Abstract

Birds must store fuel prior to the crossing of the Sahara desert, at least 1500 km with few refuelling possibilities. A major question is how inexperienced birds know where to prepare for the oncoming barrier. Experiments with caged birds showed that information from the Earth’s magnetic field close to the desert might trigger extensive fuel deposition. Blackcaps Sylvia atricapilla trapped on Cyprus in September and October were much heavier than in Sweden during the early phase of autumn migration, typical for birds preparing for crossing the Sahara desert. There is a potential cost of being fat. Fat Sedge Warblers Acrocephalus schoenobaenus on Lesvos had much poorer take off abilities than lean birds, making them more vulnerable to predators. Swallows Hirundo rustica trapped at a roost site on Rhodes showed a synchronized body mass increase and this is in agreement with their wavelike pattern of passage on Crete. In recent years, studies of fuelling behaviour and stopover duration of first-year Garden Warblers Sylvia borin have been started on Crete with the aid of radio-transmitters.

Introduction

Most of the long-distance migrants breeding in Sweden winter in Africa and about 35 passerine species have their main wintering areas in tropical Africa. Many follow the western flyway and enter Africa after passing the Iberian peninsula, like the Redstart Phoenicurus phoenicurus and the Reed Warbler Acrocephalus scirpaceus (Fransson et al. 2002, Fransson & Stolt 2005). Only a few long-distance migrants leave Sweden in a southern direction and one of these is the Spotted Flycatcher Muscicapa striata (Fransson 1986). Some other species follow the eastern flyway and pass the eastern Mediterranean, like the Thrush Nightingale Luscinia luscinia and the Blackcap Sylvia atricapilla (Fransson et al. 2005). Large numbers of soaring birds on migration to Africa avoid crossing the eastern Mediterranean Sea and concentrate in the Middle East (cf. Alerstam 1990). Many night migrating passerine birds, however, seem to cross the eastern Mediterranean Sea and this was shown already in the 1960s by radar studies carried out from an aircraft carrier (Casement 1966). In a recent study of migratory directions in SE Romania, Bulgaria and NE Greece, based on the moon-watching technique, the majority of the observed nocturnal autumn flights were directed S–SSW, which means that many birds are heading towards the Libyan desert (Zehtindjiev & Liechti 2003).

When migratory birds pass benign areas with widespread fuelling opportunities, they deposit rather small fuel loads (20–25% of lean mass). The reason for these relatively small fuel loads is probably that the advantage of larger fuel load has to be balanced against costs connected with an increased body mass, such as enlarged flight costs as well as impaired predator evasion (Alerstam & Lindström 1990). Many long-distance migratory birds have to face the challenge of passing the Sahara desert. The desert is a major obstacle for
birds that migrate to tropical Africa and distances of at least 1500 km (Figure 1) with hardly any refuelling possibilities have to be passed (Moreau 1961). In spite of this, huge numbers of songbirds regularly pass the desert in autumn and c. 5 billions have been estimated to be involved (Moreau 1972). It is well known that birds close to barriers often are found with very large fuel loads. The migration across the desert has been subject to detailed investigations (cf. Bairlein 1985, Bairlein 1987, Biebach et al. 1986) and it is now believed that two main strategies exist (Biebach et al. 2000). The birds either fly non-stop over the desert or interrupt their flight and rest during the day. They can probably shift between these two strategies depending on local weather conditions (Klaassen & Biebach 2000).

How do they know when to start fuelling?

A major question is how inexperienced birds can know where to prepare for the oncoming barrier. It has been assumed that both timing and amount of fuelling are governed by the circannual rhythm, which is fine-tuned by photoperiod (Berthold 1996; Gwinner 1996). However, variation in the time of breeding affects the timing of the onset of migration, and unpredictable weather and feeding conditions affect timing en route. Hence, a bird cannot safely deduce its latitudinal position from calendar date. In recent studies carried out at Tovetorp Zoological Research Station in Södermanland, Sweden, we have found that birds might use geomagnetic information to decide where to accumulate the extensive fuel loads necessary for successful trans-Saharan flights. Thrush Nightingales caught in Sweden during their first migration and exposed to magnetic fields simulating a migratory flight with a stopover in northern Egypt extended their fuelling period compared with control birds experiencing the ambient magnetic field in southeast Sweden (Fransson et al. 2001, Kullberg et al. 2003). It has been shown that the magnetic field can affect directional changes in migratory birds as well as in sea turtles, newts and spiny lobsters (Beck & Wiltschko 1988, Wiltschko & Wiltschko 1992, Lohmann et al. 2001, Fisher et al. 2001, Boles & Lohmann 2003). Our findings show that a change in the magnetic field also can trigger processes such as extensive fuel deposition. A non-random distribution of ringing recoveries in some species in the eastern Mediterranean area during autumn migration indicates that species-specific stopover areas occur in front of the desert (Fransson et al. 2005) and this finding supports that migrants also must use some external cues to find these places.

