



Migrating passerines can lose more body mass reversibly than previously thought

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Knowing the amount of body mass that migrants can lose is essential for the estimation of potential flight ranges, assessing the importance of stopover sites or modelling migration strategies. 'Lean' body mass, (the mass without fat stores) is often used to describe the limit of body-mass loss but birds also use protein as fuel for flight. The mean body mass of 621 passerines mist-netted in Mauritania between 2001 and 2004 with a fat score of 0 (no visible subcutaneous fat stores) and a muscle score of 0 (emaciated flight muscle) was much lower compared to the lean body mass values found in the literature. Recaptures showed that these birds were able to refuel again. The mean body mass of 122 Garden Warbler *Sylvia borin* with both a fat score and a muscle score of 0 was 12.8 g. The mean potential flight range of four Garden Warblers captured in the desert was 35% higher when 12.8 g was used for the estimation compared to the 15.0 g often used in previous studies. This has implications for future studies of the migration strategies of passerines, and suggests that, in the past, the fuel load of migrating passerines has been underestimated.

Birds need fuel for flight. Therefore migrants deplete stores of fat and protein during endurance flights. The maximum width of ecological barriers, such as oceans or deserts where there is no chance to refuel, and which birds are able to cross, is limited by the amount of fuel (fat and protein) that birds are able to deposit. The depletion of fuel stores can lead to a considerable reduction of body mass during a flight bout (eg Pilastro & Spina 1997, Salewski *et al* 2002, Battley & Piersma 2005, Bauchinger & Biebach 2005) depending on the length of the flight step and the opportunity for refuelling en route. Therefore, the body mass of migrants undertaking long endurance flights is very variable (Lindström & Piersma 1993, Piersma & Lindström 1997, Bauchinger & Biebach 2005). According to the definition of Salewski *et al* (2009) the total body mass can be divided into a variable part: the fuel (fat fuel and protein fuel) and a non-variable part: the structural mass (components of the body that cannot be used as fuel). By definition, a bird with only its structural mass should represent a bird that has just starved to death. However, for practical reasons, Salewski *et al* (2009) used the mass of living birds without visible subcutaneous fat stores and an emaciated breast muscle as an approximation of structural mass.

Knowledge of the structural mass of birds is important for assessing the actual fuel load. This has implications for estimating potential flight ranges as well as assessing how

much fuel must be deposited at a stopover site for the next migration step. Furthermore, carrying high fuel loads is not only advantageous for long-distance flights but also imposes costs, such as an increased predation risk because of reduced flight manoeuvrability and acceleration at take-off (Hedenström 1992, Witter & Cuthill 1993, Kullberg *et al* 1996, Lind *et al* 1999, but see Moreno-Rueda 2003). Additionally, the extra fuel load needs additional power to be carried, resulting in a higher basic metabolic rate and the possibility that optimal migration speeds may not be reached (Lindström & Alerstam 1992, Videler 1995, Klaassen & Lindström 1996). Therefore, for the understanding of stopover ecology and fuel deposition strategies, as well as the implementation of optimal bird migration theories, it is important to know how much fuel mass can be lost reversibly, *ie* the difference between the actual body mass and the structural mass. Hence, the structural mass must be known in advance of such analyses.

Many authors who estimated potential flight ranges of migrants (eg Hjort *et al* 1996, Pilastro & Spina 1997, Hilgerloh & Wiltshko 2000) applied the concept of 'lean body mass', *ie* treating fat as a synonym for fuel in their models (but see Pennycuik 2008). As fat is deposited in subcutaneous stores, it can be visually inspected and several scoring systems have been introduced to rank fat stores (Helms & Drury 1960, Pettersson & Hasselqvist 1985, Kaiser 1993). These scores vary in the number of categories and the distribution of fat for a given category but a score of '0' always indicates 'no visible fat stores' *ie* a

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account of the fact that protein as well as fat is also used as fuel on migration (Lindström & Piersma 1993, Jenni & Jenni-Eiermann 1998), although some authors have used a correction factor to account for this (Ottosson *et al* 2001). Studies that consider only fat as fuel will underestimate total fuel stores and overestimate the structural mass. Consequently, potential flight ranges are underestimated when a proportion of mass is interpreted as a load to carry instead of being fuel for flight. This problem is avoided when the concept of structural mass is used.

