Body mass of six long-distance migrant passerine species along the autumn migration route

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Summary

We analysed body mass and moult data of six passerine species along their autumn migration route from northern Europe to North Africa and derived hypothetical models of the organisation of their migration in terms of fuel store accumulation. We analysed data of 46,541 first-year birds from 34 trapping sites, sampled in a network of collaborating European and African ringing stations. After accounting for effects of time of day and size, there were marked differences between the six species examined in the change of body mass along the migration route and in the timing of moult. Garden Warblers (*Sylvia borin*) and Pied Flycatchers (*Ficedula hypoleuca*) underwent their postjuvenile moult prior to migration and increased their average body mass along the migration route. Sedge Warblers (*Acrocephalus schoenobaenus*) also increased body mass towards the south, but started the migration bout without further refuelling well before the Sahara and moulted mainly in the wintering grounds. Reed Warblers (*Acrocephalus scircpaceus*) and Whitethroats (*Sylvia communis*) migrated while still moulting and did not increase average body mass towards south. They accumulated the energy needed to fly over the Sahara just before it. Spotted Flycatchers (*Muscicapa striata*) behaved in the same way, but contrary to Reed Warblers and Whitethroats they did not accumulate much fat stores in North Africa, which might urge them to stop and fuel up regularly in the Sahara. In the course of the season average body mass of all species increased slightly, which enabled them to migrate faster. In general, average body mass of first-year birds in northern and central Europe during the migration period was comparable to that of adults during breeding.

Key words: Passerines, body mass, migration route, migration strategy, moult

Zusammenfassung

Körpermassen von sechs Arten von Langstreckenziehern entlang des Herbstzugweges

Wir analysierten Körpermassen- und Mauserdaten von sechs Singvogelarten auf dem Herbstzug entlang ihres Zugweges von Nordeuropa bis Nordafrika. Die Körpermassen von 46 541 diesjährigen Vögeln, die auf 34 Beringungsstationen im Rahmen eines internationalen Projektes gesammelt wurden, sind die Grundlage dieser Untersuchung. Neben der Entwicklung der Körpermassen entlang des Zugweges untersuchten wir den Einfluss der Mauser, des Fangdatums, der Tageszeit und der Körpergröße auf die Körpermasse. Mausernde Vögel waren schwerer als nichtmausernde mit der gleichen Fettmenge. Die Körpermasse nahm im Laufe der Saison und im Verlauf des Tages zu. Große Vögel (mit ei-

ner längeren 8. Handschwinge) waren schwerer als kleine. Gartengrasmücken (*Sylvia borin*) und Trauerschnäpper (*Ficedula hypoleuca*) wurden entlang des Zugweges kontinuierlich schwerer. Beide Arten machten die Jugendteilmauser hauptsächlich noch im Brutgebiet durch. Schilfrohrsänger (*Acrocephalus schoenobaenus*) wurden nach Süden ebenfalls etwas schwerer, aber sie begannen mit einem Reiseabschnitt ohne weiteren Fettaufbau schon in Mitteleuropa und mauserten ihr Kleingefieder hauptsächlich erst in Afrika. Die Körpermassen von Teichrohrsängern (*Acrocephalus scirpaceus*) und Dorngrasmücken (*Sylvia communis*) blieben nach Süden weitgehend konstant. Beide Arten lagerten die nötigen Energiereserven zum Überfliegen der Sahara erst kurz davor an. Sie trennten Jugendteilmauser und Zug nicht vollständig. Ähnlich verhielten sich Grauschnäpper (*Muscicapa striata*), doch im Gegensatz zu den zwei vorherigen Arten, wurden sie auch im Mittelmeergebiet nicht wesentlich fetter. Sie scheinen daher regelmässig in der Wüste zu rasten und zu fressen.

Introduction

Within the European-African bird migration system, birds face two large ecological barriers, the Mediterranean Sea and the Sahara desert. Both offer very few opportunities for refuelling (oases, islands) over a large distance. Therefore birds should have accumulated enough energy before starting to cross these barriers. Many birds seem to circumfly the Mediterranean Sea via the Iberian peninsula or via the Middle East (Bruderer & Liechti 1999) and, therefore, do not need much extra fuel for crossing this barrier. The Sahara desert, however, cannot be avoided and birds should carry enough energy stores for a 2000 km flight without refuelling (but possibly with stopover; Bairlein 1985, Biebach et al. 1986). There are two main ways to accumulate the energy stores needed: (a) on the way to the northern desert edge, which would require that birds accumulate at each stopover place more energy than

they use for the next flight bout, or (b) at one site before the desert. In the former case one would expect an increase in body mass along the migration route, but not in the latter case.

The main aim of this paper was to investigate whether the body mass of six long-distance migrant passerine species (Reed Warbler *Acrocephalus scirpaceus*, Sedge Warbler *A. schoenobaenus*, Garden Warbler *Sylvia borin*, Whitethroat *S. communis*, Pied Flycatcher *Ficedula hypoleuca*, Spotted Flycatcher *Muscicapa striata*) changes along their autumn migration route and to derive conclusions about the organisation of their journey. We present theoretical considerations about how much and where fuel could be accumulated and used along the migration route from the breeding grounds to the southern border of the Sahara. A further aim was to identify whether body mass increased in the course of the autumn migration season. The speed of migration, calculated from the total distance migrated and the total time used including stopovers, is often higher later in the season (Ellegren 1993), which is achieved if birds can manage longer flight bouts. This requires larger amounts of stored fuel, and hence higher body mass later in the season. Other variables likely to influence body mass, such as time of capture, body size and year, were also included in the analysis.

Juvenile feathers have a frail texture and are replaced shortly after fledging. Most juvenile birds therefore undergo a partial moult in an early phase of life (Jenni & Winkler 1994). Since moult (Murphy 1996) and the deposition of fat are energy demanding, the two phases cannot operate at maximum intensity when performed simultaneously. Timing of and energy allocation to either phase has to be optimised and embedded within the annual life cycles of the birds. Therefore, the timing of moult is likely to have a direct influence on the migration strategy. We investigated the consequences of timing of moult on body mass development along the migration route.

Methods

Trapping sites and species

The ringing data of six species captured at 34 sites were analysed (Table 1, Fig. 1): Reed Warbler, Sedge Warbler, Garden Warbler, Whitethroat, Pied Flycatcher and Spotted Flycatcher. All species considered breed over large areas in Europe and winter in Africa south of the Sahara. The trapping sites were distributed over 30.7° of latitude along the migration route from northern Europe to North Africa. Their locations were classified as coast, island or mainland. The data were collected 1994−1996 in a joint project of ringing stations within the European Science Foundation Network (Bairlein 1997).

Data collection

At all ringing stations, the following data were collected for each bird in a standardised way (Bairlein 1995): date and time of capture (to the nearest h), age (after Svensson 1992 and Jenni & Winkler 1994), feather-length of primary 8 (to the nearest 0.5 mm, Jenni & Winkler 1989), body mass (0.1 g), fat score (9 levels, Kaiser 1993) and a score for moult intensity of body feathers (0: no body feather growing, 1: between 1 and 20 body feathers growing, 2: more than 20 body feathers growing). Time of capture was defined as the time elapsed since local sunrise, calculated with procedure 'daylength' in

GENSTAT 5.3.2 (Payne et al. 1993) and used for all analyses.

To test whether the species considered moult during autumn migration, we analysed data from nocturnal captures at Col de Bretolet, a Swiss Alpine pass, collected over 12 autumn migration seasons in the years 1980–1996. Because this trapping site is not a stopover site for these species (Jenni 1984) and because only birds caught out of nocturnal migration were included, this dataset consists only of actively migrating birds.

Data selection

All analyses refer to first captures of first-year birds, because very few adults were caught at many sites. As most trapping sites were also breeding places for the species investigated, a mixture of locally born and migrating birds was often present. The interest of this study was in migrating individuals and these could not be separated individually from local birds not yet on migration. With the following data selection, we excluded most, but probably not all, locally born birds not yet on migration. The later in the season the birds are caught the more likely they are to be actually on migration. Therefore we defined for each species and each site a threshold date (Table 1), after which the birds were considered to be migrants, and only those were included in the analysis. This threshold date was determined based on the on-
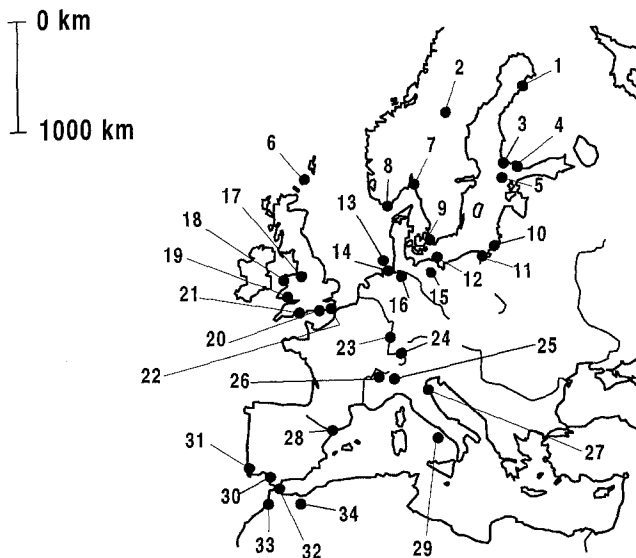
Fig. 1. Geographical distribution of the 34 ringing sites where birds were captured for this study. Numbers refer to Table 1.
Abb. 1. Lage der 34 Fangorte. Die Nummern entsprechen denjenigen in Tab. 1.

