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Article

Body size shapes inter-specific migratory behaviour: evidence from individual tracks of long-distance migratory shorebirds

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Migration is a common phenomenon across many animal taxa. Understanding how migration scales with body size across species is fundamental in the development of migration theory and in making size-related predictions. Although aerodynamic theory and ecophysiological scaling laws have assisted greatly in generating such predictions, their verifications have been limited by a lack of empirical data across a range of body sizes. The recent development of ultra-light tracking devices and its rapid application to migration now allows us to put theory to the test. We used tracking data of seven closely related migratory sandpiper species (family Scolopacidae) along the East Asian-Australasian Flyway to compare their migratory behaviour when migrating towards the breeding grounds as a function of size (50–750 g). We found a marked decline in migration speed (migration distance divided by total migration duration, including time at stopover sites and in flight) with size. Departure date from the non-breeding (i.e. wintering) ground and arrival date at the breeding ground also scaled negatively with size. Total migration duration, migration distance, total staging duration (the number of days staying at stopover sites plus days preparing, i.e. fuelling, prior to initial migration) and step length (distance covered within one migratory leg) were not significantly related with size. Correction for phylogeny showed consistent results for all variables. Besides improving our fundamental understanding of inter-specific variation in migration behaviours, the finding of a clear scaling with size in migration speed and migration timing highlight differential size related capabilities and constraints of migrants. Migratory birds, including sandpipers, are declining on a global scale and particularly along the East Asian-Australasian Flyway. This notion of size-dependency in migratory traits may have a bearing on their vulnerability to specific environmental disturbances along their flyways.

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Introduction

Body size correlates with nearly everything from an animal's appearance to its physiology and behaviour (Bonner 2011) and may therewith also affect animals' vulnerability to environmental change (Cardillo et al. 2005, Schipper et al. 2008, Woodward et al. 2012). Around the world, some magnificent animal migrations have already disappeared due to human activities and many are in steep decline (Wilcove and Wikelski 2008). Understanding the size-related, allometric, potentials and constraints on migration behaviours is fundamental for developing migration theory and may be of importance for the conservation of migratory species, since migrants' vulnerability to environmental change may vary with size (Lindström et al. 2014).

Migration comprises two distinct phases: flying, which comes at the expense of fuel stores, and staging at stopover sites where birds rest and refuel. Optimal bird migration theory proposes that migrants should minimize the use of time, energy or predation risk during migration to optimize fitness. These are known as time-, energy- and risk-minimization strategies, respectively (Alerstam and Lindström 1990, Alerstam 2011). According to the time-minimization strategy birds fly and deposit fuel as fast as possible to maximize their overall speed of migration, i.e. migration distance divided by the total time required to prepare/fuel and fly (Alerstam and Lindström 1990, Alerstam 1991, 2011, Lindstrom and Alerstam 1992). Such time-minimization strategy is demonstrated to be adopted during migrations towards the breeding grounds (i.e. pre-breeding migration) (reviewed by Nilsson et al. 2013), where a timely arrival may provide an advantage over competitors (Kokko 1999, Moore et al. 2005) and enables an optimal use of seasonally available local resources (Meltofte et al. 2008, McKinnon et al. 2012), benefiting reproductive performance (Bety et al. 2004).

Aerodynamic theory predicts that, for powered fliers (i.e. by frequently flapping their wings), flying speed increases with body mass (Pennycuick 1975), assisting in increasing overall migration speed. However, flying time only comprises a small proportion of total migration time and increased flight speed does not greatly add to migration speed. Generally, animals cannot complete long migratory journeys in one go (but see Gill et al. 2005), and not only need to deposit fuel prior to migration (termed as pre-migratory fuelling, Alerstam and Lindström 1990) but also refuel/rest at stopover sites en route. Such pre-migratory staging (Alerstam and Lindström 1990) and stopover staging constitute the lion's share of the animals' time spent migrating (Hedenström and Alerstam 1997, Battley et al. 2012), and thus the rate of fuel deposition during staging importantly determines the rate of migration, i.e. migration speed (Alerstam and Lindström 1990, Lindström 1991, Hedenström and Alerstam 1997). Due to ecophysiological constraints, the rate of fuel deposition decreases with an increase in body size (Lindström 1991, 2003), which yields an expected decrease in migration speed with size for migratory birds using powered flight (Lindström 1991, Hedenström and Alerstam 1998, Hedenström 2003).

