

Coastal migration and wind drift compensation in nocturnal passerine migrants

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The orientation of nocturnal passerine migrants in relation to winds and coastlines was studied by visual observations (ceilometer observations). Numbers and track directions of migrating birds passing at low altitude (<200 m) through a vertical light beam were recorded simultaneously at sites along two coastlines at opposite sides of the Falsterbo peninsula in southwestern Sweden in the autumn of 1989. The directions of the coastlines differed by 34° at the two observation sites, which were only 350 m apart. Observations were made during the first part of the night a few hours after sunset. Wind direction and speed were measured at 11 m altitude and the headings of individual birds were calculated. The observed mean track direction of the migrants differed significantly between the two sites, and coincided with the orientation of the coastline at each site. At site 1 partial compensation for wind drift was observed, while at site 2 wind compensation was complete. The results show that nocturnal passerine migrants flying at low altitude follow coastlines and that they may use the coastline to compensate for wind drift. It remains to be shown how widespread coastal migration and the use of topographical landmarks are for wind drift compensation among nocturnal migrants.

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Migrating birds are strongly affected by wind during their flights. The track of a bird over the ground is the vector sum of its heading, i.e. direction and speed through the air, and the wind direction and speed (Alerstam 1976a). Crosswinds may cause orientational complications since the bird's track is not the same as its heading and the bird will be laterally drifted by the wind. Richardson (1991) recently reviewed the effects of wind on orientation in birds. Several studies have reported that diurnal migrants compensate completely or partly for wind drift during migration. Birds probably use the apparent relative motion of topographical landmarks during the flight for wind drift compensation, but this should be more difficult at high altitudes and at night.

Many studies of nocturnal migrants show a correlation between mean track and wind direction, but it is often unclear whether this is caused by pseudodrift (Evans 1966, Nisbet and Drury 1967, Alerstam 1978b), incomplete compensation for wind drift or both (for

references see Richardson 1991). Other studies report evidence of at least partial compensation for wind drift at night (see Richardson 1991). In a moon-watch study, evidence of uncorrected lateral drift by passerines migrating overland at night was presented (Richardson 1982), while in a ceilometer study it was suggested that compensation occurred only near a large river and not elsewhere overland (Bingman et al. 1982). Radar observations of nocturnal migration in the Swiss lowlands (Bruderer 1977) and above the Alps (Bruderer 1982) showed important effects of topographical features on bird migration. According to studies of drift effects in southern Germany on night migrants (Bruderer and Liechti 1990), birds flying at low altitude in weak winds showed full compensation, whereas birds at higher altitudes and in stronger winds showed only partial or no compensation. The birds seemed to use landscape features such as mountain ridges or valleys to compensate for wind drift.

