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Department of Zoology, Physiological Ecology Section, University of Köln

Body mass of Garden Warblers *(Sylvia borin)* on migration: a review of field data*

By Franz Bairlein

Abstract. BAIRLEIN, F. (1991): Body mass of Garden Warblers (*Sylvia borin*) on migration: a review of field data. – Vogelwarte 36: 48–61.

The paper reviews body mass data for Garden Warblers from 72 different trapping sites during migration, ranging from northern Sweden to South Africa. On southward migration in autumn, the most substantial fat accumulation as reserves for crossing the Sahara seem to take place either in NW-Africa for birds migrating via Iberia and NW-Africa, or north of the Mediterranean Sea in populations migrating farther east across the central and eastern Mediterranean basin. Birds on autumn passage in E-Africa appear to fatten again before emigrating to more southerly wintering grounds. The maximum level of fat deposition before starting to cross the desert seem to be similar in autumn and spring, although spring fattening is likely to occur some distance south of the desert edge. Before continuing migration north, spring passage migrants regain body mass in the Mediterranean basin after their crossing of the Sahara.

Key words: Garden Warbler *(Sylvia borin)*, migration, body mass, fat deposition.

Present address: Institut für Vogelforschung, An der Vogelwarte 21, D(West)-2940 Wilhelmshaven, FRG

Introduction

One of the most impressive physiological adaptations to long-distance migration in small birds is the deposition of migratory fat (BERTHOLD 1975, BLEM 1980). Fat, which is stored in the bird's body in large subcutaneous deposits, is the principal fuel for migratory flights. The amounts of lipids stored, and the timing of fat deposition varies, within and between species depending on the distance to be travelled and their migration pattern (BERTHOLD 1975, BLEM 1980). In some species, migratory fat deposition exceeds 100 % of non-migratory body mass.

Though the principal facts of migratory fattening seem to be quite well known, only little is known on the amount, and spatial and temporal timing of fattening of freeliving specimens on an individual species level (BIBBY & GREEN 1981, LANGSLOW 1976, MOREAU 1969, PIERSMA 1988, RODRIGUEZ 1985, WOOD 1982). However, such data are a prerequisite for revealing species-specific migration strategies. For instance, if migration is progressive in stages rather than in long hops, little or no fat is needed, whereas, in contrast, much mass (fat) gain is necessary in birds faced with a long crossing of inhospitable areas (HELMS & SMYTHE 1969, LANGSLOW 1976, PIERSMA 1988).

Garden warblers, which breed in Europe and winter in equatorial Africa, have to cross the Sahara desert twice a year during their long-distance migrations (KLEIN et al. 1973, ZINK 1973). Though their journey across the Sahara appears to be progressive, with regular stopovers in the desert (BAIRLEIN 1985, 1988a, 1990a, BIEBACH 1990, BIEBACH et al. 1986), successful migration across that barren area depends on a substantial fuel on board prior to embarking on the trans-Saharan crossing. This means that the birds are independent of the limited feeding areas for migrants within the desert, although some specimens may benefit from the food available in the oases.

However, little is known on the spatial pattern of migratory fattening in Garden Warblers at various points along the migration route. Therefore, the objectives of the present paper are to review body mass data of Garden Warblers caught at various points along their migratory routes both in autumn and spring, and in their African winter quarters, and to draw some conclusions on the migratory strategy of this species.

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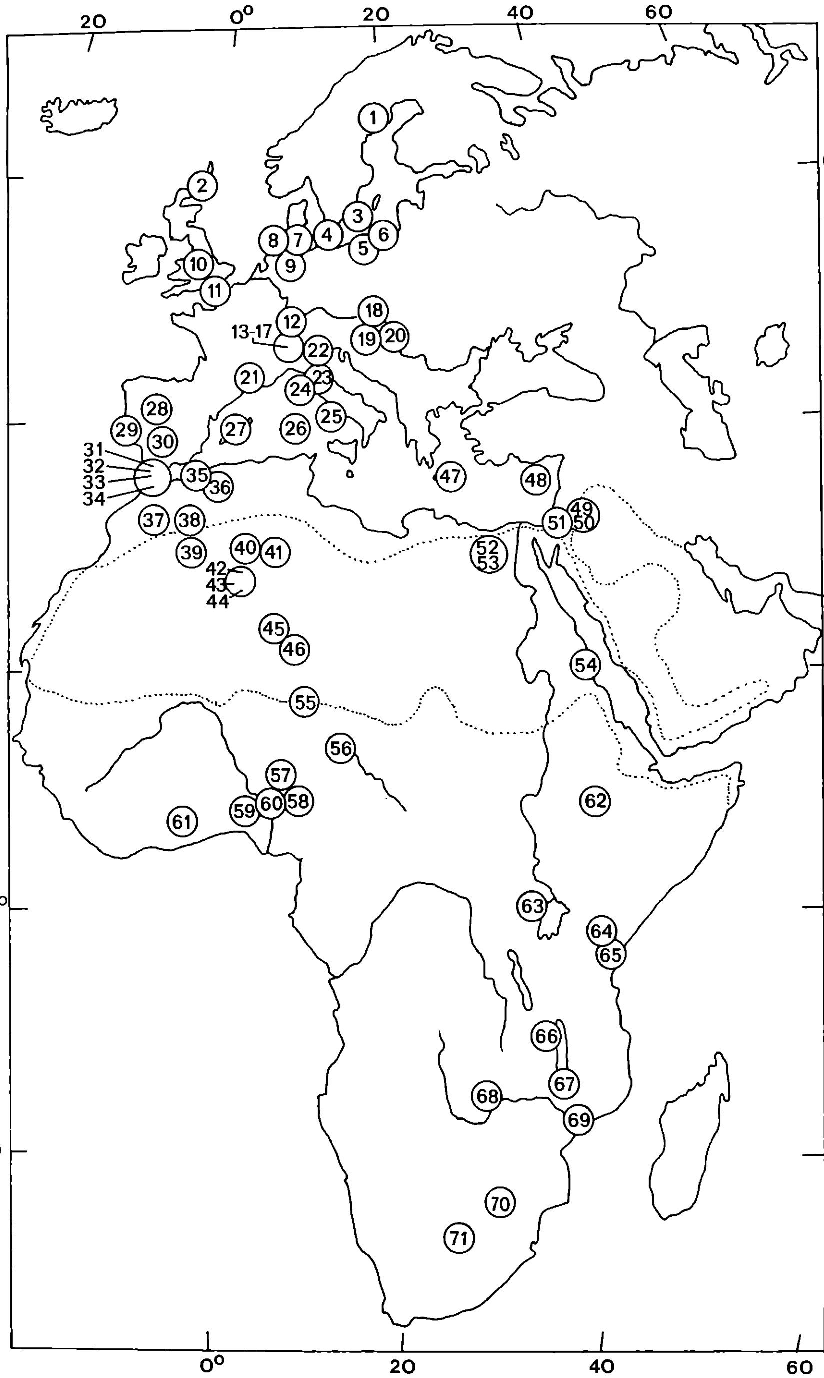

