MIGRATORY ROUTES AND STOPOVER BEHAVIOUR IN AVIAN MIGRATION

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Migratory routes and stopover behaviour in avian migration

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List of Papers


IV. **Stach R., Fransson T., Jakobsson S., Kullberg C.** No compensatory fuelling due to late autumn migration in the garden warbler Sylvia borin. *Manuscript*

V. **Fransson T., Barboutis C., Kullberg C., Stach R.** Extensive fuelling in great reed warblers following the trans-Sahara crossing in spring. *Submitted manuscript*

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Bird migration has always fascinated humans. There is something enigmatic about how migratory birds return each year to the North in spring, bringing bird songs into our lives, and then disappear before winter arrives. Migratory birds, some small and light weight as matchboxes, defies wind and weather, crosses deserts and oceans, in inter-continental migration in order to take advantage of long summer days and abundance of food at northern latitudes to breed and raise their young, and then return to southerly latitudes to wait for next spring to come.

The routes taken on migration are for many species obscure or unknown, whole or in part, and this is especially true for species that migrates nocturnally which includes the majority of passerine species. Information about migration routes and winter distributions have traditionally been collected from recoveries of ringed individuals and observation of species at various locations on the Globe in different seasons of the year (Fransson & Pettersson 2001). This has given us a rather incomplete picture about the spatio-temporal organization of migration and of the non-breeding part of the year. It is only recently that researchers have been able to track birds on a continental scale to reveal migration routes, stopover sites and wintering areas of individual birds of various species (Bairlein 2003). Through the development of miniature tracking devices, a.k.a. light level geolocators, we have now reached a breaking point in time when also small passerine species can be tracked throughout the year. This will improve our knowledge about the annual cycle in these small birds, and can also be used to direct management efforts to relevant regions for declining species (Bridge et al. 2013).

Bird migration takes place on a wide spatial scale; some species need only travel across a few degrees of latitude to find suitable areas to spend the non-breeding period while other species travel across, and between, continents, and in doing so covers thousands of kilometres each autumn and spring (Newton 2008). In the Palaearctic – African migration system
long distance migrants that spend the winters in tropical Africa need to cross the Sahara desert twice each year. This vast desert, which covers 9.4 million square kilometres, is a major ecological barrier with few feeding possibilities and has been suggested to be one of the main causes of mortality in migratory birds (Strandberg et al. 2010, Klaassen et al. 2014).

An estimated 40% of the species breeding in the Western Palaearctic migrates to winter quarters outside Palaearctic, and the majority migrates to Africa. Only a handful of species move between breeding sites in Western Europe and Scandinavia to wintering grounds in South Asia (Moreau 1952) and little is known about the migration routes used by these species.

Migratory flight can occur diurnally or nocturnally. Larger species, but also smaller passerines that migrates in flocks, tend to migrate during the day. The majority of passerines, however, migrate alone during night.

An important aspect of migration is that migratory flight is energetically costly, and this energy has to be acquired somewhere. Where, and how often, flight energy is accumulated is a fundamental part of a species migration strategy. Presumably all birds acquire some energy in preparation for migration, but a few wader species have been shown to rely entirely on fuel accumulated before departure for inter-continental flights between breeding grounds and wintering grounds (Gill et al. 2009, Klaassen et al. 2011). Most species, however, need to refuel along the route. Species that forage in flight, such as swifts and swallows, may adopt a flight and forage strategy and thus combining migration movements with foraging activity (Strandberg & Alerstam 2007, Åkesson et al. 2012), but for the majority of species flight energy is accumulated over a number of days at stopover sites. Birds use mainly subcutaneous fat as energy to fuel the flight, but protein from breast and leg muscles and internal organs may also be used, especially during periods of sustained flight when birds rely on stored fuel to last them across extensive ecological barriers (e.g. Schwilch et al. 2002).

The length of time a bird needs to stay at a particular stopover site depends on both internal and external factors. Internal factors that have been found to affect stopover duration are the birds’ physical condition at arrival at the stopover, the fuel load at departure, age, experience and dominance status (Ellegren 1991, Carpenter et al. 1993, Arizaga et al. 2008, Fusani et al. 2009, Arizaga et al. 2011, Cohen et al. 2014). External factors can either affect fuel deposition rate directly, e.g. food availability

How much energy that is stored at stopovers depends on the achieved fuel deposition rate and the migration strategy adopted by the bird. Birds are expected to prioritise between time, energy and safety aspects of migration, and the outcome will shape the birds fuelling strategies at stopovers (Alerstam & Lindström 1990). A time minimising strategy is sensitive to the achieved fuel deposition rate in that birds will accumulate larger fuel loads at stopover sites where fuel deposition rate is high and less at lower quality sites. A strategy minimising the energy used during flight on the other hand is insensitive to fuel deposition rate and birds will depart with fuel loads that maximises the possible distance that can be achieved per unit fuel mass (Alerstam & Lindström 1990). However, minimising the total amount of energy spent on migration, which also includes the energy spent on stopovers, is sensitive to fuel accumulation rate but the achieved departure fuel loads will be lower than for time minimisers (Hedenström & Alerstam 1997). A high perceived predation risk at stopovers is likely to lower the rate of fuel accumulation as birds increase vigilance and minimises the time spent exposed during feeding compared to a stopover site with a lower perceived predation risk (Lima 1985, Lindström 1990). Furthermore, since heavy fuel loads are associated with reduced flight manoeuvrability and lower escape performance birds are likely to strategically reduce the amount of fuel accumulated at a stopover with perceived high predation risk (Fransson & Weber 1997, Kullberg et al. 2000).

The way birds organise stopovers has a larger impact on the bird’s overall migration speed than alteration of the flight speed (Alerstam 2003, Nilsson et al. 2013) and thus, research on stopover behaviour and birds responses to local environmental factors at stopovers are important to fully comprehend the underlying strategy adopted by birds on migration.
Aim of thesis

This thesis focuses on two aspects of bird migration in long distance migratory passerines that differ from each other in their spatial and temporal distribution: migration routes and stopover behaviour.

By analysing routes taken by two long-distance migrants, one heading for tropical Africa and another heading for Asia, I have been able to describe how time is devoted between different staging areas used during the non-breeding season, and discuss possible reasons for the pattern observed.

