

Flight Behaviour of Passerines on Nocturnal Migration

Cecilia Nilsson



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DOCTORAL DISSERTATION

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To be publicly defended in the Blue Hall, Ecology Building, Sölvegatan 37, Lund,
Sweden on Friday the 13th of February, 09:30, for the degree of Doctor of
Philosophy, Department of Biology.

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Organization LUND UNIVERSITY Department of Biology, Evolutionary Ecology Sölvegatan 37 SE-223 62 Lund, Sweden Author (s) Cecilia Nilsson	Document name DOCTORAL DISSERTATION	
	Date of issue 7/1 2015	
	Sponsoring organization	
Title and subtitle Flight Behaviour of Passerines on Nocturnal Migration		
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Key words: Bird migration, Passerines, Flight Behaviour, Tracking radar, Optimal migration, Flight speed, Airspeed, Wind drift, Nocturnal migration, Coastline effects, Flight directions, Reverse migration		
Classification system and/or index terms (if any)		
Supplementary bibliographical information		Language English
ISSN and key title		ISBN Print: 978-91-7623-29-3 Pdf: 978-91-7623-230-9
Recipient's notes	Number of pages 188	Price
	Security classification	

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Front cover: Operator panel and signal display of stationary radar station in Lund.
Photo: Aron Hejdström

Faculty of Science, Department of Biology

ISBN (Print) 978-91-7623-229-3

ISBN (Pdf) 978-91-7623-230-9

Printed in Sweden by Media-Tryck, Lund University
Lund 2015



KLIMATKOMPENSERAT
PAPPER



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List of Papers

- I. Karlsson H, Nilsson C, Bäckman J & Alerstam T (2012) Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. *Animal Behaviour*, 83: 87–93.
- II. Nilsson C, Bäckman J & Alerstam T (2014) Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants. *Behavioral Ecology and Sociobiology*, 68:1779-1807.
- III. Nilsson C, Klaassen RHG & Alerstam T (2013) Differences in speed and duration of bird migration between spring and autumn. *The American Naturalist*, 181: 837–45.
- IV. Nilsson C, Bäckman J, Karlsson H & Alerstam T. Timing of nocturnal passerine migration in Arctic light conditions. (Submitted).
- V. Nilsson C, Bäckman J & Alerstam T (2014) Are flight paths of nocturnal songbird migrants influenced by local coastlines at a peninsula? *Current Zoology*, 60(5): 660-669.
- VI. Sjöberg S & Nilsson C. Nocturnal migratory songbirds adjust their travelling direction aloft: evidence from a radio telemetry and radar study. (Submitted).
- VII. Nilsson C & Sjöberg S. Causes and characteristics of reverse bird migration: an analysis based on radar, radio tracking and ringing at Falsterbo, Sweden. (Manuscript).
- VIII. Karlsson H, Nilsson C, Bäckman J & Alerstam T (2011) Nocturnal passerine migration without tailwind assistance. *Ibis*, 153: 485–493.
- IX. Alerstam T, Chapman JW, Bäckman J, Smith AD, Karlsson H, Nilsson C, Reynolds R, Klaassen RHG & Hill JK (2011) Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. *Proceedings of the Royal Society B*, 278: 3074–80.
- X. Chapman JW, Nilsson C, Lim KS, Bäckman J, Reynolds DR & Alerstam T. Adaptive strategies in nocturnally migrating insects and songbirds: contrasting responses to wind. (Manuscript).

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Author Contributions

- I. TA, HK and JB planned the study, HK, TA, JB and CN collected the data and HK analyzed the data. HK and TA wrote the first draft of the paper, CN made substantial revisions on which all authors gave input. CN completed the revision and is corresponding author.
- II. TA, JB and CN planned the study, CN collected the data with support from JB and TA, CN did the analysis and wrote the paper with input from the other authors.
- III. CN and TA initiated the study, CN compiled and analyzed the data, CN and TA wrote the paper and RK contributed with much input to data and manuscript.
- IV. TA, HK, JB and CN planned the study and collected the data, CN did the analysis and wrote the paper with input from all authors.
- V. TA, JB and CN planned the study. CN collected the data with support from JB, CN did the analysis and wrote the paper with input from the other authors.
- VI. CN and SS initiated the study, CN and SS collected the data, SS did the analysis and wrote the paper with input from CN.
- VII. CN and SS initiated the study, CN and SS collected the data, CN and SS did the analysis and CN wrote the paper with input from SS.
- VIII. TA, HK and JB planned the study, HK, TA, JB and CN collected the data, HK analyzed the data and wrote the first draft of the paper, CN made substantial revisions with input from all authors. CN completed the revision and is corresponding author.
- IX. TA, JWC, RK and DRR initiated the study, TA and JWC wrote the paper with input from all authors, CN and TA analyzed the bird data, JWC analyzed the moth data, and all authors contributed significantly to discussions.
- X. JWC, CN, DRR and TA initiated the study, CN analyzed the bird data, JWC and KSL the moth data. JWC, CN and TA wrote the paper with input from all authors. All authors contributed significantly to discussions.