During the project 'Bird Migration across the Sahara' of the Swiss Ornithological Institute, we recognised that many birds with fat and muscle scores of 0 had a body mass well below that indicated as 'lean body mass' according to values in the literature. Here we present data on body mass of migrant passerines mist-netted in Mauritania with fat and muscle scores of 0, which is presumably close to the structural mass. We show that this mass is considerably lower than the 'lean mass' previously used to estimate potential flight ranges or to discuss migration strategies. We further show that birds with low masses are able to regain mass and therefore that the low body masses recorded by us are reversible.

METHODS

During the entire project, between 2001 and 2004, 621 passerines of 33 species were mist-netted with both a fat score and a muscle score of 0. Body mass of birds was measured with an accuracy of 0.1 g either with an electronic scale or with a Pesola spring balance. Visible subcutaneous fat stores were estimated on a nine-digit scale according to Kaiser (1993) and the thickness of the breast muscle was scored on a four-digit scale according to Bairlein (1995). A fat score of 0 means that there are no visible fat stores and a muscle score of 0 means that the flight muscles (*musculus pectoralis superficialis* and *m. p. profundus*, Bezzel & Prinzinger 1990) are deeply depressed and emaciated. We did not correct body mass for a measure of body size: in a separate analysis based on a much larger sample but including the birds considered here, the estimated size-corrected body mass of birds with a muscle score and a fat score of 0 was almost identical with the actual mean body mass of these birds (Salewski *et al* 2009).

For the calculation of the mean body masses of birds with fat scores and muscle score of 0, only first captures were considered and therefore no bird was included more than once. To analyse whether the sometimes unexpectedly low body masses were reversible losses, we compared the initial body mass at first capture with the mass at the last recapture. To assess the impact of our results we undertook

a literature search for body mass of the species considered by us used in studies to calculate flight-range estimates.

Taking four Garden Warblers *Sylvia borin* captured in open desert as an example (for details see Salewski *et al* 2009) we show how our results may influence estimates of the potential flight range. Flight ranges can be estimated using the program 'Flight' (Pennycuick 2008). However, for analyses with this program a number of parameters (wing span, wing area, air density, altitude) have to be entered, and some parameters are given by default but can be changed manually, such as minimum energy derived from protein. One problem is that the fat and flight-muscle mass also has to be known, but this is information that is obtainable only from dead birds. However, as an approximation to body mass loss during migration, Hussell & Lambert (1980) showed that a body mass loss of 1% per hour of flight is a realistic assumption. Therefore, for flight-range estimates we followed the approach of Delingat *et al* (2008) and assumed that the body mass of migrating birds decreases by 1% per hour of flight. The potential flight range Y [km] can then be estimated according to the equation:

$$Y = 100 \cdot U \cdot \ln(1 + f) \quad \text{Equation 1}$$

where U [km/h] is the mean airspeed of spring migrants over the desert of 40 km/h (Schmaljohann *et al* 2008); f is the relative fuel load derived from:

$$f = (m - m_0)/m_0 \quad \text{Equation 2}$$

for which m is the body mass of captured birds and m_0 is either the structural mass (values from this study) or the lean body mass (other studies).

RESULTS

Of all birds with an initial fat score and a muscle score of 0, three (a Reed Warbler *Acrocephalus scirpaceus*, a Spotted Flycatcher *Muscicapa striata* and a Wheatear *Oenanthe oenanthe*) were excluded from further analyses because they were reported to have been dead. It is not clear from the original comments whether these birds were already dead in the nets or died during ringing or shortly afterwards. The number of birds considered for each species varied from one (House Martin *Delichon urbicum*, White Wagtail *Motacilla alba*, Wood Warbler *Phylloscopus sibilatrix*) to 122 (Garden Warbler). The mean body mass of these birds is listed in Table 1. A comparison of the structural mass in this study with the lean masses or similar values used to estimate flight ranges in previous studies showed that

the values of our study were from 6.2% (Willow Warbler *Phylloscopus trochilus*) to 24.3% (Common Whitethroat *Sylvia communis*) lower than those previously reported (Table 2). Two authors of this paper (VS, MH) together ringed 434 (70%) of the birds examined. Their impression was

that the great majority were apparently in a good condition with respect to their behaviour and did not appear to be moribund despite their low body masses.

