INTRODUCTION

Birds cover a wide range of different strategies to cope with seasonal environmental variations, with residents and long-distance migrants representing the extremes at different ends of a gradient (Alerstam et al., 2003; Newton, 2008); whereby the emergence of several strategies within a population in different combinations, known as partial migration, is also common (Dingle, 2008; Hegemann et al., 2008). The avian lightweights: Trans-Saharan migrants show lower lean body mass than short-/medium-distance migrants

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Abstract
Avian trans-Saharan migrants travelling long distances and crossing ecological barriers experience different constraints in terms of time, energy and safety than short-/medium-distance migrants without barrier-crossings. As such, natural selection shapes the aerodynamic properties of these groups differently. Yet, to the best of our knowledge, we lack information on whether natural selection has contributed to reducing energetic flight costs through generally lower body mass in trans-Saharan migrants. To fill parts of this gap, we investigated this eco-morphological pattern in 5,410 individuals of 22 Palearctic songbird species ranging from short-/medium-distance to trans-Saharan migrants. We used individual size-independent scaled lean body mass values based on wing length as a measure of body size and, for the first time, precisely determined lean body mass values by direct measurements via quantitative magnetic resonance technology. Scaled lean body mass for a given body size was significantly higher in short-/medium-distance migrants than in trans-Saharan migrants. Although scaled lean body mass significantly decreased with increasing migration distance in short-/medium-distance migrants, no such effect was found in trans-Saharan migrants. Our results thus show an eco-morphological pattern relating species’ lean body mass not only to migration distance but also to migration group. This suggests that selective effects of the presence/absence of ecological barriers and/or of a threshold level for migration distance on migrant birds may be more important than the linear continuum of migration distance per se.

KEYWORDS
ecological barrier, eco-morphological pattern, lean body mass, migrant, migration distance, natural selection, quantitative magnetic resonance, size-independent body mass, songbird, wing length

1 | INTRODUCTION

Birds cover a wide range of different strategies to cope with seasonal environmental variations, with residents and long-distance migrants representing the extremes at different ends of a gradient (Alerstam et al., 2003; Newton, 2008); whereby the emergence of several strategies within a population in different combinations, known as partial migration, is also common (Dingle, 2008; Hegemann et al., 2008).
et al., 2015; Lack, 1943). Although residents occupy the same area all year round and, in principle, thus, show individual spatially restricted distributions, migrants travel twice each year between their breeding and nonbreeding areas (Newton, 2008). In the latter, some birds migrate over relatively short distances mostly across benign habitats, whereas others travel thousands of kilometres between continents, which includes overcoming ecological barriers such as oceans, mountains and/or deserts (Alerstam & Lindström, 1990; Lok et al., 2015). These different constraints have led to various behavioural, physiological and morphological adaptations, selected for traits that minimize time and energy spent on and that maximize safety during migration. As such, we find eco-morphological patterns linking migration distance to inherited migratory traits, for example higher levels of migratory restlessness (Maggini & Bairlein, 2010), lower selectivity for favourable weather conditions at departure (Packmor et al., 2020), higher energy stores (Alerstam & Lindström, 1990; Burns, 2003) and more specialized aerodynamic traits (Leisler & Winkler, 2003; Lockwood et al., 1998; Milá et al., 2008; Vágási et al., 2016; Winkler & Leisler, 1992) in long- than in short-/medium-distance migrants or residents. Important aerodynamic traits are range of wing motion (Baliga et al., 2019), wing pointedness (Lockwood et al., 1998), aspect ratio (Milá et al., 2008; Vágási et al., 2016), drag coefficient and wing load (Bowlin & Wikelski, 