Abstract

Many passerines migrate during the night and at high altitudes, making their migration difficult to observe. By using tracking radars we have been able to make exact observations of the flight behaviour of passerines on nocturnal migration, which has enabled us to test several hypotheses about adaptive values and constraints regarding migratory behaviour in different ecological contexts. We have investigated the birds' flight speeds and we were able to see that birds consistently fly faster in spring than in autumn. This could be due to optimality reasons, as there might be a higher selection pressure to arrive early at the breeding grounds in spring than at wintering grounds in autumn. We have also investigated the timing of nocturnal migration by exploring how it is affected by midnight sun conditions in the Arctic, and can show that the pattern of nocturnal migration persists even in those conditions. At a site in southernmost Sweden, Falsterbo peninsula, we tested the hypothesis that coastlines affect the flight direction of migrants, and saw no evidence of small scale coastline effects. In Falsterbo we also had the unique opportunity to combine our radar data with data from a radio telemetry system on the peninsula and the longstanding ringing regime in the area. By combining methods we could see that the departure directions and directions during climbing flight differed from the directions of birds in level flight. This suggests that migrating birds adjust their orientation once aloft. We also used our combined methods to investigate what separates birds flying in reverse directions from birds continuing forward on migration. Bird flying in reverse directions flew slower, at lower altitudes and later in the night. They were also leaner and younger than birds continuing forward. All animals that fly must deal with winds, which can have a very large positive or negative effect on the flight conditions. In two comparative studies we show that nocturnally migrating moths and passerines achieve similar ground speeds and flight directions by using contrasting responses to winds.



The stationary radar station at Lund University, Lund, Sweden. Photo: Aron Hejdström



Chiff-chaff (*Phylloscopus collybita*) taking flight. Photo: Thomas Alerstam

Introduction

For millions of animals, fantastic journeys around the globe are a mere fact of everyday life. To be able to take advantage of variation in seasonal resources, these migratory animals spend large parts of their lives on the move. In many cases migration might not require any extreme adaptations, but rather fine tuning of abilities that are already present in most animals. Homing to natal sites to breed, the low cost of movement in relation to basal metabolic rate in cold weather, orientation within home ranges are all examples of adaptive behaviours that occur in both residents and migrants, and that make up a foundation for long distance migration to arise from (Cresswell et al. 2011). This has also made it possible for migration to evolve and disappear again with apparent ease in different groups of animals (Alerstam et al. 2003).

The cost of transportation puts limits on when, and for whom, migration is beneficial. Flight, being a comparatively cheap way of transportation (Schmidt-Nielsen 1972), makes birds well represented among migrants. Millions of individual birds belonging to hundreds of species move across the globe every year, including many passerines (also known as songbirds). With time, evolution has fine-tuned their behaviour in many ways, leading to a surprising degree of accuracy and modulation of behaviour in different circumstances (Alerstam 1990; Newton 2008).

Rapid technological advances have greatly increased the amount of tracking data from all over the world. Every day new data is gathered that increases our ability to critically test longstanding hypotheses and predictions regarding migratory behaviour. In this thesis I aim to test hypotheses concerning flight behaviour of passerines on nocturnal migration, ranging from optimal migration speed predictions to flight direction choices in different circumstances.