To analyse whether the low body masses of the birds in our study were reversible, we analysed recoveries and

Table 1. Body mass [g] of passerines at first capture with a fat score of 0 and a muscle score of 0. Shown are the number of birds captured (n), the mean, standard deviation (sd), minimum and maximum values of their body mass.

Species		n	Mean	sd	Minimum	Maximum
Short-toed Lark	<i>Calandrella brachydactyla</i>	3	15.27	0.95	14.2	16.0
Sand Martin	<i>Riparia riparia</i>	8	9.78	0.70	8.9	10.8
Barn Swallow	<i>Hirundo rustica</i>	75	13.40	1.03	8.8	15.6
Red-rumped Swallow	<i>Cecropis daurica</i>	2	16.20	1.00	15.5	16.9
House Martin	<i>Delichon urbicum</i>	1	12.00	-	-	-
Tree Pipit	<i>Anthus trivialis</i>	11	16.12	1.36	13.5	17.8
White Wagtail	<i>Motacilla alba</i>	1	19.10	-	-	-
Yellow Wagtail	<i>M. flava</i>	17	12.41	1.22	9.4	14.5
Nightingale	<i>Luscinia megarhynchos</i>	42	14.61	1.37	11.9	17.8
Bluethroat	<i>L. svecica</i>	5	12.36	1.23	11.0	14.3
Rufous Scrub Robin	<i>Cercotrichas galactotes</i>	5	19.20	0.84	18.0	20.0
Common Redstart	<i>Phoenicurus phoenicurus</i>	38	11.24	0.99	9.5	13.5
Wheatear	<i>Oenanthe oenanthe</i>	3	18.17	2.47	15.9	20.8
Black-eared Wheatear	<i>O. hispanica</i>	4	13.70	0.57	13.0	14.3
Whinchat	<i>Saxicola rubetra</i>	7	11.57	0.90	10.3	12.8
Garden Warbler	<i>Sylvia borin</i>	122	12.77	0.98	10.0	15.0
Blackcap	<i>S. atricapilla</i>	7	12.97	0.53	12.0	13.5
Orphean Warbler	<i>S. hortensis</i>	2	15.05	0.35	14.8	15.3
Common Whitethroat	<i>S. communis</i>	17	10.91	0.96	9.3	12.5
Subalpine Warbler	<i>S. cantillans</i>	4	6.85	0.30	6.4	7.0
Sedge Warbler	<i>Acrocephalus schoenobaenus</i>	2	8.15	0.21	8.0	8.3
Reed Warbler	<i>A. scirpaceus</i>	81	8.48	0.58	7.0	10.0
Grasshopper Warbler	<i>Locustella naevia</i>	30	9.53	0.59	8.3	10.8
Melodious Warbler	<i>Hippolais polyglotta</i>	5	8.30	0.43	7.8	8.8
Olivaceous Warbler	<i>H. pallida</i> ¹	5	8.34	0.32	8.0	8.8
Willow Warbler	<i>Phylloscopus trochilus</i>	23	6.10	0.92	4.4	8.5
Wood Warbler	<i>P. sibilatrix</i>	1	7.10	-	-	-
Chiffchaff	<i>P. collybita</i> ²	4	5.45	0.37	5.0	5.8
Spotted Flycatcher	<i>Muscicapa striata</i>	7	10.94	0.73	9.9	11.8
Pied Flycatcher	<i>Ficedula hypoleuca</i>	70	9.29	0.72	6.9	11.3
Woodchat Shrike	<i>Lanius senator</i>	10	25.38	2.56	20.3	29.5
Golden Oriole	<i>Oriolus oriolus</i>	3	50.83	9.81	41.3	60.9
Ortolan Bunting	<i>Emberiza hortulana</i>	3	17.60	0.66	17.0	18.3

¹ probably includes Eastern Olivaceous Warbler *H. pallida reiseri* as well as Western Olivaceous Warbler *H. [pallida] opaca*.

