

Stopover behaviour in migratory songbirds:

timing, orientation and departures

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DOCTORAL DISSERTATION

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List of Papers

- I. Sjöberg S, Atkinson P, Alerstam T, Åkesson S, and Muheim R. Stopover duration of migratory passerines at the Falsterbo peninsula, Sweden: effects of fuel load and weather. (*In manuscript*)
- II. Sjöberg S, Alerstam T, Åkesson S, and Muheim R. Timing of nocturnal passerine flights is determined primarily by ecological factors and not by celestial orientation cues. (*Submitted*)
- III. Sjöberg S and Muheim R. No compass calibration in free-flying birds after exposure to a cue conflict – is an unchanged star compass the explanation? (*Submitted*)
- IV. Nilsson C and Sjöberg S. Causes and Characteristics of Reverse Bird Migration: an Analysis Based on Radar, Radio Tracking and Ringing at Falsterbo, Sweden. (*Submitted*)
- V. Sjöberg S and Nilsson C. (2015) Nocturnal migratory songbirds adjust their travelling direction aloft: evidence from a radiotelemetry and radar study. *Biology Letters*, 11: 20150337.
- VI. 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. *Animal Behaviour*, 104: 59-68.

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Author contributions

- I. SS, RM, TA and SÅ initiated the study; SS collected the data and analyzed it together with PA. SS wrote the manuscript with input from all authors.
- II. RM, TA and SÅ started the telemetry project; SS, RM, TA and SÅ initiated the study; RM and SS developed the algorithm to analyse the tracking data, SS collected and analyzed the data with input from TA. SS wrote the manuscript with input from all authors.
- III. SS and RM initiated the study; RM planed the experiment, RM and SS developed the algorithm to analyse the tracking data and SS collected and analyzed the data with input from RM. SS and RM wrote the manuscript.
- IV. CN and SS initiated the study; CN and SS collected and analyzed the data. CN wrote the manuscript with input from SS.
- V. SS and CN initiated the study; SS and CN collected the data. SS analyzed the data with input from CN. SS wrote the manuscript with input from CN.
- VI. RM, TA and SÅ started the telemetry project in Falsterbo, TC started the telemetry project at FINO 2 and installed the system at FINO 2 together with AW, AS ran the receiver system at FINO 2. SS, RM, TC, TA and SÅ initiated the study; SS collected and analysed the data with input from TA. SS wrote the manuscript with input from all authors.

Abstract

Songbird migrants use stopovers between flight bouts to rest and refuel for the upcoming flights. Behaviours affecting where, when and how long to stay at stopover sites will affect how successful the overall migration will be, which has significant consequences for the overall fitness and mortality of the birds. The main purpose of this work was to investigate stopover behaviours in free-flying migrants to understand the effects of intrinsic (age and body condition) and environmental (weather) factors on the behaviours that guide birds as they depart from migratory stopovers. I studied some of our most common migratory songbirds using an automated radiotelemetry system at the Falsterbo peninsula, Sweden. Our results show that stopover duration is affected by fuel load and weather conditions, and that they differ between the migratory seasons. Furthermore, timing of departures on nocturnal flights appears primarily determined by ecological factors, and are to a large degree affected by the lengths of the nights. Birds with larger fuel stores departed before lean individuals, indicating that they prepared for a longer flight. We found that reverse movements during migration are slower, take place at lower latitudes and later in the night than movements in the expected migratory direction, and are most common in juvenile or lean individuals. Route choice across the Baltic Sea after departure from Falsterbo is largely affected by wind directions. In cue conflict experiments between magnetic compass and celestial cues at sunset we found no recalibration of the magnetic compass. We suggest that access to stars during calibration is necessary for all compasses to be calibrated when the birds depart for a night's flight. Comparisons between departure directions and directions of birds in climbing and level flight revealed that birds adjust their directions after take-off, once at cruising altitudes. Winds were the primary factor affecting flight duration for the first 50 km of flight after departure. Interestingly, cloud coverage affected flight duration negatively, while fuel load affected it positively. Collectively, this work shows how intrinsic and environmental factors modulate stopover behaviours in migratory songbirds, with essential implications on the birds' migratory schedules.

Stopover behaviour in migratory songbirds

The performance of millions and millions of birds travelling back and forth between their breeding and wintering grounds is to me, and has been to many people before me, astonishing. By migrating, birds become as well prepared as possible for the next breeding season, thereby increasing fitness. Bird migration is incredibly diverse. Different species or groups of birds use different strategies to accomplish a successful migration. Some move in flocks while others perform their migration solitarily, some fly during the day while others fly during the night. Most do not fly the entire way between their breeding and winter quarters in a single flight, but alternate flight periods with resting and refueling periods, usually referred to as stopover periods or just stopovers. To me, it is not the great daytime movements of large raptors, or the variety of species that make the show. Rather, it is the nocturnal movements of small migrants, often weighing just 10-15 g, which fascinates me most. Not only do they make it to their wintering grounds on the other side of the Earth, even the youngest, thus most inexperienced individuals, make it on their own.

I think about migratory behaviour as a chain of behavioural responses to both intrinsic and environmental factors, which together will guide the bird on its migration. Since my research is focused on the behaviours connected to stopovers, I start with the question of how long a bird will stay at a stopover. I then continue with the behaviours involved in take-off, orientation and timing of the actual departure, followed by flight behaviours, once the bird is in the air. I end with the question of when and how birds terminate their flights, and where they stop, although these final questions are those that we cannot yet say much about, at least not for small songbirds. The main purpose of my work was to understand stopover behaviours in free-flying songbirds on migration, both to confirm the results from studies of caged birds, and to try to understand the importance of intrinsic and environmental factors on departure and flight behaviours.

The importance of stopover behaviour

Songbird migrants use stopovers between flight bouts to rest and refuel for the upcoming flights (e.g. Schaub & Jenni, 2001). The migratory schedules of songbirds are to a high degree endogenously programmed, especially in first year migrants (Berthold, 1996), but the structure of the migration is expected to be modified by environmental factors (Jenni and Schaub, 2003a). It has been shown that birds not only spend more time (about 88%) on stopover than flight during migration (Alerstam & Lindström, 1990; Hedenström & Alerstam, 1997), but also that, overall, more energy is consumed at stopovers (Wikelski et al., 2003). It is estimated that 67% of the energy spent on migration is spent during stopovers (Hedenström and Alerstam, 1997). Behaviours affecting where, when and for how long a migrant should stay at stopover sites will affect how successful the overall migration will be (e.g. Newton, 2006), and consequently, the reproductive success of the coming years (e.g. Bauchinger et al., 2008, 2009; fig. 1). Hence, behaving optimally during stopovers is expected to be under strong selection (Hedenström and Alerstam, 1997), especially since mortality is higher during stopover than during the actual flight (Wikelski et al., 2003; Newton, 2006). This increased mortality during stopovers makes stopover sites, in addition to the wintering and breeding sites, important from a conservation perspective.

The knowledge about the general patterns of stopover behaviour, and how they relate to the prevailing conditions, is vague. There is a solid base of optimality theories for migration, predicting how birds should behave in order to perform the migration in either a safe way, or in a time- or energy minimizing way (e.g. Alerstam & Lindström, 1990; Hedenström & Alerstam, 1997). However, experimental studies trying to elucidate these patterns in free-flying birds have often resulted in contradictory results (e.g. Dänhardt & Lindström, 2001; Schmaljohann & Dierschke, 2005). The problem with finding common patterns could be a result of highly individual strategies, but it can also be a reflection of the disparities between different study systems. With new techniques we now have the opportunity to circumvent at least some of these problems, which will hopefully result in a better understanding of the behaviours.

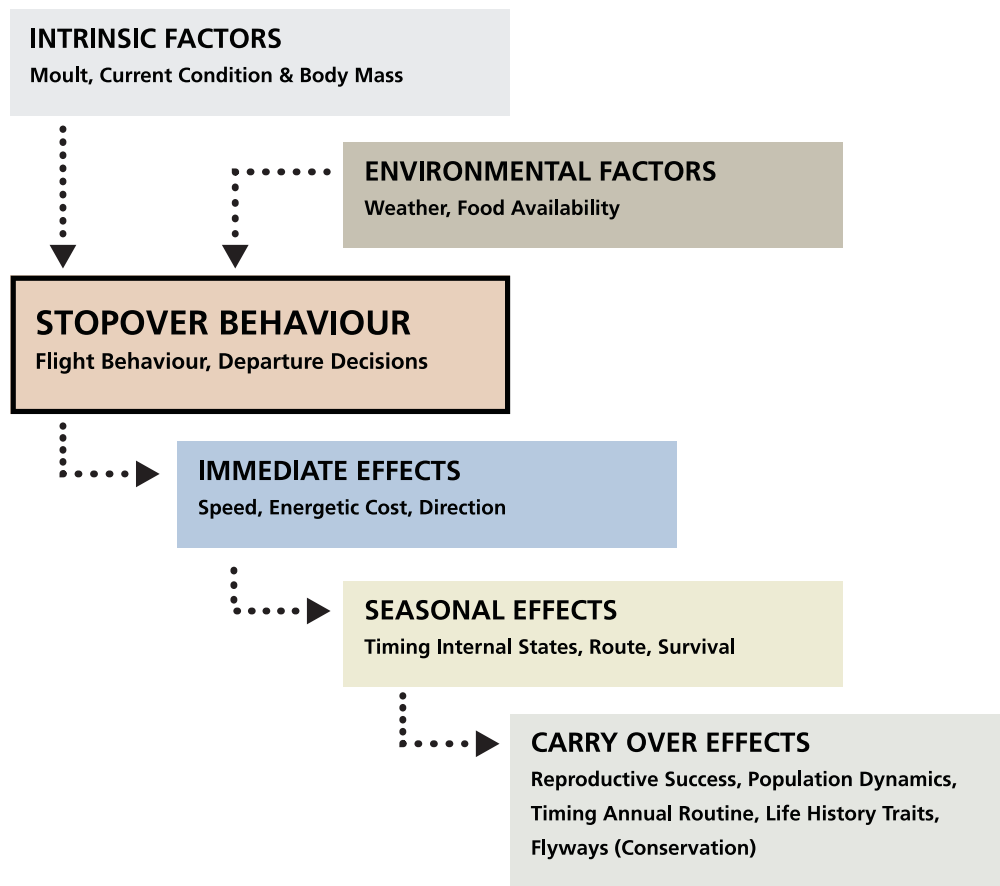


Figure 1. Decisions made by migrants on stopover sites are affected by intrinsic and environmental factors. These will have effects on the overall success of migration, the annual cycle and future reproductive success. Redrawn from Shamoun-Baranes, Bouten, & Van Loon (2010).

The aim and outline of this thesis

The main purpose of my work was to investigate stopover behaviours in free-flying migrants and to understand the effects of intrinsic (age and body condition) and environmental (weather) factors on the behaviours that guide birds as they depart from migratory stopovers. The intention was both to test to what degree results from previous experiments on caged birds apply to free-flying migrants, and to gain a deeper understanding of the causes of variation in stopover behaviours. This thesis summarizes what we know about the different behaviours of birds before, during or immediately after departures from stopovers. It is divided into chapters relating to the different behaviours.