There has been little systematic evidence of coastal

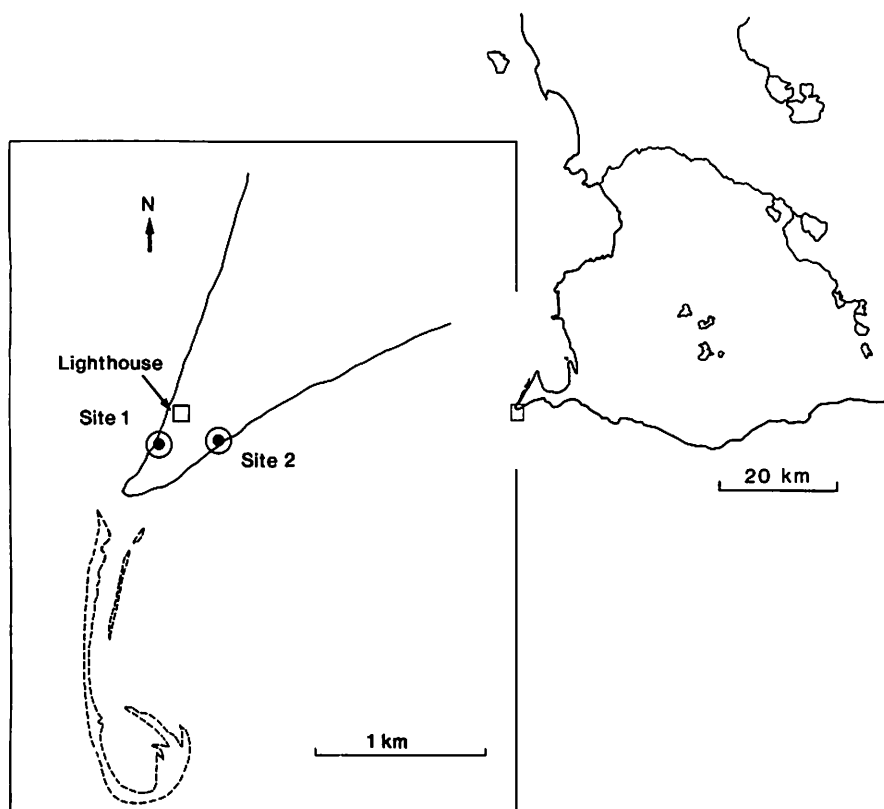


Fig. 1. Map of the study area at the Falsterbo peninsula (55°23'N, 12°50'E), the southwesternmost point of Sweden. The broken line refers to a flat island of bare sand, which is continuously transformed and moved by wave action.

migration at night in earlier studies. However, there is previous circumstantial evidence of concentrations of birds over coasts at night and of birds flying parallel to the coastline to avoid overwater flights (Lowery 1951, Vleugel 1954, Bagg and Emery 1960, Adams 1962, Lack 1963, Kippenheuer and Linsenmair 1965, Lowery and Newman 1966, Bellrose 1967, Richardson 1978). In a radar study, Richardson (1978) reported that many landbirds crossed coastlines at acute angles while others changed course parallel to the coastline.

In this study I investigated whether nocturnal passerine migrants fly along coastlines and whether those flying near coastlines use topographical landmarks to compensate for wind drift. To examine these questions I made ceilometer observations of night-migrating passerines, flying at low altitude, through a vertical light beam at two sites along the coastlines of the Falsterbo peninsula in SW Sweden (55°23'N, 12°50'E) during the autumn migration period.

Methods

Ceilometer observations were made at two nearby sites, approximately 350 m apart, close to the coastlines at

opposite sides of the Falsterbo peninsula (sites 1 and 2 in Fig. 1). I used one stationary and one portable ceilometer (both 100 W halogen light) placed 10–15 m from the two coastlines. The diameter of the reflector was 30 cm and the opening angle of the beam was approximately 5°. The orientation of the coastline was 21°/201° at site 1 and 55°/235° at site 2 (Fig. 1). Fig. 2 shows an aerial photo of the peninsula taken from SW. Note the distinct shoreline consisting of sandy beaches.

Almost all observations were made simultaneously at the two sites during 13 (site 1) and 9 (site 2) nights between 29 September and 19 October 1989. Observation bouts lasted at least 60, and up to 120 min, during the first part of the night (from two to five hours after sunset). The observer was placed horizontally on the ground in a fixed position (head towards south), and with a pair of binoculars (10×) she/he observed and estimated the track direction of migrating birds passing through the ceilometer light beam overhead. The tracks of the birds were estimated according to a clock-face to the nearest half-hour, read into a portable tape recorder, and later converted to track directions for individual birds as described by Gauthreaux (1969).

The birds observed were all small and medium sized passerines, up to the size of a thrush *Turdus* spp. A few of them were identified and most of these were Robins *Erithacus rubecula*. Other identified species were



Fig. 2. Aerial photo of the Falsterbo peninsula, taken from SW. The two observation sites 1 and 2, are indicated by numbers. Note the clearly visible shoreline which consists of sandy beaches. Photo taken by Mikael Kristersson.

Redwing *Turdus iliacus*, Song Thrush *T. philomelos* and Redstart *Phoenicurus phoenicurus*. The majority of the observed birds were flying at low altitudes, approximately between 10 and 100 m above ground.

