Causes and characteristics of reverse bird migration: an analysis based on radar, radio tracking and ringing at Falsterbo, Sweden

Cecilia Nilsson and Sissel Sjöberg

C. Nilsson (cecilia.nilsson@biol.lu.se) and S. Sjöberg, Dept of Biology, Lund Univ., Ecology Building, SE-223 62 Lund, Sweden.

That birds migrate in the reverse direction of the expected is a phenomenon of regular occurrence which has been observed at many sites. Here we use three different methods; tracking radar, radiotelemetry and ringing, to characterize the flights of these reverse migrants and investigate possible causes of reverse migration of nocturnally migrating passerines during autumn migration at Falsterbo peninsula, Sweden. Using these different methods we investigated both internal factors, such as age and fuel load, and external factors such as weather variables, competition and predation risk. Birds flying in the reverse direction were more likely to be lean and to be juveniles. Reverse migration was also more common with overcast skies and winds with north and east components. We did not find any effect of temperature, visibility, number of migrating sparrowhawks, or the total number of ringed birds at the site on the day of departure. We found that reverse migration is characterized by slower flight speeds (airspeed) at high altitudes and that it takes place later in the night than forward migration.

During migration it is common to observe birds migrating in the reverse direction of what would be expected for the season. However, not much is known about these reverse movements, and previous studies have given contradictory results as to what causes them (Alerstam 1978, Richardson 1982, Åkesson et al. 1996b, Zehnder et al. 2002). Falsterbo peninsula is a migratory hotspot in southern Sweden, where millions of migrating birds pass each year. Coastlines are in many cases poor stopover habitats, especially at hotspots where many migrants pass, leading to high competition and high predation risk (Alerstam 1978, Woodworth et al. 2014, see also Stach et al. 2015). Poor stopover habitats may increase the amount of reverse migration, and birds have been shown to perform reverse movements to a higher degree at coastal stopover sites such as Falsterbo compared to inland stopover sites (Åkesson 1999).

We investigated the factors that distinguish forward from reverse migrating birds during autumn migration at Falsterbo peninsula to gain insights into what causes reverse migration and what characterizes reverse flights compared to forward migratory movements. Both internal factors relating to the state of the bird, and external factors such as weather variables could potentially affect if a bird continues forward or makes reverse movements (Sandberg and Moore 1996). To get an as broad understanding as possible, we combined information about the passage of migrants at the Falsterbo peninsula from tracking radar, radiotelemetry and ringing recoveries. By combining these three methods, we investigated possible causes, both internal and external factors. We

also characterize the flight behavior during reverse migration. The possible causes and characteristics of reverse migration that we aim to investigate in this study are summarized in Table 1. Below we describe the predictions to be tested concerning these internal and external factors as well as characteristics in reverse migration.

Internal causes of reverse migration

To be able to cross a barrier, even a modest sea crossing as between Falsterbo peninsula and continental Europe (Fig. 1), birds need to have enough fuel. Birds with low amounts of stored fuel are known to more frequently reverse their movements, especially in front of barriers (Lindström and Alerstam 1986, Schmaljohann and Naef-Daenzer 2011, Smolinsky et al. 2013). Juveniles have been shown to make more reverse movements than adults, which could be due to them being less efficient foragers (requiring them to search for other stopover sites) or a lack of experience (Moore 1984, Lindström and Alerstam 1986). Species-specific strategies, such as migration distance, might also affect the tendency to make reverse movements. Short-distance migrants could be less constrained in their migratory schedules, and thereby more likely to make reverse movements (Åkesson et al. 1996b, Nilsson et al. 2014). To gain information on the internal states of birds making reverse movements, we mainly used radiotelemetry and short-term ringing recoveries. Factors investigated were species, migration distance, body condition and age (Table 1).

Table 1. Summary of possible causes and characteristics of reverse migration and the methods used to investigate each factor (RT 5 radio-telemetry, R 5 ringing recoveries, RA 5 radar tracking).

Factors	Method
Possible causes of reverse migratory flights	
Internal factors	
Species	RT
Migration distance	RA
Age	RT, R
Fuel load	RT, R
Immediate/later departure	RT
External factors	
Wind	RT, RA
Cloud cover	RT, RA
Temperature	RT, RA
Visibility	RA
Predation risk	RT
Competition	RT
Characteristics of reverse migratory flights	
Departure time	RT, RA
Flight speed	RA
Flight altitude	RA

External causes of reverse migration

Wind direction and wind speed can considerably impair or assist migratory flights, and it is therefore not surprising that winds are known to affect departure decisions, (Åkesson and Hedenström 2000, Covino et al. 2015). However, in other cases winds had little or no effect (Schmaljohann and Naef-Daenzer 2011, Smolinsky et al. 2013).

Access to celestial cues are important for orientation during migration, and cloud cover could affect directional choices, with birds reversing their directions or being more scattered in their departure directions in overcast weather (Sandberg et al. 1991, Åkesson et al. 2001). We investigated if weather variables differed between forward and reverse migrants for birds tracked with radar or radiotelemetry (Table 1).

Competition with conspecifics and predator pressure both affect the quality of a stopover area, and could thereby influence whether birds continue on migration or decide to make reverse movements (Alerstam 1978, Lindström and Alerstam 1986). We used ringing information from the peninsula about the total number of birds caught, the number of birds of the same species caught, and the number of migrating sparrowhawks *Accipiter nisus*, as measures of competition and predation risk on the day of departure for radio tracked birds (Table 1).