Methods

Passerine migratory flight is difficult to observe. Most passerines migrate at high altitudes (from 100 to 3000 m above ground level) and during the night, so massive movements of millions of birds often go completely unnoticed. By using radar technology we have a unique opportunity to observe the behaviour of these birds, very precisely, during flight and without having to handle the birds. The tracking radar emits a signal that is reflected by objects and then registers the signal reflected back, giving exact information on the distance, position and speed of the object. The position of the bird can be

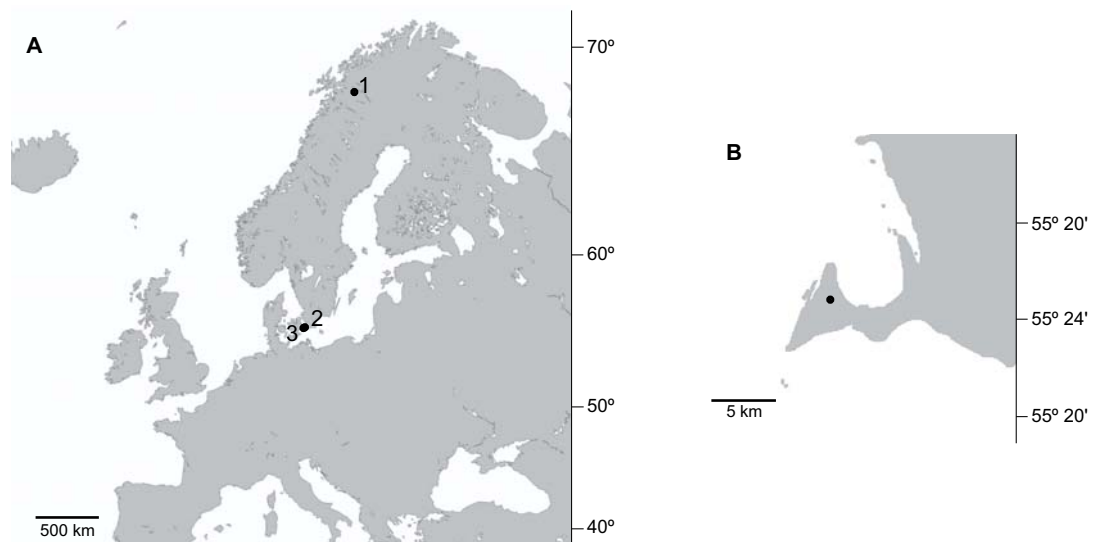


Figure 1. A) Map (mercator projection) of northern Europe with our three study sites indicated, 1. Abisko, 2. Lund and 3. Falsterbo. B) Study site Falsterbo peninsula with radar position indicated. Maps from Maptool (Seaturtle.org, 2002).

determined to an accuracy of 0.06 degrees in elevation and azimuth, and 10 meters in range and a new position is obtained every second (Bäckman & Alerstam 2003). A small bird can be tracked by the radar up to approximately 10 km away. The strength of the reflected signal depends on a number of different factors, including the area of the object that reflects the signal. When a bird beats its wings, the echoing area of its body changes and this makes the reflected signal vary in strength with the wing beat pattern. When tracking birds with radar during the night you cannot see the birds, which of course means that identifying the species of the bird being tracked is very difficult. But by using the changes in the returning signal strength, the wing beat pattern, we get clues as to which species are involved. Different flight modes, such as bounding flight, are also distinguishable by variations in the radar echo signal. Only passerines use bounding flight, and therefore we have focused on nocturnally migrating birds confirmed to show a bounding flight pattern in our analysis. Our sample will likely reflect the most common night migrating passerines in the respective areas, mainly warblers and thrushes.

I have used two different tracking radar stations, one stationary at the Ecology building at Lund University and one mobile station that has been at different sites (Figure 1). The analyses in this thesis are based on data from three different sites in Sweden: Lund (stationary station), Abisko and Falsterbo (mobile station, Figure 2). Abisko is situated in the very most northerly part of Sweden, approximately 200 km north of the Arctic Circle, Figure 1. This makes it a special site for several reasons. As the amount of land north of Abisko is limited, we can be quite sure that we here are tracking birds at the start of their journey in autumn and the end of their journey in

spring. Another special thing with Arctic sites is that the sun does not set during the summer, including periods that partially overlap with the migration season. Based on ringing and census data from the area it is likely that a large part of our material from Abisko consists of species like willow warbler (*Phylloscopus trochilus*), pied flycatcher (*Ficedula hypoleuca*), brambling (*Fringilla montifringilla*), redstart (*Phoenicurus phoenicurus*), meadow pipit (*Anthus pratensis*) and wheatear (*Oenanthe oenanthe*) (Strann & Bakken, 2004, see also Karlsson et al 2010).