Although the scaling of migration behaviours is fundamental to our understanding of migration decisions, studies investigating scaling predictions have been limited and the evidence equivocal, notably of those using ringing or sighting rather than more accurate tracking data (Ellegren 1993, Woodward et al. 2012, La Sorte et al. 2013, Watanabe 2016). Ringing data, for instance, has been shown to consistently underestimate migration speed compared to estimations based on satellite tracking (Strandberg et al. 2009). Watanabe (2016) investigated the effect of size on avian migration behaviour using individual tracking data. Remarkably though, among other size-related patterns, he only found weak support ($R^2 = 0.14$) for the expected negative relationship between migration speed and size. However, a number of potentially confounding factors warrant further investigation into this relationship and the, thus far, apparently weak support for a predicted negative relationship between migration speed and body size (Lindström 1991, Hedenström and Alerstam 1998, Hedenström 2003). Firstly, migration speed is ideally calculated by dividing total migration distance by total migration duration, but the pre-migratory fuelling period during which birds deposit body stores before initial departure (Alerstam and Lindström 1990) was not included in Watanabe (2016). Consequently, migration speed was structurally overestimated to variable degrees, depending on the length of the initial migratory leg, potentially distorting the relationship between migration speed and body size. Secondly, migration distance was calculated as the shortest distance between the breeding and wintering grounds, which may substantially deviate from the actual total distance covered along the migration pathway. Thirdly, each species was represented by one data point and detailed individual data within species was missing. Fourthly, Watanabe (2016) pooled pre- and post-breeding migration data, ignoring that species may potentially adopt a time-minimization strategy during pre-breeding, but not during post-breeding migration. Since migration speed is predicted to be constrained by size (Lindström 1991, Hedenström and Alerstam 1998, Hedenström 2003), only pre-breeding migration may be the adequate season for investigating size-related migration speed. For post-breeding, migration behaviour may vary more with factors other than size, such as physiological capacities (Gwinner 1996) and environmental conditions (Gill et al. 2014); potential interfering factors during post-breeding migration could obscure any potential size-related patterns. Finally, Watanabe (2016) combined data from species across several orders and widely different ecological responses (e.g. combining short- and long-distance migrants), further increasing among-subject variation and reducing the chance of discerning robust relationships between size and migration behaviour. Taking consideration of all these five factors, we restricted our study to tracks of individuals of seven closely related (family Scolopacidae within the order Charadriiformes), long-distance (9000–16 000 km)

migratory species across a large size range (50–750 g in lean body mass), using a single flyway (the East Asian-Australasian Flyway, EAAF) and during pre-breeding migration only.

Besides migration speed 1), other aspects of migration behaviour may also scale with body size. Indeed, in addition to migration speed (1, predicted to scale negatively) a range of other predictions have been made, including 2) total staging duration, the number of days staging at stopover sites plus pre-migratory staging duration (predicted to scale positively), 3) total migration duration (positively), 4) total migration distance (negatively), and 5) step length (negatively) (Hedenström 2003, 2006). Given constraints on fuel deposition rate and the reduced migration speed in large birds (Lindström 1991, 2003), Hedenström (2003) proposed that in order to cover a certain distance, total staging duration 2) should scale positively with size. Considering that total migration duration 3) is mostly determined by total staging duration 2), we accordingly also expect total migration duration 3) to scale positively with size. However, besides migration and breeding, migrants also need to fit moult within the confines of the annual cycle. Since both breeding (Hedenström 2006) and moulting (Hedenström 2006, Rohwer et al. 2009, Dietz et al. 2015) take longer in large birds, large species seems under higher time constraints. For instance, every year the annual cycle of the large Far Eastern curlew *Numenius madagascariensis*, leaves little or no time to spare. It spends an average of four months on primary wing moult while at its wintering grounds (Higgins and Davies 1996), three months on pre-migratory fuelling and migration from wintering to breeding grounds where it subsequently stays for about two months, followed by three months of post-breeding migration. Given these potential time constraints and constraints on migration speed 1), in large birds we might thus predict that either a) after an initial increase with size, both total staging duration 2) and total migration duration 3) level off in still larger birds, or b) that both total staging duration 2) and total migration duration 3) keep increasing in larger birds, but that larger birds may migrate shorter distances 4) and evolve to breed closer to their wintering grounds.