Characteristics of reverse flights

Previous studies have shown that birds during reverse flights fly at lower altitudes and at slower flight speeds (Bruderer and Liechti 1998, Komenda-Zehnder et al. 2002). The propensity to continue on forward migration might also change during the night, especially as birds reach a barrier (Zehnder et al. 2002, Schmaljohann and Naef-Daenzer 2011). We investigated the characteristics of reverse and forward migratory
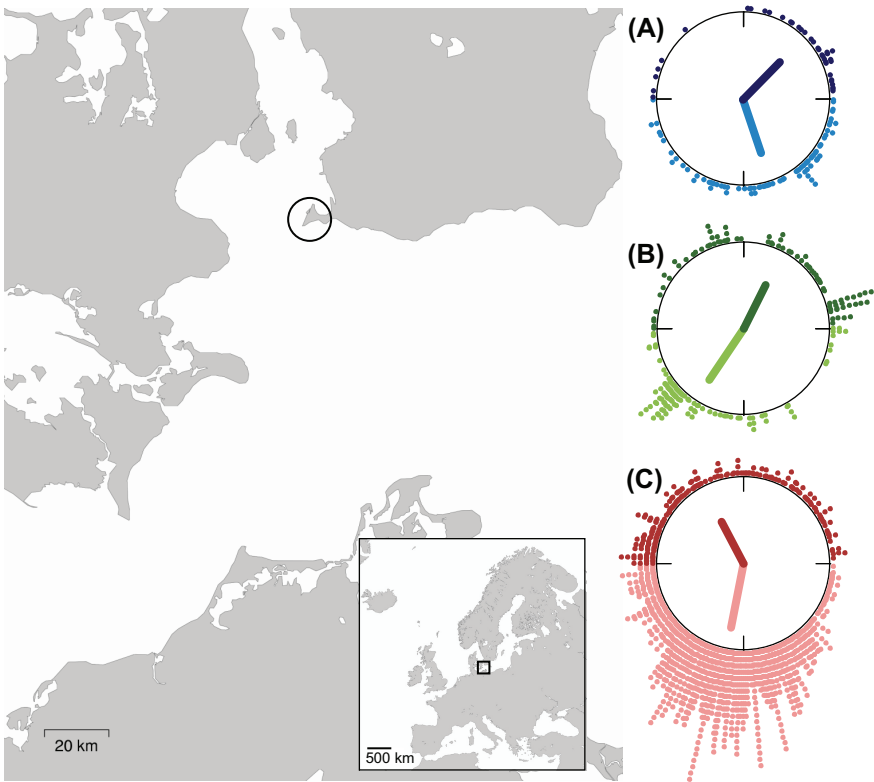

Figure 1. Map of Falsterbo (black circle) area with departure directions from radiotelemetry ((A) blue), direction between capture site and ring recovery site ((B) green) and track directions from radar tracking ((C) red). Reverse migrants in dark colors and forward migrants in light colors. Inserted map shows the location of the region (black box) in Europe. Maps from Maptool (Seaturtle.org 2002).

flights in terms of flight speed, altitudes and time of night by using tracking radar data from Falsterbo peninsula.

Predictions

We predicted that juvenile and lean individuals will perform reverse movements to a higher degree than adult and fat birds, and that reverse migration would be more common among short-distance migrants than long-distance migrants. We predicted that reverse migration would be more likely in opposed winds (winds against north), overcast conditions and low visibility, and when there is high competition (many birds ringed) and high predation pressure (many migrating sparrowhawks). We also predicted that the reverse movements would occur later during the night, at lower altitudes and at slower flight speeds (airspeeds).

Methods

Falsterbo

Falsterbo peninsula (55°24′50″N, 12°52′12″E, Fig. 1) is a migration hotspot in the south-west of Sweden. Migrants are funneled there during autumn migration, presumably by avoiding sea crossings as long as possible. A long-standing ringing regime has been running since the 1940s at Falsterbo Bird Observatory (Karlsson 2009). The peninsula has two small villages and consists mainly of sandy beaches, open areas with grass and shrubs (including two large golf courses), small areas with wetlands and reed beds and a heath that separates the peninsula from the mainland.

Radiotelemetry

We used an automatic radiotelemetry array on the Falsterbo peninsula (Fig. 1) to track nocturnal migratory passerines during their stopover in the area during autumn migration 2009–2012. The array consisted of three receiver stations (SRX600; Lotek Wireless, Newmarket ON, Canada). For setup and monitoring regime see Sjöberg et al. 2015. We used ID coded radio transmitters (NTQB-2, except for song thrushes *Turdus philomelos* that were equipped with NTQB-3-2 during 2010 and 2011, Lotek Wireless), all stable within their own burst rate (4.9–5.2 s in 2009–2010; 2.9–3.1 s in 2011–2013), but altered in order not to collide and overwrite data. All birds were caught as a part of the standardized ringing scheme at Falsterbo Bird Observatory; for method see Ringing recoveries) and a radio transmitter was glued to the back of the birds after being ringed and measured and thereafter immediately released. We selectively tagged individuals of different ages and with different amounts of stored fat (fat score 1–8) of four different nocturnally migrating passerine species. We used song thrushes and European robins *Erithacus rubecula*, medium-distance migrants leaving Scandinavia for southern Europe during the winters (Cramp 1988), and willow warblers *Phylloscopus trochilus* and garden warblers *Sylvia borin*, long-distance migrants wintering in Africa (Cramp 1992).

