Ibis (2005), **147**, 750–757

Garden Warbler *Sylvia borin* migration in sub-Saharan West Africa: phenology and body mass changes

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The Garden Warbler is a classic subject for the study of Palaearctic–African bird migration strategies. Most studies have considered the situation close to the breeding areas, while the African and especially the sub-Saharan part of the species' migration have received comparatively little attention. Here we use autumn and spring ringing data from Nigeria and The Gambia to study the movements and energetics of the species in West Africa during the non-breeding season. The first Garden Warblers arrive south of the desert around the beginning of September, roughly at the same time as the median date for their passage through the Baltic Sea region and *c.* 3 weeks before their median passage date through southern Italy. In the Nigerian Sahel savannahs, where, owing to the rainy season and its associated increase in food availability, many more Garden Warblers stop over in autumn than in the dry spring, the median date of passage is 1 October. The body mass on arrival south of the desert is normally only a few grams more than the lean body mass (LBM; 15 g) – with a mean of 16.6 g (sd = ±1.8 g) in The Gambia and 17.4 g (sd = ±1.8 g) in the Nigerian Sahel. After resting and refuelling in the Sahel, Sudan and Guinea-type savannahs the Garden Warblers depart during November–December for wintering areas further south. Before leaving, they again increase their body mass, with an average fuel load of *c.* 20%, and often more than 50% relative to LBM. Some of the birds passing through Nigeria probably spend midwinter around the Congo Basin. During spring they return northwards to the Guinea savannah zone in April and fuel-up there for the trans-Sahara passage. At this time they normally increase their body reserves to around 50% of the LBM, but *c.* 10% of the birds gain 100%, thus doubling their mass. The passage there peaks around 20 April and continues well into May. That the main take-off northwards is directly from the Guinea savannahs is indicated by the very low numbers trapped in the Sahel during spring.

The Garden Warbler *Sylvia borin* is probably the best studied long-distance migrant passerine in the Old World and has been a focal species for many studies (e.g. Bairlein 1991, Fransson 1995, Grattarola *et al.* 1999, Schaub & Jenni 2000a, 2000b). However, the African, and especially the sub-Saharan part, of its migration are still comparatively little known. The aim of this paper is to add to this information.

The journey between breeding and wintering grounds must be divided into shorter steps, as the total energy demand needed to complete each biannual migration leg exceeds the amount the bird can store and still fly (e.g. Alerstam & Lindström 1990, Weber *et al.* 1994). The fuel used for the migration is mainly fat, which is accumulated immediately prior to the periods of higher demand, and especially before the passage over ecological barriers such as the Sahara (Bairlein 1991, Phillips 1994, Stoate 1997, Schaub & Jenni 2000a, 2000b, Totzke *et al.* 2000, Ottosson *et al.* 2002).

With regard to the migratory journey itself, and especially the passage over the Sahara, different logistic theories have been put forward, including non-stop flights, intermittent flights (flying during nights, sheltering in shade during the heat of the day),

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or migration along particularly favourable routes, e.g. using oases as stopovers (Lavee *et al.* 1991, Bairlein & Totzke 1992, Biebach *et al.* 2000, Klaassen & Biebach 2000).

Results from the large-scale Italian ringing scheme Progetto Piccole Isole (Spina *et al.* 1993) showed that Garden Warblers in spring migrate on a broad front across the Mediterranean Sea, and although largely nocturnal, they also have to migrate during daylight hours when passing this broad ecological barrier (Grattarola *et al.* 1999). During autumn migration some refuelling occurs in the Algerian oases, but the birds doing this seem too few to represent a significant part of the population (Bairlein 1985, 1988).