2008; Burns, 2003; Vágási et al., 2016). Wing load represents the ratio between body mass and wing area (Pennycuick, 2008). It affects the birds’ flight performance, with a lower ratio leading to lower flight transport costs and energy expenditure (Bowlin & Wikelski, 2008; Fiedler, 2005). Therefore, long-distance migrants are thought to experience a stronger natural selection pressure towards a lower wing load than short-/medium-distance migrants or residents (Fiedler, 2005; Vágási et al., 2016). A lower wing load can be obtained through longer wing length, as it is strongly correlated with wing area (Blem, 1975), or lower body mass. Although previous studies found that longer migration distances lead to a longer wing length at an intraindividual level (Fiedler, 2005; Milá et al., 2008; Nowakowski et al., 2014), the results are less clear when comparing among species, presenting no (Calmaestra & Moreno, 2001), only weak (Mönkkönen, 1995) or strong correlations (Vágási et al., 2016). These contrasting results suggest that there may not be a uniform pattern in the relationship between wing length and migration distance. Probably, other body components besides wing length are also specifically adapted to an increasing migration distance and play an essential role in explaining part of the variation in this more general pattern. We suggest that natural selection may favour, in addition to wing length, a generally lower (lean) body mass, leading to a further reduction of transport costs and energy expenditure due to a lower wing load (Fiedler, 2005; Vágási et al., 2016) when flying longer distances. Body mass is an important life-history trait that can adaptively evolve depending on the demands (Vágási et al., 2016). Previous studies provide opposing findings when observing body mass in relation to migration distance, with body mass either increasing (Mönkkönen, 1992; Winkler & Leisler, 1992), decreasing (Jones & Witt, 2014; Kaboli et al., 2007; Sol et al., 2005) within species with longer migration distances or showing only weak associations (Vágási et al., 2016). Reasons for this might be that, apart from migration, several selective forces act on the evolution of body size in migrants (Winkler & Leisler, 1992) and, importantly, that actual body mass of migrant birds is strongly influenced by the individual’s accumulated fat stores (Kelsey & Bairlein, 2019; Klaassen et al., 1997; Lindström & Piersma, 1993; Odum, 1960). These vary strongly between cycles of fattening at stopovers and energy-burning during migratory flights (Schmaljohann & Eikenaar, 2017), over the course of day (Bontner et al., 2007; Delingat et al., 2009), by date in the season, among years and between habitats (Dunn, 2000) as well as between different flight types and aerodynamic properties (Vincente et al., 2019). Therefore, we argue that natural selection acts more strongly on the bird’s “invariant” lean body mass with respect to wing load or wing length as a measure of body size (Gosler et al., 1998) than on other body mass measurements; although this may also be subject to variation within a species (Salewski et al., 2012). Obtaining direct and accurate individual lean body mass data is, however, extremely difficult because it requires either fresh carcasses (Child & Marshall, 1968; Piersma & Jukema, 1990), which is not applicable when observing live birds, or specific methods such as total body electrical conductivity (Castro et al., 1990; Walsberg, 1988), which are rarely available. On the other hand, estimating lean body mass requires, for example individuals without fat (Fiedler, 2005), which are difficult to obtain and thus rare. Other possibilities are to use either lean body mass values from other individuals in one’s own data set or to use even values from the literature (Calmaestra & Moreno, 2001). However, these latter two approaches only provide rough estimates of lean body mass and do not capture between-individual variation. We overcame these problems by taking accurate measurements of the quantitative magnetic resonance (QMR) technology EchoMRI™ (Guglielmo et al., 2011; Seewagen & Guglielmo, 2011). This allows us to directly measure and precisely determine the lean body mass of each individual in this study and hence to investigate a possible eco-morphological pattern between migration distance and the lean body mass of the birds.