The exact burst rate of the transmitters was calculated from the decoded binary files from the receivers and in order

to clear the radiotelemetry data from false signals it was filtered by the burst rate, allowing a maximum error of $\pm$ 10 ms and at least 3 signals per minute. Vanishing bearing was calculated as a circular mean from the birds' last 10 min at the last receiver station it was in contact with at the Falsterbo peninsula, weighing each signal by signal strength. The statistical uncertainty (95% confidence intervals indicating the consistency of the directions within the last 10 min period) of the calculated vanishing bearings (216 individuals, autumn and spring data) was in the range of $\pm$ 0°–51.7° (6 vanishing bearings had CI 95% $> \pm 11.5°$, 2 vanishing bearings had CI 95% $> \pm 20°$), with mean CI 95% $= \pm 4.0°$. The numbers of signals within the last 10 min (n) ranged from 2–158 signals, mean n $= 46.0$ signals. We estimated the bias of the calculated bearings by doing measurements with transmitters on dead birds attached to helium balloons at known positions (0.3–3 km distance from the receiver station, altitudes 50–100 m), and calculated the bias to 9.5 $\pm$ 12.1° (mean $\pm$ SD, n $= 10$). For more details see Sjöberg and Nilsson 2015. As we don't know the exact preferred migration direction for the individual migrants, we judged all movements (vanishing bearings) towards the southern semicircle (n $= 79$, 90°–270°) as forward migration and movements towards the northern semicircle (n $= 37$, 270°–90°) as reverse movements (Fig. 1A).

The last signal from a bird was used as departure time, and the sample was divided into three departure time groups, daytime (06:00–18:00), sunset (18:00–22:00) and night (22:00–06:00) in order to avoid circular data. We classified the birds' strategies at this particular stopover site as 'immediate departure' (birds' leaving the area the first night after tagging) or 'later departure' (staying in the area for at least one night after tagging). This does not necessary correspond to the true stopover duration, since the birds could have arrived at the peninsula a number of days before being trapped. However, we chose to include this factor as a measure of how long the birds stayed in the area after being released with radio transmitters. Fat score at release was used as a measure of how large fuel reserves the birds carried. The birds were grouped into two age categories, juveniles on their first migration and adults.

The Swedish Meteorological and Hydrological Inst. (SMHI) collected weather data every third hour at the location of Falsterbo Bird Observatory. Data from the weather observation closest in time to departure was used as weather at departure. Temperature, wind speed and direction are automatic measurements, whereas degree of overcast is visually estimated on a 9 degree scale. The north/south component and east/west component of the wind direction was calculated as cos(wind dir) and sin(wind dir), respectively.

We used the daily capture sums from the bird observatory (see 'Ringing recoveries' for methods) during the morning before the birds departed to test whether there was any relationship between the probability of departure of the tagged individuals in a forward or reverse direction and the total number of birds caught, or the total number of birds caught of the same species. As sparrowhawks on migration are one of the most common predators of passerines on the peninsula, we also included the number of sparrowhawks counted by an observer at the tip of the peninsula (standardized autumn migration counts, Karlsson 2009) as a measure of predation

risk. Capture data and observations of sparrowhawks were logged as their distributions were skewed.

A logistic regression was performed to identify the factors related to whether the birds performed forward or reverse migration. Species, age, fat score at release, strategy, departure time group, temperature, degree of overcast, wind speed, log of the total number of ringed birds, log of the total number of ringed birds of the same species, log of the number of migrating sparrowhawks and the north- and east-wind component were included in the original model. Also included were the interactions species × age, species × strategy and age × fat score. None of the variables where highly correlated to each other (no Pearson's r above 0.5). We used backward (likelihood ratio) elimination by p-values ($p > 0.05$) to get the final model. Mean values for the different variables are shown in Supplementary material Appendix 1.

Ringing recoveries

Falsterbo Bird Observatory has been ringing birds during spring and autumn migration since 1947, with a standardized ringing scheme starting in 1980. The autumn ringing scheme consists of daily ringing between July 20 and November 10 in the lighthouse garden and between July 20 and September 30 in the reed beds of Flommen, a nature reserve north of the lighthouse garden. All birds are trapped in mistnets and are ringed, measured and immediately released at the ringing site. Mistnets are up 30 min before dawn, for at least 6 h or as long as more than 10 birds are caught during one hour. The birds are aged according to plumage characteristics, wing length (maximum cord) is measured to the closest mm, body mass to the closest 0.1 g and fat score is visually estimated on a scale from 0–9 (Pettersson and Hasselquist 1985, revised and extended with fat score 7–9 at Falsterbo Bird Observatory).

We selected ringing recoveries of passerines found within 10 d of ringing, and at least 5 km away from the ringing site. Only records of birds with known age and biometrics (fat score) were included. The birds were ringed during autumn seasons between 1954 and 2013 and in total we have used 192 ring recoveries. The most common species were Eurasian reed warbler *Acrocephalus scirpaceus*, goldcrest *Regulus regulus*, European robin, sedge warbler *Acrocephalus schoenobaenus* and willow warbler. We calculated a direction (orthodromic) between the ringing and the recovery point, and divided the sample into forward (n = 111, 90°–270°) and reverse (n = 81, 270°–90°) migrants (Fig. 1B).