Fig. 1: Map showing the various sites from which body mass data are available.

Abb. 1: Lage der Untersuchungsorte, von denen Daten zur Verfügung standen.

Material and methods

The sources of information for the current review are both published and, in particular, many unpublished reports on body mass of Garden Warblers taken at many sites during migration and in the wintering areas. These data were compiled without further transformation or correction for body size or time of day when the bird was caught since, in most cases, appropriate data are not reported.

Comparisons of body mass data taken at various sites or in different seasons may be biased due to factors such as age, size, food availability, time of day, season of the year or inter-year variation (e.g. CLARK 1979), or, presumably, because of different populations are involved in different seasons or at different sites. However, the geographical body size variations in Garden Warblers are small (BAIRLEIN 1991), resulting in only minor errors. Furthermore, a few examples (Vom/Nigeria: SMITH 1966; Imesi/Nigeria: LUDLOW 1966; Camargue/S-France: BAIRLEIN & HOFFMANN in prep.) showed that fall and spring birds trapped at the same site are of the same population. Moreover, no significant difference between the sexes was detected (BRÖCKEL 1974).

Despite the wealth of complex factors which affect them, the mass of grounded migrants can be used to reveal body fat variations during migration. Body mass variations in migrating passerines are most attributable to the migratory bird's fat level, though some muscle hypertrophy as well as minor changes in other body compartments may occur (BAGGOTT 1975, FRY et al. 1972).

To indicate the extent of fattening in the migrating population at a particular site, the proportion of mass over 22 g is taken. At this mass a Garden Warbler would be capable to fly for about 2000 km with the most favourable following wind conditions, and to cross the western Mediterranean and western Sahara by one single nonstop flight (BAIRLEIN 1987).

The proportion of birds weighing 22g or over is calculated either from the original frequency distributions of body masses, or from the reported means and standard deviations of larger sample sizes assuming normal distribution of the mass data. The assumption of normal distributed body mass data is based on refined analyses of large original data sets (e.g. Helgoland: BRÖCKEL 1973; Mettnau/Bodensee: Vogelwarte Radolfzell; Camargue: BAIRLEIN & HOFFMANN in prep.), and, therefore, may provide a reasonable standard for comparisons.

Acknowledgements. I should like to thank all who submitted the unpublished data mentioned in the summary tables 1–3. Furthermore, I wish to thank P BERTHOLD and C. MEAD for critically reading the manuscript.

Table 1: Body mass (g) of Garden Warblers (*Sylvia borin*) on autumn migration (the different localities from which data are available are listed from North to South; the numbers in front of the name of the sites refer to Fig. 1).

Tab. 1: Körpermassen (g) von Gartengrasmücken während des Herbstzuges. Die Untersuchungsorte sind von N nach S gelistet; ihre geographische Lage ist Abb. 1 zu entnehmen.

locality	n of birds	mass mean	SD	min	max	% > 22	source
(1) Umea/N-Sweden	31	19.6	2.1			12[2]	P LUNDBERG (in KÜHN 1979)
(2) Fair Isle	50	17.2		11	25.4		WILLIAMSON (1968)
(3) Ottenby/Sweden	219	17.4					PETTERSSON (1985)
(4) Falsterbo/Sweden	23	19.0	2.0				SCOTT (1965)
(5) Mierzeja Wislana/Poland	100	19.8	2.1	14.5	28.0	13[1]	Operation Baltic (A. PETRYNA)
(6) Kurishe Nehrung/SSSR	1262	19[3]					DOLNIK & BLUYMENTHAL (1967)
(7) Schleswig-Holstein/N-Germany	8	18.5		15	22		DENKER (1981)
(8) Helgoland/N-Germany	13	18.6		16.2	21.2		GROEBBELS (1930)
	237	19.4	2.2	12	26	6[1]	BRÖCKEL (1973)
(9) Reit/N-Germany	645	18.7	1.5	15.0	25.4	5[1]	Vogelwarte Radolfzell
(10) Great Britain	118	19.2	2.4	12	27.2	9[1]	BTO (cf Ch. MEAD)
Cheshire/GB	84	18.3	1.9	15.0	23.0	4	NORMAN et al. (1988)