The first two chapters of this introduction provide background information on why it is important to study stopover behaviours and on the methods that I have used, which includes a short introduction to the stopover site, Falsterbo, and the different species that I have studied. In chapter 3, I discuss stopover duration, i.e., how long birds stay at stopovers and which factors affect the duration of their stay. The results from paper I are summarized in this chapter. Chapter 4 describes the timing of departures on nocturnal flights and puts the results from paper II in context. In chapter 5, I briefly summarize the different cues that birds use for orientation and discuss the calibration of the different compasses. The chapter further deals with the causes for shifts in travelling direction and route choice. It summarizes the results from papers III-VI and puts them into perspective. Chapter 6 discusses duration and speed of migratory flights and puts the results from paper VI in context. Finally, chapter 7 gives concluding remarks and suggestions for future work.



In the individual papers included in this thesis, the following principal questions are addressed:

Paper I. How does the general pattern of stopover duration in Falsterbo compare to that at other stopover sites in other types of habitats and topographical locations? Are there any differences between species (song thrushes, robins, willow warblers, garden warblers and blue tits), birds of different ages (juveniles/adults), or migratory seasons (autumn/spring)? Which weather conditions distinguish departure days from non-departure days?

Paper II. Is the timing of nocturnal departures in passerines determined by ecological factors or by celestial orientation cues? How do passerine migrants time their nocturnal departures? Are there differences in timing between the migratory seasons (autumn and spring) and between different species of long- and medium-distance migrants? Do intrinsic (age, fuel store, departure direction) and environmental factors (wind strength and direction) cause variation in the departure timing of the migratory passerines?

Paper III. In which way do passerine migrants calibrate their different compass cues in order to get consistent directions out of them?

Paper IV. Which factors make birds reverse their flights? Which internal factors (age and fuel load) affect the probability of a passerine to continue on forward or reverse migration? Is it determined by environmental factors such as weather variables? Which flight behaviours characterize reverse migration?

Paper V. Do birds determine travelling direction already before departure or do they adjust their heading direction also after take-off?

Paper VI. Which individual characteristics (species, age, fuel reserves) determine the likelihood of migratory passerines to perform a trans-barrier flight across the Baltic Sea instead of taking a detour around the Baltic Sea? Are there differences in behaviour (departure timing and directions) and/or the prevailing environmental conditions (wind direction, wind speed, cloud cover, visibility, time of season) between birds that cross and birds that do not cross the Baltic Sea? What determines the flight duration of a departure flight (first 50 km of flight) – does it vary because of species-specific traits, individual characteristics (age, fuel reserves), behaviour (departure orientation) or environmental conditions (winds and weather)?

Methods

Falsterbo

Located at the southwestern tip of Sweden, Falsterbo peninsula is probably the point of the Scandinavian Peninsula where the largest number of birds concentrate on their way south during autumn migration (fig 2). Birds are channeled here when trying to avoid flying over open water. The intense diurnal migration of raptors in the area is a much visited spectacle for birdwatchers. Falsterbo is only a small peninsula, about 10 km long and to a large extent surrounded by water, with two small villages, sandy beaches, and grassy and shrubby habitats in between the urbanized areas. A contrasting effect of the geographical location, that causes the heavy migration during autumns, is that the peninsula is not as strategic on northward migrations, hence spring migration is much more scattered than autumn movements. Furthermore, Falsterbo is not expected to be a high quality stopover habitat, especially not during autumn, when large numbers of birds gather in the area. Coastlines are in many cases poor stopover habitats, and the large number of birds leads to high competition and high predation risk (Alerstam, 1978; Woodworth, Francis, & Taylor, 2014). Radio telemetry is ideally suited for following avian migrants during stopover in this area, since the peninsula has a flat topography, is fairly small and well-defined by the surrounding water.

Bird migration has been thoroughly investigated on the peninsula since the 1940s, with hundreds of scientific publications produced with data from the area. Falsterbo Bird Observatory (55°38'N, 12°82'E) has been running since 1955, and from ringing and bird migration counts, we have today a good understanding of the patterns of migration, species composition, phenology and conditions of birds passing the area (Karlsson, 2009). There is also a weather station at the location of Falsterbo Bird Observatory, with weather data being collected every third hour by the Swedish Meteorological and Hydrological Institute (SMHI).

Study Species

I have focused my studies on a few of the most common passerine species migrating from Sweden during autumn migration and returning during the spring. The different species are selected because they are regularly caught in the standardized ringing programme at Falsterbo Bird Observatory and because they have different migratory strategies. I have mainly focused on nocturnal solitarily flying species, but I have also included the flocking diurnal blue tit, *Cyanistes caeruleus*, for comparisons of stopover duration. The species are among the most studied migratory passerine species within the Palaearctic-African migratory flyway, which facilitates comparisons to other studies.

I have studied two medium-distance migrants, European robins, *Erithacus rubecula* (hereafter “robin”), and song thrushes, *Turdus philomelos*. Both species occur throughout most of the Western Palaearctic, with the breeding populations of Scandinavia migrating to winter in southwestern Europe (Cramp, 1988). The robin is considerably smaller and weighs about 15-20 g compared to the song thrush that weighs about 60-80 g. In order to enable comparisons with long-distance migrants, I also studied willow warblers, *Phylloscopus trochilus*, and garden warblers, *Sylvia borin*. They too breed throughout the Western Palaearctic, but migrate longer distances and spend the winter in tropical Africa south of the Sahel region (Cramp, 1992). Willow warblers are small warblers of about 7-11 g, whereas garden warblers are medium sized warblers of about 17-20 g. As mentioned above, blue tits were included in order to enable comparisons with a diurnal migrant. Blue tits are small (10-12 g) partial migrants; some individuals stay in their breeding range in the Western Palaearctic throughout the year, while others migrate short distances during the winter (Ulfstrand, 1962; Nilsson, et al., 2006). Ringing recoveries show that all species migrate in southwesterly directions from southern Sweden in autumn (Fransson and Karlsson-Hall, 2008).

The radiotelemetry system

All studies in this thesis are performed using an automated radiotelemetry system that was installed at the Falsterbo peninsula in 2009 (fig. 2). The automatic receiver system consists of three terrestrial stations at Falsterbo, and one offshore station at the research platform FINO 2 (installed in 2011). The stations at Falsterbo are located along the coastline running northeast – southwest, approx. 2.9 km apart from each other. They are mounted 1) on top of a 25 m high lighthouse surrounded by a golf course, 2) on top of a 43 m high water tower in a village on the peninsula, and 3) 5 m above ground on the roof of a farm building in an area with grass/shrubby habitat and sandy beaches. The offshore receiver station at FINO 2 is located 47 km southeast of



From upper left: garden warbler, European robin, willow warbler, song thrush and blue tit

Falsterbo, approximately 60 m above sea level. A sea crossing flight to Germany via FINO 2 is associated with a distance over sea of at least 80 km in a southeasterly direction from Falsterbo. A sea crossing flight in a southwesterly direction from Falsterbo towards Denmark is associated with a distance over sea of 23-50 km. Each telemetry station is equipped with a radiotelemetry receiver (SRX600; Lotek Wireless, Newmarket ON, Canada) with two to five antennas.

The receivers continuously scanned for radio signals from the transmitters that were attached to the feathers of the back of the birds. The radio transmitters were small, 0.35 – 0.67 g (0.35g transmitters for all species and field seasons except song thrushes that were equipped with 0.67g transmitters during 2010 and 2011) and ID-coded, which made it possible to release several birds at the same time. The transmitters sent out a signal every third second and had a life-span of up to 25 days.

The system provided high resolution data on when and how the birds depart from the peninsula. The last received signal gives the timing of the departure and a circular mean of the signal strengths received by the different antennas at a station gives the vanishing bearings (cf. paper V). Furthermore, from the departure times from Falsterbo and the timing of the first signal at the offshore station at FINO 2, we could calculate the flight durations for the first 47 km of the flight of those birds that took this route after departure. All birds were caught using mist nets as a part of the standardized ringing programme at Falsterbo Bird Observatory. Prior to attaching the radio transmitter, I determined the age of each bird on the basis of plumage characteristics, its wing length measured to the closest mm, body mass to the closest 0.1 g with a Pesola spring balance, and fat stores on a 0-9 visual scale (based on Pettersson and Hasselquist 1985, but adapted for Falsterbo Bird Observatory and extended with fat classes 7-9). The birds were either released with radio transmitters directly after ringing, or they were first experimentally manipulated (paper III) and then released with radio transmitters to examine how the treatment affected their free-flying behaviours.

Radar

During 2009-2012 a customized x-band tracking radar (200 kW peak power, 0.25 μ s pulse duration, 504 Hz pulse repetition frequency, 1.5° pencil beam width) was placed in Falsterbo. The radar was manually operated, and tracked one bird, the target, at a time. The wing beat frequency can be detected since the echo back to the radar gets modulated when the birds flap their wings. This is used to identify flight mode, and thereby to identify passerines using bounding flight (a flight pattern distinctive of small and medium-sized passerines). On selected nights without precipitation, the radar was operated from sunset until a few hours after midnight. Data from the radar gives the groundspeed and the track direction vector, which



Figure 2. Maps showing (a) the location of Falsterbo in Scandinavia (black star), (b) the locations of the radiotelemetry receiver stations at Falsterbo peninsula (1: the Falsterbo light house, 2: the water tower, 3: the farm) and (c) the location of the offshore radiotelemetry receiver station at FINO 2 (white star) in relation to Falsterbo (black star). The arrow shows the direct flight route from Falsterbo to FINO 2. Adapted from Sjöberg et al., 2015.

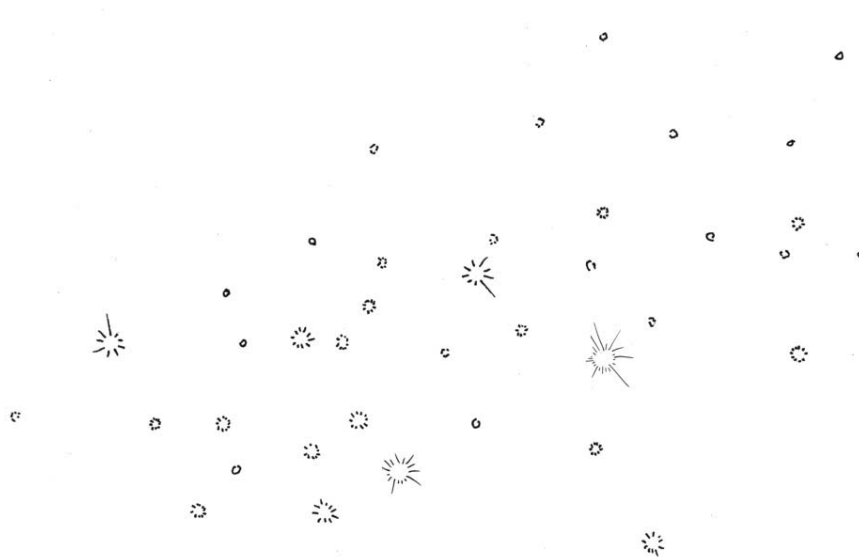
together with the wind speed and wind direction vector, enables calculation of airspeed and heading. I used data from the radar in paper IV and V to compare departure behaviours recorded by radiotelemetry with flight behaviours recorded by radar.