² may include Iberian Chiffchaff *P. ibericus*.

recaptures of the birds considered. Of the 618 birds with a fat score and a muscle score of 0 which were released alive after ringing, one Barn Swallow *Hirundo rustica* with

a mass of 11.7 g was found dead the next morning and one Pied Flycatcher *Ficedula hypoleuca* with a body mass of 8.2 g was recovered dead seven days after ringing and

Table 2. Comparison of structural mass found in birds in the present study with 'lean body mass' or a related mass from some other studies. Shown are the values for the respective masses, the definition of the masses used by the previous studies and the respective references. Many studies did not give the sd or se, or the number of individuals considered, and often the values are rounded to the first decimal place. We therefore refrain from giving sd and n when available and round our own values from Table 1 to one decimal place.

Species	Structural mass [g] (this study)	'Lean' mass [g] (other studies)	Selection criterion	Reference
Short-toed Lark	15.3	19.0	Fat score = 0	Pilastro & Spina (1997)
Tree Pipit	16.1	17.4	Fat score = 0	Pilastro & Spina (1997)
Yellow Wagtail	12.4	13.5	Fat score = 0	Pilastro & Spina (1997)
Nightingale	14.6	17.6	Fat score = 0	Pilastro & Spina (1997)
Common Redstart	11.2	12.3	Fat score = 0	Pilastro & Spina (1997)
Wheatear	18.2	19.4	Fat score = 0	Pilastro & Spina (1997)
Black-eared Wheatear	13.7	15.3	Fat score = 0	Pilastro & Spina (1997)
Whinchat	11.6	12.8	Fat score = 0	Pilastro & Spina (1997)
Garden Warbler	12.8	15.0	Assumed fat-free weight	Bairlein (1987)
"	"	14.0–17.0	Fat-free mass (fat score 0) related to wing	Ellegren & Fransson (1992)
"	"	14.8	Fat score = 0	Pilastro & Spina (1997)
"	"	16.1, 15.8 ^{1*}	Fat score = 0, corrected by wing length	Hilgerloh & Wiltschko (2000)
Blackcap	13.0	15.4	Fat score = 0	Hjort <i>et al</i> (1996)
"	"	14.3, 15.7, 16.1, 17.2 ²	Fat score = 0	Izhaki & Maitav (1998)
"	"	15.3	Fat score = 0	Ottosson <i>et al</i> (2001)
Orphean Warbler	15.1	19.8	Fat score = 0	Ottosson <i>et al</i> (2001)
Common Whitethroat	10.9	14.4, 11.7 ³	Fat extracted	Baggott (1986)
"	"	12.2	Fat score = 0	Hjort <i>et al</i> (1996)
"	"	12.2	Fat score = 0	Pilastro & Spina (1997)
"	"	12.9	Fat score = 0	Ottosson <i>et al</i> (2001)
Subalpine Warbler	6.9	8.6	Fat score = 0	Pilastro & Spina (1997)
"	"	9.0	Fat score = 0	Ottosson <i>et al</i> (2001)
Sedge Warbler	8.2	10.5, 9.5, 10.3 ⁴	Fat extracted	Baggott (1986)
"	"	9.6	Fat score = 0	Pilastro & Spina (1997)
Reed Warbler	8.5	10.0	Fat score = 0	Pilastro & Spina (1997)
"	"	10.2	Fat score = 0, corrected by wing length	Hilgerloh & Wiltschko (2000)
Grasshopper Warbler	9.5	11.6, 11.9, 12.4 ⁵	Fat extracted	Baggott (1986)
"	"	11.0	Fat score = 0	Pilastro & Spina (1997)
"	"	7.7, 8.0, 7.6 ⁶	Fat extracted	Baggott (1986)
"	"	7.0	Fat-free mass	Biebach (1990)
"	"	6.5	Minimum mass with no energy reserves	Biebach (1992)
"	"	7.2	Fat score = 0	Pilastro & Spina (1997)
Willow Warbler	6.1	7.6	Fat score = 0, corrected by wing length	Hilgerloh & Wiltschko (2000)
Wood Warbler	7.1	7.8	Fat score = 0	Pilastro & Spina (1997)
Spotted Flycatcher	10.9	12.1	Fat score = 0	Pilastro & Spina (1997)
Pied Flycatcher	9.3	10.2	Fat score = 0	Pilastro & Spina (1997)
"	"	10.6	Fat score = 0, corrected by wing length	Hilgerloh & Wiltschko (2000)
Woodchat Shrike	25.4	30.2	Fat score = 0	Pilastro & Spina (1997)
Golden Oriole	50.8	56.1	Fat score = 0	Pilastro & Spina (1997)
Ortolan Bunting	17.6	21.0	Fat score = 0	Pilastro & Spina (1997)