Larger fuel loads may support longer non-stop flights, i.e. greater step lengths. Given that the relative fuel load capacity (fuel load relative to lean body mass) decreases with size (Hedenström and Alerstam 1992), aerodynamic theory predicts that step length 5) decreases with size (Hedenström 2006, 2008). Moreover, given that breeding is limited to a short season on the breeding grounds and that large birds generally need more time to complete their breeding cycle (Klaassen 2003, Hedenström 2006), we may expect the phenology of migration, i.e. departure date 6) from the wintering grounds and arrival date 7) at the breeding grounds, to be advanced in large compared to small birds (i.e. scale negatively with size) to ensure sufficient time for breeding.

Tracking devices such as satellite transmitters and light-level geolocators, in combination with Bayesian (Sumner et al. 2009) or state-space (Patterson et al. 2008) frameworks incorporating behavioural models and environmental auxiliary data, provide increasingly more accurate and detailed information on individual migration itineraries, for instance through using R-packages 'SGAT' (Lisovski et al. 2016a) and 'FlightR' (Rakhimberdiev et al. 2017). Additionally, tracking devices have become increasingly smaller and have now been deployed on species across a large size range, making the examination of the scaling of migration behaviour possible. Our objective in this study was to test the time-minimization-strategy-based prediction on the scaling of migration speed and other key migration behaviours, using detailed individual tracks obtained from geolocators.

Material and methods

We defined wintering grounds as the non-breeding grounds at the southernmost end of the distribution range of the populations of each of the seven focal species, i.e. where the birds spend most of the northern-hemisphere winter and where pre-breeding migration starts. For our analysis, we used individual and complete pre-breeding (i.e. from wintering to breeding grounds) migration tracking data from seven shorebird species: sanderling *Calidris alba* (n=12), ruddy turnstone *Arenaria interpres* (n=63), red knot *Calidris canutus* (n=2), great knot *Calidris tenuirostris* (n=8), grey-tailed tattler *Tringa brevipes* (n=3), bar-tailed godwit *Limosa lapponica* (n=16) and Far Eastern curlew (n=8). All movements were inferred from either unpublished light-level geolocator data or from previously published geolocator studies (for details see Table 1).

Three different types of light-level geolocators were used across the seven species, BAStag, Biotracks and Integio (Table 1). Integio is the new logger generation that records the near full range of light intensity, its range being wider than the two old generations, BAStag and Biotrack. Two methods were used to process light intensity to estimate locations. Geolocator data of sanderling, ruddy turnstone and great knot were processed using the R-package 'SGAT' following Lisovski et al. (2016a). Movements of grey-tailed tattler, red knot (Tomkovich et al. 2013), great knot (Lisovski et al. 2016b), bar-tailed godwit (Conklin et al. 2010) and Far Eastern curlew (Minton et al. 2010, 2011) were extracted from publications or obtained from personal communications. In most cases the thus obtained geolocator data were analysed using the BASTrack software provided by the British Antarctic Survey. Only for great knot data R-package 'SGAT' was used (Lisovski et al. 2016b). Sanderlings, turnstones, red knots, great knots and some bar-tailed godwits breed north of the Arctic Circle where the 24-h daylight conditions required methods developed by Lisovski et al. (2016a) to estimate the breeding locations. For turnstones equipped with BAS and Biotrack loggers, which did not record the full range of light intensity variation under 24-h daylight, breeding position was assigned as

Table 1. Details of the seven sandpiper species migrating along the East Asian-Australasian Flyway between their wintering and their breeding grounds. All species were tracked using geolocators. Species are ranked by their lean body mass.

Species	Lean body mass (g)	Wintering site	Geolocator type	n
Sanderling	50[a]	South Australia	Integio[b]	12
Ruddy turnstone	93[a]	Tasmania, Victoria, South Australia	Integio, BAStag, Biotracks[c]	63 (34, 22, 7)
Grey-tailed tattler	108[d]	Queensland	BAStag[e]	3
Red knot	113[f]	New Zealand, north western Australia	BAStag[g]	2
Great knot	135[a]	North western Australia	Integio[h]	8
Bar-tailed godwit	285[i]	New Zealand	BAStag[j]	16
Far Eastern curlew	743[a]	Victoria	BAStag[k]	8