Ringling recoveries

Migratory birds have been ringed at the Falsterbo peninsula since 1947, and a standardized ringing programme has been run by the bird observatory since 1980. In paper IV, I used short-term (within 10 days) ringing recoveries from birds ringed at the bird observatory, and compared these with data from the radiotelemetry system and radar to investigate how intrinsic and environmental factors have an effect on whether or not birds reverse their flight direction.

Cue-conflict experiments

Birds are known to use a number of compasses to determine a migratory direction (Box 1). For the different compasses to make sense, and to refer to the same direction, a bird should calibrate them against each other before and during migration (Able & Able, 1999; Bingman, 1983; Muheim & Åkesson, 2002; Muheim, et al., 2006a; Wiltschko, et al., 1998). The calibration of the compasses during migration is thought to take place during the sunset and sunrise hours. To understand the hierarchy of these compasses, and the way they are calibrated with each other, I exposed birds to a cue-conflict where the natural relationship between the cues was artificially manipulated (paper III). I exposed garden warblers to an artificially deflected magnetic field, while at the same time the birds had a full view of the celestial cues associated with a natural sunset. The deflected magnetic field was generated by a magnetic coil system that allows the horizontal component of the magnetic field to be shifted within the coil. I used a 80 × 80 cm magnetic coil system powered by a 12-V car battery to shift the horizontal component of the magnetic field by 90 degrees (for details see Sandberg, et al., 1988). After exposure to this cue-conflict from 30 min before until 30 min after sunset, the birds were equipped with radio transmitters and released. The vanishing bearings of the birds exposed to the cue-conflict were compared to the vanishing bearings of birds exposed only to the natural ambient magnetic field in order to see whether or not the birds had calibrated the compasses.



Stopover duration

Passerine migrants have been found to stay at regular stopovers for 1-15 days, but have longer stopovers (up to 20 - 25 days) before longer flights across ecological barriers (reviewed in Chernetsov, 2012). The pattern of stopover durations in Falsterbo (paper I) did, contrary to our expectations, not show any pronounced differences from other stopover sites in northern Europe. The different species we investigated had estimated mean stopover durations between 2.5 – 15.4 days (fig. 3). We had expected shorter stopover durations in the area since the peninsula is exposed during bad weather, has high expected predation and competition rates and thus was predicted to be a low-quality stopover site. The migratory schedule of passerines, with longer periods of stopover alternating with several successive nights of flights (Fransson, 1995; Bolshakov, et al., 2003; Bolshakov & Bulyuk, 2003; Hall-Karlsson & Fransson, 2008), entails that some birds, when landing after a night's flight, will only stay at the landing/stopover site for one day and continue on migration the next night (referred to as 'transients' or 'flyers'), while other individuals will stay in the area for a longer time (referred to as 'non-transients' or 'feeders') (Rappole and Warner, 1976). It is unclear whether this pattern is predefined already before arrival at a stopover, or whether internal and environmental factors at the stopover site determine whether the bird will continue or stay (Jenni and Schaub, 2003). A relatively high proportion of transients were observed in Falsterbo (paper I, fig. 3). There are only a few studies that have investigated the proportion of transients (e.g. Chernetsov, Bulyuk, & Ktitorov, 2007; Schaub, Jenni, & Bairlein, 2008; Chernetsov, 2010), generally, the proportion of transients was very similar to those measured in Falsterbo. However, we identified transients in almost all species (except the diurnal blue tit) and during both seasons, while most other studies found transients only some cases (Chernetsov et al., 2007). The large number of transients might be an effect of the poor quality of Falsterbo as a stopover site. Possibly, the birds that could have stayed to fuel for a number of days moved inland to fuel, instead of staying in this relatively harsh environment (e.g. Alerstam, 1978; Schmaljohann & Naef-Daenzer, 2011). This could be reflected in the higher proportion of reverse migration in Falsterbo when compared to an inland site (Åkesson, 1999).

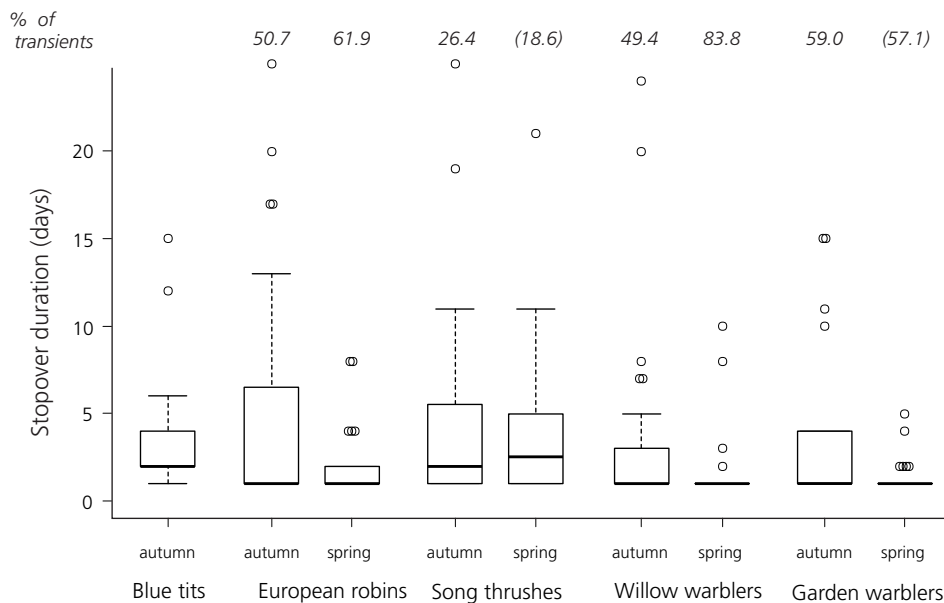


Figure 3. Stopover duration in the different species during autumn and spring migration. Boxes indicate median and the upper and lower quartiles, whiskers indicates SD and outliers are marked as circles. The figure is a descriptive illustration of the spread in the data and does not take the recontact (recapture) probability into account; the given proportions of transients are from the model with an age-related term separating transients from non-transients. If the proportion of transients is given in brackets the transient model was not significantly better than the model with constant survival probability. See paper I for further details.

Different species and populations with different migratory strategies (long-/medium-distance migrants) are expected to behave differently at stopovers. Speed of migration is expected to increase with migratory distance (Alerstam & Lindström, 1990; Ellegren, 1993; Hildén & Saurola, 1982), which could be expected to translate to shorter durations in long-distance migrants. Furthermore, differences in habitat and food preferences have been observed to affect stopover times, probably due to differences in fuel deposition rate (Schaub & Jenni, 2001b). At Falsterbo we did not observe any clear differences in stopover duration between the species with different strategies (paper I). However, we observed higher proportions of transients in the long-distance migratory species, indicating a higher overall speed of migration.

Fuel deposition rate and stopover duration

How long birds should stay on stopover depends, according to optimal migration theory, on how fast they can deposit energy for the upcoming flight in a safe way. Fuel deposition rate (FDR) depends on site quality (food abundance; Lindström, 1991), physiological constraints (if food is abundant, there is an upper limit for how much fat a bird can deposit; Lindström, 1991), competition for food with other individuals (Moore & Yong, 1991), predation risk (Schmaljohann and Dierschke, 2005) and the

prevailing weather conditions (Lindström, 2003). Furthermore, it is never advantageous for birds to stay on a site, if they do not gain fat (Lindström and Alerstam, 1992). There is a substantial amount of evidence that lean birds often stay longer at stopover sites than birds with larger fuel reserves (e.g. Biebach, Friedrich, & Heine, 1986; Moore & Kerlinger, 1987; Stach, et al., 2015), which stresses the importance of fuel stores on stopover duration. As expected, fat score at release affected the probability of birds to leave Falsterbo (paper I), with lean robins and willow warblers staying longer than individuals with larger fuel stores. In a study at 54 different stopover sites using a capture-recapture method on a variety of passerine migrants, Schaub et al. (2008) found that birds with an intermediate FDR were the last to depart from the sites. This is in agreement with the idea that birds with a low or even negative FDR should leave the area to find another site, and that birds with a very high FDR have the possibility to continue migration quickly since they have gained enough energy. Schmaljohann and Dierschke (2005) showed in a field study with northern wheatears, *Oenanthe oenanthe*, that departure fuel load was positively correlated with FDR. However, they also observed that predation pressure (number of over-flying raptors) affected FDR negatively and pointed out that the risk to be predated possibly affected timing of departure.

In front of a barrier

When facing larger ecological barriers, for example the Sahara desert, birds need to deposit extra large fuel reserves and, as a consequence, stopover duration increases. The crossing of the Baltic Sea during southward migration from Falsterbo is covered by one regular night of flight (a flight of at least 23-80 km over open water), thus birds are not expected to prolong their stopover in the area. In a radio telemetry study on juvenile garden warblers in southern Greece, birds stayed at the stopover site for more than two weeks during autumn migration, increasing their body mass by more than 100% by foraging on fig fruits (Fransson, Barboutis, Mellroth, & Akriotis, 2008). It is not fully understood what triggers this fuelling and the extended stopovers before a barrier crossing in inexperienced, juvenile birds, but both the endogenous circannual cycle of the birds (Berthold, 1996) and external spatial cues (Jenni & Schaub, 2003; Alerstam, 2006; Fransson et al., 2008) are thought to be involved. The trigger of fuelling has been studied in a series of experimental studies exposing passerines to a simulated migration along their natural route with artificial magnetic fields. Juvenile thrush nightingales, *Luscinia luscinia*, exposed to a simulated migration from Sweden to Egypt significantly increased their fat deposition compared to birds exposed to the ambient magnetic field of Sweden (Fransson et al., 2001; Kullberg, et al., 2003; Henshaw et al., 2008). In a follow-up study, the authors found a reduction in adrenocortical response in the experimental nightingales compared to the control birds (Henshaw et al., 2009). Corticosterone is thought to be involved in fuelling during migration (Landys et al.,

2004). The adrenocortical response is discussed by Henshaw et al. (2009) to be part of the reason for the extensive fuelling also in juvenile birds facing an ecological barrier.

Seasonal differences

The conditions for migration differ between spring and autumn, because of the birds' annual routine (with breeding in summer), and there are indications that this affects the disposition of the journey. Studies have shown that birds often migrate faster in spring, and one of the main reasons for a faster spring migration seems to be less time spent on stopover (reviewed in Nilsson, et al., 2013). The underlying cause for shorter stopovers during spring is not fully understood and may be linked to several different factors. Factors suggested to explain the seasonal differences in stopover duration include longer days for feeding (Bauchinger and Klaassen, 2005), more extensive pre-migratory fuelling during spring, seasonal differences in feeding intensity and behaviour, and stopover time used for other activities than fuel deposition (Nilsson et al., 2013). To reach the northern latitudes during spring migration, it might be beneficial to overload fuel at the beginning of the journey in order to avoid the risk of ending up on a stopover site without any food, which could be expected because of the late progress of spring (Alerstam & Hedenström, 1998). It might also be favorable during spring migration to stay a little bit longer and overload on fuel on the last stopover site in order to arrive at the breeding grounds with extra energy to fight for territories (Sandberg & Moore, 1996), and to have surplus energy for breeding (Klaassen et al., 2006). In line with previous studies, we found shorter stopover durations during spring compared to autumn migration in all species except willow warblers (paper I). Furthermore, we observed a higher proportion of transients during spring, indicating an overall increase of migration speed.

