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Nocturnal autumn bird migration at Falsterbo, South Sweden

Susanna Zehnder, Susanne Åkesson, Felix Liechti and Bruno Bruderer

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We investigated the patterns of nocturnal bird migration in autumn 1998 at a coastal site on the Falsterbo peninsula in south-western Sweden, by means of a passive infrared device. In total 17411 flight paths, including track direction and altitude, of migrating birds were recorded for 68 nights from August to October. Mean migratory traffic rate per night varied between 6 and 6618 birds $\text{km}^{-1} \text{h}^{-1}$, with an average of 1319 birds $\text{km}^{-1} \text{h}^{-1}$. Migration at Falsterbo showed a similar seasonal pattern to that reported for central Europe, with pronounced peaks of migration and intermittent periods with relatively low migratory intensities. Weather factors explained two thirds of the variance in the intensity of bird migration. During nights with intense migration, associated with weak winds, the mean track direction was close to that in central western Europe (225°). Birds usually maintained a constant heading independent of wind directions and, in consequence, were drifted by the wind. The mean orientation clearly differed from that of the nearest coastline, suggesting that the birds did not use the topography below to compensate for wind drift.

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The migratory behaviour of birds is controlled by endogenous factors and influenced by various environmental factors. Important exogenous factors are weather and topography (Alerstam 1976a). At the mid-latitudes in Europe the seasonal pattern of bird migration is strongly influenced by the itinerant low-pressure systems. Heavy autumn migration occurs mainly to the east of high-pressure areas, often immediately after a depression has passed (Richardson 1978, 1990, Alerstam 1990, Bruderer 1997). Alerstam (1990) stated that once wind and precipitation conditions are taken into account to explain the intensity of migration, other factors do not play any major role. It has been widely established that wind has a paramount effect on migratory patterns, flight directions and altitudes (Alerstam 1979, Richardson 1991). Weak tail winds lead to large numbers of migrants aloft. Wind drift and compensation have mainly been investigated in relation to topography (e.g. Koch 1934, Williams et al. 1977, Bingman et al. 1982, Åkesson 1993a, Liechti 1993, Liechti et al. 1996, Bruderer 1997, Bruderer and Liechti 1998a, b).

Birds appear to follow topographical structures to compensate for wind drift. Mountain ridges, valleys, rivers or coastlines are often used by diurnal migrants as leading lines, but have as well been shown to be used by nocturnal migrants for wind compensation (Bingman et al. 1982, Åkesson 1993a, Bruderer and Liechti 1998b). The effect of a leading line increases the more it is orientated in the general migratory direction and the lower birds are flying (Bruderer et al. 1989).

Falsterbo, at the south-western tip of Sweden, is the most famous site for observing the passage of diurnal autumn migration in Scandinavia (Alerstam and Ulfstrand 1972, 1975, Alerstam 1978). Each year thousands of passerine migrants are ringed at Falsterbo Bird Observatory (Karlsson 1993). The orientation of nocturnal passerine migrants captured at this site has been investigated in orientation cage experiments (e.g. Sandberg et al. 1988, Åkesson 1993b, 1994, Åkesson and Bäckman 1999) and by ringing recovery analysis (e.g. Sandberg et al. 1988, Åkesson et al. 1996b). However, little is known about the nocturnal passage and those



Fig. 1. Map of southern Sweden. The star on the inset shows the location of the observation site on the Falsterbo peninsula (55° 23' N, 12° 50' E).

studies addressing it have been done for short periods only, using either surveillance radar (Alerstam 1972, 1976b) or observations of birds flying through a vertical light beam (ceiometer study, Åkesson 1993a). Åkesson (1993a) showed that nocturnal passerine migrants flying at low altitude follow the coastlines of the outermost parts of the Falsterbo peninsula and use the coastline to compensate for wind drift.

In this paper we present an almost complete seasonal survey of the course of nocturnal autumn migration at Falsterbo based on absolute numbers of migrating birds. We recorded the temporal pattern of nocturnal migration at a coastal site on the Falsterbo peninsula with a passive infrared device to study its variation with weather conditions. Seasonal and nightly patterns of

migratory intensity, flight directions and altitudes are analysed in relation to wind and topography. We investigated whether birds migrating at high altitudes, like low altitude migrants (cf. Åkesson 1993a), flew along the coastline to compensate for wind drift.

Study site and methods

Nocturnal migration was monitored by using an infrared device at the southern tip of the Falsterbo peninsula (55° 23' N, 12° 50' E; 5 m above sea level, ASL) in south-westernmost Sweden (Fig. 1). The observation point was located at the Falsterbo Lighthouse, which is surrounded by a small stand of bushes and trees in otherwise open country.