[a]Calculated as the median body mass of individuals captured during November–December on their wintering grounds in Australia (unpublished data Victorian Wader Study Group and Australasian Wader Studies Group) and multiplied by 0.94 (Zwarts et al. 1990), or [b]Lisovski et al. (2016a). [c]Unpublished tracks from Victorian Wader Study Group, Australia. [d]Johnsgard (1981). [e]Unpublished tracks from Queensland Wader Study Group, Australia. [f]Battley (1997). [g]Tomkovich et al. (2013). [h]Lisovski et al. (2016b). [i]Gill et al. (2005). [j]Conklin et al. (2010). [k]Minton and Gosbell (2011).

the median breeding longitude and latitude of the conspecifics tracked using Intigeo loggers. Red knots were captured at their breeding grounds and their precise breeding location was thus known (Tomkovich et al. 2013). Three out of 16 bar-tailed godwits bred north of the Arctic Circle and their breeding position was assumed based on their known breeding region (Conklin et al. 2010). Far Eastern curlews breed south of the Arctic Circle and therefore do not face the issue of 24-h daylight. Their breeding position could thus be determined using BASTrack software.

Some individuals of Far Eastern curlew migrated around the equinox, when daylenght around the globe is similar and thus accurate estimation of latitude is problematic. Since Far Eastern curlew conducts a rapid and long initial migration step from southeast Australia towards the east Asian coast, resulting in drastic changes in sunrise and sunset times, these marked changes in geolocator recordings greatly assisted to identify departure and arrival times (i.e. accurate assessment of temporal patterns may still be possible even when accurate estimation of locations is limited (Lisovski and Hahn 2012)). To further improve on our assessments of the timing of migrations we also used geolocator conductivity data, which allowed to judge whether a bird was flying or was sitting on land with contact to salt-water.

Seven migration variables depicting aspects of the migratory itineraries were extracted from the published and unpublished tracks, namely 1) migration speed, 2) total staging duration, 3) total migration duration, 4) migration distance, 5) step length, 6) departure date from the wintering ground and 7) arrival date at the breeding ground. We measured migration duration as the number of days elapsed from departure date to arrival date, and total migration duration 3) as migration duration plus pre-migratory duration. For each species, average pre-migratory staging duration was estimated using segment regression of body mass data of birds captured on the wintering grounds against date (for details see Supplementary material Appendix 1). We defined 'true' staging sites as sites where birds stopped for a duration of at least four days (see Warnock 2010 for definition of staging and stopover site) and the number of migratory legs 4) was

calculated accordingly. Total staging duration 2) was calculated as the sum of days at each stopover site, including sites where birds stayed less than four days, plus pre-migratory staging duration. Migration distance 4) was the sum of distances travelled in each migratory leg from one 'true' staging site to the next via a great circle route. Step length 5) is the total distance flown between the wintering and the breeding grounds, divided by the number of migratory legs from wintering/staging site to the next staging/breeding site, using 'true' staging sites only.

Migration speed is calculated by dividing the total migration distance by the total migration duration, including both migration duration and the pre-migratory staging period prior to migration (Alerstam and Lindström 1990). This pre-migratory staging period, however, was impossible to ascertain from the tracking data. To ensure that any pattern we might detect in migration speed with size was not caused by our subjective selection of methods, we used three methods to calculate migration speed, naming them as traditional migration speed, partial migration speed and overall migration speed. First, following a frequently used method (La Sorte et al. 2013, Sergio et al. 2014, Watanabe 2016), we calculated traditional migration speed by dividing total migration distance by migration duration. This traditional method thus ignores the pre-migratory staging period and thus overestimates migration speed. To avoid overestimation, we alternatively calculated partial migration speed by excluding the first migratory leg, dividing migration distance between the first staging site and the breeding location by the time elapsed from the date of arrival at the first staging site and the date of arrival at the breeding grounds. For this calculation, we assumed birds arrive at their first staging site with very low fat stores. This is a reasonable assumption for migrants in this study, where many individuals fly non-stop for 2000–10 000 km from Australia/New Zealand to the southeast Asian coast (Battley et al. 2000, Choi et al. 2009). Although thus generating an accurate estimate of migration speed for each individual, partial migration speed reflects migration speed over only part of the migratory journey. Therefore, we also calculated overall migration speed, dividing total migration distance between wintering and breeding

location by the sum of total migration duration (migration duration plus pre-migratory staging duration). Although thus relying on a species-specific average correction of pre-migratory staging duration (Supplementary material Appendix 1) rather than a preferred individual correction, overall migration speed provides an estimate of overall speed across the entire migratory journey from wintering to breeding grounds. Although partial migration may be considered the least biased estimate of an individual's migration speed, we consider that collectively the three estimates provide a better insight in migration speed variations among the focal species.