Table 1. Location of the sites, sample sizes and onset of the "migratory period" for each spezcies. The numbers in front of the sites correspond to Figs. 1 and 2. The sites are ordered from north to south. Mig. per.: migratory period as defined in this study. All birds caught after the date indicated in the table were included in the analysis. M denotes sites where the species does not breed and the sample consists entirely of migrants.

Tab. 1. Fangorte, Stichprobengröße und Beginn der „Zugperiode" für alle Arten. Die Nummern vor den Fangorten entsprechen denjenigen in Abb. 1 und 2. Die Fangorte sind von Norden nach Süden sortiert. Mig. per.: Zugperiode, so wie sie in dieser Arbeit definiert wurde. Alle Vögel, die nach diesem Datum gefangen wurden, wurden für die Auswertungen verwendet. M bezeichnet Fangorte, wo die entsprechende Art nicht brütet, sondern nur als Durchzügler auftritt.

Site	Latitude	Longitude	Location	Reed Warbler Mig. per.	n	Sedge Warbler Mig. per.	n	Garden Warbler Mig. per.	n	Whitethroat Mig. per.	n	Pied Flycatcher Mig. per.	n	Spotted Flycatcher Mig. per.	n
1: Tauvo (SF)	64.8	24.6	coast	–	–	M	12	>29 Jul.	44	–	–	>24 Jul.	34	>3 Aug.	26
2: Annsjön (S)	61.3	12.5	mainland	–	–	–	–	>29 Jul.	17	–	–	>29 Jul.	46	–	–
3: Rauvola (SF)	60.4	22.3	coast	>3 Aug.	1427	>29 Jul.	2608	>3 Aug.	170	>29 Jul.	109	>29 Jul.	32	>3 Aug.	10
4: Hanko (SF)	59.8	22.9	coast	–	–	M	55	>3 Aug.	307	>29 Jul.	44	>29 Jul.	138	>3 Aug.	105
5: Jurmo (SF)	59.8	21.6	island	–	–	–	–	–	–	–	–	M	110	>3 Aug.	269
6: Fair Isle (GB)	59.4	–1.6	island	–	–	–	–	M	83	–	–	–	15	–	–
7: Jomfruland (N)	58.9	9.6	island	–	–	–	–	>3 Aug.	103	>3 Aug.	19	>3 Aug.	138	–	–
8: Lista (N)	58.1	6.6	coast	>3 Aug.	1239	>29 Jul.	1069	>3 Aug.	473	>3 Aug.	161	>29 Jul.	138	>3 Aug.	38
9: Falsterbo (S)	56.4	12.8	coast	>3 Aug.	4107	>29 Jul.	2048	>3 Aug.	343	>3 Aug.	157	>3 Aug.	200	>3 Aug.	142
10: Rybachy (RU)	55.2	20.8	coast	>3 Aug.	1292	>29 Jul.	1698	>3 Aug.	2079	>29 Jul.	302	>3 Aug.	466	>3 Aug.	243
11: Mierzeja Wislana (PO)	54.3	19.3	coast	–	–	–	–	>3 Aug.	112	M	11	>3 Aug.	86	>3 Aug.	60
12: Greifswalder Oie (D)	54.3	13.9	island	M	16	>29 Jul.	36	>3 Aug.	657	>3 Aug.	112	>3 Aug.	673	>3 Aug.	162
13: Helgoland (D)	54.2	7.9	island	M	21	–	–	M	261	M	57	M	132	M	16
14: Oldeoog (D)	53.8	8.0	island	M	52	–	–	M	302	M	263	M	193	M	18
15: Galenbecker See (D)	53.6	13.7	mainland	>3 Aug.	2161	>29 Jul.	177	>3 Aug.	270	>3 Aug.	36	>3 Aug.	18	–	–
16: Reit (D)	53.5	10.1	mainland	>3 Aug.	753	>29 Jul.	18	>3 Aug.	26	>3 Aug.	166	–	–	–	–
17: Woolston (GB)	53.4	–2.5	mainland	>3 Aug.	179	>29 Jul.	238	>3 Aug.	27	>3 Aug.	44	–	–	–	–
18: Bardsey (GB)	52.8	–4.8	coast	–	–	M	25	>3 Aug.	20	>3 Aug.	17	>3 Aug.	35	>3 Aug.	34
19: Kenfig (GB)	51.5	–3.7	mainland	>3 Aug.	229	>29 Jul.	346	>3 Aug.	27	>3 Aug.	64	–	–	–	–
20: Stodmarsh (GB)	51.3	1.2	mainland	>3 Aug.	683	>29 Jul.	720	–	–	–	–	–	–	–	–
21: Dungeness (GB)	50.9	1.0	mainland	>3 Aug.	318	M	72	>3 Aug.	68	>3 Aug.	198	M	93	–	–
22: Portland (GB)	50.6	2.5	coast	–	–	M	33	>3 Aug.	34	>3 Aug.	19	>3 Aug.	22	>3 Aug.	12
23: Münchhausen (F)	48.9	8.1	mainland	>8 Aug.	569	M	27	–	–	–	–	–	–	–	–
24: Mettnau (D)	47.7	9.0	mainland	>8 Aug.	2975	M	181	>3 Aug.	447	>8 Aug.	22	>8 Aug.	38	>8 Aug.	19

Table 1. (continued)
Tab. 1. (Fortsetzung)

Site	Latitude	Longitude	Location	Reed Warbler Mig. per.	n	Sedge Warbler Mig. per.	n	Garden Warbler Mig. per.	n	Whitethroat Mig. per.	n	Pied Flycatcher Mig. per.	n	Spotted Flycatcher Mig. per.	n
25: Bolle di Magadino (CH)	46.2	8.9	mainland	>13 Aug.	961	M	94	>13 Aug.	77	–	–	M	138	>8 Aug.	150
26: Col de Bretolet (CH)	46.2	6.8	mainland	M	62	–	–	>8 Aug.	209	M	19	M	632	M	75
27: Campotto (I)	44.6	11.8	mainland	>18 Aug.	1243	M	587	M	381	–	–	M	18	>8 Aug.	19
28: Ebro delta (ES)	40.7	0.9	coast	>23 Aug.	1518	M	89	M	11	>13 Aug.	18	M	95	–	–
29: Capri (I)	40.5	14.2	island	–	–	–	–	M	380	–	–	–	–	–	–
30: Coto de Doñana (ES)	37.2	–6.5	coast	>7 Sep.	189	–	–	M	1539	>28 Aug.	134	M	217	>18 Aug.	268
31: A Rocha (P)	37.2	–8.6	coast	–	–	–	–	–	–	>28 Aug.	12	–	–	–	–
32: Gibraltar (GI)	36.2	–5.4	coast	–	–	–	–	M	72	M	11	M	86	–	–
33: Bou Rhaba (MO)	34.3	–6.7	mainland	M	77	–	–	M	12	–	–	M	19	–	–
34: Moulaya (MO)	34.1	2.5	mainland	M	337	–	–	–	–	–	–	M	68	>18 Aug.	46
Total sample size					20408		10133		8551		1995		3742		1712

set of migration at trapping sites where the species does not breed and based on literature about the onset of migration (Cramp 1992, 1993, Glutz von Blotzheim & Bauer 1991, 1993). With these restrictions, a total number of 20,408 Reed Warblers, 10,133 Sedge Warblers, 8551 Garden Warblers, 1995 Whitethroats, 3742 Pied and 1712 Spotted Flycatchers were available for analysis. As we intended to evaluate the influence of moult on body mass we included moulting and non-moulting individuals.

Statistical analysis

First, we analysed, for each species separately, the effects of six variables on the body mass of the individual birds with a type I analysis of covariance. Thus, the effect of a variable is evaluated only after adjustment for the ones entered previously. We first entered (and adjusted for) the variables time of capture and its square (in order to model a non-linear curve), length of primary 8 and moult intensity, before testing for differences between sites. Hence, effects of sites are independent of time of capture, size of bird and moult intensity. Then, effects of date and year as well as interactions between site and other variables were evaluated. Because of the large sample sizes, almost all variables revealed statistical significance at a low alpha level (0.001), though their effect may not be biologically relevant (Yoccoz 1991). Therefore, we considered how much of the total variability was explained by each variable (partial r^2).