Continuation of Table 1:

locality	n of birds	mass mean	SD	min	max	% > 22	source
(11) Dungensess/GB	13	20.2	2.3			21[2]	Scott (1965)
(12) Mettnau/S-Germany	6804	19.8	2.3	11.3	32.1	16[1]	Vogelwarte Radolfzell
(13) Aargau/Switzerland	176	19.2	2.0	16.0	28.0	8[2]	L. Jenni
(14) Neuenburgersee/Switzerland	231	19.5	2.0	15.0	26.0	11[2]	L. Jenni
(15) Tessin/Switzerland	151	18.8	1.6	13.5	22.5	2[2]	L. Jenni
(16) Col de Bretolet/Switzerland	958	19.1	2.0	14.0	27.0	7[2]	L. Jenni
	185[4]	18.4	2.0	14.0	25.0	4[2]	
	773[5]	19.3	2.0	14.0	27.0	9[2]	
(17) Wallis/Switzerland	347[6]	18.8	1.7	15.5	25.5	3[2]	L. Jenni
(18) Marchauen/E-Austria	60	22.7		16	29.5		Mazzucco (1974)
(19) Illmitz/E-Austria	246	19.9	2.2	10.8	26.7	16[1]	Vogelwarte Radolfzell
(20) Hungary	10[7]	23.8					Schmidt (1964)
(22) Campotto/N-Italy	429	20.7					F. Spina
(23) Toscana/N-Italy	30	23.6	3.0			70[2]	N. Baccetti
	15	20.9	2.3				
	15[8]	26.3	3.7		32		
(24) Montecristo/N-Italy	101	19.8	2.4	15	26	18[2]	N. Baccetti
(25) Capri/Italy	11	22.0	3.9				Baccetti et al. (1985)
	103	23.2	3.9			62[2]	Scebba et al. (1985)
(26) Sardinia	65	24.3	3.2			74[2]	Baccetti et al. (1985)
(21) Camargue/S-France	4305	20.8	2.7	10.2	34.4	27[1]	L. Hoffmann
	84	20.1	2.5	14.6	29.1	21	Norman et al. (1988)
(28) Spain	50			14.7	27.2		Mead (1966)
(30a) Almeria/SW-Spain	94	21.0	3.2	14.5	29.5	33[1]	W. & R. Wiltschko
(30) Sierra Morena/SW-Spain	84	20.3					Jordano (1981)
(31) Coto de Donana	384	22.0		13.4	30.0	56[1]	Herrera (1974)
	96	19.8	3.0	14.9	27.0	26[1]	Gardiazabal (1986)
(32) Sanlucar/SW-Spain	133	18.7	2.7			11[2]	Hilgerloh (1986)
(29) S-Portugal	52	21.4		16.0	30.6	39[2]	Thomas (1979)
	21[8]	23.8	4.5	16.7	30.6	65[2]	
	31[9]	19.7	2.9	16	27	21[2]	
	647	20.6	3.2	10.6	29.8	30[1]	G. Vowles
	79	21.5	3.9	14.6	30.2	42	Norman et al. (1988)
(33) Gibraltar	45	20.0	3.3	15.5	28.9	18[1]	Finlayson (1981, pers. comm.)
(35) Ancor/N-Algeria	20	18.7	1.6	16.1	22.0	0[1]	Bairlein (1988a)
(36) Mohammadia/N-Algeria	357	19.6	2.8	15.0	29.9	16[1]	Bairlein (1988a)
	55[8]	20.9	3.6	15.7	28.7		
	302[9]	19.4	2.5	15.0	29.9		
(37) Morocco	23	21.4	2.6	15.5	25.0	42[1]	G. Rheinwald
(40) H. Touiel/Algerian Sahara	6	24.6		22.7	27.0	100[1]	Bairlein et al. (1983)
(41) H. Hadjar/Algerian Sahara	49	24.7	1.8	20.7	27.9	92[1]	Bairlein
(43) H. Nebka/Algerian Sahara	25	22.0	4.4	11.7	29.6	68[1]	Bairlein
(44) H. Marroket/Algerian Sahara	49	22.9	3.8	13.2	28.8	76[1]	Bairlein (1985)
(45) Arak/Algerian Sahara	13	19.5	1.5	17.5	23.0	8[1]	Bairlein (1985)
(46) Hoggar/Algerian Sahara	2	17.7		16.9	18.5		Bairlein et al. (1983)
(47) Crete	17	22.6	7.0	13.5	28.5	54[2]	Phillips & Round (1975)
(48) Cyprus	43	21.8		14	27.4		Flint & Stewart (1983)
(51) Beit Jimal/Israel	9	19.4	2.8	16.0	23.5	33[1]	U. N. Safriel & I. Izhaki
(51a) S-Sinai/Egypt	15	20.7	2.4			30[2]	Safriel & Lavee (1988)
(52) „desert"/Egyptian Sahara	44	23.4	2.3	17.0	32.4	77[1]	H. Biebach
(53) Sadat Farm/Egyptian Sahara	31	18.1	3.7	13.3	27.0	13[1]	H. Biebach
(54) Port Sudan/Sudan	526	16.4	1.6			0[2]	G. Nikolaus & B. Raddatz
(56) Malamfatori/Nigeria	103	17.4		14.0	22.6		Dowsett & Fry (1971)