Observations were carried out between 7 August and 28 October 1998, hence they covered the main autumn passage (Karlsson 1993). If not prevented by precipitation, the recordings started one hour before sunset and lasted until one hour after sunrise. The overall nocturnal pattern showed two minima of migration intensity, the first approximately at sunset and the second 80 min before sunrise. In order to exclude the potentially confounding influence of diurnal movements, which increased considerably already before sunrise, the analyses were restricted to the time interval between the end of civil twilight at dusk and the beginning of civil twilight at dawn (Fig. 2). According to this definition, nights lasted from 21:53 to 4:34 h (6.7 h) in early August, and from 18:24 to 7:20 h (13.0 h) at the end of October (UTC + 2 h).

The thermal imaging equipment consisted of a passive infrared device (Long-Range-Infrared System LORIS, IRTV-445L, Inframetrics, Massachusetts, USA), a video recorder, a video peak store (Video Peak Store 493, Colorado Video Inc.), and a monitor. The camera with an opening angle of 1.45° was placed in a vertical upward position on the ground and was adjusted towards north with the aid of a compass. The camera was focused periodically on an object a few kilometres away in order to ensure a well-focused image from 300 m to infinity. Thermal radiation emitted

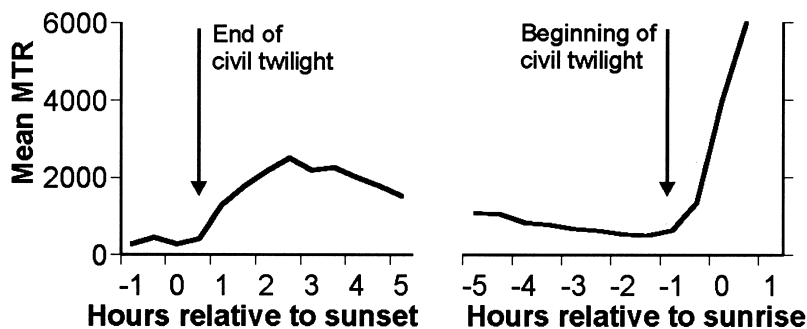
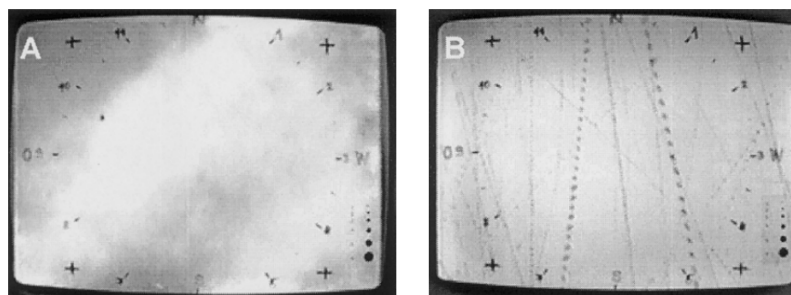


Fig. 2. Nocturnal pattern of mean MTR relative to sunset and sunrise, based on pooled data from the entire season. The arrows indicate the end of civil twilight at dusk and the beginning of civil twilight at dawn, respectively.

Fig. 3. (A) Monitor showing the picture of a night with cloud passage. Clouds and birds appear dark in contrast to the cold sky. A single bird of size 4 is visible near ten o'clock. (B) Monitor showing a peak store picture (similar to a long term exposure). Each line of dots corresponds to a single bird. The flight direction of the bird is determined according to the closest numbers of entrance and exit of the clock face. The bird's altitude is estimated according to the scale marked in the lower right hand corner.



by any kind of material can be detected if contrasting by at least 0.06°C against the background. Birds are normally seen as unstructured silhouettes. A bird of the size of a small passerine can be detected from very low altitudes up to 3000 m above ground level (AGL) as has been shown by direct comparisons with tracking radar (Bruderer and Liechti 1994, Liechti et al. 1995). Birds flying below 300 m AGL are increasingly out of focus, but clearly visible down to the lowest observed flight levels at roughly 25 m AGL (direct comparison with the height of the lighthouse).

Clouds seriously impair applicability of the technique because they contrast strongly with the clear sky and birds cannot be detected through them (Fig. 3A). Therefore, a cloudless sky meets the requirements for optimal observations. Because the infrared picture is built on heat differences, completely overcast and clear skies cannot be distinguished on the screen. The base of the clouds represents the upper limit for bird detection. All observations were recorded on video tapes and later analysed, for cloudless and completely overcast skies by means of video peak store. This device produces a picture on the screen similar to a long-term exposure. A bird's flight path appears as a line of dots, which is easier to observe than a moving silhouette crossing the screen (Fig. 3B).