Birds from northern and eastern populations often have longer and more pointed wings than those of southern and western populations (Klein et al. 1973). Because of their longer migration, they may carry more fuel stores for their size than birds from southern and western populations, and hence may show a disproportionally high body mass. As a result, the adjustment of body mass according to the length of primary 8 with one single slope for all populations taken together might lead to overestimations of the effect of size on body mass. If such an effect is present, we would expect to find a correlation between the site-specif-

ic slopes of body mass on size and latitude or longitude. We derived the site-specific slopes of body mass on size from a model with body mass as the dependent variable and time of capture, its square, moult intensity, length of primary 8, site and the interaction length of primary 8 x site as independent variables. With one exception (Sedge Warbler: latitude, $r = 0.488$, $p = 0.03$; longitude, $r = 0.378$, $p = 0.10$; $n = 20$), all correlations between the site-specific slopes of body mass on length of primary 8 and longitude or latitude were not significant (all $p \geq 0.09$). This indicates that there was no geographical change in the slopes of body mass on size along the north-south or the east-west axis and that the use of a single slope for all sites for the adjustment of body mass on size introduced no bias, except possibly in the Sedge Warbler. Size-independent body mass of this species is likely to be higher in the south and lower in the north than reported here.

Secondly, we tested whether mean values of body mass per site were correlated with their geographic position (latitude, longitude and location). For this, we first adjusted the body mass values of all birds with respect to the time of capture, its square and size (length of primary 8). The estimates for these adjustments were derived from a linear model with body mass as dependent and time of capture, its square and length of primary 8 as independent variables. From the adjusted body mass values, we calculated the site specific means. They became the dependent variable in another analysis of covariance with location (coast, island or mainland), longitude, latitude and the interaction longitude x latitude as independent variables. All sites were given the same weight. All statistical analyses were performed with GENSTAT 5.3.2 (Payne et al. 1993).

Results

Effects of time of capture, length of primary 8, moult, date, year and site

The models explained between 29.5 % (Spotted Flycatcher) and 39.2 % (Reed Warbler) of the total body mass variability (Table 2). Not all variables had the same explanation power in all species. Variables that accounted on average for more than 2.5 % of total variation were time of capture, length of primary 8, moult and site.

Time of capture and its square together were important sources of variation. Except in the Reed Warbler, the square of time of capture had only a marginal influence, indicating that body mass increase over the day could be approximated linearly. The average body mass increases per hour (derived from a linear model with body mass as dependent variable and time of capture, its square and length of primary 8 as independent variables, calculated over a 12 h period) were 0.053 g $\pm$ 0.009 s.e. (Sedge Warbler), 0.074 g $\pm$ 0.019 (Garden Warbler), 0.102 g $\pm$ 0.028 (Whitethroat), 0.043 g $\pm$ 0.008 (Pied Flycatcher) and 0.067 g $\pm$ 0.017 (Spotted Flycatcher). In the Reed Warbler, the increase was much lower (0.003 gh^{-1} $\pm$ 0.006 s.e.). This low increase most likely had no biological reasons, but was due to a peculiar distribution of the capture times: most Reed Warblers were caught in the hours around sunrise.

The length of primary 8, as a correlate of body size, was an important source of variation for body mass in the Garden Warbler and even more so in the Sedge Warbler. Larger birds were heavier by 0.157 g $\pm$ 0.006 s.e. (Reed Warbler), 0.206 g $\pm$ 0.006 (Sedge Warbler), 0.271 g $\pm$ 0.012 (Garden Warbler), 0.119 g $\pm$ 0.019 (Whitethroat), 0.112 g $\pm$ 0.011 (Pied Flycatcher) and 0.109 g $\pm$ 0.014 (Spotted Flycatcher) per mm of length of primary 8. These estimates were obtained from the same model as above.

The moult of body feathers affected body mass particularly in Reed Warbler and Whitethroat (Table 2), and much less in the other species. Moulting birds were lighter. The effect of moult was similar at all sites because the site x moult interaction explained much less variation than the main effect of moult. Newton (1968) and Chilgren (1977) found that moulting birds are heavier than non-moulting birds because of a higher water content. In this study we found the opposite, but this discrepancy can be attributed to the fact that non-moulting birds often had higher fat scores, which in turn increased body mass (Table 3). This was especially pronounced for the species with the

Table 2. Analyses of covariance for body mass in response to the factors site, moult and year and to the covariates time, length of primary 8 and date. df: degrees of freedom, ss: sum of squares, p.r²: partial r². partial r², + p > 0.05. Note that the variables were entered in the order given here and that effects of one variable refer to values corrected for the previous variables (see text).

Tab. 2. Kovarianzanalysen mit Körpermasse als Zielvariable und den Faktoren Fangort, Mauserintensität und Jahr, sowie den Größen Fangzeit, Länge der 8. Handschwinge und Datum als unabhängige Variablen. df: Freiheitsgrade, ss: Summe der Abweichungsquadrate, p. r²: partielles r², + partielles r² p > 0.05. Die Variablen wurden in der angegebenen Reihenfolge ins Modell integriert, weshalb der Effekt einer Variablen bestimmt wird, nachdem die Zielgröße nach den Variablen korrigiert wurde, die vor der betreffenden aufgeführt sind.

Species	Reed Warbler			Sedge Warbler			Garden Warbler			Whitethroat			Pied Flycatcher			Spotted Flycatcher		
Source	df	ss	p.r²	df	ss	p.r²	df	ss	p.r²	df	ss	p.r²	df	ss	p.r²	df	ss	p.r²
Time	1	3.3+	0.0	1	161.5	1.2	1	679.3	1.4	1	242.4	4.3	1	191.0	3.5	1	152.1	5.0
Time²	1	380.9	1.0	1	37.2	0.3	1	0.1+	0.0	1	14.8	0.3	1	9.3	0.2	1	10.0	0.3
Primary 8	1	1363.4	3.7	1	1388.5	10.1	1	2577.1	5.4	1	101.9	1.8	1	143.0	2.6	1	103.0	3.4
Moult	2	6400.7	17.3	2	313.1	2.3	2	798.0	1.7	2	588.7	10.5	2	63.9	1.2	2	76.5	2.5
Site	21	3897.4	10.5	19	959.1	7.0	28	8721.3	18.2	22	350.7	6.3	25	838.0	15.5	18	135.7	4.4
Site × Time	21	115.8	0.3	19	77.4	0.6	28	391.8	0.8	22	62.8+	1.1	25	194.0	3.6	18	58.3	1.9
Site × Time²	21	75.5	0.2	19	36.9	0.3	28	367.7	0.8	22	75.0	1.3	25	46.4	0.9	18	38.4	1.3
Site × Moult	38	394.5	1.1	35	57.2	0.4	45	339.7	0.7	34	171.7	3.1	33	34.2+	0.6	31	111.4	3.6
Date	1	336.7	0.9	1	328.5	2.4	1	111.7	0.2	1	92.5	1.7	1	56.9	1.1	1	18.7	0.6
Site × Date	21	355.9	1.0	19	268.3	2.0	28	737.7	1.5	22	146.5	2.6	25	170.1	3.1	18	45.6	1.5
Year	2	673.8	1.8	2	56.7	0.4	2	172.3	0.4	2	38.1	0.7	2	27.9	0.5	2	14.6	0.5
Site × Year	29	522.7	1.4	27	321.8	2.3	41	477.2	1.0	24	100.7	1.8	33	160.4	3.0	23	137.7	4.5
Residual	20 248	22 532.1	60.8	9986	9691.9	70.8	8344	32 571.6	67.9	1840	3595.9	64.4	3567	3469.6	64.2	1577	2157.4	70.5
Total	20 407	37 052.6		10 132	13 698.1		8550	47 945.7		1994	5581.6		3741	5404.7		1711	3059.4	

largest proportion of moulting birds, Reed Warbler and Whitethroat. Intensely moulting birds (moult score 2) with fat score 1 were heavier (Reed Warbler by 0.23 g ± 0.04 s.e., Whitethroat 0.47 g ± 0.12, Garden Warbler 0.75 g ± 0.09, Pied Flycatcher 0.28 g ± 0.07) than non-moulting conspecifics with fat score 1 (all p < 0.001). This showed that moulting birds with low fat stores were indeed heavier than non-moulting conspecifics with the same fat score. However, moulting Spotted Flycatchers with fat score 1 had a similar body mass to non-moulting ones ($F_{2, 588}$ = 0.1, p = 0.877), and moulting Sedge Warblers with fat score 1 were lighter (0.26 g ± 0.06) than non-moulting conspecifics ($F_{2, 2196}$ = 11.6, p < 0.001).

After adjustment for time of capture, its square, size and moult, body mass differed between sites in all species, but the amount of variability explained by site varied considerably between species. Body mass varied substantially between sites in Garden Warbler and Pied Flycatcher, but only little in Spotted Flycatcher (Table 2).