Approximately 1 450 km south of Abisko we find our second and third sites, Lund and Falsterbo peninsula (Figure 1). Lund is a town 10 km from the coast, mostly surrounded by agricultural fields. Falsterbo is at the south-west tip of Sweden and is a well known place for birdwatchers, mainly for viewing intense diurnal bird migration in autumn. Birds on migration gather towards the peninsula, presumably to avoid flying over open water. Falsterbo is a hot spot not only for migration but also for science, with hundreds of scientific



Figure 2. The mobile radar station and operator on site in Falsterbo, south Sweden. Photo: Johan Bäckman

studies published, many in connection to the longstanding ringing program at Falsterbo bird observatory (Karlsson 2009). Based on the ringing information, species like European robins (*Erithacus rubecula*), goldcrests, (*Regulus regulus*), chiff-chaffs (*Phylloscopus collybita*), willow warblers (*Phylloscopus trochilus*), redstarts (*Phoenicurus phoenicurus*) and song thrushes (*Turdus philomelos*) are likely to be numerous among the nocturnal migrants passing the peninsula. A radio telemetry system has recently been installed at the peninsula, giving us the possibility of making interesting comparisons between movements of tagged birds, were we know much more about the state of the individuals, and the radar observations.

The radar stations are X-band stations that have been customized to track bird targets. They have 200 kW peak power, 0.25 μ s pulse duration, 504 Hz pulse repetition frequency and 1.5° pencil beam width. Data has been collected between 2007 and 2012, (Abisko 2007-2008, Lund 2004-2008, Falsterbo 2009-2012).

The wind situation is of great importance for the birds, to a large degree influencing the amount of energy needed to cover a certain ground distance as well as potentially causing displacements. It is therefore crucial to have an exact knowledge of the wind situation each bird encounters. To make this possible we track weather balloons with the radar, so that for many of the tracks we have very precise information of the wind situation at the flight altitude of the bird (within 150 m) and close in time (within 2 h) to when the bird flew.

Flight speed

Birds on migration are expected to behave optimally, but what constitutes optimal behaviour will differ according to what currency the birds are constrained by. This has a direct bearing on the choice of flight speed by birds. The relationship describing the power required to fly in relation to airspeed together with the fuelling rate at stopovers predicts that the bird should use slightly different speeds depending on what currency they want to optimize. The fastest airspeed would be expected if the birds want to minimize the time on migration (V_{mt}), a slightly lower speed is predicted if they want to minimize the energy used for migration and an even slower airspeed (V_{mr}) is predicted if they want to maximize the distance flown on a certain amount of fuel, see Alerstam & Lindström 1990; Hedenström & Alerstam 1997. These characteristic speeds differ only slightly from each other, and are not to be confused with the maximum or minimum