Thus, we assume that during the flight over the Mediterranean Sea and the Sahara there are no possibilities to feed en route for the majority of Garden Warblers, and most other desert-crossing species. In the autumn there are also limited possibilities for feeding on the North African coast (Bairlein 1991, Schaub & Jenni 2000a, 2000b), but conditions there are much better in spring, after the winter rains (Grattarola *et al.* 1999). With a fat-free lean body mass of *c.* 15 g (Bairlein 1987), the required body mass for crossing the Sahara and the Mediterranean Sea has been variously suggested as: (1) more than 22 g, on the basis of comparing departure mass and arrival mass from different sites along the migratory route (Bairlein 1985, 1988, 1991, Totzke *et al.* 2000); (2) more than 27 g with no tail-wind assistance, using Pennycuick's model in still air with re-estimated body drag coefficients (Pennycuick 1989, Pennycuick *et al.* 1996), or less with wind assistance (Spina *et al.* 1993, Pilastro & Spina 1997, Grattarola *et al.* 1999); and (3) 24.7 g from West African data, mainly from Nigeria (Bairlein 1991).

It is important, however, to study the migrants at the 'correct' latitude, as it seems that birds increase to the greatest mass only when close to the border of a major ecological barrier. This was illustrated recently in an experimental setting where Thrush Nightingales *Luscinia luscinia* were monitored in cages under simulated latitudinal migration (Fransson *et al.* 2001).

In the present study we analyse body mass and phenology data from three sites south of the Sahara: (1) Malamfatori near Lake Chad and (2) Amurum near Jos, both in Nigeria, and (3) Ginak Island in The Gambia. We examine the post-desert-crossing body mass in September–October, refuelling in October–November for the continued southward passage, and then the final pre-trans-Saharan fat accumulation in spring. In midwinter, Garden Warblers are mostly south of the areas studied by us, e.g. recoveries of birds ringed on Capri in Italy (Pettersson *et al.* 1990) suggest that many spend that time around the Congo Basin (see also Elgood *et al.* 1994).

MATERIALS AND METHODS

Birds were trapped in mist-nets as part of general ringing programmes at Malamfatori during 1999–2000 (in Sahel-type savannah at 13°33′N, 13°23′E; Ottosson *et al.* 2001) and at Amurum during 2001–04 (in a variety of Guinea-type savannah on the Jos Plateau at 9°53′N, 8°59′E; Vickery & Jones 2002), both in Nigeria, and on Ginak Island in The Gambia during 1994–2000 (in a coastal variety of Sudan-type savannah at 13°40′N, 16°30′W; King 2000) (Fig. 1). Timing and duration of ringing activities changed from year to year, but at Malamfatori the whole spring and autumn seasons were sampled in 2000. At Amurum, since November 2001, regular ringing has been based on a Constant Effort Site programme, with additional trapping effort during migration time. In The Gambia, ringing activities also varied between years. The numbers of Garden Warblers trapped each season at each site are summarized in Table 1.

Trapped birds were ringed and standard measurements, such as wing length and body mass, were

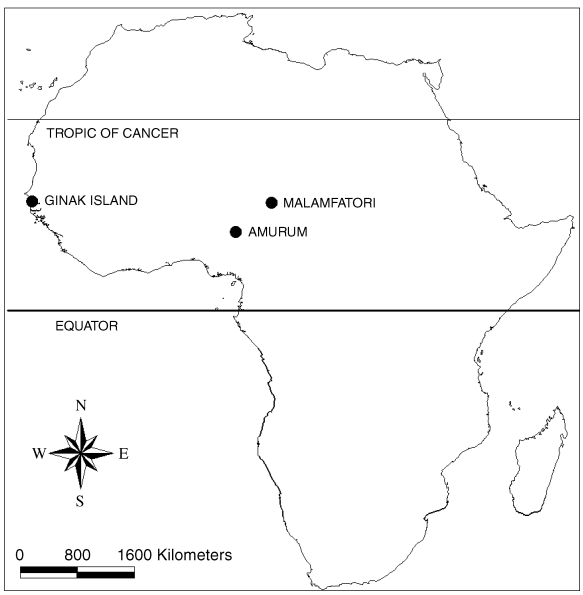

Figure 1. Africa with positions of the ringing sites.

Table 1. Numbers of measured Garden Warblers at each study site and study period.