Sometimes bird-shaped silhouettes or indications of flapping phases can be seen, but the identification of species remains impossible. Therefore, it cannot be excluded that a very small fraction of the observations is due to hunting or migrating bats (e.g. Ahlén 1997). Insects are much more numerous than bats but radiate less heat. Even large insects produce roughly 10 times less heat than small birds. Heat radiation decreases by distance squared. This suggests that even for large insects detectability would decline rapidly beyond 30 m. Comparisons with parallel radar measurements in Switzerland gave no indication that insects detected by radar (min. distance 100 m) could be detected by the infrared device (unpubl. data). Due to the narrow beam at short distances the passage through the field of view is very fast, at least for large insects. Medium-sized

insects would only be visible up to a few metres; they would, therefore, be much out of focus and provide relatively large bubble-like targets. Such targets were excluded from the counts. Small and weak fast-moving targets were also considered to be insects and were excluded. The quality of the picture deteriorates at sunset and sunrise due to the sun's infrared radiation. Hence, the quality of thermal imaging is severely reduced under daylight conditions and cannot be compared quantitatively with nocturnal observations.

The higher a bird flies above the camera the smaller the silhouette appears on the screen and the longer it takes to cross the field of view. Silhouettes were classified into seven size classes. The largest (class 7) was often out of focus, but was much darker than the bubble-like targets classified as insects. Classes 6 to 1 were compared with a reference scale (points of different size) mounted on the screen (Fig. 3). The estimates of flight altitude for each size class, according to radar measurements, are given in Table 2. The vast majority of nocturnal migrants are passerines of the size between a warbler and a thrush (Bloch et al. 1981). The size differences between the real silhouettes vary, therefore, within narrow limits. In contrast, the heat transmitted towards the infrared device decreases at least with the square of the distance in clear air. Thus, the usual size differences between various passerines are negligible compared to the influence of distance.

The flight directions, i.e. track directions, were determined according to the clock face method suggested by Lowery and Newman (1955) for the moon-watching technique (12 o'clock = N; 6 o'clock = S; clockwise). A circle was marked on the screen (see Fig. 2). For each bird the closest full hours of entrance and exit were registered; thus, 24 different flight directions were possible. Only birds flying through the circle were analysed. The circle on the screen corresponded to 1.4° opening angle of the field of view. The conical shape of the controlled space leads to an altitude-dependent detection probability of birds aloft. Therefore, numbers of observed birds were transformed into migration traffic rates (MTR) (Lowery 1951, adjusted to the metric

system). The MTR gives the number of birds crossing a line of one kilometre perpendicular to the flight direction during one hour (birds km⁻¹ h⁻¹), calculated according to the following approximation:

$$\text{MTR} = \frac{\sum_{i=1}^7 x_i \cdot (d_i \cdot (\sin \phi))^{-1}}{\Delta t} \quad (1)$$

where i = height classes 1 to 7, x_i = number of birds in height class i , d_i = flight altitude (km), ϕ = opening angle of the camera and Δt = observation interval (h). For each night the mean MTR was calculated. For specific analyses, nights were classified into three intensity classes. The average night included 1.4% of the seasonal passage. Therefore, we defined intense migration nights as those including > 2% of total passage of the season, intermediate nights as those with 0.5–2% and low migration nights as those with < 0.5%. The sum of MTR of the intense migratory nights ($N = 16$) accounted for 73% of the total passage, intermediate nights ($N = 20$) for 21% and low migratory nights ($N = 32$) for 6%.

Weather data for Falsterbo were provided by the Swedish Meteorological and Hydrological Institute (surface wind direction and speed, temperature, dew point temperature, altitude of cloud base, degree of cloud cover, air pressure, visibility; 3-hourly measurements). For all analyses mean values based on the 21, 00 and 03 UTC measurements were used. The 24-h changes of temperature and air pressure were calculated as the difference between the measurements at 00 UTC of two consecutive nights. Surface winds were used to calculate the headings of birds at 0–1000 m ASL. This extrapolation is possible due to the plain topography. For the headings of birds at 1001 m–3000 m ASL the average wind direction and speed was calculated based on the 23 UTC radio sonde from Kastrup Airport, Denmark (25 km NNW of Falsterbo).

The track of a bird over the ground is the vector sum of its heading (direction and speed with respect to the air) and the wind (direction and speed). Hence, mean heading directions were calculated as follows:

$$\text{Heading} = \alpha - \arcsin\left(\frac{v_w \cdot \sin(\alpha - \omega)}{v_a}\right) \quad (2)$$

where α = mean track direction, ω = wind direction, v_w = wind speed (m s⁻¹) and v_a = average air speed of the bird (m s⁻¹). For these calculations the bird's air speed was estimated at 12 m s⁻¹ (Liechti and Bruderer 1995, Bruderer and Liechti 1998a).

For each night a tail wind component was calculated as follows:

$$\text{Tail wind component} = [\cos(\beta - \omega)] \cdot v_w \quad (3)$$

where β = basic direction, defined as mean track direction under low wind speed conditions ($v_w \leq 5$ m s⁻¹) where birds are expected to fully compensate for wind drift (Bruderer et al. 1989), ω = wind direction and v_w = wind speed (m s⁻¹). At Falsterbo the basic direction of nocturnal migration in autumn 1998 was $\beta = 225^\circ$. Negative values of tail wind correspond to head wind.