Date and the interaction date × site was another source of body mass value variation. The interaction term often accounted for more variation than date alone. Hence the change in body mass in the course of the season was not equal at the sites. We estimated the average change in body mass per day for each site with a model con-

Table 3. Median fat scores of the 3 moult intensity classes (n = sample size). Moult scores: 0 – 2 (non-moulting to heavily moulting, see methods), fat scores: 1 – 4 (very little fat to furcular depression filled with fat, according to Kaiser 1993).

Tab. 3. Mediane der Fettklassen für die 3 Mauserklassen (n = Stichprobengröße). Mauserklassen: 0 – 2 (nicht mausernd bis stark mausernd; siehe Methoden), Fettklassen 1 – 4 (sehr wenig Fett bis Vertiefung zwischen den Gabelbeinen mit Fett gefüllt; nach Kaiser 1993).

Moult score	0		1		2	
	Fat score	n	Fat score	n	Fat score	n
Reed Warbler	4	7589	2	4362	1	9020
Sedge Warbler	2	8454	2	1259	1	848
Garden Warbler	3	7867	2	906	1	710
Whitethroat	3	976	2	367	1	715
Pied Flycatcher	1	762	1	197	1	189
Spotted Flycatcher	2	1343	2	229	1	279

taining body mass as dependent variable and time of capture, its square, length of primary 8, moult, site, date and the date x site interaction as independent variables (Fig. 2). Although the standard errors of the estimates were often quite large, the seasonal changes at several sites were significantly different from zero. Where this was the case, the birds were heavier later in the season in 42 out of 46 species-site combinations. The seasonal increase in body mass of Pied Flycatchers was higher at the southern sites than at northern sites ($F_{1,20}$ = 25.1, p < 0.001, r^2 = 53.4), whereas there was no geographical trend for the other species. The average seasonal body mass increases over all sites were 0.010 gday^{-1} ± 0.001 (Reed Warbler), 0.012 gday^{-1} ± 0.001 (Sedge Warbler), 0.010 gday^{-1} ± 0.002 (Garden Warbler), 0.019 gday^{-1} ± 0.003 (Whitethroat), 0.013 gday^{-1} ± 0.002 (Pied Flycatcher) and 0.011 gday^{-1} ± 0.003 (Spotted Flycatcher) when estimated with a linear model with body mass as dependent and time of capture, its square, length of primary 8, moult and date as independent variables. Over a migration period of two months, all species were less than 1g heavier at the end of the season, except the Whitethroat (1.14 g).

Body mass also differed between years, most especially in the Spotted Flycatcher. Since the interaction year x site explained a larger proportion of body mass variability than year alone, differences in body mass between years were not parallel at all sites. The largest differ-

ences in average body mass between the three years were found for Reed Warblers in the Coto de Doñana (1.15 g), for Sedge Warblers in the Ebro Delta (2.57 g), for Garden Warblers at Mierzeja Wislana (3.82 g), for Whitethroats on Helgoland (2.03 g), for Pied Flycatchers on Oldeoog (2.81 g) and for Spotted Flycatchers at Mierzeja Wislana (2.61 g). These estimates were derived from the maximal models (Table 2).

From the maximal models, we estimated site-specific average body mass at sunrise of non-moulting birds in 1994 by inserting site-specific average values of date and length of primary 8 (Table 4). Hence, these values were not corrected for size and date, but for moult, year and time of capture. It appeared that average body mass of first-year birds during autumn migration did not differ from than that of adults during the breeding season at most sites (body mass during the breeding season: Reed Warbler 12.0 – 13.0 g, Sedge Warbler 11.7 – 13.4 g, Garden Warbler 17.8 – 19.8 g, Whitethroat 13.9 – 15.8 g, Pied Flycatcher 11.0 – 14.9 g, Spotted Flycatcher 14.8 – 16.2 g; Glutz von Blotzheim & Bauer 1991, 1993).

Moult of body feathers during migration

The proportion of moulting birds (Table 5) depends both on the proportion of locally born birds not yet on migration (which generally moult body feathers) and of birds moulting on migration; hence the latter proportion is diffi-

cult to determine. However, sites with no or very few moulting birds indicate that migrating birds are not moulting. Direct information on the proportion of moulting birds on migration is provided by birds caught during night migration at the Alpine pass Col de Bretolet (Table 5). There, a considerable proportion of actively migrating Reed Warblers, Whitethroats and Spotted Flycatchers were still moulting, whereas the proportion of moulting Garden Warblers and Pied Flycatchers was much lower. With this in mind, the following conclusions can be drawn.

The Pied Flycatcher migrated through western and central Europe usually after completion of moult. This also applied to western and central European birds which were rarely caught during moult. Similarly, Garden Warblers generally started migration after moult or at the end of moult, as indicated by low proportions of moulting birds at Col de Bretolet and in southern Europe. Sedge Warblers usually delayed the postjuvenile moult until arrival in sub-Saharan Africa and only completed the juvenile plumage (Redfern & Alker 1996). In contrast, Whitethroats often seemed to extend moult into the first leg of migration up to central Europe with an appreciable proportion of moulting night migrants at Col de Bretolet. By the time they arrived in southern Europe, moult had apparently finished. Reed Warblers often moulted during migration, as also found in Belgium (26 – 82 %, Herremans 1990), but it remains unclear whether the high percentage of moulting birds in southern Europe is due to locally born or migrating birds. The Spotted Flycatcher also often migrated while moulting, showing the highest proportion of moulting individuals at Col de Bretolet of all species. However, it remains unclear why there was such a low proportion of moulting Spotted Flycatchers in Britain.

Body mass change along the migration route

In order to test average body mass for geographical trends between sites, we estimated mean body mass at each site accounting for the time of capture and the length of primary 8. In contrast to the values given in Table 4, these mean values were corrected for size and the time of capture, but not for moult, date and year.

Mean size-corrected body mass increased significantly towards the south in four species, but not in Reed Warbler and Spotted Flycatcher (Fig. 3, Table 6). The slope for the Sedge Warbler was quite flat (0.10 g $\pm$ 0.18 s.e. per 10° of latitude) and the total increase in body mass from the northernmost to the southernmost site of this study was only 0.24 g. Mean body mass increased more markedly along the north-south axis in Pied Flycatcher (0.41 g $\pm$ 0.12 per 10° of latitude; 1.26 g over the entire range) and in Whitethroat (0.44 g $\pm$ 0.23 per 10° of latitude; 1.07 g over the entire range). Garden Warblers increased in body mass towards the south, but also towards the east. Furthermore, the increase along the north-south axis was larger in eastern Europe than in western Europe, as indicated by the significant interaction term latitude × longitude (Table 6). For example, the increase in mean body mass was 0.27 g $\pm$ 0.21 per 10° of latitude at 0° E, while it was 1.41 g $\pm$ 0.33 per 10° of latitude at 20° E (Fig. 3). For the other species there was no east-west gradient in average body mass (Table 6). Average body mass did not differ significantly between coastal, island and mainland sites. However, location was just significant in the Pied Flycatcher (heaviest on coasts, 0.32 g lighter on islands and 0.08 g lighter on the mainland).