However, important the selective effect of migration distance is on shaping migratory traits, it is probably superimposed and/or overridden by the presence of ecological barriers en route, representing an additional important natural selection pressure on migrant birds (Corman et al., 2014; Dierschke & Delingat, 2001). Within the Palearctic African migration system, trans-Saharan migrants have to cross the inhospitable Sahara Desert as such a barrier (Bairlein, 1992; Jiguet et al., 2019; Schmaljohann et al., 2007) and need to accumulate large energy stores near their maximum capacity (Hedenström & Alerstam, 1992), mainly stored as lipids (Jenni
& Jenni-Eiermann, 1998). However, accumulation of energy stores is limited by a maximum portable total body mass because above a certain size, available power is not sufficient to support flight (Ellington, 1991; Norberg, 1990). In this case, we predict that, rather than influenced by migration distance alone, lean body mass for a given body size measurement would be lower in trans-Saharan than

| Species                          | Sample size | Migration group | Lean body mass (g) | Wing length (mm) | Mean migration distance (km) |
|----------------------------------|-------------|----------------|-------------------|-----------------|-----------------------------|
| Willow Warbler                  | 296         | Trans-Saharan  | 7.83 ± 0.71       | 67.00 ± 3.21    | 7,150                       |
| Phylloscopus trochilus           |             |                |                   |                 |                             |
| Common Chiffchaff                | 368         | Trans-Saharan  | 6.98 ± 0.68       | 59.56 ± 3.24    | 3,000                       |
| Phylloscopus collybita           |             |                |                   |                 |                             |
| Eurasian Reed Warbler            | 24          | Trans-Saharan  | 11.16 ± 0.65      | 67.71 ± 1.39    | 6,350                       |
| Acrocephalus scirpaceus          |             |                |                   |                 |                             |
| Icterine Warbler                 | 12          | Trans-Saharan  | 12.75 ± 0.36      | 78.79 ± 1.67    | 8,700                       |
| Hippolais icterina               |             |                |                   |                 |                             |
| Eurasian Blackcap                | 401         | Pre-Saharan    | 16.46 ± 1.19      | 75.69 ± 1.91    | 2,500                       |
| Sylvia atricapilla               |             |                |                   |                 |                             |
| Garden Warbler                   | 305         | Trans-Saharan  | 16.81 ± 1.21      | 79.98 ± 1.95    | 7,300                       |
| Sylvia borin                     |             |                |                   |                 |                             |
| Lesser Whitethroat               | 14          | Trans-Saharan  | 10.45 ± 0.62      | 66.39 ± 1.85    | 4,900                       |
| Sylvia curruca                   |             |                |                   |                 |                             |
| Common Whitethroat               | 175         | Trans-Saharan  | 13.43 ± 0.66      | 73.60 ± 1.76    | 5,850                       |
| Sylvia communis                  |             |                |                   |                 |                             |
| Eurasian Wren                    | 126         | Pre-Saharan    | 8.42 ± 0.66       | 48.85 ± 1.79    | 1,300                       |
| Troglodytes troglodytes          |             |                |                   |                 |                             |
| Common Starling                  | 72          | Pre-Saharan    | 76.24 ± 5.27      | 132.60 ± 2.70   | 1,900                       |
| Sturnus vulgaris                 |             |                |                   |                 |                             |
| Common Blackbird                 | 989         | Pre-Saharan    | 90.12 ± 6.12      | 133.06 ± 3.95   | 1,500                       |
| Turdus merula                    |             |                |                   |                 |                             |
| Redwing                          | 151         | Pre-Saharan    | 55.51 ± 4.06      | 119.06 ± 3.95   | 2,650                       |
| Turdus iliacus                   |             |                |                   |                 |                             |
| Song Thrush                      | 520         | Pre-Saharan    | 62.93 ± 3.94      | 119.12 ± 2.71   | 2,600                       |
| Turdus philomelos                |             |                |                   |                 |                             |
| Spotted Flycatcher               | 68          | Trans-Saharan  | 14.03 ± 0.96      | 88.63 ± 2.08    | 8,200                       |
| Muscicapa striata                |             |                |                   |                 |                             |
| European Robin                   | 690         | Pre-Saharan    | 15.24 ± 0.99      | 73.41 ± 1.84    | 3,000                       |
| Erithacus rubecula               |             |                |                   |                 |                             |
| European Pied Flycatcher         | 82          | Trans-Saharan  | 11.39 ± 0.59      | 79.87 ± 1.36    | 6,500                       |
| Ficedula hypoleuca               |             |                |                   |                 |                             |
| Common Redstart                  | 313         | Trans-Saharan  | 13.52 ± 0.72      | 80.41 ± 1.94    | 5,350                       |
| Phoenicurus phoenicurus          |             |                |                   |                 |                             |
| Northern Wheatear                | 288         | Trans-Saharan  | 22.60 ± 2.26      | 100.36 ± 4.65   | 6,800                       |
| Oenanthe oenanthe                |             |                |                   |                 |                             |
| House Sparrow                    | 20          | Pre-Saharan    | 27.56 ± 1.94      | 77.15 ± 2.37    | 0                           |
| Passer domesticus                |             |                |                   |                 |                             |
| Dunnock                          | 375         | Pre-Saharan    | 18.44 ± 1.26      | 71.11 ± 1.83    | 2,100                       |
| Prunella modularis               |             |                |                   |                 |                             |
| Meadow Pipit                     | 105         | Pre-Saharan    | 15.98 ± 1.29      | 80.83 ± 2.70    | 2,750                       |
| Anthus pratensis                 |             |                |                   |                 |                             |
| Tree Pipit                       | 16          | Trans-Saharan  | 19.35 ± 0.97      | 87.50 ± 2.42    | 5,900                       |
| Anthus trivialis                 |             |                |                   |                 |                             |

Note: Given are sample size per species, migration group (pre- or trans-Saharan), mean lean body mass and wing length with corresponding standard deviation as well as mean migration distance, which was rounded up to the nearest 50 km. For further details, see methods.

*Listing of the species and authority for the names can be looked up in the IOC World Bird List, version 10.1 (https://www.worldbirdnames.org/).
in short-/medium-distance migrants in an inter-specific comparison. This would allow the former to carry larger amounts of fuel required for the barrier crossing without exceeding the maximum portable total body mass.

To the best of our knowledge, we lack detailed evidence of such a fundamental inter-specific eco-morphological pattern. Thus, to fill parts of this gap in our understanding, we directly collected individual wing length and lean body mass data of 22 Palearctic songbird species, ranging from short-/medium-distance to trans-Saharan migrants. Using these parameters, we calculated the species’ size-independent scaled lean body mass (sLBM). Herein, we wanted to assess whether (a) sLBM differs between short-/medium-distance migrants and those migrants having to cross the Sahara Desert, that is trans-Saharan migrants, whether (b) migration distance explains the variation of sLBM and whether (c) its effect is comparable between both migration groups.