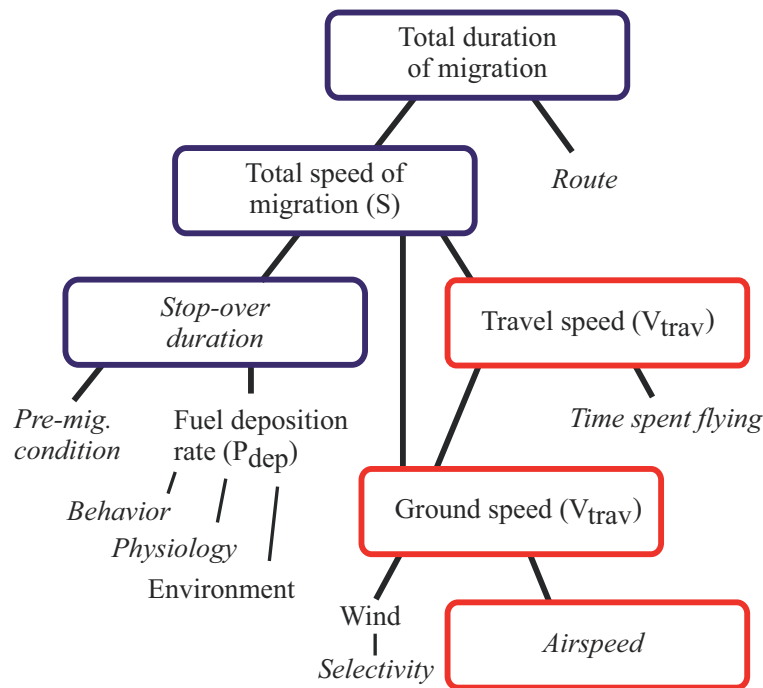


Figure 3. Schematic overview of factors that determine total speed and duration of migration. The total duration of migration depends on the overall speed of migration and the route taken. The total speed of migration depends on the duration of stopovers and the daily travel speed. Stopover duration depends on premigratory condition and the fuel deposition rate, P_{dep} , which, in turn, depends on foraging rate and -efficiency (food abundance, competition, duration of daylight, behavioral and physiological factors). The travel speed is determined by the daily travel time and the ground speed during travelling. Ground speed is in turn the result of the birds' own flight speed in relation to the surrounding air (airspeed) and wind conditions. Selection to increase total migration speed (or reduce duration) may operate on behavioral and other traits shown in italics. Variables related to flight behavior are indicated in red and variables dependent also on foraging behavior are indicated in blue. Adapted from paper III, Nilsson et al. 2013.

flight speeds, which are both very costly to maintain and therefore not appropriate for long distance movements.

The flight speed of a bird can be described in two different ways. As the self-propelled speed of the bird in relation to the surrounding air – the airspeed, or as the speed at which the bird moves over the ground, which is a result of the airspeed and the effect of the wind on the bird, known as ground speed. The total duration of the migration journey is determined not only by the flight speed (air and groundspeed) but also by the time spent flying each day, the time spent on stopovers and the route taken (Figure 3). Many of these factors can be affected by the bird through its behaviour, but some factors depend on the environment (e.g. winds, food availability).

In **paper I** we investigate the flight speed during migration in different circumstances and describe how airspeeds are consistently higher in spring than in autumn at our sites in Abisko and Lund. The difference in airspeed is similar to what theory predicts to be the difference between time minimizing

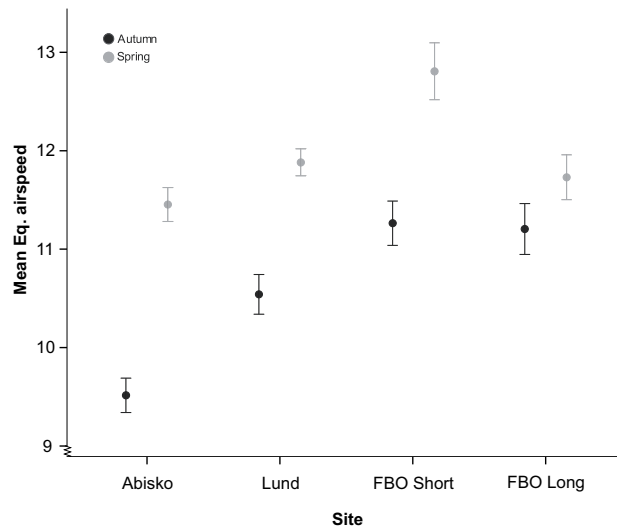


Figure 4. Mean equivalent airspeed with 95 % confidence intervals of nocturnal passerine migrants in Abisko and Lund and Falsterbo during autumn (dark grey) and spring (light grey). Falsterbo (FBO) data is divided into short (short) or long distance (long) migrants based on time of passage at Falsterbo. Adapted from paper II, Nilsson et al. 2014b.

(higher airspeeds) and energy minimizing (lower airspeeds) migration. This could be explained by birds being more time restricted in spring than in autumn, given that it is beneficial to be among the first to arrive at the breeding site. The first to arrive in spring will benefit in the competition for breeding territories (Kokko 1999), while there might not be the same benefit of speeding up in autumn. There could however be other reasons that we observe a higher mean airspeed in spring, such as a higher proportion of more slow flying juveniles in autumn.

We investigated this difference in airspeed further, and in **paper II** we compare airspeeds during spring and autumn at our third site, Falsterbo. Not only is spring airspeed faster than autumn airspeeds here as well, but there also seems to be a difference in the degree of seasonal modulation of airspeed between long distance and short-distance migrants (Figure 4). Short distance migrants show a larger difference in airspeed between spring and autumn, which might be due to them being more flexible in their annual schedules and more prone to migrate slowly in autumn. This is also supported by short distance migrants being more likely to wait for good wind situations during autumn migration, which decreases the amount of energy needed for migration, but might be costly in terms of waiting time (Alerstam 1979).