We used a logistic regression to test which factors separated forward and reverse migrants. Age, fat score and the interaction between age and fat score were included. Age and fat score were not significantly correlated (χ^2 test). We used backward (likelihood ratio) elimination by p-values ($p > 0.05$). Mean values are shown in Supplementary material Appendix 1.

Tracking radar

We used a customized x-band tracking radar (200 kW peak power, 0.25 μs pulse duration, 504 Hz pulse repetition frequency, 1.5° pencil beam width) to track nocturnal migrants flying over the Falsterbo peninsula (Fig. 1). The radar is manually operated and tracks one individual target at a time. As the birds flap their wings, the echo back to the radar changes and the wing beat signature can be recorded. This was used to identify flight mode, and thereby to select tracks of passerines using bounding flight. The radar was operated from sunset until a few hours after midnight on selected nights without precipitation during the autumn seasons (19 August–21 October in 2009, 11 August–14 September in 2010 and 24 August–24 October in 2011). Every night wind measurements were made by releasing helium balloons that were tracked by the radar to get an exact wind profile. Airspeed and heading were calculated from the measured track vector (ground speed and track direction) and the wind vector (wind speed and direction) at the altitude of the target. Only targets for which wind measurements were available at the same altitude (± 150 m) and within 2 h of the bird track were included in the analyses. A few tracks with unrealistic airspeeds (below 5 m s⁻¹ or above 20 m s⁻¹) were excluded from the analyses. To make airspeeds at different altitudes comparable, equivalent airspeed was calculated by adjusting airspeed for air pressure at different altitudes, for details, see Nilsson et al. 2014. For details on radar operation and data processing, see Bäckman and Alerstam 2003, Karlsson et al. 2012. Targets were classified as long or short distance migrants based on the time of season they were recorded, ringing data shows that long distance migrants pass the area before short distance migrants in autumn and the other way around in spring, Nilsson et al. 2014. The total sample of 1161 tracks was divided into forward migrants (n = 961, track directions 90°–270°) and reverse migrants (n = 200, track directions, 270°–90°), Fig. 1C. Weather variables were obtained once per night (23:00 local time) from observations made by the SMHI at Falsterbo Bird Observatory (see radiotelemetry methods).

We use a logistic regression to investigate the factors that differed between forward and reverse migrants. Equivalent airspeed, altitude, time of night (before/after midnight), vertical speed, temperature, degree of overcast, visibility, wind speed, migration distance, the north wind component and east wind component were included in the original model. Also included was the interaction between altitude and equivalent airspeed. None of the variables where highly correlated to each other (no Pearson's r above 0.6). We used backward (likelihood ratio) elimination by p-values ($p > 0.05$) to get the final model. See Supplementary material Appendix 1 for mean values of all variables.

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.k3882 > (Nilsson and Sjöberg 2015).

Results

The proportion of reverse migrants was highest in the radiotelemetry departure data (47%) and ringing recoveries (43%), and lowest in the radar sample (21%).

The final logistic regression model based on the radiotelemetry data (Table 2) included species, age, log of the number of birds caught of the same species and a interaction between age and fat score. Age and fat score remained in the final ringing recovery model (Table 2). The radar data final

Table 2. Variables showing significant relationships to the probability of reverse versus forward migration according to logistic regression analyses (final models) for radar, radiotelemetry and ringing data, respectively. Also included are mean values of continuous variables for reverse and forward migrants and percentages forward and reverse for categorical variables. Variables not included in final models were for radar data: vertical speed, altitude, temperature, migration distance, equivalent airspeed, wind speed and visibility. For radiotelemetry: fat score at release, departure time group, temperature, degree of overcast, wind speed, log of total no. of ringed birds, strategy, log sparrowhawk count, species × age interaction, species × strategy interaction, the north wind component and the east wind component. For ringing recoveries: age × fat score interaction.

Method	Variable	Group	Log reg. Change in –2 log likelihood	DF	sig	exp(B)	Reverse Mean	SD	%	n	Forward Mean	SD	%	n
Radiotel.														
	Species		10.72	3	0.013									
		Song thrush							18	6			82	27
		Willow warbler				0.58			29	9			71	22
		Robin				0.14			44	16			56	20
		Garden warbler				0.72			38	6			63	10
	Age		6.90	1	0.009									
		Juveniles							38	25			62	41
		Adults				27.91			24	12			76	38
	Age × Fat score		5.18	1	0.023									
	Log same species capture		6.66	1	0.010		0.84	0.72		37	1.02	0.63		79
Ringing Rec.														
	Fat score		22.90	1	0.000	0.57	3.37	2.14		35	5.31	1.44		81
	Age		4.76	1	0.029									
		Juveniles							47	77			53	86
		Adults				0.22			14	4			86	25
Radar														
	Cloud cover		8.94	1	0.003	1.13	4.12	2.78		200	3.53	2.70		961
	North wind comp.		49.01	1	0.000	0.36	–0.17	0.63		200	0.27	0.55		961
	East wind comp.		30.39	1	0.000	2.46	–0.25	0.72		200	–0.50	0.61		961
	Before/after midn.		24.52	1	0.000									
		Before							13	88			87	588
		After				0.42			23	112			77	373
	Altitude × Eq. airspeed		28.96	1	0.000	1.00								

model included; before or after midnight, degree of overcast, north wind and east wind components as well as the interaction altitude and equivalent airspeed (Table 2).

Internal causes of reverse migration

Juvenile birds were more likely than adults to undertake reverse migration according to ringing recoveries (Table 2, Fig. 2).