2 | MATERIALS AND METHODS

2.1 | Data collection

During spring migration 2017–2019 and autumn migration 2017–2018, 5,410 individuals of 22 Palearctic songbird species (Table 1) were routinely caught in the trapping garden of the Institute of Avian Research ‘Vogelwarte Helgoland’ on Helgoland (54°11’N, 07°55’E), a small island only ca. 50 km off the German North Sea coastline (Hüppop & Hüppop, 2011). Almost all of the birds caught here are migrating songbirds that cross the German Bight when travelling towards or from their Scandinavian breeding grounds (Hüppop & Hüppop, 2011), showing high variation in body condition and carried fuel load within species (Kelsey et al., 2019; Packmor et al., 2020). Body mass (+0.1 g) using an electronic balance and maximum wing length (i.e. maximum chord, ±0.5 mm), a reliable measurement (Gosler et al., 1998) and the only measure of body size routinely collected for all bird species on Helgoland, were taken for each bird. Hereafter, we used the EchoMRI™ (EchoMRI Body Composition Analyser E26-262-BH, Zinsser Analytic GmbH, Frankfurt am Main, Germany) to directly measure for each bird (a) QMR fat mass, that is all fat molecules, and (b) QMR lean mass, that is the sum of all water-containing body parts (EchoMRI, 2016). Afterwards, birds were released.

The EchoMRI™ is designed to scan small animals up to a standard mass limit of 500 g to distinguish between the different hydrogen spin relaxation rates of the different body tissues and fluids (EchoMRI, 2016). Guglielmo et al. (2011), Seewagen and Guglielmo (2011) and Kelsey and Bairlein (2019) demonstrated that this method yields precise, accurate and repeatable measurements to track changes in body composition of individual birds over time. For more details on the validation and physics of the QMR technique, see Taicher et al. (2003) and Tinsley et al. (2004). For scanning, birds were placed in appropriately-sized ventilated holding tubes to minimize bird movement. Following Kelsey and Bairlein (2019), we scanned three consecutive times, allowing individual mean estimates. After Kelsey et al. (2019), we needed differently-sized tubes for the different sized birds with two associated EchoMRI software settings (‘BA50’ with a signal amplifier, ‘BIRD’) with an accumulation of three. The EchoMRI™ needs calibration once a week using the software ‘system test’ and canola oil standards from the manufacturer, cf. Guglielmo et al. (2011) and Kelsey and Bairlein (2019). Additionally, we calibrated the QMR unit daily before starting the actual scanning of the birds to ensure correct functioning of the machine. For further details on correct use, see also Guglielmo et al. (2011) and Kelsey and Bairlein (2019).

Individual measurements are used here from those published in Kelsey et al. (2019), where repeatability of QMR data was already tested within the three scans of each bird for all individuals of the 21 avian species considered in this study, except for *Passer domesticus* L. (House Sparrow). This showed a median repeatability of 0.93 for QMR fat mass and 0.81 for QMR lean mass. The House Sparrow was measured during the same time period, but not included in Kelsey et al. (2019), and showed comparable high repeatability for the QMR fat mass (0.92) and lean mass (0.96).

2.2 | Migration group and distance

We classified birds according to two main migration groups (Table 1): (a) short-/medium-distance migrants (hereafter pre-Saharan migrants), and (b) long-distance migrants (hereafter trans-Saharan migrants). Additionally, we were able to sample the local breeding population of the House Sparrow. This species is known to show dispersal movements, with few individuals moving further than 30 km (maximum: appr. 320 km), rather than true migration (Summers-Smith, 1956). In fact, the breeding population on Helgoland usually stays on the island year-round (Dierschke et al., 2011) and can, therefore, be considered ‘resident’ (Förtschler & Geiter, 2010). As many ‘resident’ and pre-Saharan species show partial migration, where transition between dispersal movements and true migration is flexible (Chapman et al., 2011), and only one resident species was considered in this study, we included the House Sparrow as pre-Saharan migrant in our models.

To estimate each species’ mean migration distance (Table 1), we determined their mean breeding and wintering areas using descriptions in the ringing atlases of Germany (Bairlein et al., 2014; Dierschke et al., 2011), Norway (Bakken et al., 2006) and Sweden (Fransson & Hall-Karlsson, 2008) by manually plotting corresponding polygons into the program Google Earth Pro™, version Google 2020. Since this program does not allow calculation of the exact centre of the areas, we benefitted from the function ‘image-overlay’, which displays an earth-curvature adjusted rectangle with a central cross. Manually adjusting the rectangle to be equivalent to the specific area, we could use the cross to individually define each centre, which was marked using the function ‘placemark’. To measure the great circle distance, that is the shortest route between two locations or as the crow flies, between the centre of the breeding and
wintering area for each species (rounded up to the nearest 50 km), we used the function ‘ruler’ between the two placemarkers set.

One special case is the *Oenanthe oenanthe* L. (Northern Wheatear) because two subspecies with significantly different migration distances pass Helgoland during migration. The *O. o. leucorhoa* subspecies breeds in eastern Canada, Greenland and Iceland, whereas birds of the nominate form *O. o. oenanthe* passing Helgoland breed mainly in Scandinavia (Delingat et al., 2011). Since both subspecies winter in the same region in sub-Saharan West Africa (Bairlein et al., 2012; Schmaljohann et al., 2016), their mean migratory distances differ. We generated the mean migratory distance for each subspecies (*leucorhoa* = 7,750 km; nominate = 5,850 km) and then used the average distance of these two (= 6,800 km) for analysis.

