When and where to fuel before crossing the Sahara desert – extended stopover and migratory fuelling in first-year garden warblers *Sylvia borin*

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Large numbers of passerine migrants cross the Sahara desert every year on their way to-and-from wintering areas in tropical Africa. In the desert, hardly any fuelling opportunities exist and most migrants have to prepare in advance. A central question is how inexperienced birds know where to fuel. Inexperienced garden warblers *Sylvia borin* were studied in Greece just before the desert crossing in autumn. Body mass data collected at two sites indicate that most birds do not fuel for the desert crossing further north. For the first time, detailed information about stopover duration close to the Sahara desert was studied by using light weight radio-transmitters. Results from Crete show that most first-year garden warblers arrive with relatively small fuel loads in relation to lean body mass (<30%), stay for 13–20 d and depart with an average fuel load of about 100%. Radio-tagged birds performed small scale movements initially and took advantage of fig fruits. Birds trapped at fig trees were heavier than birds trapped with tape lures, showing that tape lures can bias the sample of migrants trapped. The precise fuelling pattern found indicates that first-year migrants must also include external spatial cues to make the preparation for crossing the desert in the right area.

In the western Palaearctic, most long-distance passerine migrations involve crossing a vast ecological barrier, the Sahara desert, covering at least 1,500 km with hardly any possibilities to refuel (Biebach 1990). The problems connected with the desert crossing have been under focus for a long time (Moreau 1961, 1972), and radar studies have shown that most passerine migrants seem to use an intermittent flight strategy when crossing the desert, with flight during night and rest during daytime (Biebach et al. 2000, Schmaljohann et al. 2006). The majority of passerine migrants crossing the Sahara desert need to have extensive fuel loads before they start the flight and it is well known that close to the desert migrants often carry very large fuel loads (cf. Fry et al. 1970, Finlayson 1981, Fransson et al. 2006). It has also been shown that different populations of swallows *Hirundo rustica* show variation in fuel load in relation to the distance that they have to cross before reaching the southern border of the desert (Rubolini et al. 2002). Migration routes of several species passing through the eastern Mediterranean area from northern Europe have been shown to converge at specific areas close to the Sahara desert, areas assumed to be important for the preparation before crossing the desert (Fransson et al. 2005).

One central question is how inexperienced migrants know that they have to put on a very large fuel load in preparation for an oncoming desert crossing, and it has been assumed that this is governed by their endogenous rhythm (Berthold 1996, Gwinner 1996). Much of the migratory program of passerine birds is under endogenous control and fine-tuned by photoperiod (Gwinner 1996). It is, however, believed that this program alone can not guide inexperienced birds during their first migration and that other external cues should be involved as well (Gwinner 1996, Thorup and Rabøl 2001, Jenni and Schaub 2003, Alerstam 2006). To make the appropriate fuelling decision just before crossing the Sahara desert is one detail that has been believed not to be handled by the endogenous program alone (Jenni and Schaub 2003). Thrush nightingales seem to use the magnetic field as a spatial cue and first-year birds experimentally exposed to a magnetic field close to the desert, increased their fuelling as if they were preparing for the oncoming desert crossing (Fransson et al. 2001, Kullberg et al. 2003). Detailed information about fuelling when birds are preparing for the desert crossing, however, is still rare (but see Bairlein 1987, Ottosson et al. 2002, Ottosson et al. 2005). The aim of this study was to
find out where and how inexperienced first-year garden warblers *Sylvia borin* prepare for crossing the Sahara desert in autumn.

**Methods**

Garden warblers were trapped at two different sites in Greece, one northern and one southern (Fig. 1). The northern site was at Charamida (39° 01’N 26° 33’E) on the island of Lesvos, in the eastern Aegean Sea. The southern site was in the central part of Crete, at Partira Lake (35° 07’N 25° 14’E) and sites close to the village of Kalyvia further south (35° 03’N 25° 13’E). The distance from the trapping site on Lesvos to the study area on Crete is about 450 km and the direction is 195° (SSW). Adult garden warblers start autumn migration earlier than first-year birds (cf. Fransson 1995) and since their passage in Greece was not covered adequately, data from adult birds have not been included and hence no comparisons between age classes have been made in this study.

Birds were trapped on Lesvos during the years 1998–2002 and on Crete during 2001–2004. Garden warblers were attracted by tape lures and trapped in mist-nets from dawn until noon. Trapped birds were aged according to Svensson (1992) and weighed to the nearest 0.1 g. Maximum wing length (Svensson 1992) was recorded as a measurement of size. In total, 146 first-year garden warblers were trapped on Lesvos and 414 on Crete by using tape lures. The trapping effort differed between years and the earliest bird was trapped on Lesvos on 30 August and the latest on 11 October, while on Crete birds were trapped between 30 August and 5 October. In 2004, field work was carried out during the period 3–29 September and during this period a further 45 garden warblers were trapped during eight days at fig trees *Ficus carica* close to the village of Kalyvia on Crete, without the use of tape lures.