The second main aim of the thesis concerns the organisation of stopovers. By studying stopover behaviour at different stages of migration (in two long-distance migrants): at northern latitudes well in advance of any barrier crossing and just after crossing of a barrier my aim has been to reveal how birds adopt their fuelling behaviour to different circumstances encountered. Another question that has been studied is how the progress of the season affects fuelling decisions in a long-distance migrant.

Paper I investigates the migration routes and wintering areas of the thrush nightingale (*Luscinia luscinia*). The species migrates to southeast Africa but the spatio-temporal distribution of the species on the African continent was previously not well known and paper I focuses on the wintering strategy of the species.

Paper II describes the unknown migration routes and wintering areas of the western population of the common rosefinch (*Carpodacus erythrinus*). Although the species is known to winter in Asia, from Pakistan to southeast China, the routes taken, and the temporal organisation of migration, has previously not been thoroughly studied.

Paper III focuses on the spatial distribution and fuelling behaviour of garden warblers (*Sylvia borin*) at a stopover site in a coastal area in southeast Sweden. We expected birds with small fuel loads to redistribute inland from the coastal capture site to find suitable feeding
conditions, and to put on moderate fuel loads before continuing migration since the birds did not face a major environmental barrier.

In paper IV we continue to explore the fuelling behaviour of garden warblers but this time in relation to the progress of the season. We test the hypothesis that birds migrating late in the migration season refuel at a higher rate, and deposit larger fuel loads, than birds migrating early in the season in order to increase migration speed.

Paper V investigates the fuelling behaviour of great reed warblers (*Acrocephalus arundinaceus*) after crossing the Sahara desert in spring. We expected that birds, after the strenuous crossing, should arrive very lean and that they should continue migration as soon as they had obtained enough fuel stores for one continued flight stage to the north.
Methods

Species

The thrush nightingale (fig. 1 top right) is a medium sized passerine with a wide breeding distribution, including south Scandinavia, northeast Europe and further east to about 90 degrees longitude. The male song is strong and unmistakable but the birds are often very difficult to spot due to their cryptic reddish brown plumage and their secretive habits. They prefer deciduous forests with dense underbrush, or thick shrubberies, and are often found in lush vegetation along rivers or wetland edges (Cramp 1988). Males and females are undistinguishable outside breeding season. They winter in tropical East Africa and pass into Africa on autumn migration following the eastern flyway, via Greece, Turkey and Egypt (Fransson et al. 2005). Ring recoveries from the winter areas south of Sahara, from birds ringed in Sweden, are very rare (Fransson and Hall-Karlsson 2008).

The common rosefinch (fig. 1 top left) is a relatively new immigrant to Sweden after a range expansion in the middle of the twentieth century (Stjernberg 1985). The population size increased in Sweden until the 1990's but has since steadily declined (Green & Lindström 2014). The species has a very wide breeding distribution, from Norway in the East all the way to eastern Siberia, although the breeding range of the nominate subspecies (C. e. erythrinus) only stretches as far as 90 degrees East where it is succeeded by the eastern sub-species C. e. grebnitskii (Cramp & Perrins 1994). Adult males are easily distinguishable from females and young birds by their reddish plumage on the head and chest. The habitat is usually a mosaic of open areas and young growing forest and shrubbery (Stjernberg 1979). Males often sing from a high vantage point in taller trees and are then fairly exposed. The species winters in South Asia, from Pakistan and India to southeast China (Ali & Ripley 1974). Long distance ring recoveries from the Scandinavian countries are scarce and no bird has been recovered in the wintering area (Paevskii 1973, Bakken et al. 2006, Bønløkke et al. 2006, Fransson & Hall-Karlsson 2008, Piha 2014).
The garden warbler (fig. 1 *bottom right*) is a common bird that breeds in the entire Western Palaearctic except for in the very north and south, and winters in Central Africa south of the Sahara (Cramp 1992). Sexes are indistinguishable from each other. This species prefer open forest with a dense layer of underbrush, often found in glades or fringes to deeper forests, or in dense scrubland (Cramp 1992). During the breeding season the garden warbler feed mainly on arthropods, but like several other *Sylvia* species changes to a mix diet of insects and fruit and berries during migration and also at the winter quarters (Jordano 1987, Pearson 1972).

The great reed warbler (fig. 1 *bottom left*) has a wide breeding range. The nominate sub-species breeds from the Iberian Peninsula and France in

**Fig 1.** Birds studied in the thesis. From top left: common rosefinch¹ (*Carpodacus erythrinus*), thrush nightingale² (*Luscinia luscinia*), great reed warbler¹ (*Acrocephalus arundinaceus*), garden warbler¹ (*Sylvia borin*).

Photo¹ T. Fransson¹, C. Kullberg²
the west, to southern Scandinavia in the north and eastward to the Caspian Sea. The species winters in Africa south of Sahara, from West Africa to South Africa (Cramp 1992). It is the largest warbler species in Europe. Sexes are similar although males are a little larger than females. The species is associated with tall reed beds in lakes and wetlands, but can in the winter quarters also utilise dense vegetation, tall grasses and bushes in swamps and along streams (Cramp 1992).

**Geolocators**

We used light-level geolocators (hereafter called geolocators) to investigate the spatiotemporal organisation of migration in thrush nightingales (paper I) and common rosefinches (paper II). The birds carried the geolocators on the back (fig. 2 left), with a leg-loop harness around the thighs made from 1 mm EPDM rubber cord (Rappole and Tipton 1991). We used two models of geolocators, the MK12S from British Antarctic Survey (BAS) and the Intigeo-P65 from Migrate Technology Ltd (fig. 2). Both models were similar in weight and with the harness attached weighed around 0.8–0.9 grams.

The geolocator is constructed with a light sensor, microchip, internal memory and battery, all sealed in an epoxy coating to withstand the forces of the environment. The models we used had the light sensor mounted on a stalk (MK12S), or had the light guided to the sensor by a ‘light tube’ (Intigeo-P65), to avoid shading from the wings when folded on the back (fig. 2).