We included the House Sparrow with an average migration distance of 0 km in the group of pre-Saharan migrants (see above). This group had significantly shorter mean migration distances (mean: 2,046 km, 95% CrI: 1,193/2,852 km, range: 0 – 3,000 km, n = 10) than trans-Saharan migrants in our study (mean: 6,345 km, 95% credible interval (CrI): 5,624/7,076 km, range: 3,000–8,700 km, n = 12; Table 1).

### 2.3 Statistics

Statistics were conducted using R (R Development Core Team, 2019, version 3.6.2). For each bird, mean values of repeated QMR scans of fat and lean mass were determined, excluding outliers. Following Kelsey et al., (2019), we defined outliers as single scan measurements resulting in an individual standard deviation outside the 95% quantile of the standard deviation of the species-specific data set.

To estimate the bird’s lean body mass, we followed the approach described by Kelsey et al., (2019). Our QMR lean mass measurements (EchoMRI, 2016) do not capture the mass of water-free body parts, such as the skeleton, feathers, beak and claws. Excluding the latter for estimating the bird’s lean body mass would lead to an underestimation. Therefore, QMR fat was subtracted from the actual body mass to calculate the individual lean body mass.

For each species, mean ± standard deviation was determined for wing length (mm) and lean body mass (g); see Table 1 and Figure 1. To adjust the individuals’ lean body mass to a size-independent lean body mass of each species, we quantified the birds’ body mass in relation to their body size. Various nondestructive approaches are based on these body mass and body size measurements, for example the scaled mass index (SMI) developed by Peig and Green (2009), which is based on a standardized major axis (SMA) regression or, alternatively, on an ordinary least squares (OLS) regression. SMI has proven to be a reliable and powerful tool in various species when determining size-independent body mass (English et al., 2018; Peig & Green, 2010). However, using a SMA regression has been criticized as it, for example relies on the ratio of error variances being unity, which is mostly incorrect (Revell, 2011). Further, monomorphic species have their own body plan distinct from other species, and therefore, body condition should not be estimated on an inter-species level (Peig & Green, 2010), as in our study.

An alternative dominant approach is to calculate residuals from an OLS regression of body mass against size (Hayes & Shonkwiler, 2001; Jakob et al., 1996; Schulte-Hostedde et al., 2001, 2005). This ‘residual’ approach is considered very reliable because it does not vary with body size (Jakob et al., 1996; but see Kotiaho, 1999) and has been used, including variations of these...
indices, for many different taxa like birds, fish and invertebrates (Bailey, 1979; Bolger & Connolly, 1988; Jakob et al., 1996). However, Green (2001) showed that even this approach can violate key assumptions, for example functional relationship between mass and body size being linear.

Due to these controversially discussed approaches to estimate sLBM, we calculated sLBM using both approaches including possible variations thereof, resulting in seven different approaches (Appendix S2). sLBM values provided by each of the seven approaches strongly correlated with each other and presented similar/comparable results. We decided to report sLBM values calculated using the ‘residual’ approach based on a GLS regression (Appendix S2f), controlling for phylogeny by including a phylogenetic tree of the species considered (Appendix S1). The GLS regression was based on the natural logarithm of lean body mass and the natural logarithm of wing length. Phylogeny was captured by the argument ‘correlation =corPagel()’ using the R-package ‘nlme’ (Pinheiro et al., 2019).

We chose wing length as body size measurement as it is the only measurement routinely taken for all bird species during captures on Helgoland (see above), and it is known to be a reliable and repeatable measure of body size among different songbird species (Gosler et al., 1998). However, we know that wing length as body size measurement is debated in ornithology especially due to a possible correlation with migration distance (e.g. Vágási et al., 2016). Other body size measurements and/or a combination of different measurements may be preferred (Rising & Somers, 1989). We want to draw attention to this controversial aspect by detailing it in the discussion.

The calculated sLBM values were then used in the following models. To control for the effect of the species’ phylogenetic relationship, we fitted a generalized linear mixed-effects model by implementing Markov chain Monte Carlo techniques (MCMCglmm; Hadfield, 2010), including a phylogenetic tree of the species considered (Appendix S1). MCMCglmm allows to control for a source of nonindependency (i.e. phylogeny) and measurement error under a Bayesian statistical framework by including the phylogenetic effect as a random term. It provides for the model parameters the posterior distribution (see Hadfield (2010, 2019) and Korner-Nievergelt et al., (2015). sLBM was the dependent variable. In a first model (hereafter ‘full model’), migration distance (km), migration group (two level-factor: pre- and trans-Saharan migrants) and their two-way interaction were explanatory variables. The interaction was included to assess whether variation in migration distance differentially affected sLBM between the migration groups. To evaluate the pure difference between the two migration groups, we analysed a second model (hereafter ‘migration group model’) with migration group as the only explanatory variable. As sample size heterogeneity can have an important impact on the reliability of the mean estimates, and we had high differences in sample size between species (Table 1), we implemented a weighted factor into our MCMCglmm models by defining a measure of error variance (= 1/sample size) for each species.