In order to investigate the fuelling behaviour close to the desert in more detail, field studies have been carried out in the eastern Mediterranean in collaboration with Greek ornithologists. Different areas have been visited over the years. This article presents an overview of these visits as well as some examples of results that have been achieved so far.

Fieldwork

The first study was carried out in the western part of Greece during two weeks in September 1988. The year after, in 1989, two weeks (24 September – 7 October) of ringing was carried out in the Akrotiri peninsula on southern Cyprus. In 1997, the island of Lesvos in the Aegean Sea was visited during a three weeks period (28 September – 19 October). During the period 26 September – 10 October 2000, ringing was carried out on Rhodes in the Dodecanese. From 2001 until 2004 fieldwork and ringing was carried out on Crete (9–23 September 2001, 8 September – 6 October 2002, 28 August – 11 September 2003, and 2–30 September 2004). The ringing on Cyprus was carried out with permission from the Cyprus Ornithological Society and in Greece with permission from the Ministry of Agriculture and in collaboration...
with the Hellenic Bird Ringing Centre. During these periods of fieldwork, a total of 4933 birds were ringed. The locations of the different places are shown in Figure 2.

Results and discussion

Blackcaps and Willow Warblers on Cyprus

The ringing on Cyprus in 1989 took place south of the Akrotiri Salt Lake and close to a small water reservoir called the Bishops Pool. Recoveries show that many Blackcaps from Sweden pass this area in autumn and Blackcaps were indeed present in fairly large numbers. The Blackcaps on Cyprus carried much larger fuel loads than birds on autumn migration in Sweden do (Figure 3). A distribution of body mass data similar to the one found on Cyprus has also been found in northern Israel (Izhaki & Maitav 1998). The Blackcaps trapped on Cyprus and in northern Israel probably consist of a mixture of birds in different state of fuelling, but it is obvious that many of them were in preparation for crossing the Sahara desert, having as high fuel loads as 75% of lean body mass. Blackcaps are wintering on Cyprus, but otherwise only small numbers are found in the Middle East during winter (Cramp 1992) indicating that most of the birds found during migration in this area are heading for wintering areas in East Africa.

The most commonly trapped species was the Willow Warbler *Phylloscopus trochilus*, with 504 individuals ringed. A cold front with some rain showers in the beginning of October forced large numbers of migrants to interrupt migration and to rest in the trapping area. This was probably the reason for the unusually large proportion (38%) of adult Willow Warblers trapped. Most of the adult Willow Warblers were investigated for moult and about one third (34%) of them had unmoulted secondaries. This is the same proportion (34%) as found in Sweden (Hedenström et al. 1995) indicating that some of them had a Swedish origin. The proportion of birds with unmoulted secondaries was much higher in females (<68 mm wing length) than in males (>67 mm), being 46% and 18% respectively. This pattern has also been found in Sweden, where 44% of the females and 23% of the males showed suspended moult (Hedenström et al. 1995). This is a result of that breeding incurs a larger energy stress in females than in males, resulting in a later onset of moult. Compared with the Blackcaps, the average body mass in Willow Warblers on Cyprus was surprisingly low (mean: 9.2g, SD=0.96, range: 6.2–11.7g, n=425). This body mass is similar to that found in Willow Warblers in Sweden during the early phase of migration (Lindström et al. 1996). This indicates that Willow Warblers differ from Blackcaps in how or where they prepare for the desert crossing. It is possible that Willow Warblers, by effectively feeding on small flying insects, can fuel closer to the barrier crossing or even in the desert.