Continuation of Table 1:

locality	n of birds	mass mean	SD	min	max	% > 22	source
(57) Zaria/Nigeria	14	17.8		15.0	20.5	0	Fry (1971)
(58) Vom/Nigeria	85	17.3	1.5	14.5	23.0	1[2]	Smith (1966)
(59) Imesi/Nigeria	9	16.6	2.4	13.0	22.0		Ludlow (1966)
(60) Nigeria	78	16.8	2.1	12	23	1[2]	R. Sharland
(63) Kampala/Uganda	125[10]	18.9					Pearson (1971)
(64) Ngulia/Kenya				16.4	25.0		Pearson & Backhurst (1976)
(66) Nyika/Zambia	5	19.7		18.3	23.1		Dowsett (1970)
(67) Nchalo/S-Malawi	19[11]	18.5		16.5	22.0		Hanmer (1979)

Notes

[1] according to the frequency distribution of original body mass data
[2] calculated from mean and S.D. according to the assumption of almost normally distributed mass data
[3] roughly calculated according to Table 5 in Dolnik & Bluymenthal (1967)
[4] daytime trappings only
[5] nighttime trappings only
[6] birds trapped in the valley compared to the mountain data from Col de Bretolet
[7] birds trapped on ripe elder
[8] birds trapped on fig-trees
[9] birds trapped elsewhere compared to note 8
[10] October/November birds only
[11] November birds only

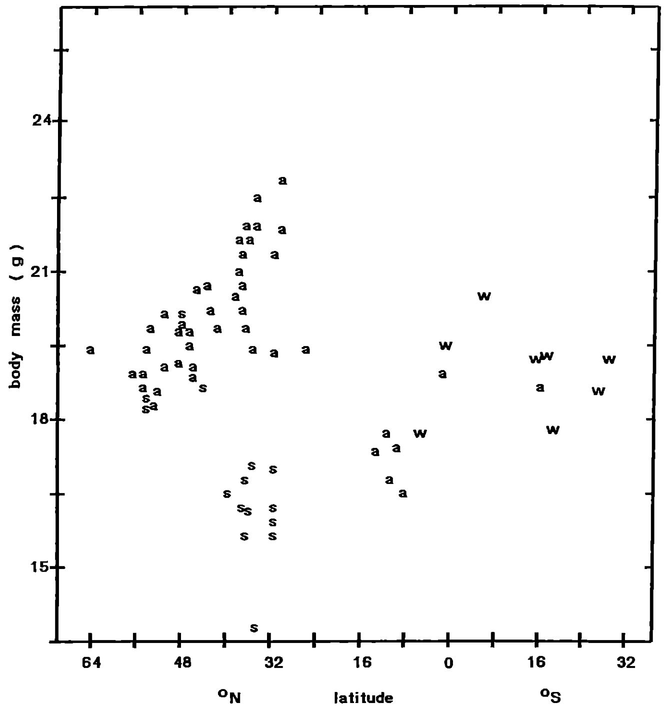

Fig. 2: Scattergram of mean body mass at various latitudes. a: autumn migration (July–November); w: winter (December–February); s: spring migration (March–April).

Abb. 2: Mittlere Körpermasse in Abhängigkeit von der geographischen Breite. a: Herbstzug (Juli–November); w: Winter (Dezember–Februar); s: Frühjahrszug (März–April).

Results

Body mass data on 107 samples of Garden Warblers during migration were available from 72 different trapping sites across the species' annual distribution (Fig. 1). The data are summarized in Tables 1–3. As obvious from a scatterplot of all site data available (Fig. 2) there is substantial geographical as well as seasonal variation.

Autumn mass (Table 1, Fig. 3)

From Scandinavia and Britain south to northern Africa the mean mass progressively increases. However, the mass gain with decreasing latitude is significantly different between sites along the southwestern migration route and those from the central Mediterranean and eastern route, respectively (Fig. 4). Average mass gain per 10 degree moved southward is 1.0 ± 0.2 (S.E.) g along the western route and 1.7 ± 0.5 g further east (t-test; $p < 0.001$), although the initial body masses are quite similar. Across Europe and south to 33°N, which is about the northern edge of the Sahara, western birds gain about 3 g mass and would attain an average of 20.8 g before their trans-Saharan flights, whereas central and eastern birds gain about 5.1 g and reach a final average body mass of 23.7 g.

The highest values of average body mass during autumn migration are reported from stopover sites in the northern Sahara. Across the desert, birds lose body mass at the rate of 6.8 ± 0.7 (S.E.) g each 10 degree of southward progress. Extrapolating this mass loss to the northern edge of the Sahara