Light-weight radio transmitters (Holohil Company Ltd. in Canada) were used on 22 first-year garden warblers in the autumn of 2004 in order to find out details about stopover behaviour. The radio transmitters were attached with glue to trimmed feathers on the back, weighed approximately 0.5 g and had a minimum life-span of 21 d (model BD-2N). All the birds tagged with radio transmitters were trapped with tape lures at a site close to the village of Kalyvia during the period 3 to 14 Sept. The habitat at the trapping site did not differ from that of the surrounding area and several fig trees were found in the neighbourhood. To be able to compare individuals and to get garden warblers assumed to be newly arrived, birds with small amounts of visible fat were chosen for radio tagging. Body mass of the 22 radio-tagged birds varied between 16.4 g and 19.7 g (mean 18.16 g). Radio-tagged birds were searched for every day and approached for an exact location within an area of about 5 × 7 km by using a hand-held receiver (RX-98X, Televilt positioning AB) connected to a four element antenna. The transmitters were normally only heard up to a distance of about 3 km. One transmitter fell off one bird and one other had its antenna broken and was not possible to follow in detail. In order to get information about body mass gain in radio-tagged birds three individuals were recaptured intentionally. A multiple linear regression analysis was applied (Schaub and Jenni 2000b) to estimate the body mass increase during the day (Dtime; g h⁻¹), and the body mass deposition rate (Ddate; g d⁻¹), for all recaptures after the third day since the initial capture. The model was designed to have a zero intercept, since the difference in body mass or fat stores is zero if there is no time difference between two capture events. The maximal model included a quadratic term for time of day in order to account for non-linear body mass gains. Size specific lean body masses estimated for garden warblers (Ellegren and Fransson 1992) have been used when calculating fuel load. According to these estimates garden warblers with a wing length of 80 mm have a lean body mass of 15.6 g and the lean body mass change by 0.32 g per mm wing length. Means are presented ± SD.

![Fig. 1. Map showing the two trapping sites in Greece and the body mass distributions of first-year garden warblers trapped with tape lures at the two sites.](image-url)
Results

Wing lengths of first-year garden warblers did not differ between Lesvos and Crete (79.53 ± 2.02 mm, n = 146 and 79.68 ± 1.62 mm, n = 414, respectively, \( t_{558} = 0.89, P = 0.35 \)). Body mass varied between 15.7 g and 29.6 g on Lesvos and between 13.3 g and 30.1 g on Crete (Fig. 1). The mean body mass differed significantly between the two sites (\( t_{556} = 2.72, P = 0.007 \)), and were 20.61 ± 2.47 g (n = 146) on Lesvos and 19.92 ± 2.67 g (n = 412) on Crete. The mean size-specific fuel loads in relation to lean body mass of garden warblers trapped were 33.0 ± 0.16% and 28.5 ± 0.2% on Lesvos and Crete respectively. The within-season pattern of body mass in first-year birds showed no variation at either Lesvos or Crete (linear regression with day of season as dependent variable; \( r^2 = 0.03, b = -0.13, n = 146, P = 0.10 \) and \( r^2 = 0.00, b = 0.003, n = 412, P = 0.96 \), respectively). Wing length did not vary with time of season at either of the two sites.

Only one of the birds attached with a transmitter disappeared after the first day. Another five birds disappeared from the area after 3–10 d. The remaining 14 birds stayed in the study area for 13–20 d (median 15 d) before their signals were lost and they were expected to have left on migration for barrier crossing (Fig. 2). During the first 9 d, movements of more than 1 km from one day to another were found in some of the birds (Fig. 3). It is therefore possible that most of the birds disappearing during the first 10 d after radio-tagging moved out of the study area, rather than departed on migration. Similar habitat is found also outside the study area where we had no possibility to regularly search for radio-tagged birds. There was no significant relationship between initial body mass and stopover duration in birds staying longer than 10 d, even though there was a tendency for lighter birds to stay longer (\( r_s = -0.37, n = 14, P = 0.19 \)). All of the birds that stayed for a longer period were found in a confined area from day 10 onwards. Almost all of the radio-tagged garden warblers were located in close connection to fig trees with ripe fruit during their stay. The last locations of most birds were within 2 km from the site where they were radio-tagged and the longest distance was about 5 km (Fig. 3).