Weather was recorded at site 1 at the Falsterbo Weather Observatory, situated in the lighthouse garden (Fig. 1). Almost all ceilometer observations were made under clear or partly covered skies (0–5/8), and 520 birds were observed in these conditions. Observations under a more or less overcast sky (7/8–8/8) resulted in 399 birds recorded. Although there was an inconsistent but significant difference in the angular scatter of track directions (r corresponds to mean vector length) between clear skies and overcast conditions at both sites (site 1: clear skies, $N = 252$, $\alpha = 210^\circ$, $r = 0.66$, overcast skies, $N = 170$, $\alpha = 225^\circ$, $r = 0.50$; site 2, clear skies, $N = 268$, $\alpha = 236^\circ$, $r = 0.54$, overcast skies, $N = 229$, $\alpha = 234^\circ$, $r = 0.80$; both $p < 0.05$, Mardia's one-way classification test, Mardia 1972), the mean track directions (α) were almost the same under clear and overcast skies and therefore all observations at each site were pooled in

the analyses. Wind speed and wind direction measured 11 m above ground were used in the calculations of heading directions (the anemometer of the Weather Observatory was situated at site 1). For these calculations the airspeed of the birds was provisionally estimated at 10 m s^{-1} , according to radar observations of flight speeds of small passerine nocturnal migrants (Bloch and Bruderer 1982). To calculate the heading of individual birds the following relationship was used:

$$\sin \gamma = \frac{\omega \cdot \sin \beta}{10},$$

where γ = angle between track and heading, β = angle between track and wind direction (with $\beta = 0^\circ$ corresponding to due following winds and $\beta = 180^\circ$ to due opposed winds), w = wind speed (m s^{-1}) and 10 (m s^{-1}) is the assumed airspeed of the birds. The value obtained for heading is $T \pm \gamma$, depending on whether the wind blew from the left ($-\gamma$) or the right side ($+\gamma$) in relation

Table 1. The relationship between observation time and number of birds recorded during onshore and offshore winds at site 1 and site 2, respectively.

	Total observation time (h)	Relative observation time (onshore/offshore)	Total number of birds	Relative number of birds (onshore/offshore)
Site 1	6.0	0.59	422	0.07
Site 2	9.5	0.80	497	1.03

to the track direction T . The birds' track and heading directions were then analysed in relation to crosswinds, where onshore winds refer to crosswinds from the sea and offshore winds refer to crosswinds from land. The observations of bird flight directions were divided into two groups with respect to crosswinds (observations during onshore and offshore winds, respectively) and the division between the two groups was made according to the orientation of the coastline at each of the two sites. Observations were made during nights with wind speeds up to 14 m s^{-1} , but most observations were associated with moderate winds $4\text{--}6 \text{ m s}^{-1}$. Since there are no obvious reasons to believe that birds migrating through the area at night are affected by other birds (observed birds were well separated in time), and the species composition of passing migrants was probably very similar (mostly thrushes and Robins) during the different observation nights, I feel confident to treat each bird as an independent observation in this analysis. Circular statistic methods used are according to Batschelet (1981) and to Mardia (1972).

Table 2. Mean observed track directions (T) and mean calculated heading directions (H) of night-migrating passerines observed during offshore and onshore winds at sites 1 and 2. The tabulated values correspond to the vectors shown in Fig. 3. All circular distributions are highly significantly oriented according to the Rayleigh test ($p < 0.001$, cf. Batschelet 1981). α = mean angle in relation to geographic North, N = number of birds, r = vector length. For further explanation see text.

			α	N	r
Site 1	Offshore winds	T_{OFF}	218°	379	0.59
		H_{OFF}	200°	379	0.62
	Onshore winds	T_{ON}	177°	27	0.62
		H_{ON}	230°	27	0.53
Site 2	Offshore winds	T_{OFF}	236°	230	0.59
		H_{OFF}	254°	230	0.54
	Onshore winds	T_{ON}	235°	239	0.77
		H_{ON}	210°	239	0.85

Results

The ratio of observation time during onshore to observation time in offshore winds and the numbers of birds observed in these wind conditions are shown in Table 1. The observation time was slightly shorter during onshore than offshore winds at both sites. The numbers of birds observed were almost the same in both wind conditions at site 2, but much fewer birds were observed in onshore winds at site 1 (Table 1).