We assessed model assumptions for the MCMCglmm models (e.g. model chain convergence) and the imbedded GLM models (e.g. normal distribution of residuals, Tukey-Anscombe Plot) according to Hadfield (2010, 2019) and Korner-Nievergelt et al., (2015). Inspections presented no violation of the model assumptions for any model. Information on the models, the phylogenetic tree and Newick code are given in the supplement (Appendix S1).

3 | RESULTS

The interaction between migration distance and migration group showed a significant effect on sLBM (full model: posterior mean: 1.29, 95% Crl: 0.23/2.31, pMCMC = 0.018; Table 2a, Figure 2a and Appendix S3). Although sLBM decreased significantly with increasing migration distance within the group of pre-Saharan migrants (full model: posterior mean = −1.67, 95% Crl: −2.66/−0.80; pMCMC = 0.001, Table 2a), we found no significant effect of migration distance in trans-Saharan migrants (posterior mean = −0.39, 95% Crl: −0.84/0.11).

**TABLE 2** Results from the MCMCglmm models analysing the scaled lean body mass (dependent) in relation to a) migration distance, migration group and their two-way interaction (explanatory variables; ‘full model’) and b) migration group alone (‘migration group model’).

|                      | Intercept (Pre-Saharan) | Migration distance | Migration group (Trans-Saharan) | Two-way interaction: Migration distance × migration group (Trans-Saharan) |
|----------------------|-------------------------|--------------------|----------------------------------|--------------------------------------------------------------------------|
| a) Full model        | −0.83 (−1.82/0.07)      | −1.67 (−2.66/−0.80) | 0.39 (−0.64/1.41)               | 1.29 (0.23/2.31)                                                          |
| b) Migration group model | 0.70 (0.13/1.27)        | −1.43 (−2.11/−0.85) |                                  |                                                                          |

Note: Posterior mean and, in brackets, 2.5% and 97.5% quantiles of the symmetric 95% Crl are provided for each model separately; in bold are significant results (Crl did not include zero and pMCMCs <0.05). For model output, see Appendix S3.
Pre-Saharan migrants showed significantly higher sLBM (migration group model: posterior mean = 0.70, 95% CrI: 0.13/1.27) than trans-Saharan migrants (migration group model: posterior mean = −0.73, 95% CrI: −1.26/−0.25, pMCMC <0.001; Table 2b, Figure 2b and Appendix S3). This strongly suggests that the presence/absence of an ecological barrier or a threshold level for migration distance may present a point of no return for the ‘light’ trans-Saharan birds.

4 | DISCUSSION

Our study demonstrates, for the first time, the eco-morphological pattern of significantly higher sLBM in pre- than in trans-Saharan migrants (Table 2, Figure 2b), based on real measurements of individual lean body mass values using quantitative magnetic resonance technology. The two-way interaction between migration distance and migration group had a significant effect on sLBM, demonstrating in our case that migration distance was only significantly related to sLBM in pre- but not in trans-Saharan migrants (Table 2, Figure 2a). This strongly suggests that the presence/absence of an ecological barrier or a threshold level for migration distance may present a more important natural selection pressure than the linear continuum of migration distance per se, shaping the apparent differences in sLBM and leading to a lower viable limit of sLBM in the ‘light’ trans-Saharan birds.

For a given body size, differences between the migration groups are probably the result of divergent natural selection pressures integrated over the annual cycle (Newton, 2008). The aerodynamic adaptations to overcome ecological barriers and travel long distances (Leisler & Winkler, 2003; Lockwood et al., 1998; Milá et al., 2008; Vágási et al., 2016; Winkler & Leisler, 1992) are realized, among others, in the birds’ relatively low lean body masses (Table 1, Figures 1 and 2) and associated aerodynamic properties, which both may allow trans-Saharan migrants to carry exceptionally large energy stores, future studies should observe birds of different migration distances at a stopover just before crossing an ecological barrier, such as the Sahara Desert or the Mediterranean Sea, where migrants are known to reach maximum energy stores (e.g. Bairlein, 1991, 2003; Berthold, 2001).

Migration group-specific variation in body mass was found, among others, in skeleton, muscle and digestive organs. Skulls are smaller and flatter in long-distance migrants than in short-distance migrants, creating a more streamlined body and less drag (Leisler & Winkler, 2003; Rayner & Maybury, 2003). As the avian skull only accounts for ca. 1% of body mass (Dumont, 2010) and especially other measurements present an opposite relationship, for example hind limbs, sternum and keel being larger in long-distance migrants (Calmaestra & Moreno, 2000; Winkler & Leisler, 1992), skeletal differences alone cannot explain the observed disparate lean body masses between the migration groups (Figure 2).