Sex- and age-dependent differences in stopover behavior

Stopover behaviour differs depending on the birds' migratory strategy (distance) and between different species, but there is also evidence for variations within species. When large numbers of migrants with the same food requirements congregate at a stopover site, competition for food will mean that subordinate individuals will get less food. Consequently, subordinate individuals will experience a decrease in FDR, potentially prolonging their stopover, which will lead to a lower overall speed of migration (Moore & Yong, 1991; Kelly, et al., 2002). Juveniles have been shown to be socially subordinate to adults (Gauthreaux, 1978), and they are also observed to be less efficient foragers (Gochfeld and Burger, 1984). This pattern is reflected in some studies of age-dependent

differences in passerines during autumn migration where juveniles carried less fat than adults and performed longer stopovers (Ellegren, 1991; Woodrey and Moore, 1997; Yong et al., 1998), perhaps as a result of a lower FDR. Adult bluethroats, *Luscinia svecica*, studied on a stopover site in eastern Sweden by capture recapture methods, were observed to stay for shorter periods than juveniles (Ellegren, 1991). In addition, the adult bluethroats had a higher fat load at the first capture, while the juveniles even lost mass in a higher proportion during the first day. In our studies at Falsterbo, we did not find an age-related effect on stopover duration (paper I) and can therefore not support these findings.

Age-dependent differences are typically observed during autumn migration. Since juveniles are expected to gain experience during their first autumn and winter, and are no longer naïve during their first spring migration, sex-dependent competition have been suggested to be more apparent than age-related differences during spring migration (Yong et al., 1998). Sex-dependent differences have been observed in a number of species during spring migration, usually discussed in view of differences in selection for overall migratory speed. A number of studies show that males return to their breeding grounds before females (Newton, 2008), but few studies directly investigating sex-dependent competition en route. Male Wilson's warblers, *Cardellina pusilla*, have been observed to have higher FDRs than females during spring migration (Yong et al., 1998). In addition, male Greenland wheatears, *Oenanthe oenanthe leucorhoa*, were shown to use a time minimizing strategy during spring migration with a FDR positively correlated with departure fuel load, whereas females did not show such a pattern, indicating instead an energy minimizing strategy (Dierschke et al., 2004). These studies do not directly demonstrate sex-dependent competition, but they may result from this kind of competition and/or differences in the general strategy between the sexes. However, it has been observed that female pied flycatchers are subordinate to males in a simulated foraging situation during spring migration (Moore, et al., 2003), which would result in more time-consuming foraging and potentially increased stopover durations for females. Hence, sex-dependent competition en route, with the dominant sex getting most of the resources, may be an additional reason for differential timing of migration between the sexes, other than just the fact that males are more eager to get back early to maximize mating opportunities (Kokko et al., 2006).

Weather influences on stopover duration

The structure of the migration is expected to be modified by environmental factors (Jenni and Schaub, 2003), and the initiation of nocturnal flights has been shown to depend strongly on prevailing weather conditions (Richardson, 1978; Richardson, 1990). Unfavourable flight conditions with precipitation and strong opposing winds have been shown to delay departure from a stopover site, and consequently prolong the

stopover duration (Åkesson, et al., 2002; Schaub, 2004; Morganti et al., 2011; Bulyuk & Tsvey, 2013). Robins have been observed to delay initiating flight during strong winds, irrespective of direction, when departing from Switzerland during autumn (Schaub, 2004). Moreover, the emigration ratio of migrating robins departing from a small Danish island was not correlated to wind direction (Rabøl 1978). Both findings indicate that wind speed, rather than directions, is the primary wind component affecting departures on nocturnal flights. Supporting these studies, we observed decreased departure probabilities in song thrushes leaving Falsterbo during spring when strong winds prevailed at sunset, but less pronounced effects of wind direction (paper I).

However, there is substantial evidence that birds prefer to initiate flights in tailwind conditions (e.g. Åkesson & Hedenström, 2000; Åkesson et al., 2002). The effect of opposing winds cannot be expected to be negligible (especially so during strong winds), even though we found no support for this. In addition to wind speed, robins departing from stopover in Switzerland were observed to be sensitive to precipitation (Schaub, 2004), similar to reed warblers departing from Sweden (Åkesson, et al., 2001) and black redstarts, *Phoenicurus ochruros*, departing from Italy (Morganti et al., 2011). We observed negative effects of rain and overcast weather on the probability to leave Falsterbo in garden warblers during spring and in blue tits during autumn migration (paper I). This pattern is further supported by an earlier study of blue tit migration in Falsterbo where blue tits were observed to be more sensitive to overcast weather and precipitation compared to other partial migrants (Nilsson, et al., 2006).



Timing of departures on nocturnal flights

Many migratory passerine species, that are normally diurnal, migrate during the night. The reason for nocturnal migration is not completely understood, but the behaviour can be adaptive for several reasons. By migrating during nights, birds make use of less turbulent wind conditions associated with night conditions, leave more time for foraging during the day, and avoid predators that to a large extent are diurnal (Kerlinger & Moore, 1989; Alerstam, 2009). Hence, nocturnal migration not only saves energy and time, but also reduces the predation risk (Newton, 2008). The timing of nocturnal flights has been suggested to be related to the different scales of movements, with true migratory departures taking place in the period after sunset, while local scale movements for better feeding are observed to be scattered throughout the night and take place during the day (Mills et al., 2011).

Nocturnal migrants have for a long time been considered to depart on migration shortly after sunset, with a peak in intensity 1-4 hrs after local sunset (for references see Moore, 1987). However, several recent studies, including paper II & VI, have observed migratory departures that occur also much later, well into the night (Åkesson, et al., 1996a, 2001; Bulyuk & Tsvey, 2006; Bolshakov et al., 2007; Schmaljohann et al., 2013). Hence, the departure of migrants does not seem as finely tuned to the hours after sunset as previously thought. Regulating the flight period by delaying departure could be advantageous, if birds prefer to cease flight and arrive at a new stopover during morning twilight in order to be able to use visual cues to find a suitable habitat.

The focus of the relatively few studies of departure times in nocturnal migrants has often been to relate departure timing to sun elevation and the availability of orientation cues. There are a few indications that migrating passerines prefer to depart during or shortly after the nautical twilight period, possibly because of the availability of different orientation cues (both stars and polarized light are available during the nautical twilight period, but not thereafter; Åkesson, et al., 2001; Bolshakov & Chernetsov, 2004; Bolshakov et al., 2007; Schmaljohann et al., 2011;). Methodological difficulties to study nocturnal timing are probably the cause of the relatively few studies on timing of departures and the low samples often used in these studies. The development of radiotelemetry has now made it possible to follow specific individuals and to obtain larger samples. We observed (paper II) a high degree

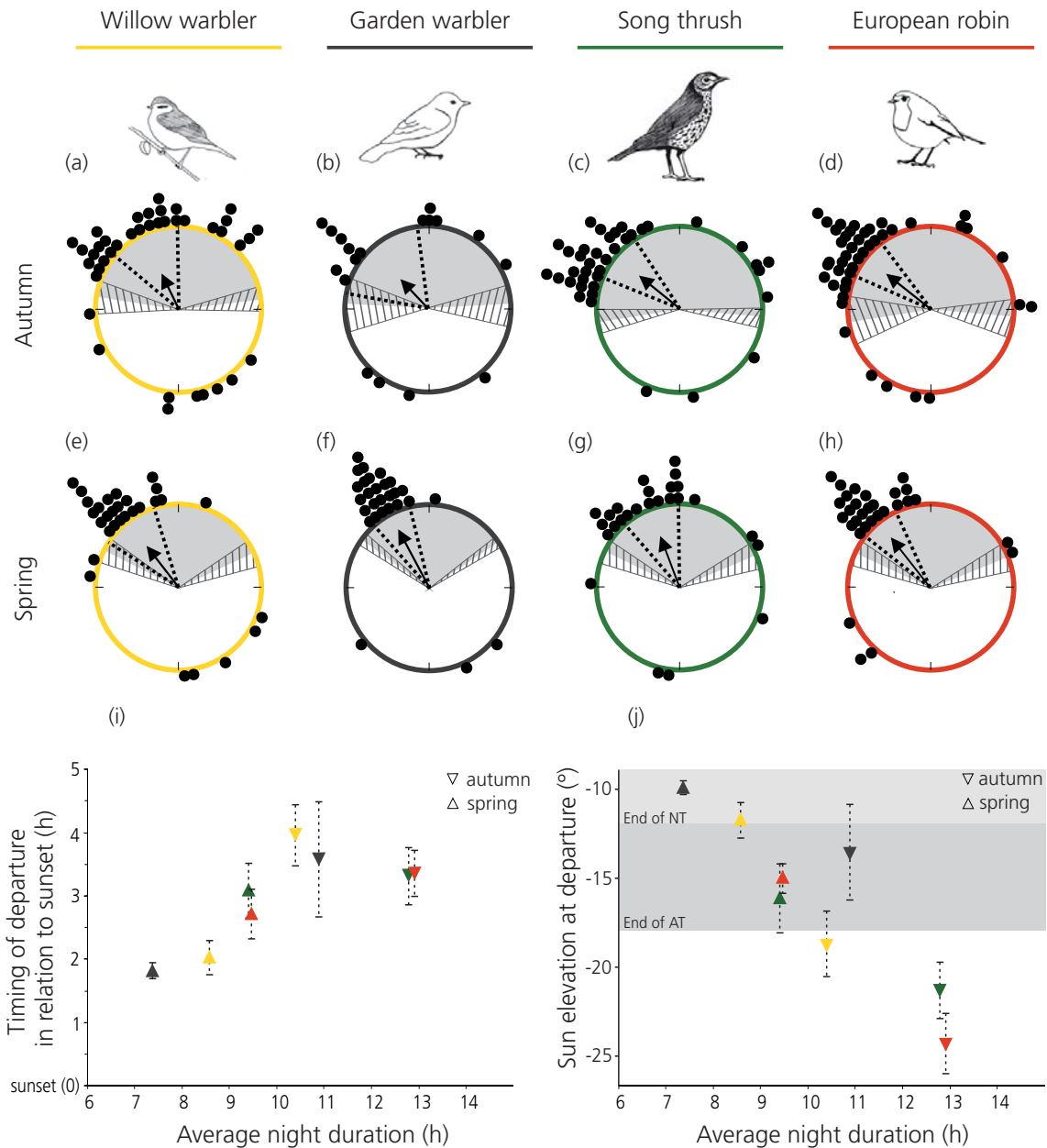


Figure 4. Timing of departures of garden warblers, willow warblers, song thrushes and robins at Falsterbo, Sweden, as recorded by automated radio telemetry. Circular diagrams (a)-(h) show departure timing for each species and season during the 24 h of day/night with 00hrs CET = 0° and 12hrs CET = 180°. Each symbol outside the circle refers to the departure time of an individual. Mean vectors (arrows) with length proportional to the mean vector length show the mean timing with 95% angular confidence intervals indicated by the dotted lines. Shaded sectors refer to the night (between mean times of sunset and sunrise) with the range of variation in sunset and sunrise times indicated by hatched sectors. Mean departure time (\pm SE) in relation to sunset for each species and season are plotted in relation to average night duration (i), and mean sun elevation at departure (\pm SE, degrees below horizon) are plotted in relation to night duration (j). Data in (i) are restricted to the period 17-07 CET, data in (j) are restricted to the period 17-00 CET. See paper II for further details.

of variability in departure timing in relation to sunset and sun elevation when birds left Falsterbo during both spring and autumn migrations (fig. 4). Contrary to earlier suggestions about the importance of celestial orientation cues, our results instead suggest adaptive responses to ecological factors (migratory season, night duration) as the primary determinants for timing of migratory flights.