Ringing-recovery data showed that reverse migrants were leaner than the forward migrants, and the radiotelemetry data showed a significant interaction between age categories and fat score (Table 2 and Fig. 3), with a larger proportion of fat adults making reverse movements than in the juvenile group.

Species differed in the likelihood of reverse migration in the radiotelemetry data (Table 2, Fig. 2), with more robins (medium-distance migrant) than willow warblers and garden warblers (long-distance migrants) moving in reverse directions. The larger song thrushes had the lowest proportion of reverse migrants. Migration distance was not included in the final logistic model of the radar data.

External causes of reverse migration

Although we investigated many weather factors, few of them were significantly related to the amount of forward or reverse movements. Only wind components and cloud cover were included in the final logistic model of the radar data. For-

ward migrants flew in winds that were more westerly and northerly compared to reverse migrants (Table 2). Forward migration was also more common on nights with less cloud cover according to radar data, see also Supplementary material Appendix 1.

We found no effect of the total number of birds ringed in the morning before departure or the number of migrating sparrowhawks, but there was an effect of the total number of birds of the same species ringed on the proportion of forward and reverse migrants. There was more forward migration on days when more birds of the same species were caugh at the bird observatory, which probably reflects days with overall good conditions for migration.

Characteristics of reverse migratory flights

Flights of reverse migrants differed from forward flights in several respects. There was an interaction between flight altitude and equivalent airspeed, with reverse migrants flying slightly faster at low altitudes and slightly slower at high altitudes (Table 2, Fig. 4). The mean altitudes were also lower in the group flying in reverse directions (Supplementary material Appendix 1). The absolute values of the mean flight altitudes should be interpreted with caution as all different altitudes were not sampled systematically; however, there is no reason to suspect that altitudes were sampled differently for forward and reverse migrants. The proportion of reverse migrants was higher after midnight than before (Table 2, Fig. 2).
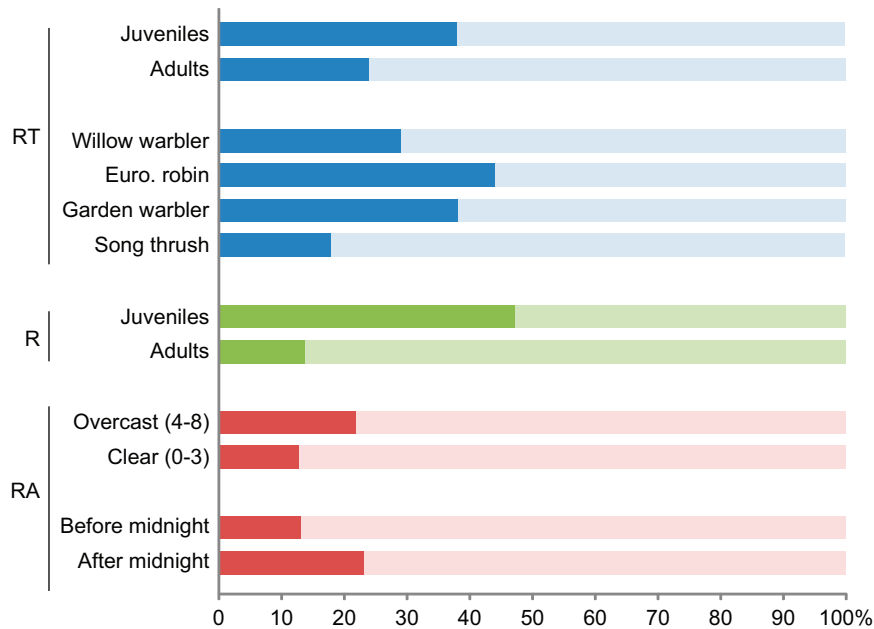
Figure 2. Proportion of reverse (dark colors) and forward (light colors) movements in different categories for radiotelemetry (RT), ringing recoveries (R), and radar (RA). The figure presents results for group variables included in the final logistic regression models based on radio-telemetry, ringing and radar data, respectively (Table 2).

Discussion

The proportion of 21% reverse migration at Falsterbo peninsula in the radar sample was higher, but still similar to previous studies, such as Bruderer and Liechti 1998: 12% and Zehnder et al. 2002: 14.1 and 10.1%. The proportion of reverse migrants in the sample of migrants aloft tracked by radar is considerably smaller than in the radio tagged and ringed birds. It is difficult to track birds at very low altitudes on the radar due to ground clutter, so some very low (below 100 m) reverse migrants might have been missed, especially if they start from the peninsula and fly very low during take-off. Further, the birds that are caught at the bird observatory have already interrupted their migration, maybe because of
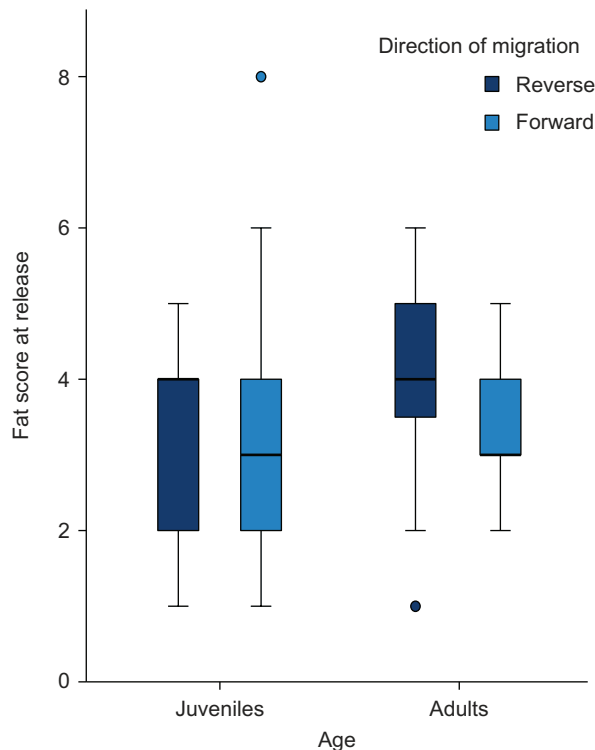