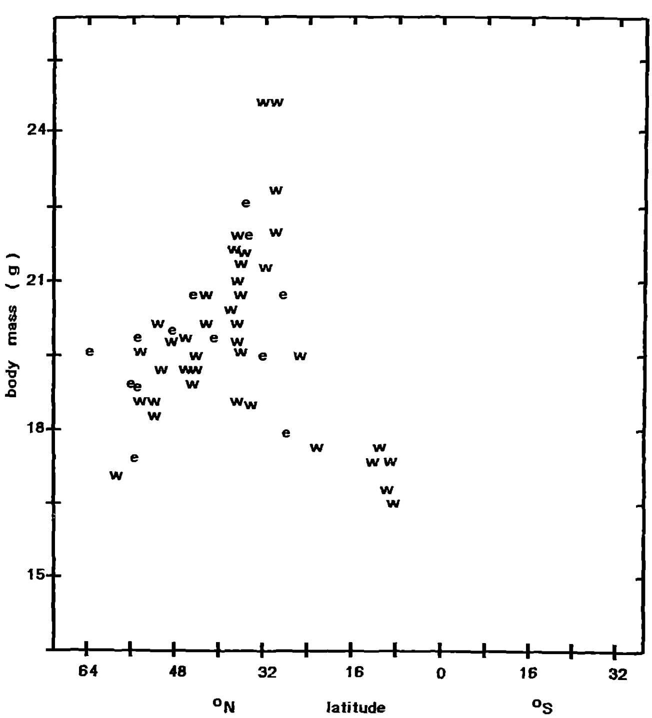

Fig. Scattergram of mean body mass at various latitudes on autumn migration. w: trapping sites west of 10.1° E; e: trapping sites east of 10.1° E.

Abb. Mittlere Körpermasse in Abhängigkeit von der geographischen Breite während des Herbstzuges. w: Orte westlich 10.1° E; e: Orte östlich davon.

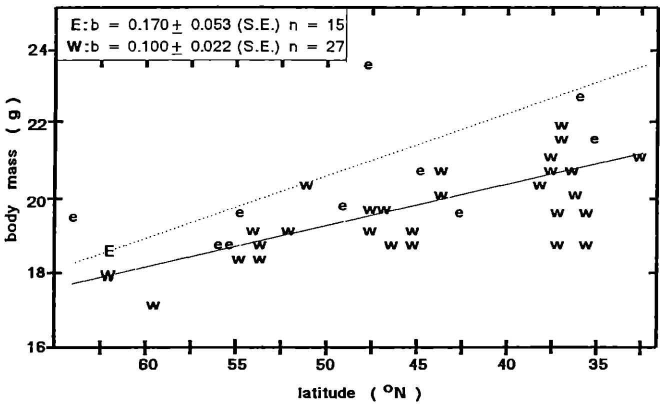

Fig. 4: Scattergram of mean body mass at various latitudes north of the northern edge of the Sahara desert belt on autumn migration. w: western flyway; e: central and eastern group.

Abb. 4: Mittlere Körpermasse in Abhängigkeit von der geographischen Breite während des Herbstzuges in Gebieten nördlich der Sahara. w: westlicher Zugweg; e: zentraler und östlicher Zugweg.

(about 33°N) reveals an estimate of average body mass at take off to the desert crossing of 25.0 g. On the other hand, extrapolating to the approximate southern edge (about 17°N) predicts arrival mass there of 14.2 g. Further south, in Nigeria, mean body masses reported from the autumn are around 17 g. Autumn passage migrants in eastern Africa are significantly heavier at approximately 19 g (χ2-test; $p < 0.025$).

Winter mass (Table 2)

Only few body mass data are available for the period December till February, when Garden Warblers are thought to be in their winter quarters. Most of them are in the range of about 18 to 20 g, with the lowest reported from W-Africa, although there is only one small sample available from there.

Table 2: Body mass (g) of Garden Warblers (*Sylvia borin*) at African wintering sites (December to February; the numbers in front of the names of the different sites refer to Fig. 1).

Tab. 2: Körpermassen von Gartengrasmücken im afrikanischen Winterareal (Dezember – Februar). Sonst wie Tab. 1.

locality	n of birds	mass mean	SD	min	max	source
(61) Ghana	11	17.6	0.9	16.0	18.8	BTO (cf Ch. Mead)
(63) Kampala/Uganda	184[1]	19.5				Pearson (1971)
(65) Amani/N-Tanzania	8	20.3	1.6	18.0	22.2	Sclater & Moreau (1933), Moreau (1944)
(67) Nchalo/S-Malawi	168	19.3		16.0	26.0	Hanmer (1979)
(68) Zambia	24	19.2		16.5	24.0	Dowsett (1965), Britton & Dowsett (1969), Peirce (1984), M. Kelsey
(69) Mopeia/Mocambique	22	18.0		16.0	22.3	Hanmer (1979)
(70) Transvaal/South Africa	1	18.5				Skead (1974)
(71) Barberspan/South Africa	14	19.3	1.6	17.8	24.2	Skead (1977)

Table 3: Body mass (g) of Garden Warblers (*Sylvia borin*) on spring migration (the different localities from which data are available are listed from South to North; the numbers in front of the name of the sites refer to Fig. 1).

Tab. 3: Körpermassen von Gartengrasmücken während des Frühjahrszuges. Sonst wie Tab. 1.