Under the assumption that mean track direction only varies according to wind, we can apply the “universal measure of drift” (Alerstam 1976a) to describe the amount of wind drift. The magnitude of drift was estimated for each night as the slope coefficient b of the relationship between mean track direction and the corresponding angle between mean track and mean heading directions. A coefficient of $b = 0$ means complete compensation and $b = 1$ full drift. An intermediate value of b indicates partial drift compensation. In order to correlate circular values in a linear function, we restricted the analysed mean track directions to 180° around the basic direction (135° – 315°).

To compensate for the altitude-dependent detection probability of birds aloft, mean track direction and mean vector length were calculated according to the increasing field of view with distance. In order to avoid pseudoreplication in the analyses of track direction and scatter in the course of the night (Fig. 8), we calculated mean vectors based on mean values for each night. Within single nights only time intervals (tenths of night) with at least five birds were included, since means based on less than five observations were considered as not representative. Circular statistics (Rayleigh test, 95% confidence interval, Watson-Williams test and a non-parametric test for dispersion) were applied according to Batschelet (1981). Chi-square and Kendall- τ tests, correlation analyses and analyses of multiple regression (stepwise forward) were done with STATISTICA 5.0 (StatSoft, Inc. 1995) software package. For the multiple regression analysis the requirement of normally distributed residuals was achieved by log-transforming the dependent variable (mean MTR) according to Stahel (1995). For the analysis of weather factors, originally all weather variables recorded at Falsterbo, the calculated trends, and the tailwind component were included as independent variables.

Results

Temporal patterns

Observations were carried out during 51 entire nights, while in 17 nights observations were interrupted due to occasional precipitation. Fifteen nights had to be excluded because of rain. In total, 17411 birds were registered in 632.3 h of observation. The mean migration traffic rate per night fluctuated between 6 and 6618

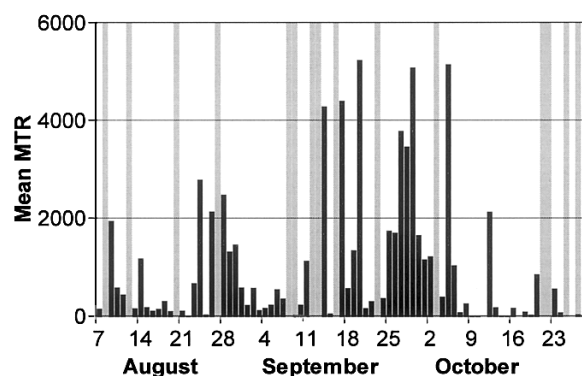


Fig. 4. Seasonal pattern of mean MTR (birds $\text{km}^{-1} \text{h}^{-1}$) per night. Nights without observations due to precipitation are marked with grey bars.

birds $\text{km}^{-1} \text{h}^{-1}$ (Fig. 4), with an average of 1319 birds $\text{km}^{-1} \text{h}^{-1}$ and a median of 566 birds $\text{km}^{-1} \text{h}^{-1}$ for those nights with observations. Assuming that missing nights had a MTR of 0, the mean migration traffic rate for the period between 7 August and 28 October was 1081 birds $\text{km}^{-1} \text{h}^{-1}$ and the median 327 birds $\text{km}^{-1} \text{h}^{-1}$. Nightly mean MTRs were moderate in the first half of the season and peaked in the second half of September. In October the MTR declined considerably.

Wind speed, tailwind component, air pressure and change in air pressure accounted for 66% of the variance in MTR (Table 1). Nightly mean MTR was high in conditions of low wind speed, large tailwind component, high and rising air pressure. Temperature and temperature change, humidity, dew point temperature, distance to the cloud base, and degree of cloud cover had no significant influence on the numbers of birds observed.

The median of the nightly passage (MTR) was reached on average after 40% ($\text{SD} \pm 15\%$) of the night's duration (Fig. 5). On average this corresponds to 4 h 53 min ($\text{SD} \pm 1 \text{ h } 47 \text{ min}$) after the end of civil twilight. The median was not correlated with the end of civil twilight at dusk, neither for all nights ($N = 66$, $r = 0.14$, $p = 0.28$), nor for nights with intense migration only ($N = 16$, $r = 0.39$, $p = 0.14$).

Table 1. Result of a multiple regression analysis (forward and backward stepwise, type III) relating mean MTR per night (log-transformed) with weather variables ($R^2 = 0.657$, $F_{(4,63)} = 12.309$, $p < 0.001$, S.E. of estimate = 0.386). Mean MTRs are shown in Fig. 4.