Fig. 3 shows the distribution of observed track directions of all birds observed at sites 1 and 2, as well as the orientation of the coastline. The arrow indicates the mean track direction (α) of the birds at each site and the length of the arrow (r = mean vector length) is a measure of the scatter of the circular distribution (r ranges between 0 and 1, being inversely related to the angular scatter, cf. Batschelet 1981). The significance levels correspond to the Rayleigh test (Batschelet 1981). At site 2 the mean track direction does not differ significantly from the orientation of the coastline (95% confidence

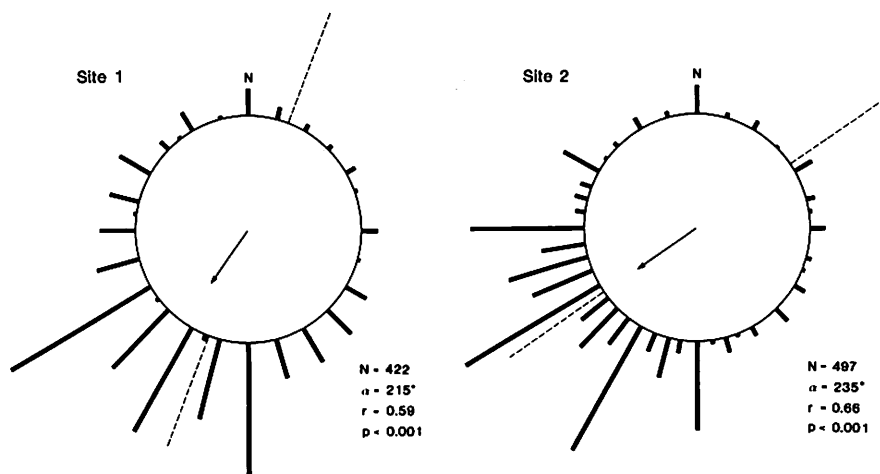
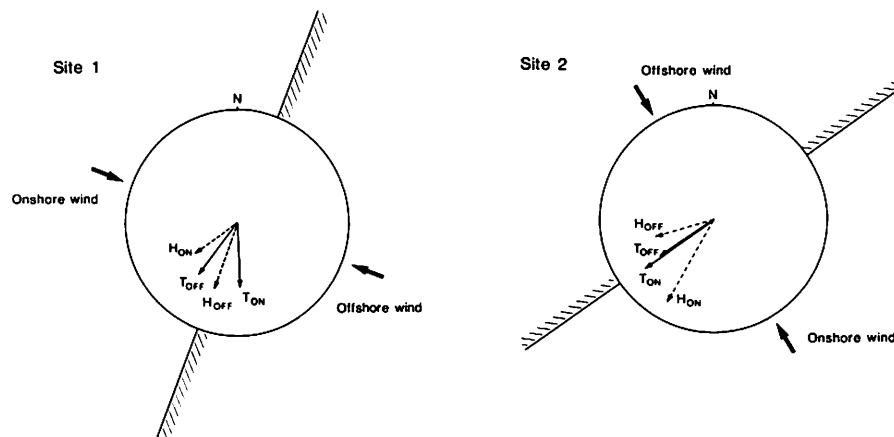


Fig. 3. Distribution of observed mean track directions of the total number of birds recorded at the two observation sites (α = mean track direction). The length of the arrow (r = mean vector length) is a measure of the scatter of the circular distribution and ranges between 0 and 1. Significance levels are according to the Rayleigh test (Batschelet 1981). The orientation of the coastline at the study site is indicated by a broken line.