Discussion

Limits of interpretation

The way the data have been collected results in two main limitations in interpretation. First, the variation in mean body mass along the migration axis does not necessarily reflect the change in body mass of an average individual during its migration. All species considered in this study breed over wide areas of Europe. Therefore, the potential recruiting area of the birds caught at a given site increases along the migration route: towards the south, pro-
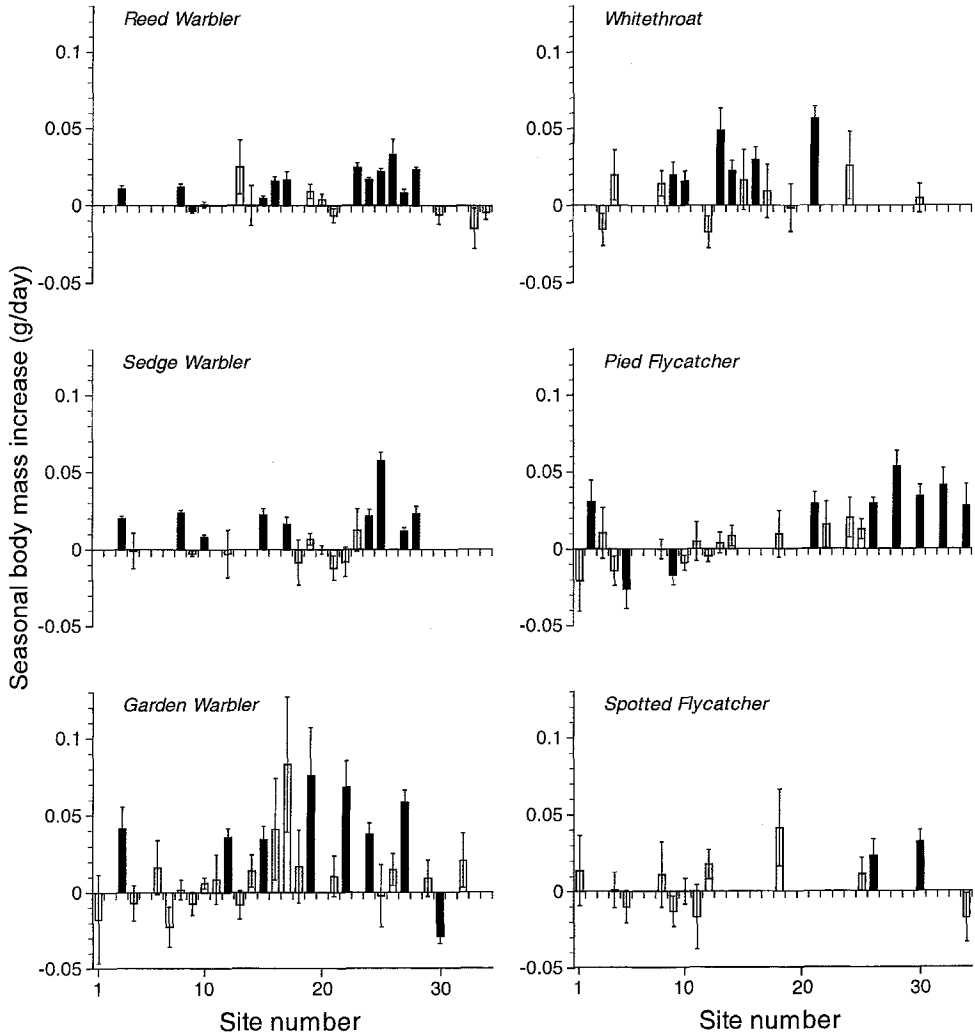
Fig. 2. Average body mass increase during the season for each species and site. The site numbers refer to Table 1. Lines represent standard error. Open bars: no significant body mass change during the season, black bars: significant body mass change during the season (p < 0.05). Sites with less than 20 captures were omitted.

Abb. 2. Durchschnittliche saisonale Körpermassenänderung (g/Tag) für alle Arten und Fangorte. Die Nummern sind identisch mit denjenigen in Tab. 1. Die Linien bezeichnen den Standardfehler. Weiße Säulen: keine signifikante Änderung während der Saison. Schwarze Säulen: signifikante Änderung während der Saison (p < 0.05). Fangorte mit weniger als 20 Fänglingen wurden weggelassen.

gressively more southern populations are added to the samples, but possibly also populations with a more western or eastern origin when migration routes converge (e.g. towards Iberia). Hence, it is likely that an increase in mean body mass along the migration route of a northern population was underestimated with our data, because progressively more southern individuals with probably lower body mass mix in. On the other hand, popula-

Table 4. Mean body mass (standard error) of non-moulting birds in 1994 at sunrise with site specific average length of primary 8 and median date of passage, estimated from the models presented in Table 2.* calculated for 1995, as no data were available for 1994.

Tab. 4. Mittlere Körpermasse (Standardfehler) von nicht-mausernden Vögeln im Jahre 1994 bei Sonnenaufgang. Diese Werte wurden mit den in Tabelle 2 aufgeführten Modellen geschätzt unter Berücksichtigung der ortsspezifischen mittleren Längen der 8. Handschwinge und des Durchzugsmedians.* für 1995 errechnet, da für 1994 keine Daten vorlagen.

Site	Reed Warbler	Sedge Warbler	Garden Warbler	Whitethroat	Pied Flycatcher	Spotted Flycatcher
1: Tauvo (SF)	–	10.6 (0.68)*	17.6 (0.82)	–	12.2 (1.15)*	15.3 (0.70)*
2: Annsjön (S)	–	–	18.7 (2.50)	–	12.6 (0.60)	–
3: Rauvola (SF)	12.5 (0.12)	11.8 (0.05)	18.7 (0.37)	15.0 (0.44)	12.9 (0.46)	13.8 (0.98)
4: Hanko (SF)	–	11.2 (0.28)	19.0 (0.24)	14.9 (0.67)	12.0 (0.22)	15.2 (0.33)
5: Jurmo (SF)	–	–	–	–	11.7 (0.20)	14.9 (0.29)
6: Fair Isle (GB)	–	–	18.8 (1.57)	–	–	–
7: Jomfruland (N)	–	–	20.4 (1.58)	14.1 (0.94)*	13.1 (0.99)*	–
8: Lista (N)	12.3 (0.06)	10.8 (0.06)	18.9 (0.19)	14.8 (0.32)	12.1 (0.20)	14.6 (0.58)
9: Falsterbo (S)	12.4 (0.03)	11.5 (0.04)	18.5 (0.21)	14.7 (0.26)	11.8 (0.15)	14.3 (0.22)
10: Rybachy (RU)	12.6 (0.08)	11.7 (0.06)	19.5 (0.13)	15.1 (0.24)	12.1 (0.11)	15.1 (0.25)
11: Mierzeja Wislana (PO)	–	–	17.5 (1.54)	14.3 (1.16)*	11.7 (1.03)	16.1 (0.41)*
12: Greifwalder Oie (D)	11.8 (0.71)	11.6 (0.26)*	18.4 (0.16)*	15.0 (0.24)*	12.1 (0.08)*	15.4 (0.20)*
13: Helgoland (D)	11.8 (0.83)	–	18.9 (0.33)	14.9 (0.60)	12.4 (0.27)	14.8 (1.74)*
14: Oldeoog (D)	12.5 (0.35)	–	19.3 (0.23)	15.8 (0.28)	12.0 (0.15)	13.3 (1.42)
15: Galenbecker See (D)	11.5 (0.13)	11.5 (0.19)	18.1 (0.37)	14.0 (0.61)*	11.8 (0.68)	–
16: Reit (D)	12.1 (0.14)	10.9 (0.85)	17.9 (1.09)	15.3 (0.34)	–	–
17: Woolston (GB)	11.2 (0.30)	10.4 (0.17)	19.4 (0.89)	13.4 (0.66)	–	–
18: Bardsey (GB)	–	10.1 (0.75)	18.4 (0.82)	14.1 (1.73)	12.2 (0.41)	13.8 (0.92)
19: Kenfig (GB)	11.9 (0.24)	11.2 (0.16)	18.4 (1.54)	13.7 (0.54)	–	–
20: Stodmarsh (GB)	11.8 (0.12)	9.4 (1.18)	–	–	–	–
21: Dungeness (GB)	12.3 (0.21)	10.8 (0.23)*	18.8 (1.55)	15.8 (0.26)	12.7 (0.60)	–
22: Portland (GB)	–	11.7 (0.26)	18.2 (0.55)	15.4 (0.60)	12.3 (0.32)	13.7 (1.17)
23: Münchhausen (F)	12.5 (0.62)	10.6 (0.41)*	–	–	–	–
24: Mettnau (D)	11.8 (0.08)	11.2 (0.29)	19.0 (0.32)	13.5 (1.36)	12.8 (0.85)	14.9 (0.99)
25: Bolle di Magadino (CH)	12.3 (0.08)	11.7 (0.23)	19.2 (0.46)	–	12.7 (0.19)	14.9 (0.33)
26: Col de Bretolet (CH)	12.2 (0.23)	–	18.8 (0.22)	16.1 (0.58)	12.2 (0.07)	14.8 (0.34)
27: Campotto (I)	11.0 (0.10)	11.1 (0.08)	22.0 (0.23)	–	14.4 (0.40)	17.3 (0.58)
28: Ebro Delta (ES)	11.4 (0.10)	12.4 (0.22)*	21.1 (1.94)	13.5 (0.84)*	15.3 (0.58)	–
29: Capri (I)	–	–	19.6 (0.19)	–	–	–
30: Coto de Doñana (ES)	12.8 (0.18)	–	17.1 (0.14)	14.0 (0.30)	12.3 (0.12)	14.1 (0.32)
31: A Rocha (P)	–	–	–	19.0 (1.26)*	–	–
32: Gibraltar (GI)	–	–	18.8 (1.69)	12.8 (0.95)*	13.1 (0.25)*	–
33: Bou Rhaba (MO)	11.9 (0.21)	–	17.1 (1.39)	–	11.9 (0.42)	–
34: Moulaya (MO)	11.3 (0.12)	–	–	–	13.4 (0.31)	17.2 (0.83)

tions with migration routes diverging from or overflying the sites sampled may not be represented anymore. In our data, this probably was the case in eastern populations of Sedge Warblers, Garden Warblers, Whitethroats and Spotted Flycatchers which migrate towards south-eastern Europe (Zink 1973, 1981) where no sites were sampled. However, for these four species the populations west of 10° E migrate along a north-eastern – south-western axis which generally coincides with the main axis of sites (Fig. 1). On a finer scale, different populations may have evolved different migration strategies with respect to

Table 5. Percentage of moulting birds (moult score 2) in Northern Europe (sites north of 53.5°N), Western Europe (sites on the British Isles), Central Europe (between 49.0°N and 46.2°N), southern Europe (south of 46.2°N), and on the Alpine pass Col de Bretolet. Mean values were calculated from the site-specific proportions of moulting birds (number of sites in parentheses), except for the Col de Bretolet for which the percentage of moulting individuals (number of individuals in parentheses) caught during nocturnal migration is given.