Time stamped light data is stored on the internal memory and the only way the researcher can access the data is to recapture the bird after a successful migratory journey and download the data to a computer. This limits the use of the device to only be attached to birds in the population which can reasonably be expected to return to the same locality the following year so that they can be recaptured. For this reasons adult males are most often targeted for this kind of studies, and to lesser extent adult females, whereas young birds due to high mortality and low site fidelity to breeding sites are seldom used in geolocator studies (McKinnon et al. 2013).

Specially designed software and R packages are available for extracting and processing light data from geolocators. Details on this is not covered
in this presentation, but a short description on how geolocator works and how light data is used for inferring geographical positions follows below.

The light sensor measures the ambient light and stores the maximum recorded light level at predefined intervals, e.g. every two, five or ten minutes. The resulting curve of sampled light levels can be used to determine the time of sunset and sunrise from a pre-defined light-level threshold. The level of light that reaches the sensor is associated with the elevation of the sun, but is also affected by the behaviour of the bird. The sun elevation angle for a given light-level threshold will be higher for birds living in darker environments, e.g. forests, than for birds living in open habitats. In most cases the chosen light-level threshold is calibrated to a sun elevation during the period when the birds is stationary at a known location (e.g. the breeding site), but can also be inferred from an iterative process that minimises latitude variation (Hill-Ekstrom calibration; Lisovski & Hahn 2012).

![Fig 2. Two different geolocator models. Left Integeo-P65 with the 'light ptube' on a common rosefinch. Right BAS MK12S recovered after one year (hence the yellow tint to the coating) with the light sensor on top of stalk.](image)

Photo: T. Fransson and the Author

Position in latitude is calculated from the resulting length of day and night for each calendar date, and position in longitude is calculated from the time of local noon/ midnigh (Hill & Braun 2001). Geolocators can thus only give two locations for each 24 hours cycle, noon and midnight position.
The accuracy of estimated locations is dependent partly on internal factors, e.g. the sensitivity of the light sensor and sampling interval, but can be severely affected by external factors, e.g. cloud cover or foliage (Hill 1994). This is especially true for species that inhabit denser habitats. All types of shading of the light sensor that occur during the critical sunrise and sunset periods can alter the experienced time of sunrise and sunset. This causes variation in estimated day/night length, and to a lesser degree time of noon/midnight. This can have profound effects on the accuracy of estimated locations, and more so in latitude than longitude (Fudickar et al. 2012). Geolocators carried by forest dwelling birds have been found to be accurate within a couple of hundred kilometres in latitude (Fudickar et al. 2012).

A different kind of accuracy issue attributed to light-level geolocation is the inherent difficulty in estimating latitude from variation in day length close to autumn and spring equinoxes, when day lengths is similar across all latitudes (Hill 1994). It is thus impossible to get a reliable estimation on latitude at, or near, the dates of autumn and spring equinoxes. Longitude is, however, unaffected and can be used to infer movements during these periods if the movement involves a change in longitude position.

The low resolution (only two locations per day) and the low accuracy of the estimated locations makes the devices unsuitable for studies on fine scale movements, such as the daily movements within a particular stopover, but can be used to investigate the spatio-temporal organisation of migration on a continental scale. The approximate routes and position of stopovers and winter quarters can be obtained, as well as duration of staging and flight periods.

Radio tracking

In paper III we tracked garden warblers carrying radio-transmitters at a stopover site on southern Gotland, southeast Sweden. Radio tracking is an ideal method for studying individual movements and habitat use on a restricted spatial scale, and can be used to investigate the behaviour of birds at stopover sites.

The transmitters are attached to the back of the birds and they send out radio signals at a specified radio frequency that can be registered by a researcher equipped with a receiver and an antenna (fig. 3). Various
attachment methods exist, e.g. gluing the transmitter to feathers on the back or, as was used in paper III, with a leg-loop harness. The batteries of the transmitters are relatively short lived, up to several weeks, and the method thus only allow for short term studies.

We used two methods for determining the position of a bird; by approaching the bird to a position close enough to determine the exact location of the bird, or from triangulating the position from two, or more, compass directions. This can be very time consuming and tradeoffs must be made between the number of birds that can be managed and how closely each bird can be followed. Radio-tracking studies are, thus, often limited to study sites of a few square kilometres (Chernetsov 2005, Chernetsov & Muhkin 2006, Cohen et al. 2012). The study site of paper III encompassed the entire peninsula (125 km\(^2\)) that makes up the

Fig 3. The author listen for radio signals from tagged garden warblers on southern Gotland with the yagi-antenna mounted on a telescopic pole for better range.

Photo: T. Fransson
southern part of Gotland, with birds spreading out over a large part of the area, and this restricted us to collecting only two locations a day for each bird (present – non-present).

Bird ringing and capture-recapture

Birds used in paper I-IV were individually marked with aluminium leg rings with a unique serial number and the address to the Swedish Museum of Natural History museum which administers bird ringing in Sweden. In paper V birds were ringed with Greek rings with an address to the Zoological Museum in Athens. Researchers have been ringing birds for over a hundred years in order to investigate large scale movement patterns and infer migration routes of different species (Fransson and Pettersson 2001). In paper I and II we compare long distance recaptures of thrush nightingales and common rosefinches from the literature to our results of migration routes for these species. In paper V we use the method of capture-recapture of individual birds at a stopover site. The method is based on standardised daily capture efforts using mist nets at strategic fixed positions in the stopover area. By chance, birds moving in the area can be captured at multiple times and on different days during the course of their stay. Upon capture various biometric measurements are collected, such as wing length, amount of visible subcutaneous fat and body mass, which give valuable information about feeding conditions and fuelling rates at that particular site, and can also give an estimate on the duration of stopover (Schaub & Jenni 2000, Salewski & Schaub 2007).