Robins have previously been observed to depart earlier in relation to sunset during spring than during autumn at the Courish spit (Bolshakov et al., 2007), similar to the pattern we observed in Falsterbo. These results suggest that the flight period is adjusted to compensate for the shorter nights associated with spring migration, to avoid reducing the nocturnal flight period to the same extent as the night becomes shorter (cf. Bauchinger & Klaassen, 2005). The duration of night seems to be an important ecological factor that drives not only large parts of the timing differences between seasons, but also between different species migrating at different times. Earlier observations of departures of different species of migrating passerines have indicated differences in departure timing related to migratory strategy (long- vs. short-distance migration; Bolshakov & Bulyuk, 2001), which by extension is related to night duration, since long- and short-distance migrants fly at different times during the seasons. However, even though night duration seems to explain a large part of the variation, we observed differences associated with season and species that remain even after the effect of night duration has been taken into account. Possibly, the early departures during spring may to some degree also be caused by an urge for higher migration speed in spring compared to autumn (Nilsson et al. 2013).

Additionally, there are studies indicating that timing of nocturnal flights might to some degree be individual and governed by the individual's internal clock. The result of one track of a migratory Swainson's thrush, *Catharus ustulatus*, followed by radio telemetry revealed departure in a very narrow time frame (9-13 minutes after civil twilight) on seven consecutive nights (Cochran, 1987). This observation, together with the fixed time of flight activity observed in captive common redstarts, *Phoenicurus phoenicurus*, (Coppack, et al., 2008), supports the idea that individual time schedules are ruled by each birds' endogenous program.

The energetic hypotheses

The cause of variation in departure timing is also suggested to relate to energetic condition (Moore & Aborn, 1996), with lean birds departing later than birds with larger amounts of stored fat, since their energetic reserves will only last for a shorter flight. This pattern has previously been observed in Northern wheatears that departed earlier and in directions indicating longer flights over open sea when departing from stopover at Helgoland, Germany, with higher amounts of stored fuel compared to lean individuals (Schmaljohann and Naef-Daenzer, 2011). Similarly, Swainson's thrushes

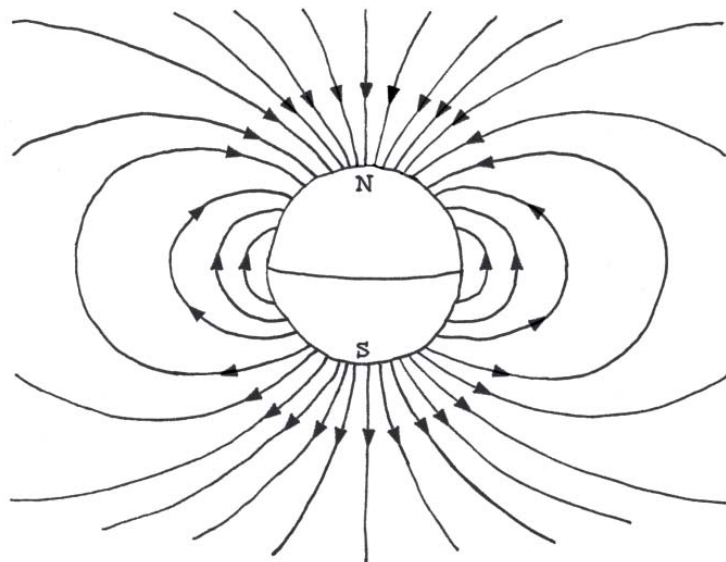
with large fuel stores departed shortly after sunset and in directions leading to a crossing of the Gulf of Mexico, while departures recorded later in the night corresponded to leaner individuals moving back inland (Smolinsky et al., 2013). This pattern is further supported by our observations at Falsterbo where robins, song thrushes, willow warblers and garden warblers with larger fat deposits depart before individuals with smaller fuel stores (paper II). In addition, birds that took a longer flight across the Baltic Sea than necessary, and passed the offshore receiver station at FINO 2, departed more concentrated in time just after sunset, compared to birds that departed on other routes from Falsterbo (paper VI). More studies of flight durations and landing times are needed in order to confirm that these adjustments in timing of departures on nocturnal flights relative to stored fuel correspond to the upcoming flight range.

Variation in departure timing caused by weather conditions

Birds have not only been observed to postpone departures to wait for more favourable weather conditions (see above), but also to delay departures within the night when the prevailing winds at sunset are unfavourable. The delay of departure under poor flight conditions may be adaptive for at least two reasons: first, since conditions may have improved when birds depart later in the night, and second, flight duration will be reduced on nights with unfavourable winds. We found that the birds in Falsterbo delayed their departure when wind conditions during sunset were not optimal, with opposing winds and high wind speeds (paper II). Additionally, Swainson's and Hermit thrushes, *Catharus ustulatus* & *guttatus*, have been observed to depart on migratory flights from stopover on Lake Erie, Ontario, Canada, earlier after sunset under favourable wind conditions, but scattered throughout the night under unfavourable conditions (Mills et al., 2011). Moreover, clouds and visibility have been discussed to affect timing of departure, either since the availability of orientation cues around sunset deteriorates, or as a direct effect on flight conditions, when visibility decreases. European reed warblers, *Acrocephalus scirpaceus*, departing from Falsterbo initiated migratory flights later during the nights when the cloud cover was reduced after sunset and celestial cues became visible (Åkesson et al., 2001). Contrary to this observation, neither we nor several studies on robins at the Courish Spit (Bulyuk & Tsvey, 2006; Bolshakov et al., 2007; Bulyuk, 2012) found any support for departure timing being related to cloudiness. Birds are shown to be sensitive to changes in air pressure (e.g. Åkesson et al., 2002; Dänhardt & Lindström, 2001; Bulyuk, 2012) and might use this to anticipate changing weather conditions.

Orientation & route choice

Birds are known to use multiple cues to determine and keep their migratory direction (reviewed in Wiltschko & Wiltschko, 2003). Juvenile inexperienced individuals on their first migration are expected to orient according to their inherited vector programme (Gwinner & Wiltschko, 1978), whereas experienced adults may make use of their knowledge about the goal area and orient by true/goal navigation. This difference is observed in a number of displacement studies where adults are capable of correcting for displacements while juveniles keep their original directions (e.g. Perdeck, 1958; Thorup et al., 2007; Chernetsov et al, 2008). The different compasses include a magnetic compass (Wiltschko & Wiltschko, 1972; Wiltschko & Wiltschko, 1995); star compass (Emlen, 1970; Emlen, 1975) and a sun/polarized skylight compass (Able, 1982; Moore, 1982, 1987; Schmidt-Koenig, 1990; c.f. textbox).



Box 1. Compasses

The star compass. As a result of the Earth's rotation around its axis, the starry sky is experienced to rotate, with the center of rotation indicating directions towards the geographic poles. In the northern hemisphere, the polar star is at the center of the rotation, thus providing a true reference towards north. By observing the pattern of the rotation of the starry sky around the polar star as nestlings, birds are able to use the position of stars to determine geographical directions (Sauer 1975; Emlen, 1970, 1975).

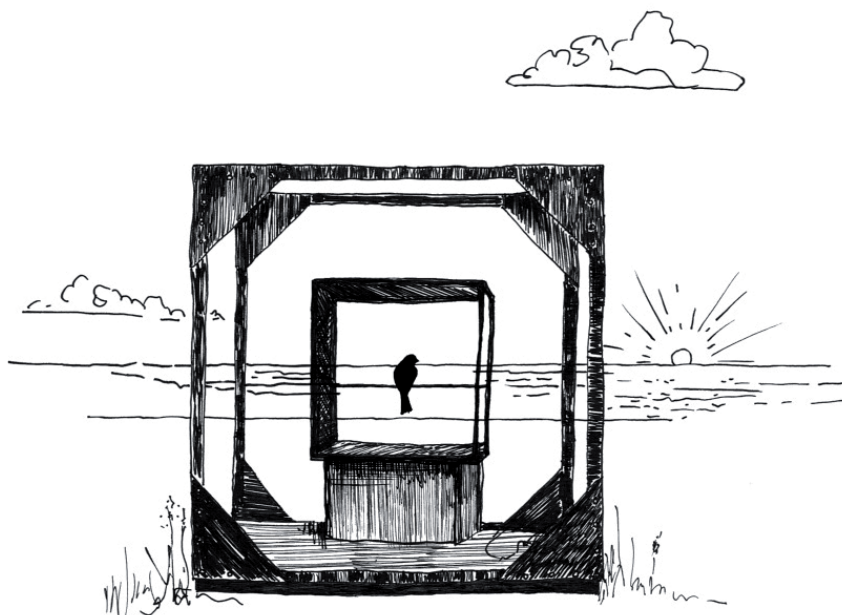
The sun compass. The sun compass is a time-compensated compass mechanism which depends on both the sun's azimuth and the circadian clock of the birds. By combining these two components, birds are able to determine an accurate orientation direction (Moore, 1982, 1987; Schmidt-Koenig, 1990).

Skylight polarization. Sunlight gets polarized when it passes through the atmosphere, and a band of maximal polarization is formed perpendicular to the sun's azimuth (also called e-vector) (Brines & Gould, 1982). The e-vector of polarized light has been suggested to provide directional information (Moore, 1986, 1987). Birds have been shown to be sensitive to the e-vector orientation in behavioural experiments (Able, 1982), and it has been suggested as the primary reference cue that birds use to calibrate their compasses (e.g. Muheim, et al., 2006a,b). It is unclear, however, whether polarized light acts as a compass on its own or whether it is used to calculate the position of the sun, when the sun itself is hidden (Muheim, 2011).

The magnetic compass. The Earth's magnetic field is a dipole field generated by movements in the Earth's outer core. Migratory birds use the inclination of the field, not the polarity, which provides them with directional information towards the equator and the poles (Wiltschko & Wiltschko, 1972, 1995). The magnetic inclination compass is known to be light-dependent (Wiltschko, et al., 1993, 2010; Muheim, et al., 2002) and there are theoretical indications that birds see the magnetic field superimposed on the retina (Ritz, et al., 2000).