Tab. 5. Prozentualer Anteil mausernder Vögel (Mauserklasse 2) in Nordeuropa (Fangorte nördlich von 53.5°N), Westeuropa (Fangorte auf den Britischen Inseln), Zentraleuropa (Fangorte zwischen 49.0°N und 46.2°N) und Südeuropa (Fangorte südlich 46.2°N). Die Werte wurden berechnet als Mittelwerte des ortsspezifischen Anteils (Anzahl Fangorte in Klammern), ausser für den Col de Bretolet, für den der Anteil mausernder Individuen (Anzahl Fänglinge in Klammern) auf dem Nachtzug angegeben ist.

	N-Europe	W-Europe	C-Europe	S-Europe	Col de Bretolet
Reed Warbler	38.1 (9)	52.7 (4)	27.8 (4)	15.4 (5)	16.1 (236)
Sedge Warbler	3.6 (9)	15.7 (6)	3.0 (3)	0.7 (2)	–
Garden Warbler	17.1 (14)	8.3 (6)	14.3 (3)	0.1 (6)	7.0 (585)
Whitethroat	38.6 (12)	41.7 (5)	10.1 (2)	0.0 (4)	17.1 (35)
Pied Flycatcher	32.9 (14)	0.0 (3)	2.9 (3)	0.0 (6)	5.0 (2364)
Spotted Flycatcher	18.6 (11)	2.9 (2)	44.8 (3)	8.3 (3)	26.2 (302)

where and when to fatten up. Since we cannot distinguish between different populations, the geographic body mass changes of single populations may be masked. Furthermore, territorial birds (e.g. Pied Flycatchers in Spain, Bibby & Green 1980; Reed Warblers in Sweden, Walinder et al. unpubl. data) are possibly less likely to be caught than non-territorial (subordinates, new arrivals) conspecifics and, hence, the samples may be biased towards lower body mass values. A prerequisite for the accurate interpretation of geographical patterns in body mass along the migration route is also that the average quality of the sites sampled is similar along the migration route, e.g. that the location has no effect on body mass. We cannot evaluate the quality of the sites, but mean body mass was not significantly different between the locations (island, coast, mainland). Hence, latitudinal or longitudinal effects were therefore not masked or caused by the location of the sites.

Secondly, because body mass generally increases during stopover, our analysis should ideally be based on body mass either at arrival or at departure from each site. But our analysis was performed with body mass data of birds captured for the first time at a site. Most of those birds are not captured just after arrival, but on average several days later (Schaub et al. in press). Body mass recorded in our samples is dependent not only on body mass at arrival, but also on fuel deposition rate at the site and on the time the birds have spent at the site before first capture. However, stopover duration estimated at several sites along the migration route for Reed, Sedge and Garden Warblers was quite similar between sites and usually the first capture of an individual occurred in the middle of the stopover period (Schaub & Jenni in prep.). Fuel deposition rates of a species varied between sites, but only those of the Reed Warbler increased along the migration route (Schaub & Jenni 2000). If the analysis had been made with body masses at departure, we would not expect to find markedly different results from those presented here for Sedge and Garden Warbler, but probably a slight increase of average body mass towards the south for the Reed Warbler. In summary, there are more reasons to suppose that the body mass data analysed here underestimated, rather than overestimated, an increase in the body mass of individual birds along the migration route.
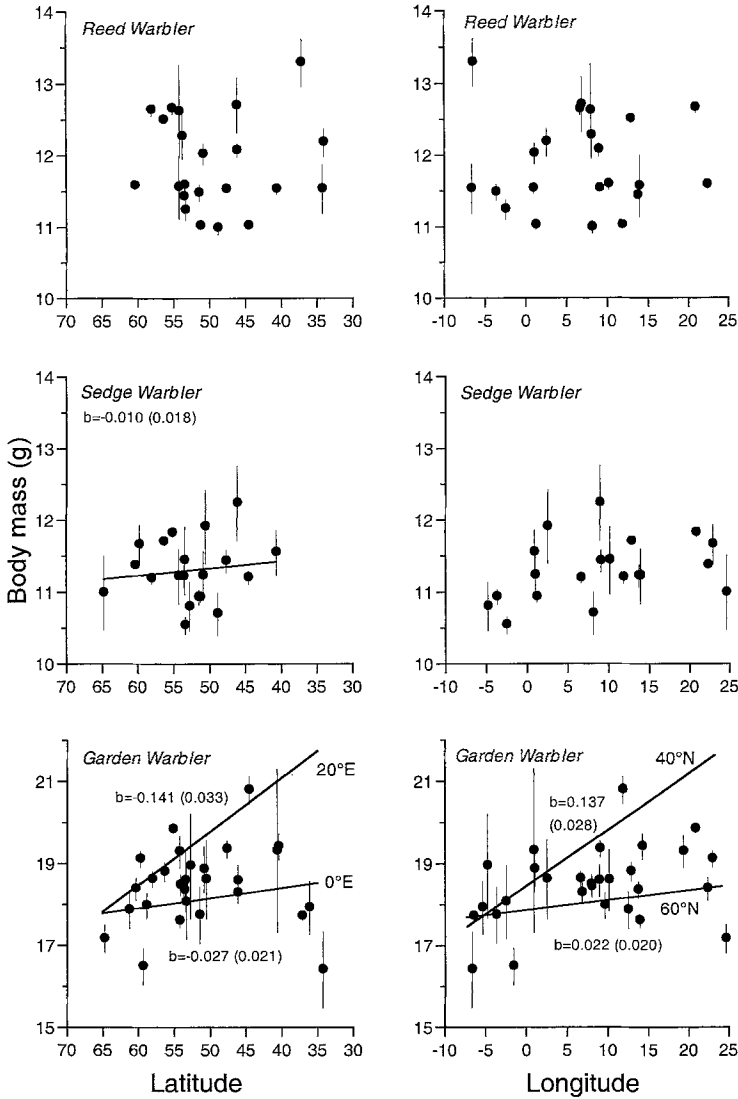
Fig. 3. Mean standardised body mass (dots) with 95 % confidence interval (lines) for each species and each site plotted against longitude and latitude. Standardisations were calculated with respect to time of capture and length of primary 8. If the relationship between body mass and latitude or longitude, respectively, was significant (see Table 6), the regression line is drawn and the slope (b) and its s.e. is shown. For the Garden Warbler, two regression lines are given in order to depict the effect of the interaction between latitude and longitude.

Abb. 3. Mittlere standardisierte Körpermasse (nach Fangzeit und Länge der 8. Handschwinge) und 95 % Vertrauensintervall aller Arten und Fangorte aufgetragen gegen Längen- und Breitengrad der Fangorte. War die Beziehung zwischen Körpermasse und Längen- oder Breitengrad signifikant (siehe Tabelle 6), so ist die Regressionsgerade eingezeichnet sowie die Steigung (b) und deren Standardfehler angegeben. Für die Gartengrasmücke wurden je zwei Regressionsgeraden eingezeichnet, um die Interkation zwischen Längen- und Breitengrad zu verdeutlichen.
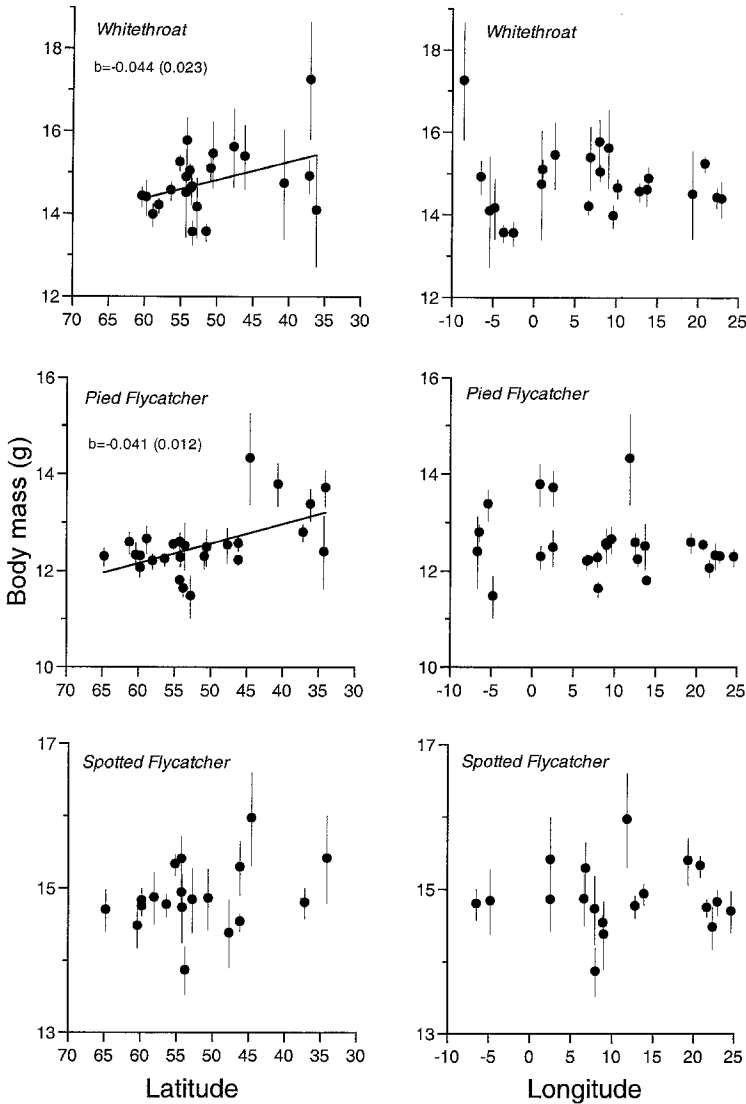
Fig. 3. (continued)
Abb. 3. (Fortsetzung)