Laboratory experiment

The thesis contains one experiment that was conducted in a laboratory where fuel deposition rate and achieved fuel load were examined in garden warblers that migrated early or late in the autumn season (paper IV). Birds were kept in laboratory facilities at Tovetorp research station (southern Sweden: 58.95 N, 17.15 E) for about two weeks and given food and water ad libitum. Body mass increase was determined from weighing the birds inside their respective cage. This was achieved by constructing
the perches to hang from inflexible, 2 mm, wires that went through holes in the roof, and attached to a wooden crossbar on top of the roof (fig. 4). A sandbag attached to the crossbar provided extra stability to the construction. Birds were weighed during the mornings when the rooms were illuminated by only a weak light. During weighing an electronic scale was placed under the crossbar. The body mass of the birds were registered when the bird landed on the perch, or if the bird had remained seated on the perch when the scale was placed under the crossbar the negative weight was recorded once the bird left the perch.

Fig 4. Garden warblers were weighed while still in the cage. The picture shows the perch hanging in metal wires that went through the roof and were attached to a wooden crossbar. An electronic scale was placed under the crossbar and the body mass of the birds was recorded once the bird returned to the perch. Alternatively, the negative body mass was recorded if the bird remained sitting on the perch while the scale was placed under the crossbar and then left the perch. The sandbag on top of the crossbar added stability to the construction.

Photo: C. Kullberg
Papers in short

Paper I

In paper I we investigated the migration routes and wintering areas of thrush nightingales by fitting male birds, captured in their territories in the beginning of the breeding season, with geolocators (mod. MK12S from British Antarctic Survey).

Two birds carrying geolocators (out of 35) were recaptured the year following deployment. The low return rate in this species is a concern but we cannot determine if this was caused by carrying the geolocators or from low site fidelity to territories between the years since data is lacking on return rates without geolocators. Carrying geolocators have been shown to increase drag which causes birds to expend more energy during flight (Bowlin et al. 2010). This could potentially increase mortality during migration and return rates have been shown to be affected in some (but not all) species that have been used in geolocator studies (reviewed by Bridge et al. 2013).

Unfortunately, both geolocators ran out of power shortly after the birds had begun their return journey but both geolocators left intact data on autumn migration and the stationary periods during winter. The following year another bird was recaptured which had carried an improved model with more battery power. This geolocator was still collecting data at retrieval and gave intact information about both autumn and spring migration and this bird is included in this presentation as 'bird 3', although not appearing in paper I.

Results and Discussion

The birds began the autumn migration journey in the middle of august. They migrated in a south-easterly direction and made a more than three weeks long stopover in the Mediterranean area before crossing the Sahara desert. Long stopovers are common close to ecological barriers and birds depart from these stopovers with fuel loads that will last across

The crossing of the Sahara took, unfortunately, place during the autumn equinox period which made it impossible to determine the route taken. A clear shift in longitude over 4-7 days during this period probably corresponds to the desert crossing and the birds ended up in southern Sudan when the positions again could be determined.

The birds arrived in the Sahel region of Sudan in the second half of September and remained in the area for 41-56 days. The birds then relocated to northern Kenya where they remained stationary for another 30-37 days. In December they again took flight and moved south to their final wintering areas, which were situated around Mozambique, Zambia and Zimbabwe, where they stayed until the second half of March when spring migration began (fig. 5).

After the desert crossing in autumn many bird species stay for prolonged periods of time in the Sahel. They arrive when the annual rain season draws to an end in the Sahel and the vegetation is still green and support abundance of arthropods which the birds take advantage of (Pearson & Lack 1992). Some species remain in the Sahel throughout the dry season but many species continue south when the area deteriorates (Morel 1973). Large numbers of birds of several species are captured on migration in November and December at Ngulia Lodge in southern Kenya, and the thrush nightingale is among the most numerous (Pearson & Backhurst 1976). We show in paper I that migration within Africa in thrush nightingales most probably is made up of three separate stages, with two sites used for extensive periods north of Ngulia. The third bird shows essentially the same pattern with three separate staging sites in Africa south of the Sahara (fig 5). The movements and stops fit well with the southward movement of the inter-tropical rain season, suggesting that birds time the inter-African movements more closely with the rain than previously shown. We argue in paper I that the stationary periods in Sudan and Kenya are too long to be considered as mere stopovers on migration but that the sites are part of the wintering strategy of the species which include inter-African movements when habitat deteriorates. Recent geolocator studies have revealed long distance movements within wintering areas as dynamic responses to changes in the habitat or food abundance (see for example Heckscher et al. 2011, Fraser et al. 2012, Jahn et al. 2013, Lemke et al. 2013, paper I and paper II).
Fig 5. Migration routes of three thrush nightingales. Bird 1 and 2 are included in Paper I. Bird 3 was recaptured a year later and is included in this thesis for comparison. It also show the spring return journey. Filled circles (autumn) and open circles (spring) represent mean positions of stationary sites. Solid lines represent migration between stationary sites and broken lines represent migratory movements undertaken during the autumn equinox. Spring migration route is indicated by dashed lines. Dates indicate time spent at stationary sites.
Not included in paper I is the spring return journey of the third thrush nightingale. The bird (bird 3) left the wintering area at the end of March and moved northeast to a stopover site in northern Kenya where it remained for 20 days (fig. 5). It then moved northeast approximately 800 km to a second stopover site in eastern Ethiopia where it remained for another 9 days. The bird continued migration on May 1 and moved along the western part of the Arabian Peninsula. It arrived back at the breeding site on southern Gotland on May 23. The entire spring migration journey took 54 days, covering approximately 9300 km (calculated as cumulative great circle distances between consecutive stopovers) which gives an average spring migration speed of 172 km day$^{-1}$. The bird, thus, performed an anti-clockwise loop-migration of the same pattern described in another geolocator study on this species (Tøttrup et al. 2012a) and which also has been shown for the red-backed shrike *Lanius collurio* (Tøttrup et al. 2012b). Anti-clockwise loop migration seem to be common in species that follow the eastern flyway into Africa and winters below five degrees South (Pearson & Lack 1992). The reason for this has been suggested to be the extremely dry conditions in Sudan in spring whereas the northward moving rain front has reached south Ethiopia and south Somalia at the time for spring migration and these areas can thus provide birds with better fuelling possibilities (Pearson & Lack 1992). Our results clearly highlights the importance of the inter-tropical rain movements for bird migration within Africa, and also the birds’ ability to find and utilise areas of high food abundance across the continent.