	n of	mass					
locality	birds	mean	SD	min	max	% > 22	source
(68) Zambia	8	21.2	1.5	19.6	23.8	25[1]	BRITTON & DOWSETT (1969) M. KELSEY
(67) Nchalo/S-Malawi	14	20.6		17.3	26.0		HANMER (1979)
(63) Kampala/Uganda	62[3]	21.2	2.3			30[1]	PEARSON (1971)
(62) Ethiopia	14	25.0	4.1	18.5	32.0	77[1]	S. TYLER
(59) Imesi/Nigeria	19	21.5		16.0	37.0		LUDLOW (1966)
(58) Vom/Nigeria	71	21.4	3.6	16.5	32.5	43[2]	SMITH (1966)
(57) Zaria/Nigeria	11	21.5		15.4	33.0		FRY (1971)
(56) Malamfatori/Nigeria	302	22.2	4.3	14.5	35.5	52[2]	DOWSETT & FRY (1971)
(55) Air/Niger	2	21.7		21.5	22.0		P BECK
(42) El Golea/Algerian Sahara	4	18.3	0.7	17.5	19.0	0	P. BECK
(39) Beni Abbes/Algerian Sahara				13	17		DUPUY (1970)
(38) Defilia/S-Morocco	17	16.3		13.3	20.8		ASH (1969)
(34) Kaifiene/NW-Morocco	42	17.1		14.4	22.7		SMITH (1979)
(33) Gibraltar	85	16.3	1.4	12.9	19.6	0[1]	C. FINLAYSON
(32) Sanlucar/SW-Spain	128	16.3	1.4			0[2]	HILGERLOH (1986)
(31) Coto de Donana/SW-Spain	39	16.7	2.3	13.0	24.0	5[1]	GARDIAZABAL (1986)
(30a) Almeria/SW-Spain	14	15.5	1.5	13.3	18.3	0[1]	W & R. WILTSCHKO
(27) Majorca	190	18.1	2.3	13.4	27.5	5[1]	K. BAKER
(21) Camargue	1152	17.2	2.0	10.8	24.5	0.5[1]	L. HOFFMANN
(25) Capri/Italy	10	16.5		15.0	18.5		SMITH (1966)
	185	16.5	1.9			0.2[2]	SCEBBA et al. (1985)
(24) Montecristo/N-Italy	278	15.0	1.6	11.5	19.5	0	N. BACCETTI
(22) Campotto/N-Italy	10	18.7	1.3	17.0	21.0	0	F. SPINA
(51) Beit Jimal/Israel	27	15.9	1.9	12.5	19.5	0	U.N. SAFRIEL & I. IZAHAKI
(51a) S-Sinai/Egypt	83	14.6	1.4			0	SAFRIEL & LAVEE (1988)
(49) Azraq/Jordania	48	17		14.8	19.8	0	NELSON (1973)
(50) Jordania	109	15.5		12.7	19.7	0	MOREAU (1969)
(48) Cyprus	272	13.9		8.5	20.7	0	MOREAU (1969)
	21	16.4		13	18.5	0	FLINT & STEWART (1983)
(18) Marchauen/E-Austria	34	20.2		16.8	26.5		MAZZUCCO (1974)
(7) Schleswig-Holstein/N-Germany	27	18.4		15	24		DENKER (1981)
(3) Ottenby	85	16.8					PETTERSSON (1985)
(2) Fair Isle	50	16.6		13.8	20.3	0	WILLIAMSON (1968)

Notes

[1, 2] see Table 1

[3] April birds only

Spring mass (Table 3, Fig 5)

In spring, the highest average body masses are reported from the northern savanna with individual maximum mass of up to 37 g (cf. Imesi/Nigeria, No. 57 in Table 3). In contrast to autumn, less data are available from sites close to the presumed start of the trans-desert flights. Mass loss between the northernmost savanna sites (Ethiopia, Lake Tschad) and the northern edge of the Sahara amounts to 4.0 ± 1.3 (S.E.) g each 10 degree latitude of northward crossing of the Sahara in spring. That predicts an average body mass at take-off on the southern desert edge of 24.7 g, and a mean arrival mass at the northern edge of 15.6 g, respectively.

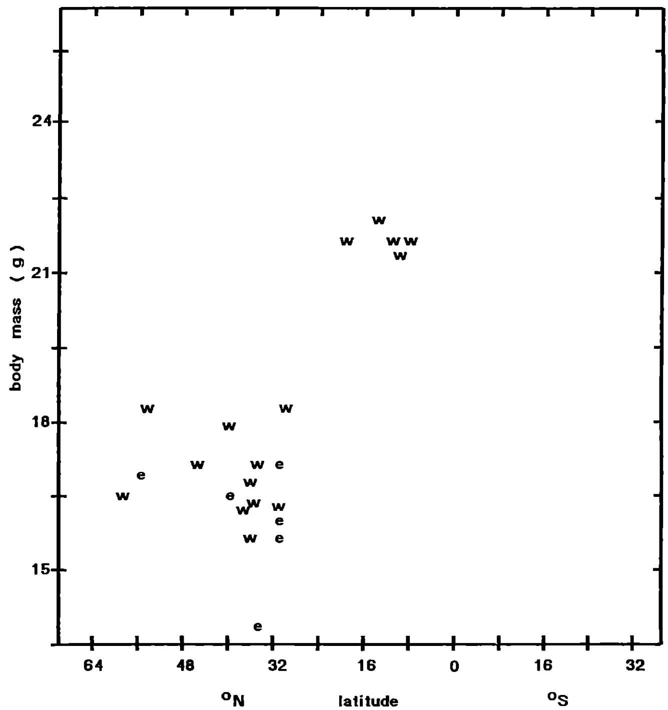

Fig. 5: As Fig. 3, on spring migration.
Abb. 5: Wie Abb. 3, Frühjahrszug.

Further north, away from the northern desert edge, comparatively light Garden Warblers, on average, are reported from some Mediterranean islands (Cyprus, Monte Cristo). However, these may be influenced by mass lost in making a landfall whilst the birds were over the Sea.

Discussion

Irrespective of some biases involved in dealing average body mass data from various sites, different years and various investigators (cf. Clark 1979), some obvious and interesting results emerged from the present review.