	B (S.E. of B)	t (53)	p-level
Intercept	26.98 (6.09)	4.43	<0.001
Wind speed	-0.11 (0.02)	-6.67	<0.001
Tailwind component	0.06 (0.01)	6.11	<0.001
Air pressure	-0.02 (0.01)	-3.87	<0.001
Trend of air pressure	0.03 (0.01)	4.78	<0.001

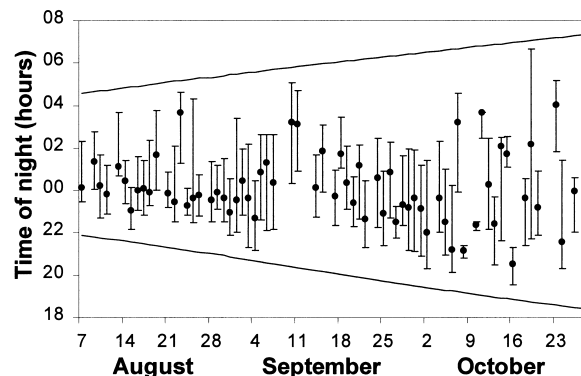


Fig. 5. Nightly patterns of migratory intensities. The duration of the night is limited by civil twilight at dusk and at dawn (lines). The dots mark the median (50% of the nocturnal migration has passed) and the T-bars show the time interval between the 25% and 75% percentiles. The time scale corresponds to local summertime (UTC + 2 h).

The duration of the main passage (50% around the median) in August and September decreased significantly with increasing migratory intensity ($N = 45$, $r = -0.50$, $p < 0.001$). But this correlation is not significant when data from October are included ($N = 68$, $r = -0.16$, $p = 0.21$). In October variability increased due to low migratory intensities, partly caused by inclement weather. The overall nocturnal pattern showed a pronounced peak of migratory intensity in the first half of the night and a prolonged decline towards the morning (Fig. 6).

The comparison of three time intervals of the night showed that during peak migratory intensity (tenths 2–5 of the night) birds flew higher than in the first tenth ($\chi^2 = 315.6$, $\text{df} = 6$, $p < 0.001$) and also higher than in the remaining part of the night (tenths 6–10; $\chi^2 = 328.3$, $\text{df} = 6$, $p < 0.001$; tests based on the seven height classes; Fig. 7).

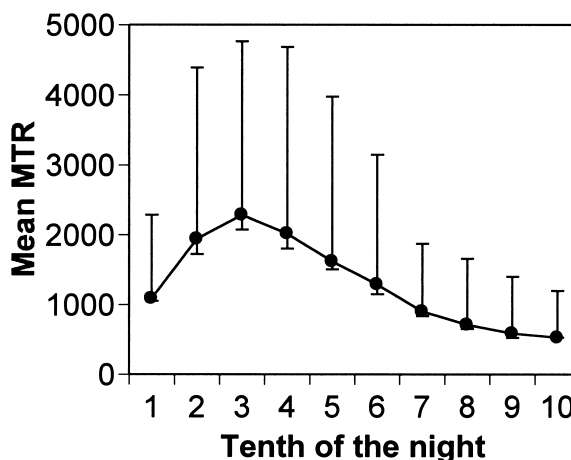


Fig. 6. Nocturnal pattern of mean MTR (birds $\text{km}^{-1} \text{h}^{-1}$) calculated from the data of the whole season. The error bars indicate the interquartile range.

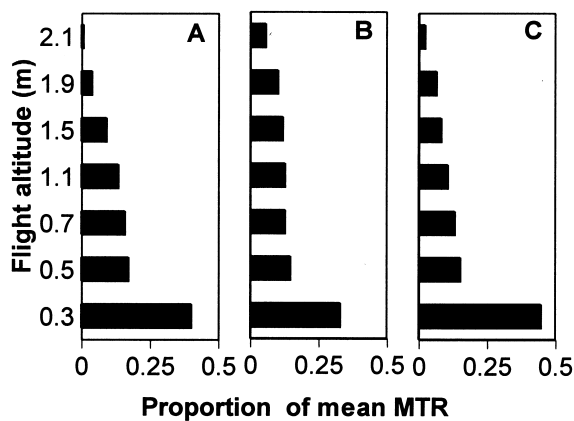


Fig. 7. Distribution of flight altitudes in three time intervals. The migratory intensity per height class is given as a proportion of the mean MTR per time interval. A includes the first tenth of the night; B tenths 2–5 of the night; C tenths 6–10 of the night.

Flight directions and wind influence

The mean track direction of all birds including all nights was 219° ($N = 17411$, $r = 0.62$, $p < 0.001$; $\pm 9^\circ$, 95% confidence interval). The higher the flight altitude was, the more southerly and more concentrated were the track directions ($N = 7$, $Z = 3.15$, $p = 0.002$; Kendall; for both relationships) (Table 2).

In the first tenth of the night, tracks were more westerly oriented than during the second tenth period (Fig. 8; $N = 89$, $F = 4.20$, $p < 0.05$; Watson-Williams test). In the second half of the night (6–10 tenth of the night) track directions gradually shifted from south-westerly directions towards more westerly directions ($N = 385$, $F = 22.21$, $p < 0.01$; Watson-Williams test). Birds recorded late at night (tenth 6–10 of the night) were more scattered, mainly because of an increasing tendency to fly towards W and NW during this period ($N = 385$, $U = 15944$, $p < 0.001$; nonparametric test for dispersion).