Effects of time of capture, size, date and year

Regressing the time of capture on the body mass at first capture can give an indication of body mass increase of individual birds within a day. As pointed out earlier, most Reed Warblers were caught during the first hours after sunrise, which resulted in an unreliable estimate of daily body mass increase, but this has only small effects on the adjustment of body mass on the time of capture. Estimates of body mass increase during the day from individual birds can be obtained from retraps. The weighted average increase obtained from the

Table 6. Effects of longitude, latitude and location (island, coast, mainland) on adjusted (with respect to time of capture and length of primary 8) site-specific mean body mass values (ANCOVA).
Tab. 6. Effekt von Längen- und Breitengrad, sowie von der Lage des Fangortes (Insel, Küste, Inland) auf standardisierte (nach Fangzeit und Länge der 8. Handschwinge) ortsspezifische Körpermassen (Kovarianzanalyse).

Species	Source	df	ss	F	p
Reed Warbler	Location	2	1.19	1.37	0.28
	Longitude	1	0.06	0.14	0.72
	Latitude	1	0.05	0.10	0.75
	Longitude*Latitude	1	0.16	0.38	0.55
	Residual	16	6.94		
	Total	21	8.39		
Sedge Warbler	Location	2	0.32	1.21	0.33
	Longitude	1	0.25	1.92	0.19
	Latitude	1	0.88	6.68	< 0.05
	Longitude*Latitude	1	0.15	1.16	0.30
	Residual	14	1.85		
	Total	19	3.45		
Garden Warbler	Location	2	1.35	2.51	0.10
	Longitude	1	3.10	11.48	< 0.01
	Latitude	1	2.47	9.17	< 0.01
	Longitude*Latitude	1	11.02	40.86	< 0.01
	Residual	23	6.21		
	Total	28	24.15		
Whitethroat	Location	2	0.16	0.13	0.88
	Longitude	1	0.11	0.18	0.68
	Latitude	1	3.81	6.25	< 0.05
	Longitude*Latitude	1	0.03	0.05	0.83
	Residual	17	10.39		
	Total	22	14.50		
Pied Flycatcher	Location	2	1.73	3.50	0.05
	Longitude	1	0.08	0.35	0.56
	Latitude	1	3.25	13.27	< 0.01
	Longitude*Latitude	1	0.18	0.73	0.40
	Residual	20	4.90		
	Total	25	10.14		
Spotted Flycatcher	Location	2	0.46	1.43	0.28
	Longitude	1	0.04	0.26	0.62
	Latitude	1	0.50	3.13	0.10
	Longitude*Latitude	1	0.45	2.82	0.12
	Residual	13	2.07		
	Total	18	3.51		

retraps of some of the sites combined was 0.061 gh^{-1} (Reed Warbler), 0.065 gh^{-1} (Sedge Warbler) and 0.079 gh^{-1} (Garden Warbler) (from Schaub & Jenni 2000). Hence, the estimates obtained in the present study were similar to the values derived from retraps of Sedge and Garden Warblers.

The speed of migration increases in the course of the season (Ellegren 1993, Fransson 1995), which is possible if the fuel deposition rates increase, as found by Schaub and Jenni (2000). The speed increase could then either be achieved by seasonally decreasing stopover durations but maintaining constant lengths of

flight bouts or by constant stopover durations but seasonally increasing lengths of flight bouts. In the former case, departure body mass would remain constant during the season, whereas in the latter case it would increase. Our findings suggest the latter. However, the seasonal body mass increase was quite small, and possibly the seasonal increase in migration speed is achieved by a combination of seasonally decreasing stopover duration and seasonally increasing lengths of flight bouts. The seasonal body mass increase was higher at southern sites in the Pied Flycatcher. This pattern is likely to occur if birds increase body mass along the migration route and if migration speed increases in the course of the season.

There are many possible reasons for variation in mean body mass between years. Food availability might change between years, weather might influence the decision of when to land or to embark, which affects the sample caught, and migration of different populations might be delayed or might follow a slightly different route in different years. Since yearly mean body mass did not vary in the same direction at all sites, it is not likely that factors governing body mass on a large scale are in operation, such as large-scale weather situations during migration or a generally late breeding season.

At most sites the average body mass of first-year non-moulting birds as predicted by the models (Table 4) were not higher than the body mass reported during breeding. Although the average values reported here might be biased downwards (see above) the species studied show on average no marked general increase in body mass over much of their migration leg in Europe. Nevertheless, birds during the migration season might have more energy reserves than during the breeding season because the body composition might have changed. Furthermore, the body masses reported here are those at first capture. The departure body mass can be much higher depending on stopover duration after capture and fuel deposition rate at the particular site.

Body mass variation between sites and timing of moult

Moult was one of the major factors affecting body mass (Table 2). Moult may energetically or physiologically compete with migration and the accumulation of energy stores (Lindström et al. 1994). Therefore, the seasonal timing of moult in relation to migration may influence the pattern of energy accumulation and, hence, body mass along the migration route.

Sedge Warbler, Garden Warbler and Pied Flycatcher separate moult and migration almost entirely (Table 5). Garden Warbler and Pied Flycatcher moult prior to migration (Jenni & Winkler 1994), whereas Sedge Warblers delay moult until they arrive in the wintering quarters (Redfern & Alker 1996).

Sedge Warblers only slightly increased body mass along the migration route. Individuals which have accumulated large energy stores usually start a non-refuelling flight from as far back as western and central Europe or the northern Mediterranean region to sub-Saharan Africa (Bibby & Green 1981). Therefore, the only birds are likely to be caught are those which have not attained the level of body mass required for embarking on such long flights. The body mass of Pied Flycatchers remained constant over northern and central Europe and increased rapidly south of 45° N (south of the Alps).

As shown earlier by Bairlein (1991), the body mass of Garden Warblers during autumn migration increased from the breeding grounds in Europe to North Africa, i.e. along the northeast – south-west migration axis. Compared with Bairlein's (1991) data, our estimates were lower for both east of 10° E (1.1 versus 1.7 g/ 10° latitude) and west of 10° E (0.0 versus 1.0 g/10° latitude; analysed in the same way as in Bairlein 1991). The three southernmost sites sampled in our study (all west of 10° E) provided particularly low body mass values (Fig. 2) and, if omitted, there is a significant increase of 0.8 g/10° latitude for the remaining sites west of 10° E. These three sites (Coto de Doñana, Gibraltar and Capri) were also in-

cluded by Bairlein (1991), but he found average body masses at least 2 g higher than in our study. It is not known why body mass collected during the three study years was so low at these three sites; the fact that Bairlein (1991) also included adult birds with generally slightly higher body mass and that he did not adjust body mass according to size and time of capture can only explain part of the difference. Bairlein (1991) had data available from more sites in SW-Europe which showed high average body mass. Despite these discrepancies, both studies found basically the same pattern, i.e. a more pronounced increase in body mass in eastern than in western birds. Western populations of Garden Warblers which migrate towards the Iberian peninsula have to cross only a small stretch of the Mediterranean Sea, find suitable stopover areas in North Africa and cross the western part of the Sahara with more oases and a shorter extension than those further east. In contrast, Garden Warblers migrating more to the east have to cross the Mediterranean Sea, find less suitable stopover sites in North Africa and cross the most inhospitable part of the Sahara (Biebach et al. 1986). Hence, the latter need larger energy stores.

Reed Warbler, Spotted Flycatcher and Whitethroat are in still moult at the onset of migration (Table 5; see also Herremans 1990 for Reed Warbler, Norman 1990 for Whitethroat). Reed Warbler and Spotted Flycatcher did not increase body mass along the migration route, and this was also true when only non-moulting birds were considered. In Whitethroats, body mass increase towards the south was significant, but not when only non-moulting birds were considered. Since the proportion of moulting Whitethroats decreased from north to south and because moulting birds were lighter than non-moulting birds, the observed body mass increase towards the south was mainly due to a decrease in the proportion of moulting birds.