Eco-morphological studies showed that less muscle mass is appointed to hindlimbs when flight musculature, as a necessity for long migration, is better developed and vice versa (Leisler & Winkler, 1991). This trade-off, with its contrasting eco-morphological adaptations, therefore makes it unlikely that weight differences in hindlimbs and/or flight musculature are solely responsible for differences in lean body mass (Figure 2).

Digestive organs related to increased fat assimilation efficiency, such as intestine, gizzard and liver (McWilliams & Karasov, 2001), are also energetically expensive (Alexander, 1999) and therefore often reduced before migrating long distances, especially across ecological barriers, to keep the payload and related flight costs low (Biebach, 1998; Piersma, 2002; Piersma & Gill, 1998). As such, these flexible organs may differ in size between pre- and trans-Saharan migrants, especially when including populations of different origin, like in our study, and possibly different inter- and intra-specific stop-over strategies, that is either long flight intervals and few stopovers or short flight intervals and many stopovers (Packmor et al., 2020).
However, the phenotypic flexibility of the digestive system enables fast reactions to changing environmental demands (Piersma, 2002). More importantly, all birds were caught on Helgoland, from where on similar routes must initially be taken by both migration groups (Bairlein et al., 2014; Dierschke et al., 2011). Most likely, environmental demands, and therefore organ flexibility, between species are low for this site and, if present, probably similar in both groups at this location. The large overlap in body condition and fuel load between the species suggest that this may be the case (Kelsey et al., 2019; Packmor et al., 2020); however, further target-orientated studies are needed.

In addition to the aerodynamic properties of wing shape – more pointed wings in long-distance migrants than in short-distance migrants yielding higher air speeds and lower drag in the former (Lockwood et al., 1998) – a lower body mass for a given bird size produces less body and parasite drag because of the decreased surface/profile area in contact with resisting airflow during flight (Pennycuick, 1975). Consequently, energy costs of transport are relatively lower in trans- than in pre-Saharan migrants, thus, allowing a more efficient flight ‘style’ (Bowlin & Wikelski, 2008; Fiedler, 2005; Pennycuick, 2001) with fewer and/or shorter stopovers for energy refuelling, resulting in higher migration speed (Schmaljohann & Both, 2017) in trans-Saharan migrants (Schmaljohann, 2019). When facing the ecological barriers en route, that is the Mediterranean Sea and Sahara Desert, trans-Saharan migrants need to accumulate energy stores near their maximum fuel storage capacity (Hedenström & Alerstam, 1992) for such crossings (Bayly et al., 2012; Odum, 1963). These are mainly stored as lipids in form of adipose tissue, as this is the best fuel type and provides 95% of total energy expenditure needed during migratory endurance flights (Jenni & Jenni-Eiermann, 1998). In contrast, proteins, predominantly catabolized from muscles and digestive organs (e.g. Hume & Biebach, 1996; Piersma, 1998; Piersma & Gill, 1998; Piersma & Jukema, 1990), produce eight times less chemical energy per g wet mass and require 10 times more maintenance energy than fat (Scott & Evans, 1992) and, therefore, only contribute around 5% of the energy needed (Jenni & Jenni-Eiermann, 1998). In order to keep the total body mass to be carried, that is the transport costs low, on the one hand, and to carry large amounts of energy-rich fuel stores for the enduring barrier-crossings, on the other hand, it is most viable to possess a low lean body mass in relation to a high fat mass. Thus, the presence/absence of barriers may represent a stronger selection, or at least an important additional pressure, on reducing the bird’s lean body mass than the migration distance alone, because crossing benign land throughout migration does not require as high energy stores as crossing ecological barriers.

However, the possibility to reduce lean body mass is limited, as a specific body mass, especially muscle mass, is needed to enable flight ability (Norberg, 1990). This fact may help explain the significant two-way interaction between migration distance and group, where migration distance only had a significant effect on sLBM in pre- but not in trans-Saharan migrants (Table 2, Figure 2a). Within the pre-Saharan migrant group including ‘heavy’ species, species that travel longer migration journeys benefit from lower lean body mass due to a more efficient flight ‘style’ with less transport costs and higher migration speed (La Sorte et al., 2013; Schmaljohann, 2019), similar to the pattern described above. Trans-Saharan migrants, on the other hand, comprise of the ‘lighter’ species and may already demonstrate the lower limit of the viable lean body mass components for a specific body size. For instance, even though birds can survive with emaciated flight muscles (Salewski et al., 2012), the pectoralis muscle and supporting supracoracoideus still comprise approximately 10-13% of body mass to meet the mechanical power required of flapping flight over a range of different flight conditions (Biewener, 2011). Further, similar minimum requirements are also placed on skeleton mass, accounting for 4% (Dumont, 2010) to 8%–9% (Bezzel & Prinzinger, 1990) of lean body mass, and feather mass, representing 6.7 to 9.5% in small bird species (Chilgren, 1977; Kelsey & Bairlein, 2019; Turček, 1960). Therefore, the respective limited components most likely rule out further dramatic reductions of the lean body mass in trans-Saharan birds, as they either reached a specific threshold of reduction related to migration distance and/or the presence of the Sahara Desert as a strong ecological barrier.