We related the mean track direction to the mean angle between track and heading direction for each night in order to analyse the birds' response to wind drift (Alerstam 1976a). In nights with high and low migratory intensity, mean track directions were positively correlated with the angle between track and

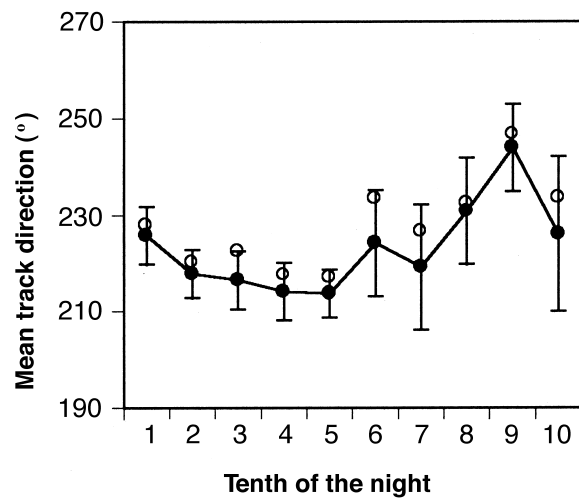


Fig. 8. Mean track direction during the course of the night. The black symbols show the mean track directions calculated based on every single track weighted by its contribution to the MTR. The error bars indicate the 95% confidence interval (Batschelet 1981). The open circles show the track direction calculated based on nightly means. During the migratory peak (tenth 2–5 of the night) tracks were significantly more concentrated and southerly oriented than in the rest of the night.

heading at altitudes below and above 1000 m ASL (linear regression for high intensity: < 1000 m: $N = 17$, $r = 0.70$, $p = 0.002$; $N = 16$, $r = 0.88$, $p < 0.001$, and for low intensity: < 1000 m: $N = 21$, $r = 0.69$, $p < 0.001$; > 1000 m: $N = 18$, $r = 0.79$, $p < 0.001$) (Fig. 9). In nights with intermediate migratory activity the correlation was positive in both flight altitude categories, but not significant. Only for one of the significant correlations, i.e. for intense migration at high altitude, the slope of the regression line was significantly different from 1, indicating partial compensation (see Fig. 9).

For the analysis of mean track directions in relation to the coastline, only low flying birds (< 600 m ASL), i.e. height classes 7 and 6 were included, since the influence of topographical structures have been shown to decrease with altitude (Bruderer et al. 1989). Under conditions of low wind speed ($v_w \leq 5 \text{ m s}^{-1}$) 51% of the migratory movements were recorded in height classes 6–10. The mean track directions of this selection differed between winds from the left ($\omega = 44^\circ$ to 226° ; $\alpha = 231^\circ$, $r = 0.49$, $N = 1536$, 95% CI $\pm 12^\circ$) and from

Table 2. Mean track directions and MTR with respect to flight altitude as given for each size class of birds. Flight altitude was estimated according to silhouette size (see Study site and methods). All directional distributions were significantly different from random ($p < 0.001$, Rayleigh test).

Size class	7	6	5	4	3	2	1
Estimated mean flight altitude (km)	0.3	0.5	0.7	1.1	1.5	1.9	2.1
Mean track direction ($^\circ$)	228	227	226	219	209	201	199
Mean vector length	0.45	0.65	0.66	0.75	0.80	0.87	0.92
MTR (birds $\text{km}^{-1} \text{h}^{-1}$)	532	218	190	167	136	108	52
Number of tracks	2517	1722	2098	2894	3216	3241	1723

the right ($\omega = 226^\circ$ to 44° ; $\alpha = 220^\circ$, $r = 0.57$, $N = 826$, $95\% \text{ CI} \pm 10^\circ$), though the 95% confidence intervals overlap. The orientation of the coastline 100 m west of the observation site ($21^\circ/201^\circ$) was not within the calculated 95% confidence intervals of the mean track direction, neither with winds from the left nor from the right.