During autumn migration across Europe, Garden Warblers progressively gain mass while moving south. By the time they had reached the Sahara desert belt, specimens migrating across the central or eastern Mediterranean area had put on much more mass than their western conspecifics. On average, the eastern birds seem to have fattened up for their desert crossing before reaching the Mediterranean Sea. As indicated in Table 1, most of them carry substantial fat (as shown by the proportion with a body mass of 22 g and over) for long flights even north of the Mediterranean belt.

In contrast, the spatial course of average mass gain along the western flyway in autumn would indicate that these birds can hardly have enough fat for a long flight across the desert embarking north of the Mediterranean Sea. However, body masses reported from the north-western desert are very high; almost all specimens are really fat (cf. Bairlein 1987, and unpubl.). Predicted take-off mass from mass losses across the desert resulted in about 25 g prior to desert crossing. This mass corresponds quite well with the mean mass of fat birds found in stopover sites in N-Algeria (24.2 ± 1.1

(S.E.) g; n = 112; BAIRLEIN 1987), and with that of retraps at last capture (23.7 ± 1.3 (S.E.) g; n = 38; BAIRLEIN, in prep.). Thus, on average, that level of mass gain is likely to have been achieved by migrating Garden Warblers to be sufficient for a desert crossing.

There is further evidence from the proportion of birds of 22 g and over, that maximum fat deposition appears to take place immediately prior to embarking on the trans-desert flights. As reported by FRY et al. (1970, 1972), the heaviest migrants may have difficulties in making height when released from the hand. Thus, in order to avoid increased vulnerability due to heavy fat loadings, migrants should embark on flights immediately after sufficient lipid levels are laid down (CALDWELL et al. 1963). Interestingly, Garden Warblers caught at Col de Bretolet/Swiss Alps at night, i.e. while in migration, exhibit a higher mean mass and higher proportion of fat birds than those caught in daylight (see Table 1, No. 16). It may be that the mean mass of trapped birds is not representative of those which are about to set off on migration. Moreover, different capture probabilities for birds of different mass (as shown in Sedge Warblers *Acrocephalus schoenobaenus* by BIBBY et al. 1976) may bias mean mass of birds at a particular site towards light birds. However, though that behaviour may underestimate the proportion of fat birds encountered by trapping, Garden Warblers migrating along the western flyway seem to lay down much of their depot fats even as far south as northwestern Africa (BAIRLEIN 1988b, BAIRLEIN in prep.).

Compared with the predicted arrival mass at the southern desert edge in autumn (about 13 g), the masses reported from Nigeria are considerably higher. Thus, these migrants may have refueled before their passage in Nigeria (SMITH 1963, 1966). Migrants, arriving in the Sahel in September are encountering the end of the wet season, and they are, therefore, faced with particular favourable feeding conditions (MOREL 1968). Thus, once over the desert, Garden Warblers seem to move slowly south, feeding on the way.

Autumn mass throughout passage in Nigeria does not change much, though some heavy birds of over 22 g are reported from the end of October and early November (SMITH 1966). In east Africa, however, there is evidence that passage migrants fatten in there before continuing south, not uncommonly exceeding 22 g (PEARSON 1971, PEARSON & BACKHURST 1976). Such fattening south of the equator in E-Africa before emigrating may indicate the preparation for movements within the species winter range towards SE-Africa, whereas the western ones appear to move less. Recently, GWINNER et al. (1988) reported a resurgence of migratory behaviour in „winter" in caged Garden Warblers.

Winter mass does not show much geographical variation, though the Ghana wintering birds appear to be lighter than the SE-African ones. At Kampala/Uganda the mass of wintering birds is relatively constant between October and March (PEARSON 1971). The usual winter mass in E-Africa is below 17 g (PEARSON 1971).

Spring mass in east Africa indicates that there is no widespread deposition of fat between Zambia and Uganda, although average body masses in spring are slightly higher than in autumn, and late passage migrants in Uganda carry some fat (PEARSON 1971), indicating that some specimens deposit fat at more southerly latitudes.

Wintering birds at Kampala left the area without putting on appreciable amounts of fat, and even in late April many departing birds on passage weighed below 21 g, thus possessing only limited reserves (PEARSON 1971). In Tsavo/Kenya only a few grounded birds were fat during northward passage (PEARSON 1980). Thus, these birds may start moving slowly northwards to their points of taking-off for the trans-Sahara flights without considerable reserves. In Ethiopia, however, high mean body mass is achieved (25 g) revealing pronounced fat deposition there or in areas further to the south.

In W-Africa, between-season variation in body mass is much more pronounced. On average, spring migrants in Nigeria are about 4 – 5 g heavier than in autumn, and exhibit about the same mass as fall migrants in the northern Sahara, and as is predicted from mass loss on spring passage of the desert. This may indicate that many of them lay down their energy reserves for crossing the desert in spring that far south of the desert edge (Dowsett & Fry 1971, Fry 1971, Ludlow 1966, Smith 1966). Presumably, they do so because of the harsh feeding conditions in the dry savannas towards the end of the dry period (Morel 1968).

