N.S.}$	