After seeing this pattern of faster spring than autumn migration at all our sites and over several years of data, we decided to test whether this was a general pattern. We also wanted to see if there was evidence of differences between seasons on other levels of migration speed (Figure 3), not only flight speed. In **paper III** we make an overview of published studies in which data from both spring and autumn are available and compare for how many of

them spring performance is faster than autumn performance. We did this on all levels from airspeed, ground speed, travel speed (distance per day) stopover duration, total migration speed (distance/total migration duration) and total migration duration. We looked at papers concerning any species and at all locations, and found a dominant pattern in which migration towards breeding grounds (spring) is faster than migration away from breeding grounds (autumn). There could of course be many reasons for this, ranging from static weather conditions giving more tailwind conditions in spring (Kemp et al. 2010) to an asymmetrical selection pressure, favouring faster speeds in spring (see above).

Nocturnal timing

This thesis is concerned with nocturnal migrants, migrants that migrate from sunset until early morning hours. There are several theories as to why they do this, from being able to free up time for foraging during the day and predation avoidance to calmer and more laminar wind situations during night (Kerlinger & Moore 1989; Lank 1989; Alerstam 2009). However, birds migrating in the high arctic are faced with a very special situation. During large parts of the spring migratory season the sun does not set below the horizon and there is no real "night". Abisko is such a site, and we investigated if a pattern where migration intensity is increasing in the evenings and decreasing in the early morning would persist also under midnight sun conditions. A tracking radar is a blunt tool to measure migration intensity, but we were still able to get a broad picture of the migration pattern in Abisko. In **paper IV** we show that the pattern of migration intensity during the night hours, with a peak around midnight, seems to persist also under midnight sun conditions, indicating that the incentive to fly during the night hours remains also under midnight sun conditions. As insect catches in the area have been shown to remain higher during the day than during the night, also under midnight sun conditions (Speakman et al. 2000), this lends support to the theory that birds migrate during the night to be able to forage during the day.

Flight directions

The track direction is the direction of the bird's movement over ground, which is a result of the way which the bird is facing (heading) and the effect of the wind (Figure 5). The heading a bird chooses is of course primarily based

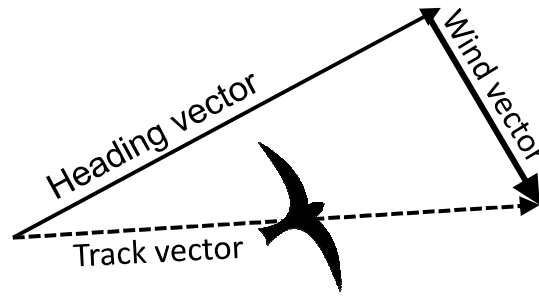


Figure 5. Triangle of velocities. The heading vector consists of the airspeed and the heading direction (body axis of bird). Track vector is the ground speed and the direction in which the bird is moving. Wind vector shows the wind speed and wind direction.

on the direction to the goal area. Birds can however make adjustments to their direction in response to the local environment, to the wind situation or to the topography. It has for example been suggested that coastlines could act as leading lines during migration, as an orientation aid or as a fixed reference point to help the birds to assess if, and to what degree, they are being displaced by wind. The coastlines of Falsterbo peninsula have been the subject of such studies, but the studies have shown conflicting results. Visual observations suggested that birds on different parts of the peninsula showed different mean directions, corresponding to the coastlines (Åkesson 1993). This was however not seen in a study using infrared detection at the same site (Zehnder et al. 2001). We decided to test the hypothesis that coast lines affect flight directions by dividing our data into three different sectors, each covering an area with differently directed coastlines. If coastlines affected the flight directions, the directions in the different areas should differ, **paper V**. The mean directions in the three areas did not differ much, and the differences did not match the directions of the coastlines (Figure 6). From this we draw the conclusion that coastlines, on the small scale of the peninsula, does not affect the flight directions of free flying nocturnal migrants, at least not the vast majority of migrants that fly above 100 m altitude. There might however of course still be an effect of coastlines on a much larger scale, funnelling the birds towards the peninsula along the Swedish west and south coasts.