Figure 3. Box plot of fat score at release for juveniles and adults, divided into reverse (dark blue) and forward (light blue) migrants.
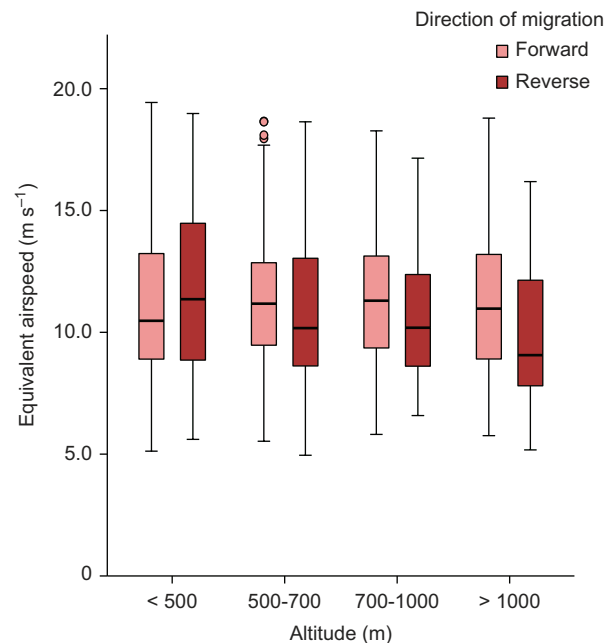

Figure 4. Box plot of equivalent airspeed in four different altitude groups divided into reverse (dark red) and forward (light red) migrants. The altitudes are grouped here for the benefit of the figure, but are otherwise used as a continuous variable.

low energy reserves, and then made the decision to reverse their movements in search of better stopover sites. There is also a possibility that the stress associated with trapping (radiotelemetry and ringing) lead to a higher proportion of return migrants.

Internal causes of reverse migration

To be able to continue on migration, especially if facing a sea crossing, it is very important for birds to have enough fuel. Consequently, fat score seems to be the factor that most reliably differs between forward and reverse migrants (Lindström and Alerstam 1986, Åkesson et al. 1996b, Sandberg and Moore 1996, Deutschlander and Muheim 2009, Schmaljohann and Naef-Daenzer 2011, Smolinsky et al. 2013, Stach et al. 2015). In our study we find the expected effect of fat score on the likelihood of ringing recoveries in forward or reverse directions, with lean birds turning backwards to a higher degree (similar to the pattern observed in Smolinsky et al. 2013). We further found an interaction between fat score and age in the radiotelemetry data (Table 2, Fig. 3). Lean and fat juveniles engage in reverse migration to the same degree, but fat adult individuals perform reverse movements to a higher degree than lean adult individuals, which was unexpected. Probably this is a result of the distribution of fat and lean individuals in the radiotelemetry data. The very leanest birds (fat score 0–1), were not (except one bird) equipped with radio transmitters, as the tagging was judged to have too adverse effects on this group, even though the weight of the transmitter would not have exceeded the recommended upper 5% limit of body mass (Cochran 1980). Most of the bird in our sample therefore probably had sufficient fuel deposits to make the rather short sea crossing across the Baltic Sea (23–100 km). This could also be a possible contributing cause to the absence of differences in fat score in itself on the vanishing bearings of the radio-tracked birds.

Furthermore, we observed a difference between experienced, adult migrants and inexperienced, juvenile migrants in ringed birds, with juvenile migrants being more likely to fly in reverse directions (Table 2). Juvenile birds have been shown to be less efficient foragers, and less able to cope with competition, possibly making them more likely to perform reverse movements (Woodrey and Moore 1997, Yong et al. 1998). They could also be more likely to hesitate at the sea crossing, not having passed it before.

Robins and some other short- to medium-distance species are known to sometimes winter in southern Sweden, and might choose to terminate migration and make reverse movements to search for suitable wintering grounds (Åkesson et al. 1996b). This pattern was supported by the radio-tracked robins more commonly returning inland than long-distance migrants, such as willow warblers and garden warblers (Table 2). The smallest proportion of reverse migrants was however among the song thrushes, which are medium-distance migrants. Song thrushes are considerably larger than the other species and may be able to better cope with bad flight conditions. Also, they are not known winter in southern Sweden to the same extent as the robins.

The reason for making reverse movements could also be non adaptive, such as orientation errors (Komenda-Zehnder et al. 2002), or that the birds had been drifted off course. Orientation errors might be more likely to occur among inexperienced juveniles, which is consistent with more inexperienced migrants making reverse movements.