Statistical analysis

Before analyses, we converted departure and arrival dates to date number. We tested the relationship between size and each of the seven migration variables using linear mixed models (LMM) (original data in Supplementary material Appendix 2). For LMM, we included size as a fixed variable and species as a random intercept. For size we used lean body mass, i.e. body mass of a bird without any migratory fuel, obtained from the literature or, if unavailable, estimated as the median body mass of individuals captured during November–December on their wintering grounds, Australia (unpublished data from Victorian Wader Study Group and Australasian Wader Studies Group) and multiplying this by 0.94 following Zwarts et al. (1990). The 10-logarithm of lean body mass (kg) was included as independent variable to normalise the data. We also 10-log transformed the dependent variables to facilitate interpretation of effect sizes (i.e. decreasing relationship when slope < 0; increasing when slope is > 0; levelling off when |slope| < 1; accelerating function when |slope| > 1). Prior to LMM analysis, to account for heterogeneity of variances in the dependent variables across the different species, we used the 'varIdent' function. We conducted LMM analyses using R-package 'nlme'.

To test for correlations between the seven migration variables (i.e. excluding traditional and overall migration speed and using partial migration speed only) we used Pearson correlation. Next, to correct for correlations between these seven migration variables and to evaluate across how many dimensions the variation in migration behaviour can be collapsed we used principal component analysis (PCA). The total number of principal components (PCs) was selected based on Kaiser's stopping rule, including PCs with eigenvalues > 1 only. Subsequently, to evaluate how the PCs scale with size, the selected PCs were examined individually in relation to the 10-logarithm of lean body mass using LMM.

Although we limited our studied species within a single shorebird family to reduce potential phylogenetic interference, phylogenetic differences still exist. To examine the potential interference of phylogeny, we used a phylogenetic mixed model to examine the effect of size on all seven migration variables and PCs. To this end, we used a Bayesian approach, applying the 'MCMCglmm' function within the R-package 'MCMCglmm'. Data were transformed prior to

analyses as outlined above for LMM. We defined the data distribution as Gaussian for all seven migration variables and PCs. For the phylogeny, we used a tree based on data provided in Thomas et al. (2004). We conducted all analyses using R ver. 3.2.3 (R Core Team).

Results

The wintering grounds of the seven sandpiper species in our study (Table 1) were located in New Zealand and Australia. From there, all birds migrated northward to their breeding grounds in northeast China, southeast Siberia and northern Russia and Alaska via East and Southeast Asia, largely following the coastline of east China and the Yellow Sea. En route between the wintering and breeding grounds, they regularly performed stopovers to rest and replenish their fuel stores. Far Eastern curlew bred in the sub-Arctic at the border between northeast China and Russia. Grey-tailed tattler bred in the Kamchatka peninsula in Russia's Far East. The other species bred in Arctic Russia and Alaska (Fig. 1).

The LMM analyses showed that three out of the seven investigated migration behaviour variables scaled with size: partial migration speed, departure date and arrival date (Table 2). As predicted, partial migration speed 1) decreased with size (Fig. 2,1B). Also as predicted, traditional migration speed (Fig. 2,1A) yielded higher estimates of migration speeds than partial and overall migration speeds (Fig. 2,1C). This bias led to traditional migration speeds double or triple the estimate of partial migration speed in most species except for Far Eastern curlew, where it was between five to nine times higher. Traditional migration speed and overall migration also tended to decrease with size, but the decline was weaker and not significant. Contrary to predictions, total staging duration 2), total migration duration 3), migration distance 4) and step length 5) did not scale with size (Fig. 2,2 to 2,5). Departure from the wintering grounds 6) was nearly two months earlier in the largest compared to the smallest species investigated (Fig. 2,6). Despite their slower migration speed, this earlier departure in larger birds also led to their earlier arrival at the breeding grounds (Fig. 2,7).

Correcting for phylogeny had no effect on the scaling of partial migration speed with size (Table 2), whereas the decline of traditional and overall migration speed became stronger. The inclusion of phylogeny marginally changed the scaling of departure date 7) and arrival date 8) with size. Similar to the LMM result, after correction for phylogeny the four migration variables, total staging duration 2), total migration duration 3) migration distance 4) and step length 5), remained unrelated to size.