¹ two different sites

² Eilat in spring, in autumn, northern Israel in spring, in autumn

³ autumn, spring

⁴ autumn, spring adult female, spring adult male

⁵ autumn first year, autumn adult, spring

⁶ autumn adult, autumn first year, spring

had apparently been dead for several days. Eighty birds of 17 species were recaptured one day or more after the initial capture (Table 3). All species for which more than three individuals were considered (Nightingale *Luscinia megarhynchos*, Garden Warbler, Reed Warbler, Grasshopper Warbler *Locustella naevia*, Pied Flycatcher) showed a positive mean body-mass change. In other species, single individuals also gained body mass within a few days (eg Bluethroat *Luscinia svecica*, Black-eared Wheatear *Oenanthe hispanica*, Orphean Warbler *Sylvia hortensis*, Ortolan Bunting *Emberiza hortulana*) although others lost body mass. The latter mainly affected diurnal migrants (Sand Martin *Riparia riparia*, Barn Swallow, Yellow Wagtail *Motacilla flava*).

There were no recoveries of the birds with an initial fat score and muscle score of 0, but of the 20 passerines ringed during the project and later recovered in Europe some had very low initial body masses that were comparable to those considered here. Three Reed Warblers with body masses of 10.3 g, 9.5 g and 9.0 g and a Pied Flycatcher at 10.0 g when ringed in Mauritania were recaptured or recovered at a later date in Europe, proving that they managed to refuel and to continue migration successfully despite their low initial body mass.

Four Garden Warblers mist-netted in April 2004 with a body masses of 22.4 g, 23.5 g, 24.4 g and 25.4 g in Bir Amrane (22°47' N, 8°43' W), a site without any possibility of refuelling, had a potential mean flight range of 1,863

± 214 km (sd), according to equation 1, when a constant flight and 15.0 g for m_0 (Table 2) was assumed. When m_0 was set to 12.8 g for the four birds (Table 1) the mean flight range was 2,507 ± 214 km (sd) or 35% higher. This result indicates that the definition of the minimal possible body mass (here structural mass instead of lean mass) has great implications for flight range estimates and the modelling of migration strategies.

DISCUSSION

We have shown that migrating passerines can lose more body mass without dying than previously thought. Some individuals with very low initial body mass gained mass within a few days and others with a low initial mass when captured in Mauritania were later recovered in Europe. This suggests that, while it is not possible to assess the fitness consequences of extreme body mass loss during migration, for example through its effect on later breeding performance, the amount of body mass lost as recorded here is reversible. Although the body masses recorded here were far below the average body masses of the respective species, and therefore indicate extreme situations, the respective individuals can regain such losses and continue migration. Therefore, it can be argued in turn that migrating passerines have more fuel available for migration

Table 3. Body mass change of recaptured birds with an initial fat score and muscle score of 0. Shown are the number of individuals per species, the initial body mass, the number of days between the initial capture and the last capture and the body mass change. When more than three individuals were considered the mean ± sd is given.