Trapping at four different fig trees in September 2004 (within 2.5 km from the tape lure trapping site) resulted in 45 first-year garden warblers, out of which seven had initially been trapped using tape lures. The mean body mass of the garden warblers at fig trees was 3.5 g higher than the mean body mass of garden warblers trapped with tape lures in the same autumn, 23.2 ± 3.6 g (n = 45, Fig. 4) and 19.57 ± 2.4 g (n = 140), respectively (\( t_{183} = 7.75, P < 0.001 \)). The trapping at fig trees resulted in a number of recaptures that gave information about fuelling rate during the stopover. Seven garden warblers, initially captured with tape lures, were recaptured 3–11 d later at fig trees and they showed a mean increase of 0.63 ± 0.50 g d\(^{-1}\). The same figure in seven garden warblers captured in fig trees and recaptured at the same place after 3–11 d was 0.99 ± 0.39 g d\(^{-1}\). The difference between these two groups was not significant (\( t_{12} = 1.5, P = 0.15 \)). There was no difference between the two groups in the elapsed time between ringing and recapture (\( Z = 0.45, P = 0.71 \)). Three of the radio-tagged birds were recaptured (after 9, 11 and 18 d) and the mean increase was 0.74 g d\(^{-1}\), which shows that they were similar to birds not tagged with radio transmitters. One of the radio-tagged birds was recaptured twice, after 12 and 18 d, respectively. During the first 12 d it increased in body mass by 0.54 g d\(^{-1}\) while for the last

Fig. 2. The numbers of days that radio-tagged first-year garden warblers were followed in a study area on southern Crete in the autumn of 2004.

Fig. 3. The 2004 study area in southern Crete showing the sites where radio-tagged birds that stayed longer than 12 d were found on their last day (squares) in relation to the trapping site (star). Lines show movements of two radio-tagged birds and beside the lines are the days since the first capture.

Fig. 4. The body mass distribution of first-year garden warblers trapped close to fig trees (black bars) and with tape lures (grey bars) in southern Crete in the autumn 2004.
6 days the increase was 1.0 g d$^{-1}$. The body mass at the last trapping occasion was 29.8 g and it disappeared two nights after this trapping. The combined recapture data of 17 garden warblers show that they gained body mass with an average rate of 0.72 g d$^{-1}$ according to the multiple linear regression analysis approach ($r^2_{\text{adjusted}} = 0.823$, $F_{3,13} = 28.9$, $P < 0.001$). The increase during the day (Dtime: g h$^{-1}$) was not significant and this could partly depend on that most birds were trapped during the same period of the day.

The estimated departure body mass of first-year garden warblers from Crete was based on radio-tagged birds that stayed longer than 12 d by using their initial body mass, the stopover duration and the mean value of daily body mass increase based on recaptures (0.72 g d$^{-1}$). Since all birds were trapped in the early part of the day we added one gram to get an estimated evening body mass, which is the amount of daily body mass increase found in birds of this size when body mass is stable (Fransson unpubl. data). The mean departure body mass was then estimated at 30.3 ± 1.43 g (range 27.3–32.7 g, $n = 14$, Fig. 5) and the mean departure fuel load in relation to size specific lean body mass for the radio-tagged birds was estimated at 96 ± 10.8% (range 75–115%, $n = 14$).

**Discussion**

To our knowledge, this is the first time that complete stopover periods in passerine birds have been followed in detail by using lightweight radio-transmitters before crossing the Sahara desert. The results clearly show that inexperienced first-year garden warblers have a very precise fuelling strategy in front of the Sahara desert in this area. Most of the first-year garden warblers seem to arrive in Crete with rather small fuel loads, stay for more than two weeks and take off with an average fuel load close to 100% of the lean body mass. The garden warbler is known to fuel extensively before crossing the Sahara desert both in spring and in autumn (photo in Perrins 1974, Bairlein 1987, Bairlein 1991, Ottosson et al. 2005). Both in Algeria in autumn and in Nigeria in spring a few garden warblers have been found to stay for more than 20 days (Bairlein 1987, Ottosson et al. 2005).

The fact that first-year garden warblers trapped on Crete were lighter than on Lesvos, a distance of about one night of migration to the south, might indicate that most continue south in Greece without fuelling to any greater extent. If birds prepare for the desert crossing further north and pass Crete without fuelling on their way south it is reasonable to believe that many of them have to land on Crete during daytime after covering a sea crossing from the north (see Fig. 1) and therefore should have appeared in the trapping as very heavy birds to a larger extent then actually found. If garden warblers prepare for the desert crossing one or two migratory flights further north, the departure fuel load from those sites is expected to be clearly larger than the one estimated on Crete, especially since the diminishing return of flight distance with an increasing fuel load is obvious when the fuel load is above 100% (Alerstam and Lindström 1990). A small proportion of garden warblers on both Lesvos and Crete was found with large fuel loads and it is not clear what strategy these birds use.