Calibration of the compasses

Since the relationships between compass cues are expected to differ along the migratory route (e.g., changing magnetic declination, the angular difference between the magnetic and geographic north pole), and because the availability of compass cues differs due to weather conditions, time of day, season and location during migration, birds have to regularly calibrate the different compasses with respect to a common reference (Muheim, et al., 2006a). It is poorly understood how this works in detail, and contradictory results from experimental data are confusing. Possibly, birds use whichever cue is best for each particular situation, and the hierarchy of the compasses is not stable. It has previously been suggested that the contradictory results can be explained by differences in cue availability during the exposure (Muheim, et al., 2006a), with access to the vertically aligned e-vector of polarized light near the horizon being the crucial cue necessary for calibration. This is supported by observations of free-flying *Catharus* thrushes that recalibrated their magnetic compass daily from celestial cues when tracked by radio telemetry in North America (Cochran et al., 2004). Similarly, savannah sparrows, *Passerculus sandwichensis*, and white crowned sparrows, *Zonotrichia albicollis*, recalibrated their magnetic compass by polarized light near the horizon at sunrise and sunset (Muheim, et al., 2006b; 2009).



Garden warbler during exposure to a shifted magnetic field at sunset

However, studies performed in Australia and Europe found no recalibration of the magnetic compass after similar exposures, and the results of these studies instead indicate that magnetic cues are the primary calibration reference (Wiltshko, et al., 2008; Gaggini, et al., 2010; Chernetsov, et al., 2011; Schmaljohann, et al., 2013; Åkesson et al., 2014). Song thrushes released with radio transmitters after exposure to a shifted magnetic field, with a full view of the surroundings, were observed to continue in the migratory direction without calibration of the compasses (Chernetsov et al., 2011).

Interestingly, a recent study indicates that an unchanged or calibrated star compass could be the reason for these contradictory results between studies performed at different continents (Giunchi et al., 2014). Pied flycatchers, *Ficedula hypoleuca*, were observed to alter their orientation in cage experiments after cue-conflict exposure to a 90 deg shifted polarization pattern during sunset. However, after being released and tracked with radiotelemetry, the flycatchers showed no response and oriented in the seasonally expected migratory direction. The authors explained these seemingly conflicting results by suggesting an unchanged star compass during the exposure (the stars were not visible until after the exposure) that the birds relied on after release. This is supported by our data (paper III) on garden warblers. After exposure to a 90 deg shifted magnetic field during sunset, the birds did not shift their direction when released with radio transmitters (which is also in agreement with previous studies from Europe and Australia suggesting magnetic cues as primary reference cue for calibration of the celestial compasses; fig. 5). The vanishing bearings did not differ between control birds or birds that had been exposed to a 90 deg shifted magnetic field with full view of the setting sun. None of the groups differed from the vanishing bearings that we observed in garden warblers released with radio transmitters immediately after ringing. Our birds had no access to stars during the exposure, but were released 1.5 hrs after sunset when stars were visible. From our data it is impossible to determine, whether the birds recalibrated the celestial and/or the magnetic compass during the exposure, but ignored those cues when they had access to stars, or if all compasses were unchanged.

To further understand the seemingly contradictory results from the different continents, we reexamined all existing cue-calibration studies, in the light of the new suggestion about the star compass (Giunchi et al., 2014). After evaluating all studies, and taking into account if the birds had access to stars during the cue-conflict exposure, we propose (paper III) the following hierarchy between the compasses:

1. Birds recalibrate their magnetic compass from celestial cues if they have access to the vertically aligned e-vectors near the horizon.
2. Birds recalibrate the celestial cues from magnetic cues if they are exposed to a cue conflict and do not have access to the polarized light near the horizon.
3. Birds recalibrate their star compass from the newly calibrated magnetic compass if they have access to the polarized light near the horizon and the exposure last until the stars appear.

- Birds do not seem to recalibrate the star compass from the magnetic compass if the cue conflict is created by a shifted polarized light pattern (possibly since the stellar and magnetic reference systems remain in the same relationship to each other, even though the magnetic compass has been recalibrated from the polarized light pattern). After release they simply rely on their unchanged star compass.

In order to further understand the hierarchy of the compasses and how birds calibrate their compasses during migration, more studies are needed that strictly control all cues, including the stars.

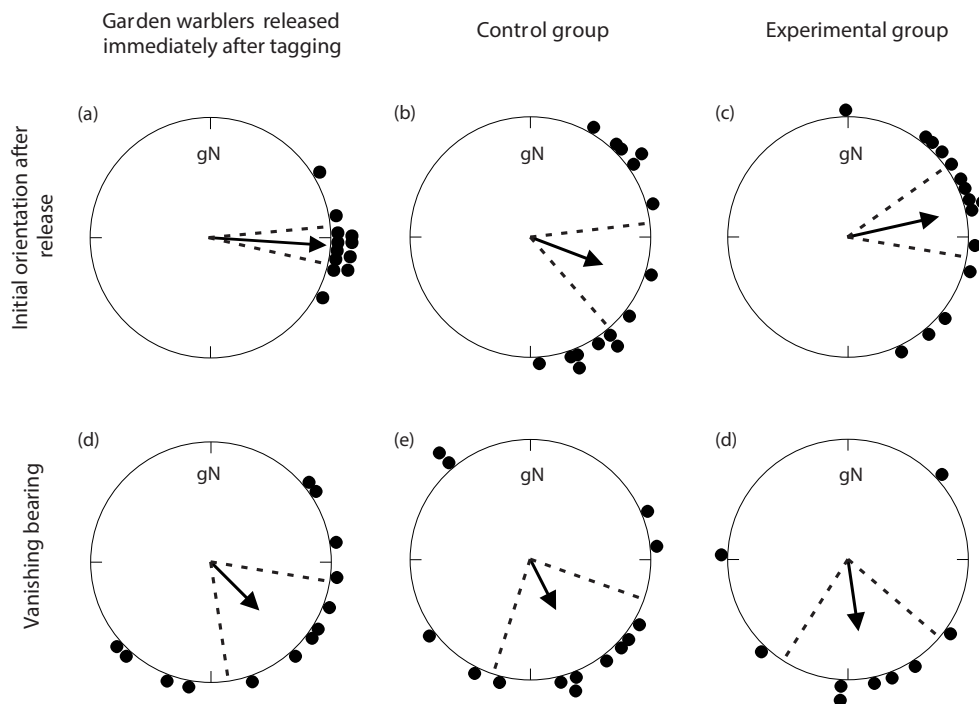


Figure 5. (a-c) Initial orientation of the first 10 min after release from the lighthouse receiver station for garden warblers (a) released immediately after tagging during daytime, (b,c) released at night after cue conflict exposure under (b) the control condition and (c) the experimental condition. (d-f) Vanishing bearings of garden warblers (d) released immediately after tagging during daytime, (e) control and (f) experimental group. If the birds would have recalibrated their magnetic compass, and used it after release, we would expect a -90 deg shift in orientation in the experimental birds. See paper III for further details.

Flights with different goals

Birds use their compass senses to find the direction towards their goal. However, during migration a bird will not always continue in the main migratory direction after a stopover, and the direction towards the goal for each particular flight could change. The cause of movements in directions other than the migratory direction during migration can be either adaptive responses of lean individuals searching for better feeding habitat, or non-adaptive reasons, like e.g. orientation errors (Komenda-Zehnder et al., 2002) or strong winds that drift the birds off course.

Reverse movements

It is frequently observed that birds fly in directions opposite to their expected migratory direction, especially in front of barriers and in coastal regions (Alerstam, 1978; Åkesson, et al., 1996b; Åkesson, 1999). In Falsterbo 47% of the vanishing bearings of radio tracked birds were directed towards the north and 43% of short-term ringing recoveries were found north of the peninsula during autumn migration (paper IV, fig. 6). 21% of the track directions from the radar sample of overflying birds at Falsterbo during autumn were northbound, which is higher, but still congruent with previous studies reporting the proportion of reverse migration (Bruderer & Liechti, 1998: 12%; Zehnder & Åkesson, 2002: 14.1% and 10.1%). We found no indication that daily variation in competition and predation risk affected the probability of reverse movements (the only significant effect was in the opposite direction from the expected). However, it cannot be excluded that the generally high level of competition and predation at coastal sites, such as Falsterbo, increases the proportions of reverse movements.

Departures on local scale flights are frequently observed during daytime or scattered throughout the entire night (Newton, 2008; Mills et al., 2011). In contrast, departures in the expected migratory direction are most commonly observed during the sunset period (Åkesson et al., 1996a, 2002; Mills et al., 2011; Smolinsky et al., 2013). Hence, the tendency to depart and continue on forward migration might also change during the night, especially when the birds are facing a barrier (Zehnder et al. 2002; Schmaljohann and Naef-Daenzer 2011). The overflying migrants tracked by radar at Falsterbo performed northerly directed flights more often after midnight. However, we did not observe more reverse departures of radio tagged birds late during the night (paper IV), and true migratory departures in appropriate directions are known to take place during the entire night (see above).

Different species may also be more or less susceptible to making reverse movements because of their species-specific strategies, such as migration distance. Short-distance

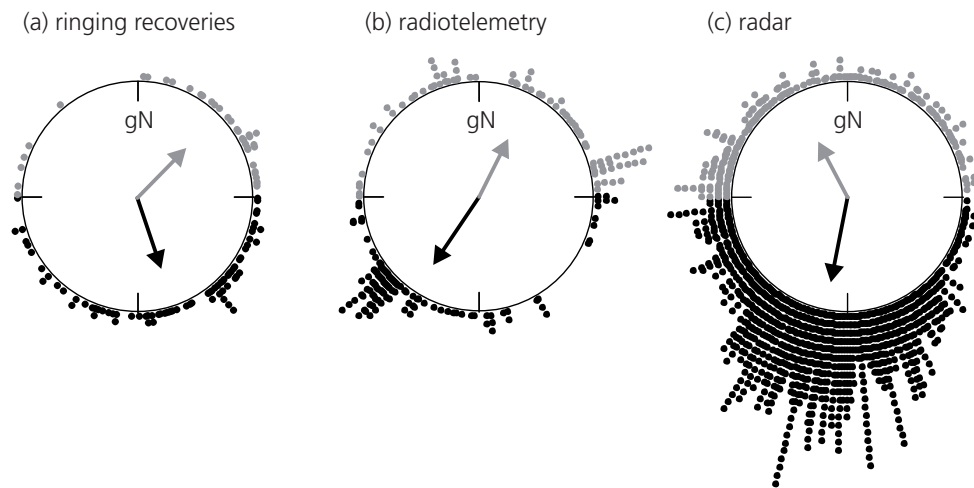


Figure 6. Departure directions from (a) radiotelemetry, (b) direction between capture site and ring recovery site and (c) track directions from radar tracked birds at Falsterbo peninsula. Reverse migrants in light grey and forward migrants in black. See paper IV for further details.

migrants are expected to be more likely to perform reverse movements, since they may be less constrained in time (Åkesson et al., 1996b; Nilsson, et al., 2014).

We found radio-tracked robins to reverse their departures from Falsterbo more often than long-distance migratory garden and willow warblers (paper IV). However, the medium-distance migratory song thrushes were the least likely to depart in directions opposite to their expected migratory directions.