Site	Period	Year	No. measured
Malamfatori, Nigeria	2 April–24 April	1999	0
	17 February–10 May	2000	14
	22 August–9 November	2000	49
Amurum, Nigeria	8 November–28 November	2001	14
	11 December–20 December	2001	0
	3 March–21 April	2002	34
	6 November–14 December	2002	18
	27 February–20 May	2003	162
	9 August–15 September	2003	6
	17 October–11 November	2003	61
Ginak Island, The Gambia	21 September–31 December 1 January–20 April (coverage varying between years)	1994–2000	537

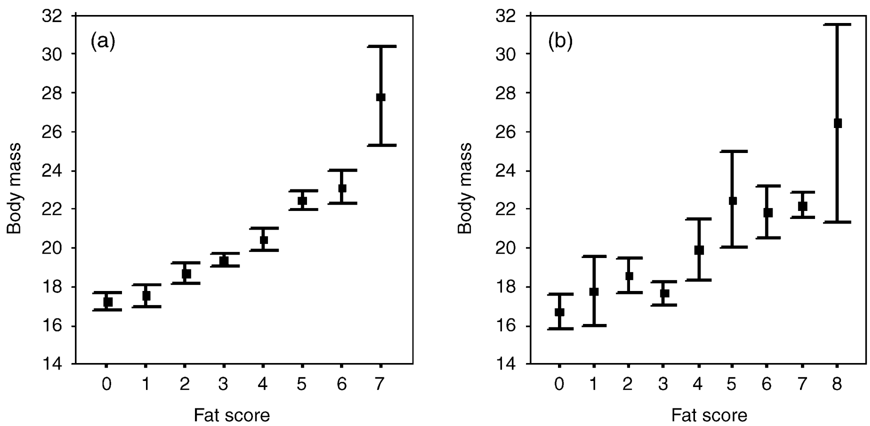

Figure 2. Ninety-five per cent confidence limits for the mean body mass (g) in relation to fat score of Garden Warblers trapped at (a) Amurum, Nigeria, and (b) Malamfatori, Nigeria.

taken. In addition, fat scores were taken at the Nigerian sites but not in The Gambia. Two different scales were used for determining fat loads: at Malamfatori the modified scale of Hasselquist and Pettersson (1985; ten scores) was used, and at Jos fat was scored according to the scale of Kaiser (1993, nine scores) (see also Bairlein 1995). The relationships between body mass and fat scores at the two Nigerian sites are shown in Figure 2.

Following Alerstam and Lindström (1990) we describe the size of fuel stores, and the rate at which they were deposited, as a proportion of lean body mass (LBM), i.e. the body mass of a bird carrying no migratory fat. We have found no data for LBM based on dissected birds, but based on low body masses Bairlein (1987) and Grattarola *et al.* (1999) estimated the average LBM of Garden Warblers to be 15.0 g.

All statistical analyses were performed using SPSS (SPSS Inc. 2001).

RESULTS

Phenology in the Sahel and Guinea savannahs

Autumn

In 2000 the first Garden Warbler on autumn migration through the Sahel zone was trapped at Malamfatori on 31 August, 13 days after trapping had started (18 August). In September and throughout the autumn, Garden Warblers were then trapped in small numbers until ringing ended on 10 November (Fig. 3). Median date of passage was 1 October (n = 49). The Garden Warblers