**Paper II**

In paper II we investigated the migration routes and wintering areas of a bird species that follow the not well studied European-Asian flyway, the common rosefinch. Male rosefinches were trapped and fitted with geolocators at two breeding locations: at Ringenäs, outside the city of Halmstad on the west coast of Sweden, and on southern Gotland in the Baltic Sea. The return rate of tagged birds was 27% (10 of 37) but only three were recaptured carrying geolocators. Three other birds were recaptured but had lost the geolocator and four birds were sighted but we were unable to capture them. All three retrieved geolocators gave intact information from the outward-bound and return journeys.
Results and Discussion

The three birds left the breeding areas in late July – early August and moved east-southeast across Russia and the Central Asian desert zone to the foothills of the mountain ranges of The Tien Shan, the Pamirs and the Hindu Kush (fig. 6). Only one bird made a longer (six days) stopover at the edge of the desert zone. This first part of autumn migration took 18–27 days to complete (3800–4500 km). The continuing southward migration through the mountain regions to the wintering sites in southern Pakistan and western India took much longer time, 39–69 days, despite much shorter distances (1200–3000 km). The reason for the slow speed was that the birds made several prolonged stops (19–28 days) along the way south. We argue in paper II that the long stops are part of a migration strategy where the birds temporarily cease migration to take advantage of local food abundances (e.g. Arlt et al. 2015).

All birds used two wintering sites, 300–850 km from the first wintering site (fig. 6). Relocation occurred in January in all birds. Rosefinches can form large flocks during winter (Cramp and Perrins 1994) and we argued that the relocation probably was a response to local food shortage due to overgrazing of seeds.

The birds followed different routes in autumn and spring, with more southerly routes in spring back to the breeding grounds than for autumn migration (fig. 6). The Central Asian deserts are extremely dry in autumn, but rain during winter makes the vegetation in the desert area flourish which allows birds use the desert zone for stopover in spring (Dolnik 1990, Bolshakov 2003). Migratory birds in this area circumnavigate, if possible, the desert zone during autumn but pass over it in spring (Dolnik 1990, Bolshakov 2003, Bulyuk & Chernetsov 2005, Chernetsov et al. 2008). European populations wintering in Asia may need to cross the desert zone but the northerly routes used in autumn may have shortened the passage over inhospitable land. The more southerly routes taken in spring may also have allowed birds to take advantage of better feeding opportunities en route from a stronger advancement in spring at lower latitudes. During spring migration the birds used one or two stopovers (8–11 days) while still in South and Central Asia and then migrated at high speed, with only a few short stops, towards the breeding grounds. One bird covered 4000 km in just 11 days!
Fig 6. Migration routes of common rosefinches. Solid lines indicate autumn migration routes and broken lines indicate spring migration routes. Dashed lines indicate migration movements during autumn equinoxes when latitude could not be estimated. Open circles (autumn) and squares (spring) show median position of longer staging sites, (used >5 days). Filled black circles (autumn) and squares (spring) show median position of shorter stops (2-5 days). Kernel densities encompass 50 and 70 % of estimated positions during wintering periods. Hatched area show the extent of the deserts of Central Asia.
The somewhat unorthodox arrangement of spring migration, where almost all of the energy for migration must have been accumulated in Asia, followed by a rapid migration over 4-5000 kilometres, surprised us. We speculate if this is a result of an extended migration distance, caused by the range expansion in the western population that has changed the migration schedule. The high migration speed in the second part of spring migration can perhaps also be attributed to selection for early arrival at breeding grounds (Morbey & Ydenberg 2001).

Paper III

In paper III we were interested in how garden warblers organise a stopover at a northern site without the influence of a major barrier ahead. The study was conducted on southern Gotland which is within reach of a night's flight from the southern coast of Finland (Hall-Karlsson & Fransson 2008). This is also true for the northern coast of Poland for the continuing flight, which makes it an ideal place to study stopover behaviour in migratory birds.

Fifty-one first–year garden warblers captured in the long term standardized bird ringing project at the southwest coast of the peninsula, at Sundre Bird Observatory, were fitted with miniature radio transmitters.

We tracked the birds daily to establish the duration of stopover and the location where the birds refuelled. We also re-trapped three birds to investigate at what rate they accumulated fuel.

All newly tagged birds were tracked throughout the first day to the place where they would spend the first night. We checked the location of all birds the following morning, and if no signal was detected from a bird that had been present at the location the previous night that bird was searched for during subsequent days until found or deemed to have left the study area. We scanned for lost signals across the entire 125 km² peninsula in the south of Gotland, by omni-directional antennas mounted on our vehicles. The exact location of detected birds was established using hand-held yagi-antennas. All birds with known locations were checked twice daily until they left the area, presumably continuing on migration. Some birds that had remained close to the capture site during the first day were tracked after sunset over open water in a southward direction when they continued migration.
Results and Discussion

The capture area consisted mainly of open, dry shrub land, dominated by Swedish whitebeam \textit{Sorbus intermedia} and juniper \textit{Juniperus communis}, but was devoid of dense shrubberies and fruit bearing plants and was thus probably not a suitable habitat for garden warblers. We found that birds with larger fuel stores upon capture were more likely to remain in nearby shrubberies during the day and continue migration the following evening. Leaner birds tended to move north from the capture area and spread out along the western part of the peninsula, up to 14 kilometres from the capture area (fig. 7). This behaviour of moving away from coastal areas, where suitable habitat may be lacking and competition and predation risk can be high, has been described for several species and mainly seems to include young birds and birds with low amount of fuel (Alerstam 1978, Åkesson et al. 1996, Nilsson & Sjöberg 2015).