As expected, Pearson correlation tests revealed a high correlation among the seven migration behaviour variables (Fig. 3). Particularly strong positive correlations existed between total migration duration and total staging duration (r = 0.98), and between departure date and arrival date (0.86). Additional strong correlations were also revealed between migration speed and departure date (0.78), arrival
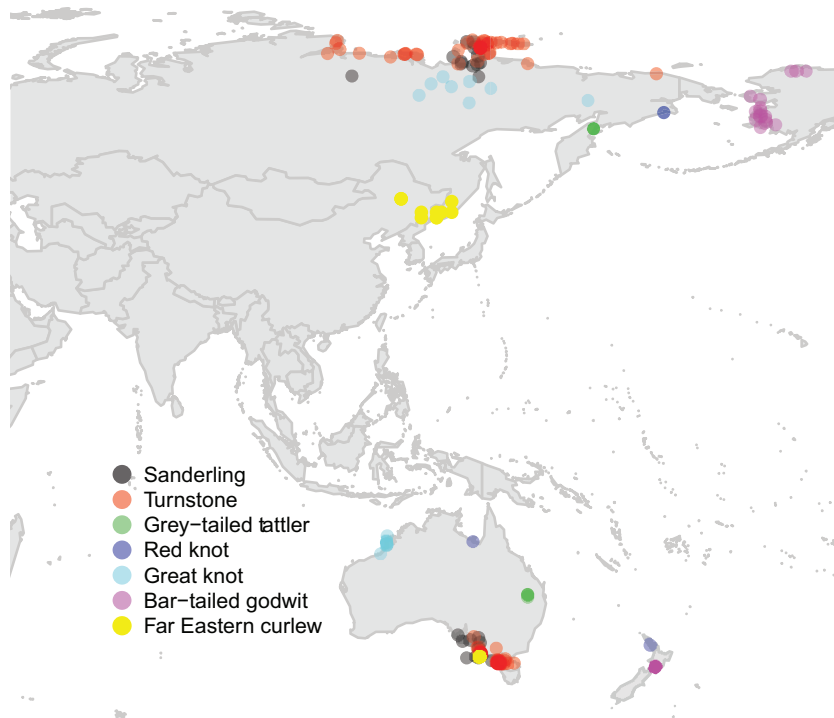
Figure 1. Wintering grounds in New Zealand and Australia and breeding grounds in northeast China and Russian Arctic for the seven sandpiper species in this study. Colours represent individual species, and dots represent individual birds.

date (0.69), total staging duration (–0.60), total migration duration (–0.56), departure date with total staging duration (–0.72) and total migration duration (–0.72), between arrival date and total staging duration (–0.55) and total migration duration (–0.50), and between step length and migration distance (0.52).

In agreement with the high correlation among many of the migration behaviour variables, the PCA revealed that a limited set of three dimensions (i.e. PC1, PC2 and PC3) explained as much as 91% of the variance in the migration variables (Table 3). Migration speed 1), departure date 7) and arrival date 8) were positively correlated with PC1

Table 2. The relationship between size (10-log transformed lean body mass, kg) and seven migration variables and their first three principal components (PCs) for seven sandpiper species migrating northward along the East Asian-Australasian Flyway towards their breeding grounds. Analyses were conducted without and with including the random effect of phylogeny using linear mixed models (LMM) and MCMCglmm, respectively. In all LMM, the degrees of freedom were 112, 7, except overall migration, for which it is 109, 6. Migration variables are ranked based on their numbering in the text. Significant slopes are highlighted in bold. R^2 represents coefficient of determination.

Migration variables[$]	LMM			MCMCglmm		
	Intercept	Slope (p value)	R^2	Intercept	Slope (p value)	R^2
1) Migration speed (km d⁻¹)						
Traditional	2.42	–0.06 (0.408)	0.05	2.37	–0.14 (0.208)	0.11
Partial	1.65	**–0.56 (0.001)**	**0.65**	1.68	**–0.50 (0.006)**	**0.48**
Overall	1.87	–0.23 (0.174)	0.20	1.85	–0.43 (0.142)	0.21
2) Total staging duration (d)	2.11	0.13 (0.189)	0.22	2.22	0.34 (0.062)	0.30
3) Total migration duration (d)	2.14	0.11 (0.226)	0.20	2.24	0.30 (0.064)	0.30
4) Migration distance (km)	4.02	–0.07 (0.453)	0.06	3.99	–0.13 (0.354)	0.08
5) Step length (km)	3.80	0.18 (0.247)	0.13	3.77	0.12 (0.518)	0.04
6) Departure date number	1.79	**–0.23 (0.010)**	**0.62**	1.79	**–0.24 (0.014)**	**0.47**
7) Arrival date number	2.01	**–0.17 (0.001)**	**0.81**	2.02	**–0.16 (0.002)**	**0.61**
PC1	–5.22	**–5.42 (0.003)**	**0.71**	–5.82	**–6.65 (0.002)**	0.61
PC2	0.99	0.68 (0.711)	0.01	1.63	1.84 (0.492)	0.05
PC3	–0.93	–1.44 (0.309)	0.11	0.02	0.462 (0.824)	0.00