When does a bird establish the direction in which it will fly? Radio telemetry data from Falsterbo show the interesting result that birds that only a few hours later pass an offshore station far south-east of Falsterbo, left the peninsula in a wide range of directions. In **paper VI** we compare the spread in directions of birds seen on the radar on migration in level flight, with birds leaving the peninsula (radio telemetry) and birds in climbing flight (radar). The spread in directions is much larger for birds departing from the peninsula

and birds in climbing flight, when compared to birds in level flight. This indicates that the final fine-tuning of direction might be made once the bird reaches its flight altitude, and that departure and climbing flights might be more affected by other factors such as winds.

Birds on migration of course generally fly in the direction that would be expected for the season, south in autumn and north in spring. It is however common to observe birds doing the exact opposite, flying north in autumn and south in spring. This is sometimes known as reverse migration, and can be due to several different reasons (e.g. Alerstam 1978; Richardson 1982; Zehnder et al. 2002). In **paper VII** we take advantage of the unique opportunity that Falsterbo peninsula offers to combine several different methods to analyze these reverse movements and migrants. The radar data gives us information on the flights of birds moving in the reversed direction, and from radio telemetry and ringing we gained information on the internal state of individuals making reverse movements. We conclude that reverse migrants fly slower than forward migrants, at lower altitudes and that reverse

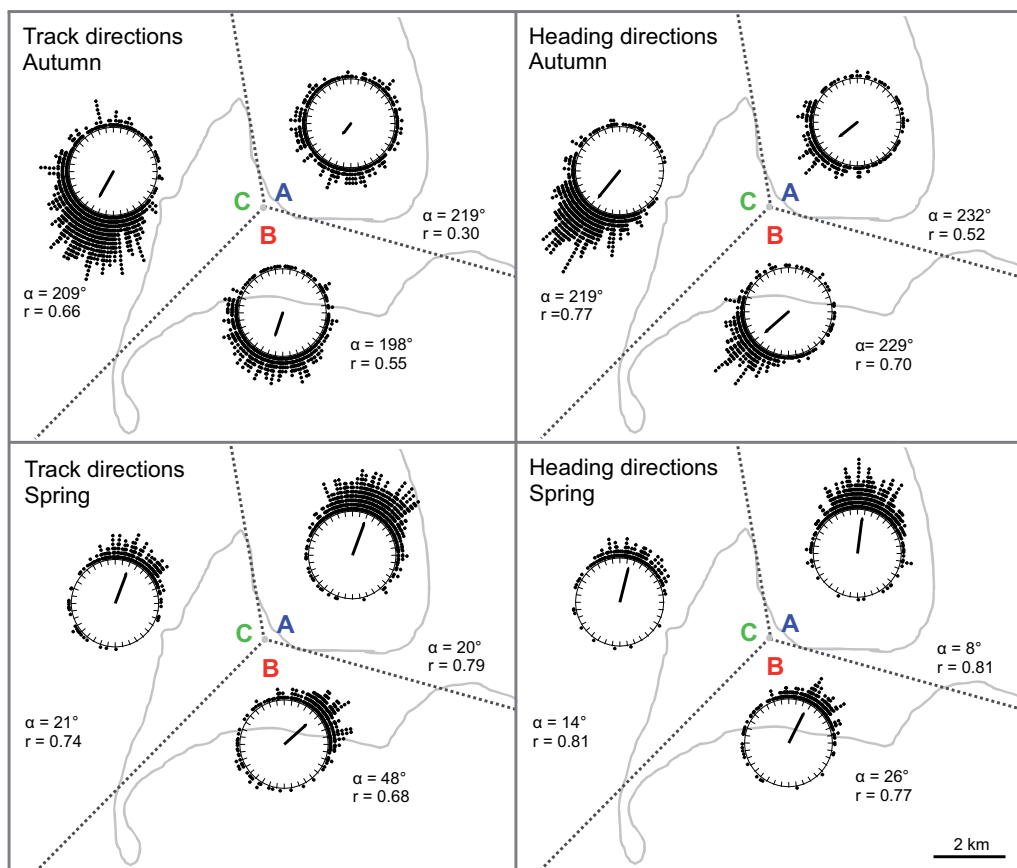


Figure 6. Mean track and heading directions in the three different areas of Falsterbo peninsula plotted on top of a map of the peninsula. The areas are defined as sectors around the radar, area A is 350°-105°, area B 105°-225° and area C 225°-350°. Within each area the mean direction (α) and r is given. Adapted from paper V, Nilsson et al. 2014a.

flights are more common later in the night. Young birds are more likely to engage in reverse migration than older birds, and reverse migrants are also more likely to be lean. We also investigated a number of weather variables, but only the amount of cloud cover and unfavourable wind directions had an effect on the amount of reverse migration. This supports the view that reverse migration is an active response by birds when they are faced with unfavourable conditions and low fuel reserves.