Fuel stores and age

The most likely cause of reverse movements during migration may be that lean birds return to previously passed stopover sites with better feeding opportunities. Predictably, fuel load seems to be the intrinsic factor that most often characterizes reverse flying migrants (e.g.; Lindström & Alerstam, 1986; Åkesson et al., 1996b; Sandberg & Moore, 1996; Deutschlander & Muheim, 2009; Schmaljohann & Naef-Daenzer, 2011; Smolinsky et al., 2013; Stach et al., 2015). Supporting previous studies, we found in short-term ringing recoveries that lean birds reversed their orientation at Falsterbo to a higher degree than individuals with larger fuel stores (paper IV). Furthermore, we observed more juvenile birds moving in directions opposite to the expected migratory direction, in agreement with previous findings (Lindström and Alerstam, 1986). The reason for age-related differences in directions is unclear. However, juveniles have been shown to be less efficient foragers than adults (see above), which may oblige them to search for alternative stopover sites when competition is high. In addition, since they lack experience, they may hesitate to cross the Baltic Sea. Orientation errors may be more likely to occur among juveniles, which could cause movements in directions other than the expected ones. Juveniles have earlier been shown to be more scattered in their orientation (Moore, 1984).

Weather

Prevailing wind conditions may significantly impair or assist migratory flights (Pennycuick, 2008). Hence, it is not surprising that winds have been observed to affect not only the probability of departures on migratory flights (see above) and the timing of the departures (see above), but also departure and travel directions (e.g. Åkesson & Hedenström, 2000; Schmaljohann & Naef-Daenzer, 2011; Covino, et al., 2014; Sjöberg et al., 2015). However, several previous studies have failed to find an effect of winds on the proportion of reverse migration (Bruderer and Liechti, 1998; Komenda-Zehnder et al., 2002; Smolinsky et al., 2013). We observed (paper IV) an effect of winds on the flight directions of migrants while aloft (radar tracking), but not on radio tracked birds departing from Falsterbo. Reverse movements were found to be more common among the birds aloft when strong winds were blowing opposite to the expected migratory direction.

In addition, northward movements during autumn migration were also more frequent on nights with more cloud cover. However, the cause for this behavioral change under overcast situations could potentially be both because of unfavourable orientation conditions causing difficulties to maintain a constant heading and/or because of low migratory motivation when flight conditions are not ideal. Accordingly, birds are known to prefer to initiate migratory flights under clear conditions (see above). Orientation accuracy might be dependent on cloud cover, and improve with increased access to celestial cues (e.g. Åkesson et al., 2001). White-throated sparrows tracked by radar, for example, have been observed to adapt a 'zig-zag' shaped flight pattern under overcast conditions (Emlen and Demong, 1978).

Route choice in front of a barrier

Passerine migrants use a variety of strategies when facing a barrier, indicating that the decisions made before flying across barriers play an essential role in the birds' migratory strategies. Straight barrier crossings and longer detours are regularly observed (e.g. Alerstam, 2001; Stutchbury et al., 2009; Åkesson, et al., 2012), as well as reverse movements (Alerstam, 1978; Åkesson et al., 1996b; Woodworth et al., 2014) and postponement of departure for more favorable weather conditions (Åkesson & Hedenström, 2000). The crossing of the Baltic Sea on southward migration from Falsterbo (a flight of about 23-80 km over open water) should not be compared with crossings of larger ecological barriers, such as the Saharan desert. All our birds equipped with radio transmitters probably had enough fuel to manage the flight across the sea. However, the sea crossing from Falsterbo is enough to make birds hesitate. Migrants have been observed to perform reverse movements more often at the peninsula than at an inland site (Åkesson, 1999).

Wind conditions considerably influence the patterns and speed of bird migration (Alerstam, 1979; Liechti & Bruderer, 1998; Richardson, 1990), potentially causing

lateral drift once the birds are in the air. Hence, it was not unexpected that we found a significant influence of wind directions on the probability of birds to pass the offshore receiver station at FINO 2 after departure from Falsterbo (paper VI). Adult individuals and individuals with larger fuel reserves have been observed to be more likely to perform straight barrier crossing crossings rather than detours where the barrier crossing can be reduced or avoided (e.g. Sandberg, et al, 1991; Schmaljohann & Naef-Daenzer, 2011; Smolinsky et al., 2013). Contrary to these findings, we found only a weak trend of age and no effect of fat score at release, or body mass relative to size-specific fat-free body mass, on the probability of a departure on a flight across the open Baltic Sea (resulting in a passage of FINO 2).



Adjustments of directions

Passerine migrants are assumed to make use of several cues when determining their departure direction (see above), and are expected to establish the migratory direction before departure from a stopover. Consequently, departure directions and vanishing bearings from stopover sites are often interpreted as intended travel direction, and have in a number of studies been demonstrated to relate to several intrinsic (age, fuel load) and environmental factors (wind conditions, cloud coverage; see above). However, while analyzing the vanishing bearings from the birds that left Falsterbo and then later passed the offshore receiver station at FINO 2 (paper VI), we realized that these birds had adjusted their headings after we lost radio contact with them at Falsterbo (fig. 7).

In order to further understand this shift in heading, we compared vanishing bearings from radio-tracked birds with radar data of overflying birds in climbing and level flight (paper V). The differences in the concentration of directions during departure and level flight illustrate a clear pattern, that birds do not just determine a direction before departure, but in addition adjust it once at cruising altitudes.

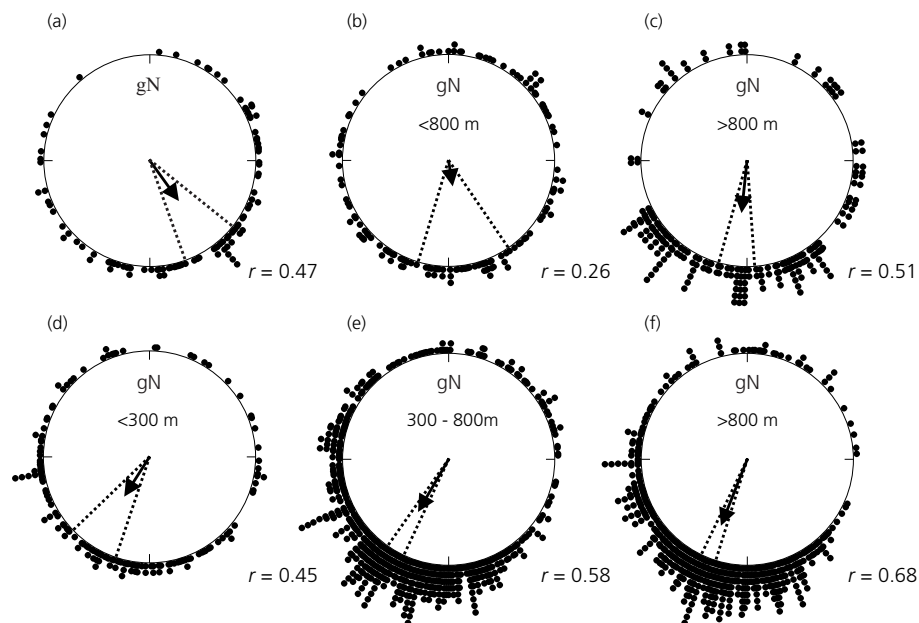


Figure 7. Circular distributions illustrating the pattern of directional adjustment at departure and cruising altitudes: (a) vanishing bearing of radio-tracked birds; track direction of birds followed by radar during: (b) climbing with altitude <800m, (c) climbing with altitude >800m, and with level flights at altitudes (d) <300m, (e) 300-800m, and (f) >800m. Arrows indicate mean direction, r-values and 95% CI, all circular distributions have p (Rayleigh) <0.001. See paper IV for further details.

As mentioned above, wind conditions have an immense effect on bird migration (Richardson, 1978,1990; Alerstam, 1979; Liechti & Bruderer, 1998), and the travelling path of a migrant aloft is the result of the heading and speed of the individual and the wind speed and direction. Migratory birds have been shown to fly with complete wind drift, as well as with partial or full compensation for lateral drift (Richardson, 1990; Liechti, 2006; Chapman et al., 2011). Winds are generally weaker at ground level, and if favorable tailwinds are found at high altitudes, a migrant will gain from increasing its altitude, even though climbing is energetically costly (Hedenström & Alerstam, 1992). Radar studies have shown that migratory passerines ascend by more or less straight climbing flight (Alerstam, 1990). Birds are expected to trade-off forward airspeed with climbing rate (Hedenström & Alerstam, 1992; Piersma et al., 1997). Migratory shorebirds have been observed to fully drift at departure over sea, and partially or fully compensate for drift at higher altitudes and in flights over land (Grönroos et al., 2012). Similarly, common and arctic terns, *Sterna hirundo* & *paradisea*, have been observed not to compensate for lateral wind drift during climbing flights (Alerstam, 1985). The adjustment of headings that we observed (paper V) could partly, but not completely, be explained by birds not compensating for lateral drift in climbing flights. Presumably birds fine-tune their orientation once in the air, which causes the major part of the adjustment in direction.



The Falsterbo lighthouse

Flight speed and the duration of flights

Flight speed

As covered in earlier chapters, time spent on migration does not only relate to how fast a bird flies in relation to the surrounding air. It also depends on the duration spent on stopovers (hence also fuel deposition rate), route choices, time spent flying (timing of nocturnal flights), and the prevailing wind conditions once the bird is in the air. How fast a bird can fly relative to the surrounding air (airspeed) is determined by the birds' body size and its wing and body morphology, and whether it uses flapping or soaring flight (Pennycuik, 2008). The maximum flight speed a bird can achieve is very costly, and birds are not expected to fly at these speeds during long-distance movements, such as migration. According to migration theory, a bird should fly at slightly higher air speeds to optimize time, rather than energy, spent on migration (Alerstam & Lindström, 1990). Radar studies have shown that small passerines, similar to the small species investigated in this thesis, fly at approx. 10 m/s during migration, while larger passerines, such as song thrushes, fly at approx. 13 m/s (Bruderer & Boldt, 2001).

Movements on different scales during migration, such as migratory flights or search for better feeding areas, may be driven by different factors. Thus, birds may not invest energy in the different behaviours to the same degree and therefore fly at different airspeeds for the different types of movements. Previous studies have observed reverse flights at lower altitudes and at lower flight speeds compared to forward movements (Bruderer and Liechti, 1998; Komenda-Zehnder et al., 2002). Similarly, we found reverse movements to be slower, although only at high altitudes (paper IV). At low altitudes, forward migration was instead slower, possibly as a result of higher proportions of climbing flights compared to birds in reverse flights flying at low altitudes.

Flight durations

Both the actual flight speed and the straightness of the flight path will affect the duration of a migratory flight. Because of methodological problems with tracking, entire flights and flight durations of small migratory passerines are still largely unknown. Ground speed is determined by the airspeed of the bird and the wind vector. Consequently, ground speed is strongly influenced by tail or head winds (Pennycuick, 2008). As expected, we observed that the prevailing wind was the primary factor affecting the flight duration between Falsterbo and the offshore receiver station at FINO 2, a flight covering the first 50 km after departure (paper VI). In addition to winds, we found effects of cloud cover and fuel store on flight duration (fig. 8). White-throated sparrows have previously been observed to adopt less straight flight paths and lower airspeeds when released under totally overcast skies compared to sparrows released under clear skies (Emlen and Demong, 1978). Moreover, there are indications that increasing cloud cover impairs orientation accuracy (e.g. Sandberg et al., 1991; Åkesson et al., 2001). Similar to the behavioral change causing more reverse directed flights in overcast weather (see above), it is unclear whether the increase in flight duration with an increase in cloud cover is related to orientation difficulties and problems with maintaining a fixed heading, or whether it is related to low migratory motivation under unfavorable conditions.