Sedge Warblers on Lesvos

In order to follow up a study carried out in Sweden about how an increased body mass affect escape performance in Blackcaps (Kullberg et al. 1996), we went to Lesvos in the autumn of 1997. The plan was to study take off flights in Blackcaps with a natural variation in body masses, also including extremely heavy birds. We used a mobile registration cage where birds could be video recorded during a simulated predator attack in close connection to the trapping. On the southeastern side of the island, at Charamida, we had the possibility to use an already established ringing site during our stay. By means of tape luring we trapped 701 Blackcaps in total during a three weeks period, but the proportion of heavy birds were much less than we expected and also different from the situation on Cyprus. We instead focused on Sedge Warblers where the proportion of heavy birds was very large. We found that an increasing fuel load from 0% to 60% reduced flight velocity by 26% (Kull-
Interestingly, we were unable to demonstrate an effect of fuel load on angle of take off in Sedge Warblers, whereas angle of take off in heavy Blackcaps studied in Sweden was affected to a larger extent than flight speed (Kullberg et al. 1996).

Extremely large fuel loads in migratory birds certainly increase the risk of being taken by predators. In the Mediterranean, the Eleonora’s Falcon *Falco eleonorae* breeds during the main passage time of migrants and judging from prey remains at a colony off Crete, Sedge Warblers are the most common prey species among the *Acrocephalus* warblers that migrate through the area (Ristow et al. 1986 in Handrinos and Akriotis 1997). Falcons probably take most of their daily catch of migrants in the early morning, at the end of the migrants’ night flights. On 6 October 2000 we made an interesting observation close to the coastline on southeastern Rhodes. In the period of dusk, between 7.15 and 7.30 p.m. we observed about 25 passerines taking off from a small reed bed. We
had the lighter part of the sky in the background and could follow the birds for a short while. Suddenly, an Eleonora’s Falcon appeared and we saw the falcon attacking several of the birds even though it was more or less dark. At one occasion the falcon hit one bird without catching it, and it was falling against the ground as if it was seriously injured. This shows that there might be a risk, not only when birds arrive to this area, but also when they depart.

Collecting morphometric measures such as wing length, body mass and fat score from migratory birds in connection with ringing can give important information about migratory strategies. The body mass of Sedge Warblers *Acrocephalus schoenobaenus* on Lesvos varied between 9.4 and 19.7 gram (Figure 4) and the visual fat score showed a strong correlation with body mass (Figure 5). The mean body mass was 15.9 gram and the mean fat score was 6.9 in the 63 Sedge Warblers trapped. The highest body masses indicate that some birds carry a fuel load of about 100% (compared with the lean body mass). Sedge Warblers breeding in Great Britain are known to fuel already in southern England and northern France, well before they reach the Sahara desert (Bibby & Green 1981) and our results from Lesvos indicate that Sedge Warblers might prepare well in advance of the barrier crossing also in this area.

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It has recently been shown that the distance to be covered across the Sahara desert, following the two main western European flyways, affects the size of the pre-migratory fuel stores in Swallows Hirundo rustica in Iberia and Italy (Rubolini et al. 2002). Swallows are common during migration in most of the Mediterranean area and it is obvious that they put on high fuel loads in the same way as other long-distance passerine migrants.

Outside the breeding season, Swallows regularly congregate at communal roosts, which often are situated in reed beds. During the visit to Rhodes in the autumn of 2000, we found a roosting site in the vicinity of the hotel area at Lardos on the eastern side of the island. We tape-lured Swallows close to dusk during ten days. The mean body mass varied between different evenings (Figure 6). The mean body mass increased for example by 3.8 grams from 29 September until 3 October, representing an average daily increase of about one gram. After 5 October, the mean body mass decreased, possibly because many heavy birds had continued migration. Our results indicate that large groups of Swallows at this point are synchronised in their fuel deposition. In agreement with this, the estimated daily numbers of Swallows observed at Partira Lake, central Crete, during a four weeks field study suggest that Swallows on Crete have a wavelike pattern of passage (Figure 7).