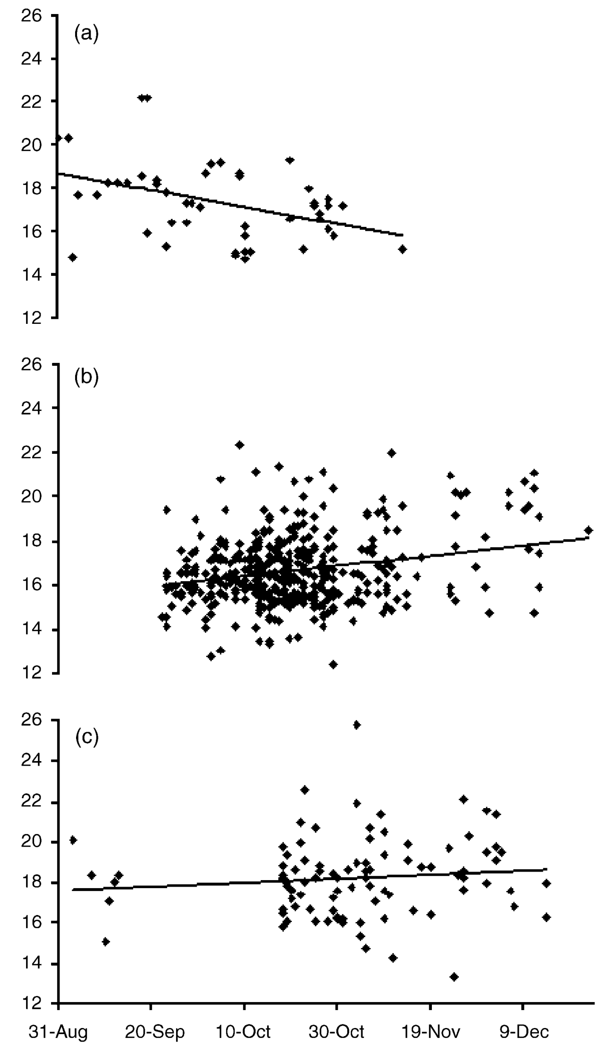

Figure 3. Body mass (g) in relation to trapping date for Garden Warblers in autumn at (a) Malamfatori, Nigeria, (b) Ginak Island, The Gambia, and (c) Amurum, Nigeria. Trend lines have been fitted to the data points.

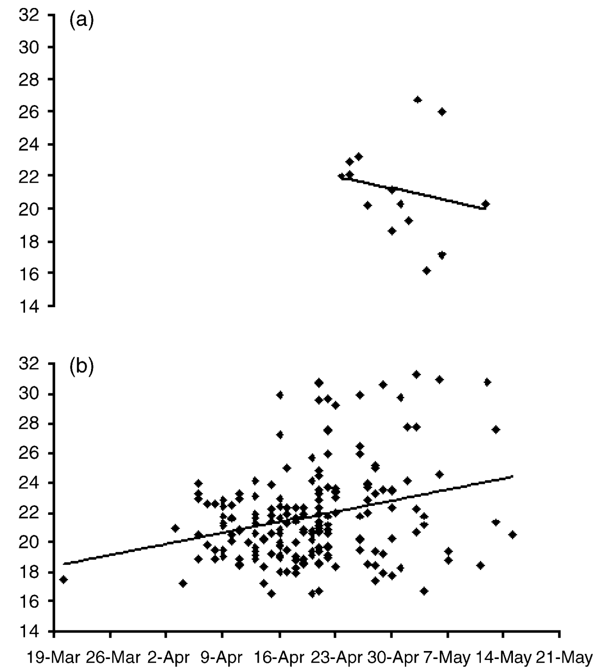

Figure 4. Body mass (g) in relation to trapping date for Garden Warblers in spring at (a) Malamfatori and (b) Amurum, Nigeria. Trend lines have been fitted to the data points.

gradually moved out of the area, probably continuing their migration.

On Ginak Island in The Gambia, in coastal Sudan savannah, the earliest Garden Warbler was trapped on 21 September and a few individuals were then trapped daily through the rest of that month (cumulative sum by date based on 7 years of trapping). The majority were, however, trapped in October, with 15 October being the median date for passage ($n = 441$). In November the numbers gradually diminished, but a few were trapped well into December, the last on 17 December.