In conclusion, the timing of moult appears to have profound effects on energy accumulation and body mass along the migration route. The fuel deposition rate of moulting birds is reduced (Schaub & Jenni 2000) which allows only a migration in short hops. Indeed, the migration speed of species moulting during migration in northern and central Europe is lower than that of the next related species not moulting during migration: in Sedge Warblers migration speed is higher than in Reed Warblers (Bensch & Nielsen 1999), in Garden Warblers it is higher than in Whitethroats (Fransson 1995, Ellegen 1993), and in Pied Flycatchers it is higher than in Spotted Flycatchers (Hildén & Saurola 1982). When moult is completed (or suspended) somewhere on the migration route, fuel deposition rate (Reed Warblers; Schaub & Jenni 2000) or body mass (Whitethroats) increases. In species which do not moult during migration, the accumulated energy at stopover places can be used entirely for migration which allows birds to build up more energy stores than are necessary to reach the next stopover sites. This makes the birds independent of high quality stopover sites before large ecological barriers nor do they need to stop for a long time at these sites.

Migration strategies

From the findings of this and earlier studies, four theoretical strategies about where and how much to fuel up emerge (Fig. 4). Birds may already start to accumulate large fuel stores well before the northern edge of the Sahara (e.g. at the first high-quality site encountered) and fly to sub-Saharan Africa without refuelling (strategy 1). This strategy is adopted by western populations of the Sedge Warblers (Bibby & Green 1981, Schaub & Jenni 2000) and possibly also by some individuals of other species. A few individuals of all species examined were very heavy and fat. The highest body mass of single birds north of the Alps exceeded the average mass of their conspecifics by 33 % (Spotted Flycatcher) to 78 % (Sedge Warbler; highest body mass: 20.0 g for Reed Warbler, 20.2 g for Sedge Warbler, 28.8 g for Garden Warbler, 21.8 g for Whitethroat, 19.4 g for Pied Flycatcher, 19.9 g for Spotted Flycatcher).
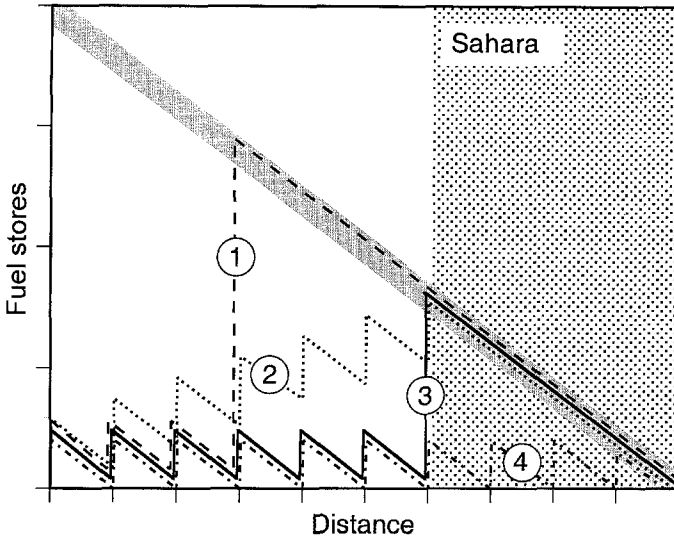
Fig. 4. Possible strategies for the migration from the breeding grounds in Europe to sub-Saharan Africa in terms of fuel stores. The diagonal grey bar-line indicates the fuel load needed for flying to the southern border of the Sahara without refuelling. The different strategies are: (1) start of non-refuelling migration well before the Sahara; (2) steadily increasing fuel load along the migration route; (3) large fuel deposition just before the Sahara; (4) refuelling in the Sahara (strippled area). Note that the relationship between fuel store and distance should be slightly curved, but is drawn as a straight line for the sake of simplicity.

Abb. 4. Mögliche Strategien für den Zug von den Brutgebieten zu den Überwintersgebieten südlich der Sahara dargestellt als Beziehung zwischen Energiereserven und Distanz. Der diagonale graue Balken zeigt an, wieviel Energie nötig wäre, um das Ziel ohne weiteres Auftanken zu erreichen. Die unterschiedlichen Strategien sind: (1) Beginn eines Fluges ohne weiteren Fettaufbau schon weit vor der Nordgrenze der Sahara; (2) Kontinuierliche Zunahme der Energiereserven entlang des Zugweges; (3) Energiereserven bleiben entlang des Zugweges konstant, erst kurz vor der Sahara werden sie markant gesteigert; (4) Energiereserven bleiben immer gleich, was Rast und Fettaufbau in der Sahara bedingt. Der Einfachheit halber wurde die Beziehung zwischen Energiereserven und Distanz linear dargestellt, in Wirklichkeit ist sie leicht konkav gekrümmt.

These individuals might have reached sub-Saharan Africa with a non-refuelling flight.

Another strategy (2 in Fig. 4) is to accumulate more energy during each stopover than is needed to fly to the next one. This results in a steady increase of body mass towards the south. In contrast to strategy 3, this avoids the accumulation of large energy stores in the southern Mediterranean region. Garden Warblers and Pied Flycatchers are likely to have adopted such a strategy. Fuel deposition rates derived from retraps (Schaub & Jenni 2000) and stopover durations (Schaub & Jenni in prep.) of Garden Warblers at sites just before the Sahara were not higher than those reported

from north and central European stopover sites, which confirms that they do not rely entirely on stopover sites just before the desert. Because eastern populations have to cover a longer distance across inhospitable area (see above), they gain larger fat stores than western populations.

With strategy 3, birds would just accumulate at each stopover site the amount of energy which is needed to fly safely to the next one. As the distance over the Sahara is longer than a one-night flight bout over continental Europe, birds are urged to fuel-up extensively just before reaching this barrier. This strategy probably involves finding high-quality stopover

sites in the southern Mediterranean region. Hence, a high body mass is probably often attained at specific places and only a few days before departure and, hence, is not easily detected. Reed Warblers and perhaps also Whitethroats adopt this strategy. Fuel deposition rates of Reed Warblers derived from retraps increased towards the south and were highest in Northern Morocco (Schaub & Jenni 2000), which is in good accordance with strategy 3. However, our data do not reflect these postulated high body masses before crossing the Sahara because the sites sampled for this study were probably not the best refueling places for each species and because we reported body mass at first capture and not body mass at departure.

The last strategy (4) is again to accumulate at each stopover site just the amount of energy needed to fly safely to the next one. But in contrast to strategy 3, refuelling sites in the Sahara are used and hence no extensive fuel-up just before the Sahara is necessary. Many passerine long-distance migrants have been found refuelling in oases (e.g. Bairlein 1985, Biebach et al. 1986, Bairlein 1992, Biebach 1995,), but it is not clear whether this is the result of an evolved strategy or whether the observed birds originally pursued another strategy but failed to carry it through. For example they might have intended to fly without refuelling over the Sahara but failed because they had not accumulated enough fuel before the Sahara. There are indications that Spotted Flycatchers adopt such a strategy but they may not rely entirely on oases. Spotted Flycatchers can be seen hunting insects in the middle of the desert (Bairlein 1992, pers. obs.), probably hoverflies *Syrphidae*, which also migrate (Gatter & Schmid 1990). The average fat score of Spotted Flycatcher (1.95) is lower than that of the other species (Reed Warbler 2.59; Sedge Warbler 2.35; Garden Warbler 2.83; Whitethroat 2.59; Pied Flycatcher 2.15) and it did not increase towards the south. Spotted Flycatchers did not accumulate much energy before the Sahara which might urge them to refuel from time to

time in the desert. The body masses of Spotted Flycatchers captured in oases and in the desert are about the same or slightly higher than the ones from Europe and they have only little fat stores on average (Moreau 1969, Bairlein et al. 1983, Bairlein 1985, Bairlein 1992). Other bird species that stop in the desert outside oases normally do not refuel (Bairlein 1985, Biebach et al. 1986) and are not included in strategy 4.

Assigning one of the four migration strategies to each of the six species is to some extent preliminary because certain data are lacking for some species. In particular, fuel deposition rates and stopover durations over a wider geographical area are not known for the two flycatcher species and the Whitethroat, but would be important information for deriving the migration strategy. Populations or individuals of a species might differ in their migration strategy. Furthermore, it is an open question how flexible individual birds are in switching to another strategy when environmental conditions change. When there are enough stopover sites of high quality before the Sahara (southern Mediterranean region), it might not be of crucial importance which strategy to adopt in terms of the success of the journey (survive or not). But if stopover sites before the Sahara become scarce, there will be a strong selective pressure against strategy 3 and against moulting during migration across Europe.

Acknowledgements

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