North of the eastern desert in spring, body mass is low, indicating that the birds have used up most of their body reserves. In contrast, spring mass in Morocco (Defilia, Kaifene) and Gibraltar are much higher. These birds appear to have accomplished some mass gain immediately north of the Sahara (Smith 1979), taking advantage of the increased food supply available after the N-African winter rains. Moreover, after the winter cooling period vegetation and feeding conditions in the Sahara itself may be much better, resulting, presumably, in more favourable feeding prospects and, consequently, less mass loss. Differences between western and eastern birds may be related to physiographic differences between the eastern and western Sahara. There are only few stopover oases in the eastern desert, contrasting with a lot more such oases in the central western Sahara. Furthermore, there is a broad belt of Mediterranean like vegetation in NW-Africa, whereas there is only a very narrow band in northern Egypt. This may also be reflected in low passage mass of birds in Cyprus (Moreau 1969), in contrast to the higher masses both at Majorca and Capri.

As reported by Finlayson (1981), Gardiazabal y Pastor (1986), or Smith (1979), and indicated by considerable higher mean body mass in the northern central Mediterranean (Camargue, Campotto) compared to the southwest (Gibraltar, SW-Spain), spring passage migrants gain some mass in the Mediterranean before continuing further north. However, this mass gain is only moderate, implying that the birds have good prospects of finding places to feed across Europe. However, there are only a few data available revealing the course of spring mass changes throughout central Europe. The relatively low masses reported from further north, at Fair Isle and Ottenby, indicate some mass loss while migrating across central Europe. However, both island sites may feature „lost“ birds. The high body mass of spring passage birds in E-Austria (Mazzucco 1974), although not supported by further data, may reflect a tendency for some further mass increase in the eastern birds. Presumably, the feeding conditions are more predictable in the Atlantic West, and therefore the birds do not require that substantial reserves, compared to their eastern conspecifics.

As the season progresses, both in autumn and spring, the body mass recorded at a particular site is changing. In autumn, at most sites from which data are reported, body mass seems to increase to a maximum at the end of the main migration, and decreases again later (Baccetti et al. 1985, Bairlein & Hoffmann in prep., Bertold 1990, Herrera 1974). In spring, in contrast, body mass appears to increase steadily, and sometimes more rapidely, with the progress of the season (Baccetti et al. 1985, Bairlein & Hoffmann in prep., Hanmer 1979, Ludlow 1966, Pearson 1971, Smith 1966). Seasonal increase in mass may reflect that later birds accumulate fat faster, or that earlier birds may have time to stay around at lower mass (Norman et al. 1988). Time available for migration seems to affect the rate of fattening in long-distance migrants, with some differences between autumn and spring (Safriel & Lavee 1988). Also the rate of mass gain may influence the timing of resumption of migration (Bairlein 1985, Biebach 1985, Gwinner et al. 1985, Riddiford & Auger 1983).

Mass gain depends largely on the food supplies available (Bibby & Green 1983). Interestingly, mean body mass achieved by Garden Warblers on fruits is significantly higher than elsewhere (cf. Table 1: Toscana (23), S-Portugal (29), N-Algeria (36)). Furthermore, the rate of mass gain on fruits appears to exceed that elsewhere (Baccetti et al 1985, Fry et al. 1970, Norman et al. 1988, Thomas 1979, Bairlein in prep.).

Concluding remarks

Prior to crossing the Sahara, Garden Warblers deposit considerable amounts of lipids as fuel for migration. There seems to be no difference, in principle, in maximum accumulation of fat between autumn and spring, though Moreau (1961, 1969, 1972) suggested some differences might be due to environmental features, in particular the probability of occurence of prevailing head-winds in each seasons. Differences observed with respect to the spatial course of fat deposition appear to be closely related to the particular feeding conditions.

Despite the gross details on body mass changes of Garden Warblers on migration, now evident from this review, much remains to be learned about the ecology and physiology of migratory fat deposition, and how the fattening process ties in with the bird's migratory strategy. The analysis of mass gain and stopover behaviour of retraps is vital and must be complemented by comparative studies under controlled conditions in the laboratory.

Zusammenfassung

Die Körpermasse von ziehenden Gartengrasmücken *(Sylvia borin)*: eine Übersicht.

Die Arbeit stellt Körpermassen von Gartengrasmücken auf dem Zug und im Winterquartier von 72 verschiedenen Untersuchungsorten zwischen N-Schweden und S-Afrika zusammen. Die zur Durchquerung der Wüste erforderlichen hohen Körpermassewerte bzw. Fettreserven scheinen auf dem Wegzug für Populationen, die über die Iberische Halbinsel nach W-Afrika ziehen, vornehmlich in NW-Afrika angelegt zu werden, für solche Populationen, die über den zentralen und östlichen Mittelmeerraum ziehen, dagegen wohl besonders nördlich des Mittelmeers. Durch O-Afrika weiter südlich wandernde Gartengrasmücken vollziehen dort offensichtlich eine weitere Depotfettanlagerung für ihren Weiterzug.

Für den Rückzug im Frühjahr scheint die Depotfettbildung etwas südlich des S-Randes der Sahara zu erfolgen, mit aber ganz ähnlichen Maximalwerten wie im Herbst. Nach Durchquerung der Sahara erfolgt vor dem Weiterzug eine geringfügige Zunahme der Körpermasse in Rastgebieten des Mittelmeerraumes.

postscript:

After revision of the final manuscript I received the paper Höser, N., & J. Oeler (1989): Körpergewicht der Gartengrasmücken *(Sylvia borin)* während des Wegzuges: Regressionsgerade in Lödla und am Bodensee. Mauritiana (Altenburg) 12: 375–380, which provides autumn body mass data from the area of Leipzig/GDR (51.0°N, 12.4°E). On average, 534 trapped individuals weighed 19.73 g, which fits well in the figures shown above.

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