External causes of reverse migration

Reverse movements were found to be more common in the radar sample in winds with strong components from the east and south, mostly corresponding to opposed winds, and also on nights with a higher degree of cloud cover (Table 2). Wind conditions will have a large effect on the attainable flight speeds and the cost, in terms of energy, of the flight (Pennycuick 2008) and it is therefore not surprising that we see more reverse migration with a higher degree of opposing winds. Cloud cover might be important for orientation, with access to stars and overall light level probably increasing orientation accuracy (Åkesson et al. 2001). We did, however, not find any effect of overall visibility on the proportion of reverse migration, indicating that perhaps access to stars was more important than visibility itself. Even though weather has a large effect on the costs and effectiveness of flight, many previous studies have failed to find an effect of weather variables on the proportion of reverse migration (Bruderer and Liechti 1998, Komenda-Zehnder et al. 2002, Zehnder et al. 2002, Smolinsky et al. 2013); however, see Schmaljohann and Naef-Daenzer 2011. Here, we find an effect on the flight directions of migrants while aloft, but not on radio tracked birds departing from the peninsula.

The number of ringed birds in total and the number of sparrow hawks were not included as significant predictors of reverse migration in the final logistic models (Table 2). The number of birds of the same species caught on the day of departure was however included in the final radiotelemetry model, with forward movements being more likely to occur when many birds of the same species were caught. This probably reflects days with species specific beneficial migration conditions. Although we found little indication of the daily variation in competition and predation risk affecting the birds' decisions about forward/reverse migration (the only significant effect was in the opposite direction from the expected), one cannot exclude that the incidence of reverse migration is still generally enhanced at coastal concentration sites because of a generally high level of competition and predation.

Characterization of reverse migration

Birds on migration are predicted to fly at optimal airspeeds to either minimize the time spent on migration or the energy used to reach the wintering grounds (Hedenström and Alerstam 1998). When making movements in the opposite directions during migration, however, birds may be driven by other factors, such as finding an appropriate stopover area. We found an interaction between altitude and equivalent airspeed, with reverse migrants flying slightly faster at low altitudes but slower at high altitudes (Fig. 4). Mean altitude was lower in the reverse migrant group (Supplementary material Appendix 1) but altitude was not included in the final logistic model of the radar data. Our results are somewhat consistent with tracks of reverse migrants in Spain,

showing decreased speed in reverse movements as well as lower altitudes (Bruderer and Liechti 1998). That birds flying in forward directions flew slightly slower at low altitudes could be due them climbing to a higher degree than birds at low altitudes flying in reverse directions.

A bird reaching the peninsula late in the night might be less likely to embark on the sea crossing than one reaching it earlier. This is supported by the radar data, in which the likelihood of a migrant making a reverse flight is higher after midnight than before midnight (Table 2), which is also in accordance with previous studies (Lindström and Alerstam 1986, Komenda-Zehnder et al. 2002, Schmaljohann and Naef-Daenzer 2011). We do not observe this pattern in the radiotelemetry sample, where there is no difference in departure time between the forward and reverse migrating birds. This might indicate that timing when departing on reverse migration from a stopover site is more similar to timing when departing on forward migration, while timing of reverse movements in birds aloft are more variable during the night. This pattern is unexpected since previous studies have shown clearly that differences in timing of departure are related to different types of migratory movements. Departures in the preferred migratory direction are observed to take place in a time-window just after sunset (Åkesson et al. 1996a, 2002, Mills et al. 2011, Smolinsky et al. 2013) and late night departures are more scattered and of local character (Mills et al. 2011), which could be expected to correspond to more reverse movements on a southerly peninsula such as Falsterbo during autumn migration.

Conclusions

The decision to continue on migration or to make reverse movements is most likely affected by a combination of factors (Sandberg and Moore 1996), with weather conditions and the condition of the bird being the two most important ones, see also Schmaljohann and Naef-Daenzer 2011. By using a unique combination of methods we have shown that during autumn migration at Falsterbo peninsula juvenile birds were more likely than adults to fly in reverse directions, and lean birds were more likely than fat birds to undertake reverse migration. Reverse movements were also more likely in opposing winds and overcast skies. Birds orienting in reverse directions flew slower at high altitudes than birds flying in the seasonally appropriate direction, and reverse movements were more likely during the later part of the night. Mainly internal factors and no weather variables were associated with the departure directions from the radiotelemetry. The radar data did however show an effect of several weather variables, perhaps indicating that birds aloft are more sensitive to weather conditions than birds during departure from a stopover area. The effect of weather variables could also be rather small in comparison with internal variables meaning that very large datasets (such as radar data) are needed to identify them. Our results indicate that reverse migration is a complex behavior that birds engage in when they are faced with problematic flight and stopover conditions along their migration routes.

References

Åkesson, S. 1999. Do passerine migrants captured at an inland site perform temporary reverse migration in autumn? – Ardea 87: 129–137.

Åkesson, S. and Hedenström, A. 2000. Wind selectivity of migratory flight departures in birds. – Behav. Ecol. Sociobiol. 47: 140–144.

Åkesson, S., Alerstam, T. and Hedenström, A. 1996a. Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. – J. Avian Biol. 27: 95–102.

Åkesson, S., Karlsson, L., Walinder, G. and Alerstam, T. 1996b. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. – Behav. Ecol. Sociobiol. 38: 293–302.

Åkesson, S., Walinder, G., Karlsson, L. and Ehnbom, S. 2001. Reed warbler orientation: initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk. – Anim. Behav. 61: 181–189.

Åkesson, S., Walinder, G., Karlsson, L. and Ehnbom, S. 2002. Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. – J. Avian Biol. 33: 349–357.