5 | OUTLOOK

A drawback of our study is the use of wing length as body size measurement, which is debated in ornithology due to a possible correlation with migration distance (e.g. Vágási et al., 2016). Migratory flight performance is considered by some to have a negligible effect on the morphology particularly in small birds (Leisler & Winkler, 2003; Rayner, 1988; Winkler & Leisler, 1992), leading to no or only a weak inter-specific correlation between wing length and migration distance (Calmaestra & Moreno, 2001; Mönkkönen, 1995). In this case, wing length can be considered a reliable general body size measurement among different songbird species, possibly even more reliable when comparing it to other body size measurements like tarsus, tail and head length (Gosler et al., 1998; Sutherland et al., 2004). Others, however, disagree, describing at least some morphological traits as likely adaptations to long-distance migration and presenting positive inter-specific correlations between wing length and migration distance (Vágási et al., 2016; Voelker, 2001). Considering this correlation, species with lower scaled values could also be those with differentially larger wings due to migratory habits, rather than those with a relatively lower lean body mass considered in this study. In this respect, maybe using other body size measurements like tarsus (Freeman & Jackson, 1990; Rising & Somers, 1989) or keel length (Senar & Pasqual, 1997) would have been more independent for our study. It is to be expected that no single measure is ideal to describe ‘true’ body size and that a combination of different measurements, for example combined in a principal components analysis (PCA), should be preferred if possible (Rising & Somers, 1989; Sutherland et al., 2004).
However, Gosler et al., (1998) only found a generally small improvement in explaining variance in body size when using a PCA than wing length alone, stating that wing length is reliable as it gives the best approximation to PC1 in most species (Gosler et al., 1998; Sutherland et al., 2004). Due to this debate, which cannot be resolved in this study, the general eco-morphological pattern found in our study should be further analysed by including other uniform body size measurements, for example tarsus or keel length, which may provide other good or even better predictors of avian body size besides wing length (Senar & Pascual, 1997), or by combining body size measurements using, for example structural size (Rising & Somers, 1989).

In our study, the ‘resident’ House Sparrow showed the highest SLBM (≈ 1.90; Figure 2a) and a mean lean body mass of 27.6 g, being heavier than migrants of identical wing length (Figure 1). Therefore, considering other resident species as a separate group in addition to pre- and trans-Saharan migrants may possibly show similarly high values, probably generally above those of pre-Saharan migrants (Figure 2).

Further analyses should include birds with different flight styles and, hence, different aerodynamic properties, such as continuously flapping flyers (e.g. waders, gulls), flap-gliding flyers with irregularly long flapping and gliding phases (e.g. swifts, bee-eaters) and soaring flyers (e.g. large raptors, storks). This may reveal further group-specific deviations, as wing morphology and the associated energetic requirements are strongly related to flight type (Ricklefs, 1996), for example leading to differences in flight speed (Alerstam et al., 2007) and the maximum accumulated energy stores (Vincze et al., 2019) between phylogenetic groups.

Despite these much-needed extensions of our study, especially in regard to the optimal body size measurement and the different flight styles, our results strongly suggest that, besides the natural selection through migration distance, selective forces experienced when crossing ecological barriers also shape the specific eco-morphological adaptations found in trans-Saharan migrants, for example the 'light' lean body mass. This gain in knowledge about migratory adaptation may have important implications for our general understanding of the performance of long-distance migration in birds. We encourage others to adopt our methodology and repeat this study in different areas where ecological barriers play a less important role for migrating birds (e.g. along the Nearctic–Neotropical flyway or East Asian flyway). In this case, we would probably expect a continuous relationship between SLBM and migration distance until a (potential) threshold is reached. Studying migration group-specific differences in lean body mass in more detail and at strategically selected areas along the different flyways will help to better understand the selective forces acting on variation in lean body mass.

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CONFLICT OF INTEREST
The authors declare that they have no conflict of interest.

ETHICAL APPROVAL
Trapping, ringing and handling of the birds comply with the law of the Federal State of Schleswig-Holstein, Germany.

PEER REVIEW
The peer review history for this article is available at https://publo ns.com/publon/10.1111/jeb.13787.

DATA AVAILABILITY STATEMENT
Derived data used in this analysis (species-specific mean and standard deviation for wing length and lean body mass as well as sample size) are freely available to access on DRYAD: https://doi.org/10.5061/dryad.31zcjrdk7. All unedited raw data are available on request.

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**Supporting Information**

Additional supporting information may be found online in the Supporting Information section.

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