Discussion

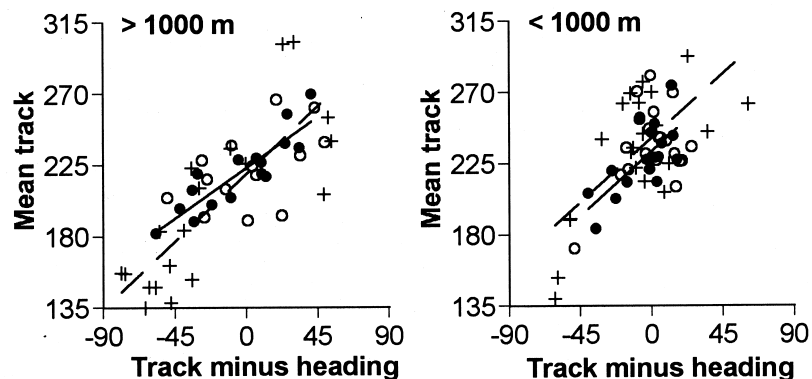
Temporal pattern of migration

The migratory intensities recorded at Falsterbo revealed large fluctuations between nights. These fluctuations are most probably due to strong weather changes that were especially pronounced in 1998 (L. Karlsson, pers. comm.), but could also reflect the variation in number of birds ready to migrate at different times of the season (Richardson 1978). The mean seasonal MTR of $1319 \text{ km}^{-1} \text{ h}^{-1}$ is the first estimate of nocturnal migratory intensity in Scandinavia. Assigning zero values to times when no observations were possible due to rain, we would come up with a mean MTR of roughly $1000 \text{ birds km}^{-1} \text{ h}^{-1}$ for the total observation period. Comparisons with other sites will be necessary to verify whether nocturnal migration is concentrated at Falsterbo or not. The nightly mean MTRs show the departure of long-distance migrants in August, a peak of migration in the second half of September, when long- and short-distance migrants pass Falsterbo, and declining numbers of short-distance migrants in October, as known from long-term ringing programs (Karlsson 1993). The number of nocturnal migrants observed aloft correlated with the number of grounded birds captured the following morning (Zehnder and Karlsson 2001). The seasonal pattern of nocturnal migration is similar to the one found by Baumgartner (1997) in

southern Germany (see also Bruderer and Liechti 1998b). Baumgartner (1997) compared long-term trapping numbers of birds at a ringing site in the Alps and radar data of one season, emphasising that it is important to account for seasonal effects when analysing weather influences. We did not include seasonal effects in the multiple regression analysis of weather factors on migratory intensity. However, almost two thirds of the variance in migratory intensity could be explained by variations in wind (tailwind component and wind velocity) and air pressure (see above). Weak tail winds are well known to be associated with heavy migratory movements (for review see Richardson 1978). By selecting nights with favourable wind conditions for migration a bird may considerably increase its flight distance covered on a given amount of fuel (Alerstam 1979, Alerstam and Lindström 1990, Liechti and Bruderer 1998, Åkesson and Hedenström 2000). Air pressure is often reported to correlate with migratory intensity, particularly in North America (see Richardson 1978, 1990 for reviews). However, Richardson (1978) emphasises that air pressure is correlated with many other weather factors. Falling and low air pressures generally are associated with deteriorating weather not suitable for migration and frequently involves rain. Rain to a large extent prevents birds from initiating migration (Parslow 1969). Indeed, we observed strong influences of wind and increasing or high air pressure on the intensity of nocturnal migration at Falsterbo in line with the findings by Baumgartner (1997). High air pressures may be taken as an indicator of a generally good synoptic weather situation, while low pressure may be taken as a substitute for the negative influence of precipitation.

We observed that most of the nights with high migratory intensity were followed by a night with relatively low migratory intensity. This pattern indicates that many nocturnal migrants that were prepared for migra-

Fig. 9. Nightly mean track direction in relation to track direction minus heading direction of birds flying above and below 1000 m ASL, respectively. Nights with intense migration are marked with a dot, intermediate intensity with an open circle and low intensity with a cross. The slope of the regression line is a measure of the magnitude of drift or compensation for drift ($b = 1$ means full drift and $b = 0$ complete compensation) (Alerstam 1976a) (Intense migration: $< 1000 \text{ m ASL}$, $b = 0.91 \pm 0.16$ (95% confidence interval), $> 1000 \text{ m ASL}$, $b = 0.71 \pm 0.07$, solid lines; low intensity migration: $< 1000 \text{ m ASL}$, $b = 0.90 \pm 0.15$, $> 1000 \text{ m ASL}$, $b = 0.92 \pm 0.12$, broken lines) (see text for more statistics).



tion departed during the limited time periods with favourable weather conditions (see above). Presumably it took some time before newly arrived migrants from further north were prepared to re-initiate migration. As shown by several studies, the vast majority of migrants depart in the first two hours after sunset (reviews in Moore 1987, Kerlinger and Moore 1989, Åkesson et al. 1996a, 2001, Bruderer and Liechti 1999). At Falsterbo the timing of the peak migratory passage was generally later at night and varied between days. Hence, birds most likely reached Falsterbo after flights of different lengths (i.e. arriving from source areas at different distances from Falsterbo). Since birds maintained their headings irrespective of wind conditions we assume that, depending on wind direction and wind speed, birds from different stopover areas were observed at Falsterbo. Winds additionally influence flight speeds, and adverse weather conditions at the beginning of the night may delay departure.