It is likely that some birds moved even further north and outside our search area since several of the tagged birds that were tracked heading north during the first or second day after capture disappeared and were not found again. The body mass of lost birds were also more similar to birds that remained in the area for some time than birds that were transients in the area which suggests that they remained on the island but outside our search area (fig. 8). Several birds made long relocation movements during the dark hours, and birds performing these movements ended up further away from the capture site than birds moving only during daytime (fig. 7). Birds that only relocated during the day settled in areas on average 3.1 ± 2.4 km from the capture site while birds that relocated nocturnally settled on average 5.6 ± 3.7 km away. While movements during the day typically occurred in protection of vegetation cover, nocturnal relocations probably allowed birds to fly above tree tops and cover greater distances in less time. The fact that birds relocate over considerable distances at stopover sites, and quite often during night, was only recently described in detail in radio-telemetry studies using an array of fixed antennas (Mills et al. 2011, Taylor et al. 2011, Woodworth et al. 2014). Mounting evidence suggests that birds landing in unfavourable habitats can move considerable distances within a general stopover area to locate a suitable feeding site, and relocations that take place during the night can be difficult to detect and instead be interpreted as the birds have continued migration.
Fig 7. Locations of stationary sites after relocation at the stopover site on southern Gotland. Squares show the locations of birds that relocated during daytime and circles show birds that relocated during the night.
The duration of stopover was 4-13 days (average: 7.9 ± 2.7 days). During this time three birds were recaptured in order to determine the rate of body mass increase at the stopover. Fuel deposition rate was 0.3 – 1.1 g day\(^{-1}\). The resulting fuel load at departure was calculated for the three birds to be 40, 50 and 56% of lean body mass. This amount of fuel was calculated to be enough for the birds to migrate to southern Europe without further stop for refuelling. This indicates that garden warblers can, and will, take advantage of high quality habitats at northern stopover sites to refuel. Birds can thus avoid further fuelling before arriving in the Mediterranean area where they will have to refuel again before crossing the Mediterranean Sea and the Sahara.

**Fig 8.** Fuel loads at capture for birds that made a longer (>2 d) stopover, short (1–2 d) stopover and birds that were lost. Error bars depict standard deviation, (**) indicate statistically different fuel loads at p-level = 0.01, and (***) at p-level = 0.001.

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**Paper IV**

In paper IV we test the hypothesis of different fuelling strategies within the migration season. Birds that migrate late in the migration season may need to compensate a late departure by increasing the speed of migration. Some studies have suggested that migration speed within species accelerates with the progress of the season (Ellegren 1990, 1993, Fransson 1995). Passerine birds spend most of the migration time at stopovers (Hedenström and Alerstam 1997) and high fuelling rates (shorter stopover durations) as well as large departure fuel loads
(decreases number of stopovers needed) at stopovers increases migration speed (Alerstam and Lindström 1990, Nilsson et al. 2013). Late migrants should thus benefit from adopting a different fuelling strategy than earlier migrants. In paper IV we studied fuelling activity in garden warblers captured early or late in the migration season (hereafter called ‘early’ and ‘late’), with the addition of a group that were captured early in the migration season but held under light conditions that simulated an advancement in time of one month (hereafter called ‘manipulated late’). All groups were held in captivity for approximately two weeks and given unlimited access to food and water. Food consumption was registered for each individual each day and body mass was recorded every third day.

Results and Discussion

We found no difference in fuel deposition rate or in maximum fuel load between the groups which show that garden warblers do not compensate a late departure on migration by altering the fuelling strategy (fig. 9). This differs from other studies of passerine species (bluethroats Luscinia svecia, Lindström et al. 1994; whitethroats Sylvia communis, Fransson 1998; thrush nightingales, Kullberg et al. 2003) which have found that the progress of the season can affect fuelling strategies. In this study all groups gained considerable in mass and the birds reached an average fuel load of 34.9 % (‘early’), 39.5 % (‘manipulated late’) and 44.5 % (‘late’) of lean body mass. Fuel load was also strongly correlated with individual rate of body mass increase (r=0.66, p<0.001). This suggests that garden warblers may differ from other species in that they seem to migrate at high speed during the entire autumn migration season which leaves little room for improving speed later in the season.

![Fig 9](image-url) (A) Fuel deposition rate, and (B) maximum achieved fuel load for birds in the three experimental conditions (mean ± SE).
Interestingly, birds in the ‘late’ group consumed significantly more food per day than the other two groups. Moreover, food consumption in ‘early’ and ‘manipulated late’ was strongly correlated with body mass increase \((r=0.82, p<0.001; r=0.71, p<0.01)\) but this correlation was absent in ‘late’ \((r=0.19, p>0.05)\). It thus appears that birds captured late in the season consumed more food but the extra ingested food did not assist the birds in gaining more body mass. We speculate if this difference is a result of higher stress response (elevated basal metabolic rate or increased nocturnal activity) or whether food choice place a role; frugivory may be more pronounced later in the season and the birds may have needed time to readjust to the protein rich food in the experimental setup. This suggests that the garden warblers did react to the progress of the season although not in the way we had predicted.

**Paper V**

In paper V we investigated body condition and fuelling strategies of great reed warblers during spring migration at a stopover site on southern Crete, at a time when the birds had just performed the laborious crossing of the Sahara desert and the Mediterranean Sea. Crete is the first major landmass which provides fuelling opportunities for birds following the eastern flyway and is thus a very suitable area for studying migration in relation to a large ecological barrier (fig. 10). Birds were captured with mist nets at Anapodaris river mouth on the south coast of Crete. The area consists of reed beds surrounding the river mouth, with bushes and olive groves along the coast line. Great reed warbler was by far the most numerous species captured at this site and a total of 56 great reed warblers were captured and ringed during one season. Twenty-five individuals (45%) were recaptured on at least one occasion in subsequent days. Nine birds were recaptured multiple times.

![Fig 10. Map showing location of study site in relation to North Africa.](image)
(up to six times) during their stopover. Birds were scored for subcutaneous fat (1-6; Pettersson and Hasselquist 1985) and size of breast muscle (0-3; Bairlein 1995) and weighed to nearest 0.1 gram. Maximum wing length was used as a proxy for size (Svensson 1992).

Results and Discussion

Birds weighed between 20.8 – 36.0 grams at first capture (average: 27.0 ± 3.8). Birds that were recaptured in subsequent days had lower body masses at first capture than birds that were not recaptured (25.2 ± 2.9 g and 28.4 ± 3.9 g respectively; fig. 11A) which indicates that leaner birds were more likely to remain in the area to refuel. The recorded body masses of great reed warblers at Anapodaris must be considered very low for this species. The body mass of male great reed warblers, with no visible subcutaneous fat, at breeding sites in Sweden have been reported to be 33.9 ± 2.4 grams (Lemke et al. 2013) and similar values are reported from a breeding site in Greece (Akriotis 1998). In our study only birds with substantial fat reserves (fat score 5-6) reached similar body masses (33.6 ± 2.1 g). This highlights the tremendous toll the Sahara crossing takes on the birds, since not only fat, but also muscle tissue and internal organs are reduced in size and used for fuelling the flight (Bauchinger et al. 2005).