At Amurum, situated in Guinea savannah at a latitude about 400 km south of Malamfatori and Ginak Island, earliest trapping was on 3 September in 2003, the only year so far with such early coverage. Trapping coverage was, however, not complete for that month, so it is possible that a few individuals occurred throughout September. In October, Garden Warblers became more numerous at Amurum, and the numbers trapped there peaked in October–November (median date 1 November, $n = 98$; Fig. 3). Numbers gradually decreased thereafter, and from late December to the end of March Garden Warblers were only present in very small numbers (R. McGregor unpubl. data).

Spring

During spring the first Garden Warbler at Amurum was ringed on 20 March 2003, 11 days after intensive ringing had started. This bird was in remex moult, and therefore was likely to have been in the area for some time. No other Garden Warblers were trapped until 3 April, after which numbers increased to a peak in the second half of that month (median date 19 April, $n = 196$; Fig. 4). Migration continued into May, with birds still being trapped on 15 May, the last day of trapping (10% of the Garden Warblers at Amurum in spring were trapped in May).

Despite continuous trapping during spring 2000, only 14 Garden Warblers were trapped at Malamfatori, all in the period 22 April–9 May (Fig. 4). No Garden Warblers were trapped on Ginak Island during spring migration, despite six years of ringing effort, but two, probably wintering, birds were trapped in late January and early February.

Body mass changes in relation to migration

Body mass was positively correlated with fat score, both at Amurum (Pearson $r = 0.797$, $n = 292$, $P < 0.001$; Fig. 2a) and at Malamfatori (Pearson $r = 0.451$, $n = 60$, $P < 0.001$; Fig. 2b), confirming that increased mass reflected increased fuel reservoirs. The difference in mean values for the fat scores 0 and 7 at Amurum (17.2 and 28.5 g, respectively) corresponded to *c.* 75% of the estimated LBM (15 g) of the species. The highest body mass measured in this study was 31.3 g (at Amurum), which is more than twice the LBM.

Autumn

Body mass in autumn showed a significant decline over time at Malamfatori (Pearson $r = -0.409$, $n = 49$, $P = 0.040$), whereas the opposite was true both on Ginak Island in The Gambia (Pearson $r = 0.241$, $n = 441$, $P < 0.001$) and at Amurum in Nigeria (Pearson $r = 0.107$, $n = 98$, $P = 0.293$). The mean body mass in autumn was lowest on Ginak Island (16.6 g, $n = 441$), intermediate at Malamfatori (17.4 g, $n = 49$) and highest at Amurum (18.2 g, $n = 98$); these represent a significant difference between the sites (one-way ANOVA, $F = 40.90$, $df = 2$, $n = 588$, $P < 0.001$). However, at all sites a proportion of the individuals had high body masses (> 22 g; Malamfatori 4.1%, Amurum 3.1%, Ginak Island 1.2%). These reserves, equivalent to 45–50% fuel reserves or more, would be sufficient for prolonged migratory flights, possibly up to 2000 km in still air according to the Pennyquick model (Pennycuick 1989, Pennycuick *et al.* 1996), assuming a wing span of 239 mm, an aspect ratio of 5.4 and an assumed fuel energy density of 30 kJ/g (Grattarola *et al.* 1999). The highest noted body mass in autumn was 25.8 g, for a bird at Amurum retrapped on 3 November. When first trapped on 18 October, it had a mass of 18.4 g, thus giving an average increase in body mass of 0.65 g per day, which is *c.* 4.3% of LBM.

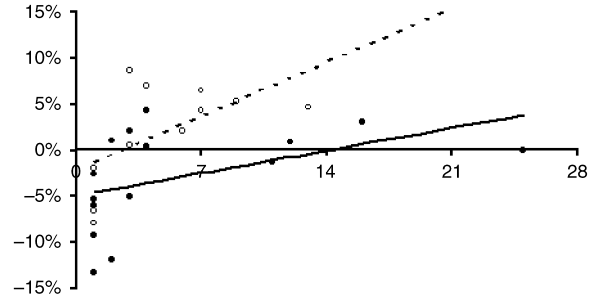

Figure 5. Mass changes in Garden Warblers from first capture to day of retrapping. The change per day (%) in relation to lean body mass is shown on the *y*-axis, and the number of days from first capture on the *x*-axis. Data from autumn are filled circles with a solid trend line, and data from spring are open circles with a dashed trend line.