The majority of the birds apparently arrived at Falsterbo after several hours of flight. Estimating a bird's flight speed at 12 m s^{-1} and by extrapolating the mean track direction we can estimate that the majority of the recorded migrants took off from the forested areas more than 100 km to the NE of Falsterbo. The majority of the migrants were seen during the first half of the night, with relatively low migratory intensities in the second half of the night. This indicates that birds presumably begin to land already after approximately 3 to 6 h of flight. Such early landings of nocturnal migrants have earlier been reported in radar studies (e.g. Bruderer and Liechti 1998b). In correspondence with this landing tendency, flight altitudes declined gradually during the second half of the night. A similar pattern has been observed at an inland site in southern Germany (Bruderer and Liechti 1998b), and thus need not indicate a landfall caused by the birds being confronted with the sea.

Flight directions and wind drift

Nights with intense migratory activity showed mean directions towards 225° at Falsterbo, which is similar to the main migratory directions reported for other sites in western Europe (e.g. 230° for southern Germany and Switzerland, Bruderer et al. 1989; 220° at a coastal site in southern Spain, Bruderer and Liechti 1998a). We also observed a more southerly mean track direction at higher altitudes which is in agreement with former observations, and presumably could be explained by the increasing wind speed with altitude. Since winds from the west predominated throughout the season, birds higher up were drifted more southwards than birds at lower altitudes. Pseudodrift might account at least for part of the change with altitude if birds with more southerly preferred migratory directions actively

choose to fly at higher altitudes (cf. Alerstam 1976b). The shift of the mean track direction during the night from SSW to SW resulted from a higher proportion of birds flying in westerly and north-westerly directions. These directions (W and NW) allow a shorter sea crossing from Falsterbo to Denmark (24 km between the closest points). In most nights the coastlines of Denmark towards W–SW are within sight of a bird flying above Falsterbo. After some hours of flight birds might be less prone to face a large sea crossing southwards due to the endogenous activity scheme or due to depleted fat stores. They may then choose, instead, to shorten the over-water flight by heading towards the Danish islands. A similar shift of the mean track direction was observed at various sites along the Mediterranean coast, where with the progress of the night birds increasingly shifted from southerly off-shore directions towards flying along the coastline (Fortin et al. 1999). Reverse movements recorded by the infrared device were rare (S. Zehnder, S. Åkesson, F. Liechti and B. Bruderer unpubl.) and much fewer than expected from an analysis of recoveries of birds ringed at this site (Åkesson et al. 1996b) and recorded by ceilometer observations (Åkesson 1995). Our observations indicate that once the birds had left the coast they usually did not return. This differs from relatively large sea-crossings at the south coast of Spain and on the island of Mallorca (Bruderer and Liechti 1998a) but conforms with various North American studies (review in Williams and Williams 1990), including very long over-water flights such as from the southern tip of Florida (Williams et al. 1977). Birds migrating at high altitudes seem to engage in sea-crossings towards the closest land on the opposite side of the sea (directed towards SW; see Fig. 1), rather than flying in reverse directions to stopover sites further inland in southern Sweden, as was reported for migrants grounded and captured at Falsterbo bird observatory (Åkesson et al. 1996b).

Migratory activity was significantly higher at low wind speeds. Surprisingly, the birds' headings rather than tracks showed a constant mean direction, indicating wind drift at low speeds, where full wind compensation could be expected (Alerstam 1976a, Liechti 1993). Birds at low wind speeds apparently maintained their preferred heading independently of wind direction and at least partially tolerated wind drift. Constant heading and lack of compensation for wind drift has been reported for different places in North America (e.g. Williams et al. 1977; review in Williams and Williams 1990). These observations might be explained by the predictions of optimal wind compensation relative to the distance to the migratory goal, since birds should allow themselves to be drifted at the beginning of the journey and over-compensate when they are close to the goal (Alerstam 1979, Liechti 1995). For the majority of the bird species recorded in this study the migratory goal is relatively far away. Since bird species or

populations with different migratory goals might select to migrate at nights with a particular wind condition (Alerstam 1972, 1975, see also Åkesson and Hedenström 2000) we cannot exclude that this pattern of wind drift, at least partly, is caused by pseudodrift (Alerstam 1976a).

Nocturnal passerine migrants at low altitudes (10–100 m ASL) have been shown to compensate for wind drift at this particular site, by flying along the coastlines of the Falsterbo peninsula (Åkesson 1993a). At the particular coastline where our observations took place (site 1 in Åkesson 1993a), the wind compensation was less marked. In the present study, we failed to demonstrate any leading-line effect. Obvious leading-line effects have been found along rivers (Bingman et al. 1982) and mountain ranges running close to the preferred flight direction (Bruderer and Liechti 1990 and references therein). Since the birds allow themselves to be drifted, we assume that for the majority of nocturnal migrants flying above 100 m AGL the local coastline does not serve as a leading line. This is in line with studies at continental coastlines and oceanic islands, where birds have been observed moving on a broad-front without deviations (Williams and Williams 1990).

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