**Temporal patterns and stopover behaviour**

In Greece, as well as in most of the Mediterranean area, the summers are normally very dry and the first rain arrives in September or later (Handri-nos & Akriotis 1997). Of the species that breed in the Mediterranean area and winter south of the Sahara desert, most leave very early, in July–August, e.g. Olivaceous Warbler Hippolais pallida and Subalpine Warbler Sylvia cantillans (Handri-nos & Akriotis 1997). The area south of the desert receives rain during the northern summer (cf. Moreau 1972) and birds might take advantage of this by an early arrival. Accordingly, few birds of these species were observed during our fieldwork. The Turtle Dove is a relatively common passage migrant in Greece and the number of birds observed at Partira Lake on Crete in 2002 clearly shows that the majority of these birds have left this area after the beginning of September (Figure 8). In 2001, fieldwork was started on the mainland of Crete and the focus of this work has been to find out where first-year Garden Warblers fuel in relation to the oncoming barrier crossing. All Garden Warblers are heading for wintering areas in sub-Saharan Africa and they are therefore more suitable to study than Blackcaps. The wintering habit of Blackcaps is complicated, with birds staying both in the Mediterranean area and in eastern Africa. For comparison, data has also been collected by Dr T. Akriotis and colleagues from Garden Warblers on Lesvos, which is about one
night of migration (400 km) to the north (Figure 2). Tape-lures have been used to attract and trap Garden Warblers in order to collect morphometric measurements. A total of 557 Garden Warblers have so far been trapped on Crete and the peak of first-year birds migration on the island is in the second week of September. The body mass varies drastically (13.3–32.8 g) indicating that birds in very different states of preparation are found on the island. The passage of adult birds is clearly earlier than the passage of first-year birds, which has also been shown for the autumn departure in Sweden (Fransson 1995). It is obvious that it takes some time to build up a large fuel load and it is interesting that an adult bird, weighing as much as 29.5 g, was trapped as early as on 30 August 2003. The first Garden Warblers are also found south of the desert around the beginning of September (Ottosson et al. 2005). To get more detailed information about the stopover behaviour in these Garden Warblers, a study using small radio transmitters (<0.5 g) has recently been initiated.

Seasonal frugivory is common in many migrants and the fact that fruits have a high content of fatty acids facilitate fuelling (Bairlein 2002). Garden Warblers are known to often eat figs Ficus carica during migration (Thomas 1979, Handri- nos & Akriotis 1997) and it has become very clear during our fieldwork and from the birds attached with radio transmitters that they are strongly attracted to fig trees during autumn stopover periods on Crete. In 2004, when at some occasions we put mist nets around single fig trees it happened that, without using tape lure, we trapped more than ten Garden Warblers during a morning. Handrinos & Akriotis (1997) pointed out that the peak of Garden Warbler migration pass Greece after the end of the main fig season, but on Crete figs regularly seem to be available until the end of September.

**Future research**

Several studies have been conducted in the desert of Egypt, Algeria and Mauritania, but few detailed studies have so far been carried out close to the desert, where many birds prepare for the extensive passage (but see Bairlein 1987, Ottosson et al. 2002, Ottosson et al. 2005). Such studies will be of great importance in order to improve our understanding about how migratory birds, including many Swedish breeding birds, prepare for crossing large inhospitable areas, like the Sahara desert. The plan is to continue and intensify these studies in collaboration with Greek colleagues and maybe also include field studies at the coast in North Africa, about one night of migration further south. The effort to ring birds during migration in Greece and Turkey has increased during the last decades. In Greece, regular ringing has been carried out on Lesvos, Antikythera in The Sea of Crete and on Gavdos (T. Akriotis pers. comm.). Gavdos is the southernmost island in Europe and situated south of Crete. In Turkey a new national ringing scheme started in 2002 and ringing of migrants is now carried out at six sites (Ö. Kesapli Didrickson, pers. comm.). These activities are very important and will definitely increase our knowledge about both the temporal and the geographical patterns of bird migration in this area.