Spring

Most body mass data from the spring were obtained at Amurum (Fig. 4). Body mass here increased with date (Pearson $r = 0.284$, $n = 196$, $P < 0.001$), which it did not at Malamfatori (Pearson $r = -0.190$, $n = 14$, $P = 0.516$). The data set from Malamfatori, however, was rather small. The mean body mass at Amurum in spring was 21.8 g ($n = 196$), and 35.7% of the Garden Warblers had a body mass exceeding 22 g; 9.2% exceeded 27 g (Fig. 4). As noted above Garden Warblers clearly utilized the Amurum area as a refattening site during the northbound spring migration, and from being nearly absent there in winter appeared in large numbers in April and into May.

Recaptures

Data are available for 15 individuals in autumn and 11 in spring (Fig. 5). The time between first capture and last recapture varied between 1 and 25 days (mean 5.4 days). Generally, fuel deposition rate (mass change per day in per cent of LBM) was negative during the first 2 days after initial capture, but positive on the following days. The initial dip in body mass could be attributed to trapping and handling effects, or to settling effects in a new environment (cf. Gosler 2001, Schwilch & Jenni 2001). Numerically, the mass gain rate was higher in spring than in autumn, with the highest recorded rate being 8.7% of LBM per day in spring and 4.3% in autumn, but the paucity of data precluded further statistical analysis.

DISCUSSION

Ringing data from our three sub-Saharan sites in West Africa document the phenology of Garden

Warbler migration, after the desert crossing in autumn and prior to it in spring. The first individuals appeared south of the desert in late August, at a time when the majority of Garden Warblers in Europe have not left the breeding areas (the median autumn trapping date at Ottenby in Sweden is 3 September and on Capri in southern Italy is 25 September; Ottenby and Capri Bird Observatories unpubl. data). As the autumn progressed, Garden Warbler numbers in Nigeria and The Gambia peaked in October after which they decreased. However, some birds were still found at these northern West African sites, at least on Ginak Island in The Gambia and at Amurum in Nigeria, well into the winter (Fig. 3). At Malamfatori, in the Sahel zone of northeast Nigeria, no Garden Warblers were trapped or observed after the autumn passage until mid-April of the next year, except for one bird on 20 February (Gustafsson *et al.* 2003).

The rains in the northern savannah zones usually fall in June–August, which should give benign conditions for migrants arriving from the north. However, after the rains have ceased the environmental conditions soon become harsher, as the dry season proceeds. Our observations indicate that in late autumn the majority of Garden Warblers continue their migration to areas south of both the Sahel and the Guinea savannah zones, as may be indicated by their mean body mass increasing with passage from north to south, and is clearly suggested by the median dates of passage. Birds trapped at Amurum in autumn carried average fuel stores of 21.3% of LBM, enough for a journey of about 900 km, more than the remaining 600 km to the coast of Nigeria where Garden Warblers arrive in December (Urban *et al.* 1997). However, the heaviest birds (weighing *c.* 70% more than LBM) carry enough fat for a journey of 2500 km or more, sufficient to reach the Congo basin, where several Garden Warblers ringed on Capri in Italy have been recovered (Pettersson *et al.* 1990). These birds thus seem prepared for a second leg of migration similar to that observed in Marsh Warblers *Acrocephalus palustris* and Thrush Nightingales in East Africa (Pearson & Backhurst 1976). In West Africa a similar strategy has been described for three *Acrocephalus* warblers, as an adaptation to the oncoming dry season (Bensch *et al.* 1991, Hedenström *et al.* 1993).