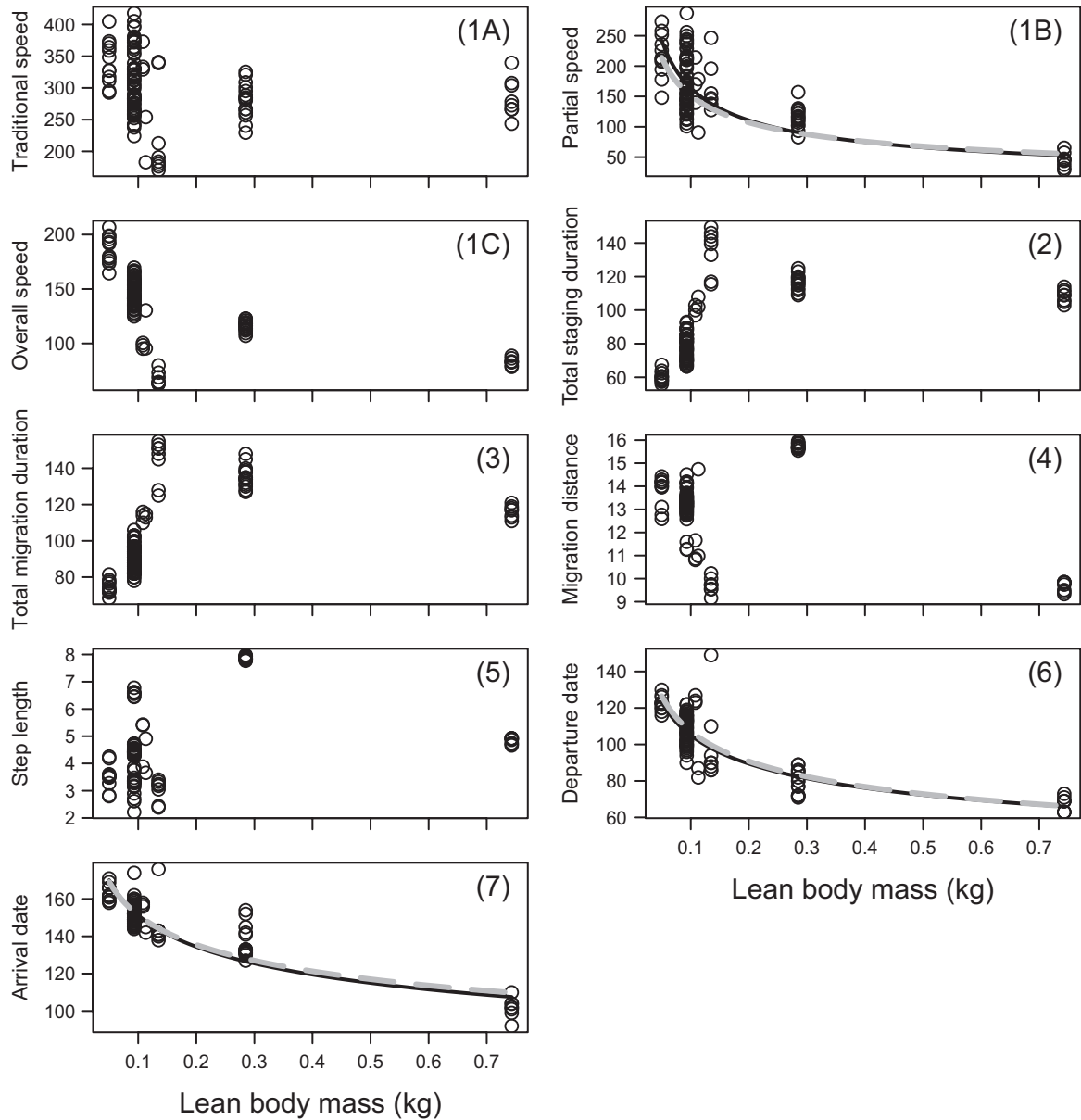[$]All migration variables were entered in the analysis as 10-log transformed.