![Fig 11](image)

**Fig 11.** (A) Distribution of body masses of great reed warblers. Black bars represent birds that were recaptured at least once after ringing while white bars represent birds that were not recaptured. (B) Relationship between fuel deposition rate and body mass at ringing.
The calculated minimum stopover time was 4.8 ± 3.1 days and two birds had a minimum stopover time of 10 days while the longest recorded stopover was 13 days. This is similar to what has been reported in great reed warblers stopping over in Morocco and Spain (Gargallo et al. 2011). In paper V we highlight the problem with using recaptures to estimate stopover duration since it is impossible to know if a bird is present in the area prior to, and after, initial and last capture (Schaub et al. 2008, Chernetsov 2011) and also because the probability of recapturing a bird may not be equal throughout the stay (Bächler & Schaub 2007, Paxton et al. 2008, Chernetsov and Muhkin 2006).

Recaptured birds showed a high average fuelling rate (1.0 ±0.4 g day⁻¹) which indicates that the reed beds provide very good feeding conditions for this species (Lindström 2003). Birds that were recaptured the first day after initial capture showed a slightly higher fuelling rate (1.3 ± 0.5 g day⁻¹) than birds captured later, indicating that birds probably could begin gaining mass immediately at arrival at the stopover. It was also shown that great reed warblers with lower body mass at first capture had a higher fuel deposition rate than birds with higher body mass (r= -0.52, p=0.007; fig 11B). This indicates that individuals are able to adjust their food intake in relation to energy reserves. The results from this study support earlier findings that migrants are very good in finding stopover sites with preferred habitat (cf. Moore and Aborn 2000, Ktitorov et al. 2008, Chernetsov 2011, paper III). This highlights the importance of carefully choosing the sites when planning stopover studies.
Concluding remarks

Although migration in birds has been extensively studied for the past hundred years or so there are still many aspects of migration that remain unknown, or where consensus has not yet been reached. One reason for this is the huge variety of migration strategies that can be seen in different taxonomic groups of birds, and even within groups, which makes the subject very complex and immensely fascinating.

In this thesis I have focused on two important aspects of migration, migratory routes and stopover behaviour, which take place at different spatial and temporal scales, and thus require different techniques to study. Knowledge about the migration routes different species follow, and what environmental conditions they encounter in space and time and how they deal with them, are essential in order to understand migration as a concept, but it is also important when it comes to guiding conservation efforts to areas that have the most negative effect on the population size in declining species. Despite their many shortcomings geolocators are currently the best tool available for tracking small migratory birds at a continental scale and they have revolutionised our knowledge and perception on bird migration.

An interesting feature of migration is that some species seem to follow different routes in autumn and spring. Loop migration was shown for rosefinches in paper II but it was also evident that thrush nightingales, when examining the routes taken by the third bird (not included in paper I) also show a loop migration pattern. In the light of recent research, loop migration seems to be fairly common and occurs when ecological features, e.g. patterns of food availability or wind directions, favours one route in one season but another route in the next season (Klaassen et al. 2010).

This thesis shows that both thrush nightingales (paper I) and common rosefinches (paper II) use multiple wintering sites. It has always been a challenge to obtain information about winter locations and behaviour at wintering sites since researchers have had to conduct studies in remote areas and often in developing countries. Although large scale movements
between winter localities have been demonstrated by ringing efforts (Pearson & Backhurst 1976) recent use of tracking technologies have shown this behaviour at a much finer spatial resolution and demonstrated that this behaviour is fairly common in many species (see McKinnon et al. 2013 for review). With the aid of tracking devices it is now possible to add a temporal component to the species winter distribution.

Paper I and II also discuss a rather unknown aspect of migration: prolonged stationary periods during migration, at sites that are not intended for preparation for crossing large ecological barriers. Some of these long stops can, as in the thrush nightingale, be explained as a winter strategy rather than being part of the general migration period (paper I), but other long stops, such as in autumn migration of common rosefinches, the stops are clearly en route and as such are not as easily explained (paper II). In paper II we propose that the long stops serve to optimise resource use along the journey when encountering abundant and predictable food sources. A different explanation was proposed for northern wheatears Oenanthe oenanthe, which made prolonged stopovers after crossing the Sahara in spring; that it could serve as a way of escaping a deteriorating winter habitat but avoiding arriving too early to sites further north where spring has not advanced enough at the time (Arlt et al. 2015).

The second main aim of the thesis concerns the organisation of stopovers. In paper III – V we primarily focused on getting a reliable measurement of fuel deposition rate and relate it to the duration of the stopover and departure fuel loads, all of which are key elements in the birds’ migration strategy. The rapid fuel deposition rate and unexpected large fuel loads in garden warblers (paper III and IV), far from ecological barriers, suggests that birds adopts a time minimising strategy (Alerstam & Lindström 1990). Rapid fuel deposition and large fuel loads were also found in great reed warblers at Anapodaris river mouth, on Crete in spring. Migration speed is often higher in spring than in autumn (Nilsson et al. 2013) which may explain the extensive fuelling at this site, but it is also possible that the birds attained an overload at this site as a preparation for the coming breeding (Sandberg and Moore 1996, Fransson and Jakobsson 1998).

We also showed in paper III how birds when forced to land in unfavourable habitats, such as coastal sites, can move considerable distances to find suitable stopover areas. This is in line with the reversed migration direction shown in other studies (Alerstam 1978, Åkesson et
al. 1996, Nilsson & Sjöberg 2015). That several of the relocation flights took place during night time, and could easily have been misinterpreted as migratory flights, show that research on stopover behaviour need to take into consideration the birds’ spatial use of the stopover area. Our finding suggests that birds that land with low fuel reserves are likely to remain in the general area but can relocate by means of short nocturnal flights if suitable feeding conditions are not found nearby. This behaviour may not only be caused by shortage in food supplies but could also be driven by high competition in the area or high risk of predation (Alerstam 1978). The extremely high recapture rate seen in paper V in the reed beds of Anapodaris river mouth also highlights the importance of carefully selecting appropriate study sites for the species in focus.