The average body mass in garden warblers trapped with tape lures on Crete is very similar to average values found in central Europe, for example 19.8 g in southern Germany, as well as in the Mediterranean area (Bairlein 1991). The difference found on Crete between birds trapped by tape lures and close to fig trees is probably a result of newly arrived birds being easier to attract by tape luring than birds that have settled and started to fuel. This is interesting and shows that trapping with tape lures at this stage biases the sample of migrants trapped. It is also in line with findings by Schaub et al. (1999) that captures when using tape lures include many birds that had performed a migratory flight the night before. The fact that a majority of the radio-tagged garden warblers stayed in the area and only one disappeared the following night indicate that most of them do not continue quickly to the Libyan coast in North Africa, which is about one night of migration further south. The Sahara desert is close to the coast in Libya and in autumn, after the dry summer period (cf. Moreau 1961, 1972), it is uncertain whether it would be possible for garden warblers to fuel in this area.

When long-distance migrants pass through Europe they most often carry relatively small fuel loads (about 20–30% of lean body mass) and this has been assumed to be a result of large fuel loads increasing flight costs, impairing predator avoidance as well as increasing the costs of foraging and maintenance (Alerstam and Lindström 1990, Klaassen and Lindström 1996, Kullberg et al. 1996). The mean stopover duration in garden warblers during autumn migration at 16 stopover sites in Europe and Northwest Africa has been estimated to be 7.7 d (Schaub and Jenni 2001). Even if different methods have been used, the stopover duration found in this study is about twice as long and it indicates that garden warblers switch from a program that they have followed on their first part of migration southward to a program preparing for the desert crossing. Garden warblers have been shown to increase their average body mass along the migration route south in autumn and this increase was found to be larger in eastern birds (Bairlein 1991, Schaub and Jenni 2000a). The successive increase in body mass towards the south has been seen as a preparation for the
oncoming barrier crossing and the larger increase in eastern birds a result of their having to cross the most inhospitable area of the Sahara (Schaub and Jenni 2000a). In spite of this increase in body mass towards the south it is clear from the results found in this study that most of the fuel needed for the crossing is accumulated close to the Sahara desert in this area. It is reasonable to believe that migrants about to fuel in preparation for a barrier crossing select species-specific habitats that can fulfil their energetic requirements (cf. Moore and Aborn 2000). Fig trees are widespread in most of Crete (Turland et al. 1993), as well as the whole of Greece, normally occurring as single trees or small clumps scattered across the landscape and this is also true in the study area. Schaub and Jenni (2000a), pointed out that they could not find the expected high body masses close to the desert in some species when analysing data from a wide range of trapping sites. They believed that this might depend on high body masses being probably attained at specific places, only a few days before departure and therefore not easily detected.

Even if the number of birds recaptured is low, the fuel deposition rate found in birds initially trapped with tape lures and later recaptured at fig trees tended to be lower than the fuel deposition rate in birds initially trapped in fig trees and recaptured in fig trees. When migratory birds arrive to a new stopover site, it has been suggested that it may take some time before they start gaining body mass because of a period of search and settling (Alerstam and Lindström 1990, Chernetsov 2006). The small scale movements found in radio-tagged birds during the first part of stopover can very well have been a result of searching for suitable places to stay, resulting in a likely lower fuel deposition rate initially as well as in some birds moving out of the study area. We regularly observed that several garden warblers fed in a single fig tree and on one occasion we estimated that about 20 garden warblers used the same tree in one morning. The fact that many garden warblers regularly used the same fig tree might also result in competition, even if no sign of this was observed by us, forcing birds to search for other feeding places. The strong connection to fig trees is in accordance with earlier findings (Thomas 1979) and the garden warblers’ well known seasonal frugivory, where figs have been found to be highly effective as food source during fuelling (Bairlein 2002). The findings in this study could have implications for nature conservation since it show that habitats close to the desert can be of decisive importance for birds’ possibility to successfully cross the desert and studies in these areas are therefore essential to carry out in the future. It remains to be studied if the pattern found in the garden warblers in this study also exist in other species in this area.

There are still unresolved questions with respect to the spatiotemporal program of bird migration, and this is especially evident when it comes to barrier crossing in passerine birds (Piersma and Lindström 2002, Jenni and Schaub 2003, Alerstam 2006). The fine-tuned pattern observed in this study clearly indicates that first-year garden warblers in this area must also include information from external spatial cues when fuelling in front of the Sahara desert.

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