Effects of wind on bird and insects

As humans we tend to think in terms of running or walking when considering movement and transportation, but when considering a animal flying in the air this can be very misleading. It is more accurate to think of flight as swimming in a river or in the currents of an ocean, since the air that animals fly through is almost constantly moving in relation to the surface of the earth. Wind speeds in the same range or larger than the airspeeds animals are able to achieve are not uncommon, and even on apparently not very windy days the wind speed will often have a substantial effect on the flight speed in relation to the ground and on the resulting track direction. Once aloft, animals can deal with flow displacement by adjusting either (or both) their heading direction and their airspeed to mitigate the effect of the wind vector on the resulting track vector (Figure 5). The movement of the air offers not only problems in terms of headwinds and displacements, but also of course great possibilities to increase the groundspeed by choosing to fly at times with tailwind conditions and thereby increase the distance covered and reduce the energy expenditure for covering a certain distance. Therefore it has often been assumed that nocturnally migrating passerines should take advantage of the wind to a large degree to be able to achieve their long journeys. However, in **paper VIII**, we show that passerines regularly migrate under all wind conditions, both head and tailwinds. Passerines will of course take advantage of days with assisting tailwinds, but we regularly observe them flying also on days with unfavourable headwinds. Somewhat counter-intuitively, this is probably due to a need for a fast total migration speed. Waiting for tailwinds to occur could take a lot of time and be costly, and might be almost impossible in some regions (Alerstam, 1979, 1990, Wikelski et al. 2003).

Birds are not the only group of animals to be faced with the challenge of coping with winds, balancing wind assistance and potential displacement. Radar is a powerful technology to observe not only nocturnally migrating passerines, but also the large quantities of insects that migrate during the

night (Drake & Reynolds 2012). The Silver Y moth (*Autographa gamma*) is a noctuid moth that migrates between northerly breeding areas and southerly wintering areas, with a migration that is in many ways similar that of passerines, see for example Chapman et al. 2012. There are of course also many differences, such as the moth migration cycle spanning over several generations. By making a broad comparison of the migration of Silver Y moths and passerines, we could see that the migration performance and flight behaviour of birds and moths of course differed in many ways, but that there were also remarkable similarities. Silver Y moths are slow flyers with airspeeds of around 4 m/s, while passerines generally reach airspeeds of 10-13 m/s. Despite this, Silver Y moths and passerines migrated with surprisingly similar ground speeds, **paper IX**. They also achieved similar distributions of tracks and headings in the different seasons. This similarity in migration flight performance, despite very different fundamental characteristics of moths and passerines, seemed mainly to be due to differences in the way they handled different wind situations. The moths adapted a more risk prone strategy of relying to a large degree on tailwinds, while birds adapted a more risk adverse strategy that gave them little wind assistance but a high degree of control.

In **paper X** we analyze more closely how passerines and Silver Y moths deal with winds. By comparing nightly mean directions in different wind situations we investigate to what degree birds and moths drift with the wind or compensate for wind displacement. We found that birds partially compensated for wind, but had a high degree of drift in autumn. The moths were drifted to a higher degree than birds in both seasons, and also showed more drift in autumn than in spring.

Conclusions

In conclusion, by gathering a large data set with observations of thousands of individual free flying passerine migrants, we have been able to investigate several aspects of their flight behaviour. With the benefit of large data sets, from several sites spanning years and different seasons, we have been able to distinguish small scale variations in behaviour. This has enabled us test several different hypotheses regarding migration flights, from optimal migration predictions of flight speed, responses to topography, the timing of nocturnal flights and differences in wind responses. These examples of fine tuned modulations of flight behaviour offers insight into what factors shape the migration of passerines in an evolutionary perspective.

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