In spring, Garden Warblers seem to embark on the trans-Saharan journey directly from the comparatively well-wooded Guinea savannah zone, as judged from the large fuel stores of the birds at Amurum, and from the very small numbers of Garden Warblers trapped at Malamfatori. The strategy suggested here for this woodland species was proposed by Bairlein (1991) and Pilastro and Spina (1997); it differs from the spring migration strategy of a dry-land bird such as the Common Whitethroat *Sylvia communis*, which fuels in large numbers by feeding on berries from the Saltbush *Salvadora persica* in the much more open Sahel savannah before the desert crossing (Stoate & Moreby 1995). No Garden Warblers were trapped on Ginak Island in spring, but here part of the reason for their absence in the ringing data could be an earlier end of ringing activities. However, in 1995 and 1997 ringing at this site continued into April (6 and 20 April, respectively), but no Garden Warblers were trapped.

Both the overall pattern of body mass against date of trapping and the documented changes in mass of recaptured individual birds show that Garden Warblers increase rapidly in mass during April. The speed with which they build up their reserves also seems higher in spring than in autumn, although the samples of retrapped individuals were rather small from both seasons (Fig. 5). The highest observed individual mass gain rate in this study was 8.7% of LBM per day. In a large review of fuel deposition rates found in migrating birds (Lindström 2003), the highest individual gain rate for a Garden Warbler was 12.5% (based on an estimated LBM of 16.0 g).

Earlier studies have suggested what departure mass Garden Warblers performing the trans-Sahara/Mediterranean passage would need to have. These figures span the interval from 22 g to more than 27 g. The figure of 22 g was based on differences in mean body mass values between populations sampled south and north of the barriers during spring migration (Bairlein 1991), and the figure of > 27 g was based on backward counting from spring arrival masses on Mediterranean islands, using the flight model simulation package of Pennycuick (1989) and an approximated flight distance across the barrier (Grattarola *et al.* 1999). Wind assistance during the migration would diminish this higher figure (cf. Hjort *et al.* 1996, Klaassen & Biebach 2000).

The mean body mass at Amurum in spring was 21.8 g, less than the 24.7 g reported from a smaller Nigerian dataset (Bairlein 1991) but still equivalent to a rather high fuel load, 45% of LBM. A closer inspection of the data (Fig. 4) shows that a non-trivial proportion of the trapped birds had very large fuel stores, some with mass more than twice the LBM. It is possible that trapping selects for lean birds in the process of fuelling, rather than for those that have already acquired sufficient stores. The true departure mass may thus be as high as 25–30 g.

To complete the picture of the migratory part of the Garden Warbler's life cycle, further study of the geography, phenology and body mass patterns of its late autumn, midwinter and early spring movements is needed. We suggest that fieldwork in southeastern Nigeria, Cameroon, coastal Gabon and the Congo Basin would achieve these aims.

We would like to thank the staff at A.P. Leventis Ornithological Research Institute (APLORI), especially Dr G.S. Mwansat. U.O. also thanks Dr A.P. Leventis for financial support, as does R.M. who was funded by the Leventis Conservation Foundation. Finance for the Swedish part of the studies at Amurum came from the Danielsson's (Swedish Ornithological Society) and Lars Hiertas Minne's foundations and from Ottenby Bird Observatory. The fieldwork at Malamfatori, within the Lake Chad Bird Migration Project, was also supported to a large extent by Dr A.P. Leventis, with other funding from the Hasselblad and Carl Trygger's foundations and Ottenby Bird Observatory in Sweden, and from Vogelwarte Helgoland in Germany and the Wetland Trust in the UK. Mr P. Hall and Mr Mari Madu gave invaluable organizational help. The Gambia data derive from the Gambia Ringing Project organized by the late J.M.B. King, in which one of us (C.H.) took part. The data have been forwarded to us from the Wetland Trust, UK, through Mr C. Matthews. We also thank Dr T. Fransson for discussions and for valuable comments on an earlier version of this manuscript. This is contribution no. 200 from Ottenby Bird Observatory and no. 12 from APLORI.

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Received 17 June 2004; revision accepted 10 June 2005;
first published online: 30 August 2005;
DOI: 10.1111/j.1474-919x.2005.00460.x.