Species	n	Initial body mass [g]	n days after initial capture	Mean body mass change [g/day]
Sand Martin	1	10.8	3	-0.27
Barn Swallow	1	13.4	1	-0.9
Tree Pipit	2	16.4/17.4	1/12	-0.40/0.11
Yellow Wagtail	3	12.7/11.2/13.5	1/1/13	-0.1/-0.7/-0.05
Nightingale	5	15.10 ± 1.6	3.0 ± 3.9	0.23 ± 0.72
Bluethroat	1	12.3	1	2.05
Common Redstart	2	11.5/10.3	1/3	-0.20/0.25
Black-eared Wheatear	1	13.5	10	0.18
Whinchat	1	11.0	1	0
Garden Warbler	21	12.5 ± 1.0	2.7 ± 1.8	0.16 ± 0.47
Orphean Warbler	1	15.3	3	0.35
Common Whitethroat	3	11.8/10.0/11.0	2/6/9	-0.13/0.33/0.58
Reed Warbler	20	8.5 ± 0.6	2.3 ± 1.6	0.47 ± 0.22
Grasshopper Warbler	8	9.7 ± 0.7	3.8 ± 3.7	0.27 ± 0.17
Willow Warbler	1	5.6	3	-0.03
Pied Flycatcher	8	9.0 ± 0.4	2.8 ± 2.1	0.16 ± 0.28
Ortolan Bunting	1	17.5	2	1.0

than previously thought, based on the visual inspection of fat scores alone (Pilastro & Spina 1997, Ottosson *et al* 2001, 2002) or the extraction of fat from dead birds (Baggott 1986, Kaiser 1992) because the extreme reversible body mass losses on migration are evidence that the lost mass was used as fuel for flight. The problem of the first approach may be that, besides ignoring protein as fuel, birds have more fat available as fuel than is apparent from a visual inspection of subcutaneous stores. This is indicated by the fact that even when muscle scores are ignored and only birds with a fat score of 0 are analysed, the body masses were distinctly below those recorded in former studies (eg $13.0 \text{ g} \pm 1.8 \text{ sd}$, $n = 211$, for the Garden Warbler; Salewski, unpublished data). The problem of the latter approach is that although fat is the most important fuel for long-distance flights, proteins that also play an important role are not considered (Lindström & Piersma 1993, Jenni & Jenni-Eiermann 1998). Protein is taken mainly from the flight muscles but also from other organs such as the leg muscles or digestive organs (Bauchinger & Biebach 2005). Salewski *et al* (2009) have shown for the Orphean Warbler that birds with a fat score of 0 can have the entire range of muscle scores (0–3). Additionally, the mass of birds with a fat score of 0 varied with muscle score. When the muscle score was also 0, the mean body mass was $15.05 \text{ g} (\pm 0.35 \text{ g sd}$, $n = 2$, this study) but, when all birds with a fat score of 0 irrespective of the muscle score were considered, the mean body mass was $17.2 \text{ g} (\pm 1.55 \text{ g sd}$, $n = 26$; muscle score 1, $16.47 \text{ g} \pm 1.12 \text{ g sd}$, $n = 10$; muscle score 2, $17.47 \text{ g} \pm 11.22 \text{ g sd}$, $n = 11$; muscle score 3, $19.67 \text{ g} \pm 0.32 \text{ g sd}$, $n = 3$). The difference in mass is additional fuel that can be used for migration. This example also shows that low body masses of birds with a muscle score of 0 are the result of a low amount of protein mass. Furthermore, Biebach (1990) found that exhausted birds close to death found in the desert showed water contents within the range of hydrated birds. Therefore, the low body masses found in this study do not merely reflect the body mass of dehydrated birds in the desert.

These results have implications for the estimation of flight ranges of migrating birds and how migrant birds have to organise their journeys. It has been known for a long time that protein is used as fuel for flight (Lindström & Piersma 1993) and therefore the concept of 'lean body mass' should be abandoned. Many studies modelling potential flight ranges of migrants used values that were derived from the application of the concept of 'lean body mass' in their models. With respect to flight-range estimates several of these studies have shown that birds carry enough fuel on spring departure from sub-Saharan Africa to cross the desert and even to enter Europe (Ottosson *et al* 2001, 2002). In contrast, other studies have suggested that this

may only be possible with wind assistance (Biebach 1992, Hjort *et al* 1996). Recent studies showed that migrating birds actively search for favourable tailwinds (Liechti 2006, Schmaljohann *et al* 2009) and, therefore, together with the findings of this study, flight ranges estimated by former studies were presumably too low. Consequently, the crossing of ecological barriers may be less costly with respect to the energy available than was previously thought (Moreau 1972).

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