Alerstam, T. 1978. Reoriented bird migration in coastal areas: dispersal to suitable resting grounds? – Oikos 30: 405–408.

Bäckman, J. and Alerstam, T. 2003. Orientation scatter of free-flying nocturnal passerine migrants: components and causes. – Anim. Behav. 65: 987–996.

Bruderer, B. and Liechti, F. 1998. Flight behaviour of nocturnally migrating birds in coastal areas: crossing or coasting. – Oikos 29: 499–507.

Cochran, W. 1980. Wildlife telemetry. – In: Schemnitz, S. D. (ed.), Wildlife management techniques manual. The Wildlife Society, pp. 507–520.

Covino, K. M., Holberton, R. L. and Morris, S. R. 2015. Factors influencing migratory decisions made by songbirds on spring stopover. – J. Avian Biol. 46: 73–80.

Cramp, S. 1988. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic: tyrant flycatchers to thrushes vol. 5. – Oxford Univ. Press.

Cramp, S. 1992. Handbook of the birds of Europe, the Middle East and North Africa: the birds of Western Palearctic: warblers vol. 6. – Oxford Univ. Press.

Deutschlander, M. E. and Muheim, R. 2009. Fuel reserves affect migratory orientation of thrushes and sparrows both before and after crossing an ecological barrier near their breeding grounds. – J. Avian Biol. 40: 85–89.

Hedenström, A. and Alerstam, T. 1998. How fast can birds migrate? – J. Avian Biol. 29: 424–432.

Karlsson, H., Nilsson, C., Bäckman, J. and Alerstam, T. 2012. Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. – Anim. Behav. 83: 87–93.

Karlsson, L. 2009. Vingar över Falsterbo, 2nd ed. – Falsterbo fågelstation.

Komenda-Zehnder, S., Liechti, F. and Bruderer, B. 2002. Is reverse migration a common feature of nocturnal bird migration? An analysis of radar data from Israel. – Ardea 90: 325–334.

Lindström, Å. and Alerstam, T. 1986. The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden. – Behav. Ecol. Sociobiol. 19: 417–424.

Mills, A. M., Thurber, B. G., Mackenzie, S. A. and Taylor, P. D. 2011. Passerines use nocturnal flights for landscape-scale movements during migration stopover. – Condor 113: 597–607.

Moore, F. 1984. Age-dependent variability in the migratory orientation of the Savannah sparrow (*Passerculus sandwichensis*). – Auk 101: 875–880.

Nilsson, C. and Sjöberg, S. 2015. Data from: Causes and characteristics of reverse bird migration: an analysis based on radar, radio tracking and ringing at Falsterbo, Sweden. – Dryad Digital Repository, < http://dx.doi.org/10.5061/dryad.k3882 >.

Nilsson, C., Bäckman, J. and Alerstam, T. 2014. Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants. – Behav. Ecol. Sociobiol. 68: 1799–1807.

Pennycuick, C. J. 2008. Modelling the flying bird. – Academic Press.

Pettersson, J. and Hasselquist, D. 1985. Fat deposition and migration capacity of robins *Erithacus rebecula* and goldcrests *Regulus regulus* at Ottenby, Sweden. – Ringing Migr. 6: 66–76.

Richardson, W. 1982. Northeastward reverse migration of birds over Nova Scotia, Canada, in autumn. – Behav. Ecol. Sociobiol. 10: 193–206.

Sandberg, R. and Moore, F. R. 1996. Migratory orientation of red-eyed vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. – Behav. Ecol. Sociobiol. 39: 1–10.

Sandberg, R., Pettersson, J. and Persson, K. 1991. Migratory orientation of free-flying robins *Erithacus rubecula* and pied flycatchers *Ficedula hypoleuca*: release experiments. – Ornis Scand. 22: 1–11.

Schmaljohann, H. and Naef-Daenzer, B. 2011. Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. – J. Anim. Ecol. 80: 1115–1122.

Seaturtle.org 2002. – < www.seaturtle.org/maptool/ > accessed 31 December 2014.

Sjöberg, S. and Nilsson, C. 2015. Nocturnal migratory songbirds adjust their travelling direction aloft: evidence from a radio telemetry and radar study. – Biol. Lett. 11: 20150337.

Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, T. and Muheim, R. 2015. Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. – Anim. Behav. 104: 59–68.

Smolinsky, J. A., Diehl, R. H., Radzio, T. A., Delaney, D. K. and Moore, F. R. 2013. Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. – Behav. Ecol. Sociobiol. 67: 2041–2051.

Stach, R., Fransson, T., Jakobsson, S. and Kullberg, C. 2015. Wide ranging stopover movements and substantial fuelling in first year garden warblers at a northern stopover site. – J. Avian Biol. 46: 315–322.

Woodrey, M. and Moore, F. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. – Auk 114: 695–707.

Woodworth, B. K., Francis, C. M. and Taylor, P. D. 2014. Inland flights of young red-eyed vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. – J. Avian Biol. 45: 387–395.

Yong, W., Finch, D., Moore, F. and Kelly, J. 1998. Stopover ecology and habitat use of migratory Wilson's warblers. – Auk 115: 829–842.

Zehnder, S., Åkesson, S., Liechti, F. and Bruderer, B. 2002. Observation of free-flying nocturnal migrants at Falsterbo: occurrence of reverse flight directions in autumn. – Avian Sci. 2: 1–12.