Fig. 4. Mean track (T) and heading (H) vectors of birds observed at site 1 and site 2 during crosswinds. Observations from one night with calm conditions are excluded. The data are divided into two groups with respect to wind direction in relation to the direction of the coastline at each study site, referring to onshore and offshore winds respectively. Mean track and heading vectors during offshore winds are referred to as T_{OFF} and H_{OFF} , during onshore winds as T_{ON} and H_{ON} . The mean angles and vector lengths of tracks and headings at the two sites are tabulated in Table 2.



interval for the birds' mean track direction = $\pm 6^\circ$; Batschelet 1981), while at site 1 the difference is significant but numerically small (95% confidence interval = $\pm 7^\circ$). The mean track direction and the distribution of observed directions at sites 1 and 2 are highly significantly different from each other (Mardia's one-way classification test, $p < 0.001$; Mardia 1972).

Mean track (T) and heading (H) directions of observed birds during offshore (T_{OFF} and H_{OFF}) and onshore (H_{ON} and T_{ON}) winds are shown in Table 2 and Fig. 4. At site 1 the mean track directions during offshore and onshore winds are significantly different from each other (Mardia's one-way classification test, $p < 0.05$), as are the mean heading directions ($p < 0.05$). At site 2, mean track directions during offshore (T_{OFF}) and onshore winds (T_{ON}) do not differ significantly either from each other (Mardia's one-way classification test, $p > 0.05$), or from the coastline direction (95% confidence interval, $p > 0.05$). In contrast, the mean heading directions (H_{OFF} and H_{ON}) at site 2 are significantly different from each other (Mardia's one-way classification test, $p < 0.01$).

Fig. 5 illustrates nightly mean track and heading directions in relation to wind direction at sites 1 and 2, respectively. Only 14 nightly mean track and heading directions were significantly oriented at site 1 and 13 at site 2. A correspondence between track directions and the orientation of the coastline irrespective of wind direction is what we expect when complete compensation occurs. Although there are very few nights of observations at site 2, the nightly mean track direction agrees rather well with the orientation of the coastline in different wind conditions, especially in the well documented nights when 80, 113 and 149 birds were observed (Fig. 5b). At site 1 most birds were observed in offshore winds (Fig. 5a), and the correspondence between nightly mean track directions and the orientation of the coastline was less pronounced and the birds were partially drifted by the wind as earlier demonstrated

(see Fig. 4). Unfortunately, there are too few nights of observations to allow any statistical evaluation based on nightly mean flight directions.

Discussion

This study shows that the mean track directions of the night-migrating passerines were significantly different at the two sites, and the mean direction coincided with the orientation of the coastline at each site. This is interesting, because it establishes that migrating birds at least at low altitudes fly along coastlines during the night and that migration along topographical landmarks may be important also in night-migrating birds. The magnitude of drift was estimated at each observation site, as the coefficient for the slope of the relationship between track directions and the corresponding angles between track and heading directions in the different wind conditions, as described by Alerstam (1976a). A coefficient of $b=0$ means complete compensation and $b=1$ full drift. According to this measure of drift the birds at site 1 were partially drifted (drift coefficient $b = 0.58$), while at site 2 the birds completely compensated for wind drift ($b = -0.02$, which is not significantly different from 0). A fraction of the observed birds at site 1 may have arrived from the eastern coast in easterly winds, making a shortcut over the flat outermost part of the peninsula. When reaching site 1 they may continue across the coastline and depart over the sea towards SW. This may have caused the observed pattern of partial wind drift at site 1. Other birds, at least at the eastern coastline (site 2) may follow the shore to the southernmost point before leaving land for a continued migration across the sea towards SW. Diurnal migrants are known to use coastlines to compensate for wind drift (see for example Alerstam and Pettersson 1977, Ri-

wind drift are great (see Alerstam and Pettersson 1977). Furthermore, the migrants may also gain partial protection from unfavourable head and cross winds along the coast (Alerstam 1978a).