One aspect of stopover that has implications for how much fuel a bird should accumulate at a stopover, given the theoretical strategies of minimising time, energy or safety, is the search and settling cost associated with arrival at a new stopover (Alerstam and Lindström 1990). The settling cost implies that birds will not be able to start accumulating fuel before having found a habitat to settle in, where food abundance and competition allow for fuel deposition. Several studies report that newly arrived birds show faster and longer movements, and with fewer turns, during the first couple of days, after which movements become more restricted in their spatial extent and with sharper turns, and this has been argued to be associated with initial search behaviour before settling in a foraging area (Chernetsov 2005, Chernetsov & Muhkin 2006, Paxton et al. 2008). A similar behaviour was shown by garden warblers in paper III when birds relocated several kilometres over the first couple of days, during which time the birds probably experienced a low fuel accumulation rate. In contrast to this, great reed warblers arriving to the reed beds in Anapodaris river mouth in spring (paper V), showed slightly higher fuel deposition rates during the first day than later, and thus did not seem to have to pay a settling cost at arrival. The study may, however, underestimate the search and settling cost experienced by the birds in the respect that we cannot be certain that the birds were captured the first day in the reed beds, or for how long they had searched to find them.

Paper III and V examine essentially the same features of stopover, fuel deposition rates and stopover duration. The different techniques used in the two studies, radio tracking and capture recapture, have both their benefits and shortcomings. In paper III we got reliable estimates on stopover durations but estimates on fuel deposition rates were hampered
due to the small sample size. In paper V stopover duration was probably underestimated but due to a high recapture rate estimate on fuel deposition rates was of high quality. By combining these two techniques in future studies, the quality of measurements on several aspects on stopover behaviour could be increased and would allow for in depth studies on stopover behaviour.

This thesis adds to the accumulated knowledge of bird migration and highlights several features in the migration of birds that shows migration to be more complex than the mere movements between summer and winter residences. I feel fortunate to have come into migration research at such an exciting time when new technology makes it possible to study migration at widely different spatial scales and address research questions that only a few decades ago seemed impossible to answer. Through the work on this thesis I have become even more fascinated by the marvels of migration and more impressed by the journey these small creatures undertake each year, the perils they face, and the never ending struggle to make life work.
Sammanfattning

Fåglars långväga säsongsbundna flyttningar har under lång tid fascinerat människan. Deras förmåga att flyga och tillryggalägga enorma sträckor under kort tid har gjort det möjligt för dem att två gånger per år flytta över, och mellan, kontinenter. De kan på så sätt utnyttja tillfälliga, men rika, födoresurser under sommarhalvåret på nordliga latituder för att häcka och föda upp sina ungar, för att sedan spendera de bistra nordliga vintermånaderna på sydligare breddgrader.

Den här avhandlingen fokuserar på två viktiga delar av migrationen som verkar på olika rmsliga och tidsmässiga nivåer, det gäller dels själva flyttningsvägarna som för fåglarna mellan häck- och vinterkvarter, och dels hur fåglarna utnyttjar rastplatser på vägen mot sina mål.

För många arter är flyttvägarna till stora delar okända. Det gäller framförallt arter som migrerar över långa avstånd och mellan kontinenter, och dessutom oftast flyttar nattetid. De traditionella metoderna att studera flyttfåglars rutter, ringmärkning och direkta fågelobservationer i olika delar av världen vid olika tidpunkter på året, har gett en översiktlig bild av var fåglarna tar vägen men många detaljer saknas fortfarande.

I artiklarna I och II studerade vi flyttningsvägarna för två arter, näktergal (Luscinia luscinia) och rosenfink (Carpodacus erythrinus), med hjälp av ljuskänsliga loggrar som man kan använda för att följa även relativt små arter under ett helt år. För båda arterna finns det väldigt få återfynd av ringmärkta fåglar från den senare delen av migrationen, och inga alls från vinterområdena. Stora delar av hur migrationen såg ut, både när det gäller den rmsliga utbredningen men även den tidsmässiga aspekten, var för båda arterna okända. I artiklarna I och II beskriver i detalj migrationsförloppen för de båda arterna.

Fåglar använder rastplatser utefter vägen framförallt för att fylla på energidepåerna som ska användas under själva flygningen. Tittar man på hur stor del av hela migrationstiden fåglar faktiskt flyger och hur stor del de tillbringar på rastplatser ser man att de till största delen av migrationen tillbringar på rastplatser. Rastplatserna är således viktiga
för fåglarna under migrationen och det är därför viktigt att studera hur de utnyttjar tiden på dessa för att förstå hur bakomliggande faktorer formar migrationen.

I avhandlingen har jag använt mig av radiosändare för att studera hur trädgårdssångare (*Sylvia borin*) på södra Gotland utnyttjar en nordlig rastplats (artikel III). Jag har även tagit in trädgårdssångare på labb för att se om födointag och viktuppgång skiljer sig åt för fåglar som flyttar tidigt på säsongen och fåglar som flyttar sent på säsongen (artikel IV). Dessutom har vi studerat hur trastsångare (*Acrocephalus arundinaceus*) fettupplagar när de under våren precis har passerat över Sahara och Medelhavet på en rastplats på Kretas sydkust (artikel V).

I avhandlingen diskuterar jag möjliga bakomliggande orsaker till resultaten som har erhållits, resultat som hade varit svåra att upptäcka utan tekniska hjälpmedel för att spåra små fåglar. Det rör sig t ex om att fåglar ibland använder olika vägar under höst och vårflytten, att de under vintern kan flytta mellan flera diskreta vinterkvarter, att de ibland gör förvånansvärt långa stopp under vägen och att de kan genomföra nattliga förflyttningar på rastplatserna. När det gäller rastplatsstudier påvänder jag vikten av att använda flera olika metoder för att få tillförlitliga data på framförallt fettupplagringstakt och hur lång tid fåglar stannar på rastplatserna.
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