**Acknowledgements**

These fieldworks would not have been possible to carry out without the devoted work of several persons. A special thank to Triantaphyllos Akriotis, Christos Barboutis, Michalis Dretakis, Paul Elfström, Milica Iovivic, Nikos Katsimanis and Tuomo Kolehmainen for assisting in the field. Triantaphyllos Akriotis, University of the Aegean, has been very helpful and arranged with ringing permits as well as rings for the work in Greece and a lot of practical assistance when we visited Lesvos in 1997. During the work on Crete, we received very important help and advice from Michalis Dretakis at the Natural History Museum of Crete. Thanks also to Christian Hjort and Åke Lindström for valuable comments on the manuscript. The fieldworks have been financially supported by Helge Ax:son Johnsons foundation, the Swedish Ornithological Society (Danielssons foundation) and the Friendship Association of the Swedish Museum of Natural History.

**References**


**Sammanfattning**

De flesta långdistansflyttande fågelarter som häckar i Sverige övervintrar i Afrika och ungefär 35 småfågelarter har sitt huvudsakliga övervintningsområde i tropiska Afrika. Flest arter flyttar mot sydväst genom Europa (t.ex. rörsångare och rödstjärt), några få flyttar söderut (t.ex. grå flugsnappare) och några flyttar mot sydost (t.ex. nätkegal och svarthätta). För småfåglarna utgör Sahara en barrier på minst 1500 km som måste passeras och där möjligheterna att födosöka är begränsade (Figur 1). De flesta måste därfor lagra upp en stor energiereserv i förväg. Antalet småfåg-
lar som varje höst passerar öknen är enormt stort och antalet har uppskattats till ungefär 5 miljarder. En huvudfråga är hur ungfåglar, som aldrig flyttat tidigare, kan veta var de ska fettupplagra inför ökenpassagen. Resultat från experiment utförda i Sverige antyder att information från jordens magnetfält kan vara en bidragande faktor som styr fåglarna att fettupplagra i rätt område. Omfattande studier har genomförts när det gäller själva ökenpassagen men få studier har utförts av fåglar som förbereder sig för passagen.


Somrarna i Grekland, liksom i en stor del av Medelhavsområdet, är normalt mycket torra och de första regnen dyker inte upp förrän i september eller senare. De fåglar som häckar i området och som flyttar till övervintringsområden söder om Sahara, t.ex rödstrupig sångare och eksångare, flyttar bort redan i juli-augusti och har lämnat området när fåglar från norrliga områden passerar i september. I områdena söder om Sahara fäller regn under sommaren och det kan därför vara fördelaktigt att så tidigt som möjligt anlända till dessa områden. Turturduvä är en vanlig art under flyttningen i Grekland och observationer på Kreta hösten 2002 visar att huvuddelen har lämnat området redan 10 september (Figur 8). Under de senaste åren har arbetet koncentrerats på att studera flyttningen hos unga trädgårdssångare på Kreta och försöka fastställa var de fettupplagar i förhållande till passagen av Sahara. Eftersom alla trädgårdssångare är på väg mot övervintringsområden
i tropiska Afrika är det en lämpligare art att studera än svarthätta, där en del övervintrar i Grekland och en del flyttar till Östafrika. Drygt 500 trädgårdssångare har ringmärkts på Kreta och den huvudsakliga passagen av ungfåglar sker i mitten av september, medan gamla fåglar passerar tidigare. Som jämförelse har grekiska kollegor samlat in biometriska uppgifter från trädgårdssångare på Lesbos som ligger ungefär en nattetapp (400 km) norrut. Vikten hos de fångade trädgårdssångarna på Kreta har varierat mellan 13,3 och 32,8 gram vilket antyder att fåglar i olika stadien av förberedelser förekommer på ön. Att lägga upp en stor fettreserv tar naturligtvis en viss tid och det är därför intressant att en gammal fågel som nästan dubblerat sin vikt och vägde 29,5 g fångats redan den 30 augusti. Att kunna fånga samma fågel vid flera tillfällen är av yttersta vikt när det gäller studier av rastningsbeteende och detta har bara varit möjligt i ett fåtal fall i samband med den vanliga ringmärkningen. För att få mer detaljerad information om hur trädgårdssångarna beter sig på Kreta (rastningens längd, rörelsemönster, viktökning och bortflyttningsvikt) har små radiosändare (<0,5 g) börjat användas med lyckat resultat. Många flyttfåglar äter frukt under höstflyttningen och under arbetets gång, inte minst genom sändarförsett fåglar, har det blivit mycket tydligt att trädgårdssångarna på Kreta är starkt knutna till fikonträd.