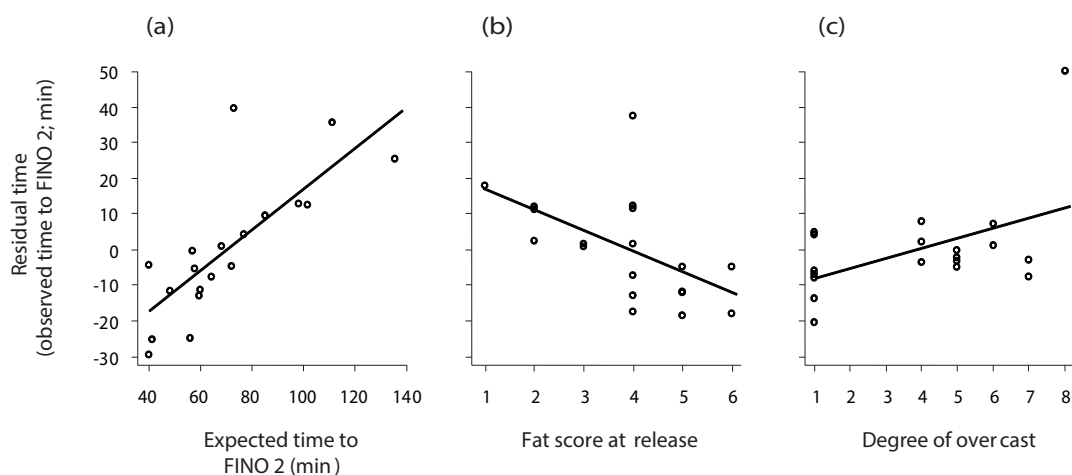


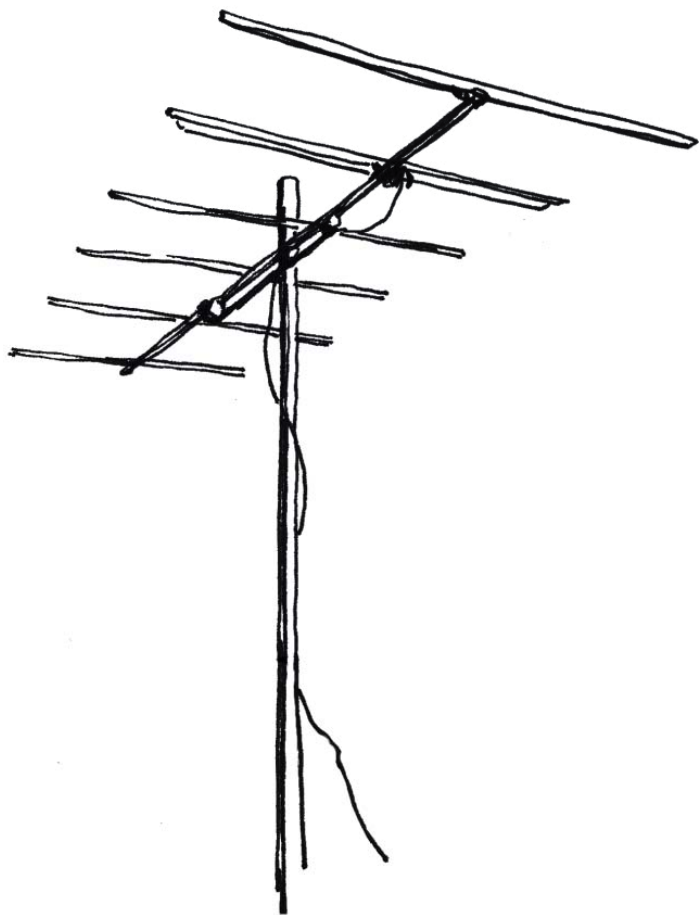
Figure 8. Observed flight time to FINO 2 was significantly correlated with (a) expected time to FINO 2 (as calculated from the surface wind situation at departure, assuming a straight flight path), (b) fat score at release and (c) degree of overcast at departure. The plots show residual times (min) after taking into account the effects of the complementary variables. See paper VI for further details.

Field and experimental studies have shown that fat birds are more prone than lean birds to depart in the migratory direction (Deutschlander & Muheim, 2009; Sandberg & Moore, 1996; Schmaljohann & Naef-Daenzer, 2011; Smolinsky et al., 2013), which potentially could affect the straightness of a flight. Heavier birds need to fly at slightly higher airspeeds compared to lean individuals, and the observed decrease in duration of the flight between Falsterbo and FINO 2 for birds with increasing fat score (fig. 8b) could partly be explained by aerodynamic theory (Pennycuick, 2008; Karlsson et al. 2012). However, we observed a reduction in flight duration relative to increased fat score that was too large to be explained by aerodynamics. Thus, additional behavioural differences between lean and fat individuals are required to explain the observed pattern. Lean individuals may be less risk-prone during departures over open sea, potentially leading to longer flight durations, if birds with larger fuel stores depart straight across the Baltic Sea.

An additional reason for higher flight speeds might be that birds need to fly at slightly higher air speeds at higher flight altitudes where the air density is lower (Pennycuick, 2008). Furthermore, birds have been observed to be selective for favourable winds once aloft (Bruderer, et al., 1995). Consequently, the reduction in duration could have been caused by fat birds flying at higher altitudes or/and in more favourable wind conditions.

End of flight

Methodological difficulties with tracking entire flights of passerine migrants are the explanation as to why almost no data exist on when and how birds cease their nocturnal flights. There are observations of nocturnal migrants not landing until the middle of the day, but those reports are often associated with landings at stopover sites after flights over open water or deserts where flight times might be extended to cross the barrier (Schmaljohann et al., 2007). It has been assumed that passerine migrants initiate nocturnal flights approx. 1-4 hrs after sunset (see above) and complete them in the middle of the night (Moore, 1987), unless they are crossing a barrier or encounter a front of bad weather. However, with the new insights that migrants initiate migratory flights throughout the entire night, there is reason to question this assumption, and there are indications that nocturnal flights often continue until morning twilight (Chernetsov 2012). The pattern of birds adjusting their departure time relative to night duration (paper II) and advancing departures when taking off on longer flights (paper VI, see above) indicates that birds prefer to land in a certain time window. Possibly, they prefer to land during dawn to be able to use visual cues to find suitable stopover habitats. New technology that facilitates tracking of entire flights even in small passerines will shed further light on how and when migrants terminate nocturnal flights.



Conclusions

Behavioural responses concerning how and when to depart from stopover sites will affect how successful the overall migration will be (e.g. Newton, 2006). The purpose of this work was to understand the effects of intrinsic (age and body condition) and environmental (weather) factors on the behaviour that guides birds as they depart from a migratory stopover. The work included investigations of the pattern of stopover duration at Falsterbo (paper I), the factors that determine how nocturnal migrants time their departures within the night (paper II), how birds calibrate their different compasses against each other in order to get consistent directions (paper III), the factors that make birds reverse their migration or perform detours around a barrier (paper IV & VI), how birds adjust their travelling directions after take-off (paper V), and the factors that affect the duration of migratory flights (paper VI).

These studies clearly illustrate the effects of intrinsic factors on the different behaviours. Birds with high fuel loads not only stayed for shorter durations in Falsterbo, they also departed earlier during the nights, indicating that they were prepared for longer flights compared to lean individuals. Furthermore, individuals with large fuel stores moved in the expected migratory direction to a larger extent than lean birds. Interestingly, fuel stores affected the flight duration during the first 50 km after departure from Falsterbo, with fat birds using less time for this flight step. To our knowledge, this was the first time fuel stores have been shown to affect flight duration in migratory passerines. All together, these results underline the increase in migratory urge that seems to characterize birds with high fuel stores; probably as a result of the increase in potential flight range. Several age-related differences have previously been observed regarding different stopover behaviours but contrary to earlier findings, we did not observe differences in stopover duration between inexperienced and experienced individuals at Falsterbo. However, we observed higher proportions of juveniles reversing their directions, perhaps as a result of juveniles hesitating more to cross the Baltic Sea, or because they had problems coping with the high rates of competition for food that are expected at coastal stopover sites such as Falsterbo.

As expected, we found large effects of prevailing weather conditions on the departure behaviours of birds leaving Falsterbo after a stopover. Rain and overcast weather decreased the probability of departures from Falsterbo, resulting in prolonged stopover durations. In addition, the proportion of flights in directions opposite to the expected migratory direction increased during nights with overcast weather. Increased cloudiness further caused an increase in flight duration between Falsterbo and the offshore receiver

station, possibly as a result of orientation issues or problems to keep a straight heading when visibility decreases. Wind direction and wind speed may considerably impair migratory flights (Pennycuick, 2008), and prevailing wind conditions are known to have great effects on bird migration. Hence, it is not surprising that birds were observed to prolong stopovers and not depart during days with strong winds. Furthermore, birds alter their timing of departure within the night and delay departures when there are strong or opposite winds during the sunset period. Additionally, more birds performed reverse movements during nights with winds opposite to the expected migratory direction. Lateral drift caused by winds, once the birds are in the air, further affects route choice and the ground speed is to a large extent determined by assistance or hindrance by tail or head winds.

The results indicate that the timing of nocturnal flights is determined by ecological factors, related to e.g. night duration and migratory seasons. The birds that departed on flights across the Baltic Sea, and passed the offshore receiver at FINO 2, departed more concentrated in time just after sunset, indicating earlier departures for longer flights. This result is in line with the finding that birds with larger fuel stores depart earlier than birds with lean fuel stores (see above). Surprisingly, the vanishing bearings from Falsterbo did not affect the probability of a flight passing FINO 2. However, this is explained by the finding that birds adjust their traveling directions also after take-off.

We also found that garden warblers did not change their departure directions after exposure to a cue-conflict between celestial and magnetic cues during sunset. From our experiments it is not possible to say whether these birds instead relied on the unchanged star compass to determine their migratory direction after release, or whether the garden warblers used magnetic cues as the primary reference cue and not the celestial cues as has been suggested earlier (Muheim, et al., 2006a).

Our results further support previous findings of higher overall speed during spring migration (Nilsson et al., 2013) and behavioral differences between species related to differences in migratory strategy (migratory distance; e.g. Ellegren, 1993; Nilsson et al., 2014).

In the future, longer tracks of departing small passerines, with better resolution, will hopefully shed further light on the behaviours that guide birds along their migratory route. Individual timing between different sites and seasons will give more information on how the birds make their way towards the breeding or wintering grounds thousands of kilometers away. Furthermore, information on how birds choose when and where to terminate flights is important, not only to fully understand the migratory performance of birds, but also to understand which stopover sites are important from a conservation perspective.

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