The importance of topographical landmarks in orientation and wind drift compensation in nocturnal migrants is not known, but some of the reasons for coastal migration in diurnal migrants also apply to night migrating birds. First, nocturnal migrants may benefit from coastal migration by facilitated orientation in relation to visible landmarks to minimize the risk of disorientation over the sea. Coastlines are probably quite visible to a low-altitude migrant during the night, since skylight is reflected in a different way from the water surface than from land, and also waves breaking towards the coast increase the visibility of shorelines (see Bellrose 1971, Martin 1990). Second, it may also be advantageous to follow coastlines extending in a direction not too different from the preferred migratory direction in order to reduce the risk of extra energy expenditures and longer flight distances and flight times caused by wind drift in strong opposing or side winds over homogeneous land or over the sea (cf. Alerstam and Pettersson 1977, Richardson 1991). The risk of predation over the sea or the gain of energy from wind sheltered flights as suggested for diurnal migrants (Alerstam 1978a, 1990b), are probably of minor importance in night migrating passerines.

Nocturnally migrating passerines are generally believed to migrate alone or in loose flocks (see e.g. Bruderer 1971). Most authors report that such birds migrate on a broad front irrespective of the topography below them (Sutter 1957, Lack 1958, Eastwood and Rider 1966, Bellrose 1971, Balcomb 1977; but see Bruderer 1982, who reported important deviations along topographical features). Radar measurements of flight altitudes of nocturnally migrating passerines in Europe and North America, show that 90% of the birds fly below 1500–2000 m above ground level (AGL). Some authors believe that the majority of birds fly between 400 and 1000 m AGL (Lack 1960, Eastwood 1967, Alerstam 1990a), but most radars are biased towards high flying birds. Bruderer (1971) and Bruderer and Steidinger (1972) showed that 50% of nocturnal bird migration in the Swiss lowlands is below 700 m, with most birds in the lowest 250 m. Many studies of nocturnal migrants report drift or partial drift and the landscape is suggested to be of minor importance for wind drift compensation during the night (Richardson 1982, 1991, Cochran and Kjos 1985, Cochran 1987), but other studies provide evidence for complete compensation for wind drift at night (Drury and Nisbet 1964, Evans 1966, Alerstam 1976b). Bruderer and Jenni (1988, 1991) and Bruderer and Liechti (1990) showed that drift, partial compensation, and full compensation occur; weak winds (up to 5 m s^{-1}) are usually fully compensated for; with increasing wind speed and increasing flight level compensation is reduced.

Radiotelemetric studies of migrating thrushes in North America have shown that individual birds, regardless of the speed and direction of the wind, cloud cover or landscape maintained a constant heading and airspeed during the flights (Cochran and Kjos 1985, Cochran 1987). To mitigate wind drift the thrushes selected the flight altitudes with the most favourable winds, which indicates that the birds were aware of the drift and that they tried to reduce it. Only a few studies have reported that landscape features can be used in wind drift compensation by nocturnal migrants. Bingman et al. (1982) based on a ceilometer study, reported wind drift compensation near a river but not elsewhere overland. Bruderer and Liechti (1990), studied nocturnal bird migration over hilly country in southern Germany. They showed that weak winds from both sides were compensated for by birds flying below 1000 m along the Suebic Alb. Partial compensation by birds flying at higher levels indicates that birds also at high altitude may see and use such topographical features during migration flights. Earlier circumstantial evidence exists that during the night migrating birds may concentrate over land in coastal areas and that they may fly parallel to the orientation of the coastline (see Introduction). This indicates that coastlines may, at least in certain wind and weather conditions, be used as leading lines by nocturnally migrating birds.

In conclusion, this study has demonstrated that, in a coastal area, night-migrating passerines at low altitudes fly along the coast and in some cases apparently use the coastline to compensate for wind drift. Probably most birds have the potential to fly along coastlines during the night, and facilitated orientation and minimization of wind drift probably provide adaptive value to this behaviour in certain conditions. Coastlines presumably constitute clearly visible and audible (see D'Arms and Griffin 1972, Griffin and Hopkins 1974) leading lines at night, even for birds at rather high altitudes. The adaptive value of coastal migration probably depends on the status of the migrating bird as well as on environmental factors such as wind direction, wind speed, the orientation of the coastline in relation to goal direction and the distance of overseas flight. It remains to be shown how widespread coastal migration is among nocturnal migrants, at different altitudes and along differently oriented coastlines.

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