Figure 2. Relationships between seven migration variables and lean body mass for seven sandpiper species migrating northward along the East Asian-Australasian Flyway towards their breeding grounds: (1A) traditional migration speed (km d^{-1}); (1B) partial migration speed (km d^{-1}); (1C) overall migration speed (km d^{-1}); (2) total staging duration (d); (3) total migration duration (d); (4) migration distance ($\times$ 1000 km); (5) step length ($\times$ 1000 km); (6) departure date (date number) from the wintering grounds and (7) arrival date (date number) at the breeding grounds. Black solid and grey dashed lines are drawn according to the back-transformation of equations presented in Table 2, estimated from LMM and MCMCglmm, respectively.

(Table 3), with PC1 explaining 58% of the variance in migration variables (Table 3). Migration distance 4) and step length 5) were highly negatively correlated with PC2, explaining another 22% of the variance (Table 3). Total staging duration 2) and total migration duration 3) and arrival date 7) were positively correlated with PC3, with PC3 explaining another 11% of the variance in the migration behaviour variables (Table 3). PC1 declined with size (with and without correcting for phylogeny p = 0.003 and 0.002, respectively, Table 2 and Fig. 4). PC2 and PC3 did not vary with size (Table 2).

Discussion

Few of the theoretical predictions on the scaling of migration variables in relation to size, ranging from fuelling rate (Lindström 1991), migration duration (Hedenström 2003) to migration speed (Lindström 1991, Hedenström and Alerstam 1998, Hedenström 2003), have been put to the test. Our study is one of the two studies, the other being Watanabe (2016), to place a comprehensive suite of allometric predictions under empirical scrutiny using individual migratory
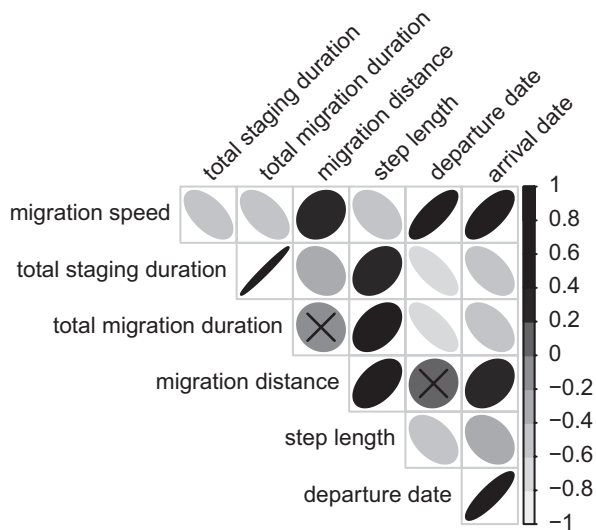
Figure 3. Pearson correlation matrix between seven migration variables extracted from seven sandpiper species migrating northward along the East Asian-Australasian Flyway towards their breeding grounds. Darkness of shading, shape and direction of ovals indicate strength, variation and direction of the correlations, respectively, with dark and narrow ovals indicating strong correlation, forward ovals indicating positive correlation, and with a cross depicting $p > 0.05$.

tracks. Despite the data used originated from a variety of studies, each having their specific methodologies inherently leading to noise in the results, the individual tracks across seven closely related sandpiper species provided support for the prediction that migration speed scales negatively with size in powered fliers (Lindström 1991, Hedenström and Alerstam 1998, Hedenström 2003). Besides migration speed, we examined an additional suite of migration variables in relation to size. Although a range of species-specific and environmental factors are known to influence migration behaviour (Alerstam 2003, Newton 2010) our analyses highlight

Table 3. Principal component analysis (PCA) loadings for the first three PC axes of a PCA on seven migration variables extracted from seven sandpiper species migrating northward along the East Asian-Australasian Flyway towards their breeding grounds. Values show the eigenvectors for each of the migration variables, ranked in order of numbering used in the text. For each migration variable, the highest of the three eigenvectors is emboldened. At the bottom the (cumulative) proportion of the variation across all seven migration variables as explained by each of the PC axes is depicted.

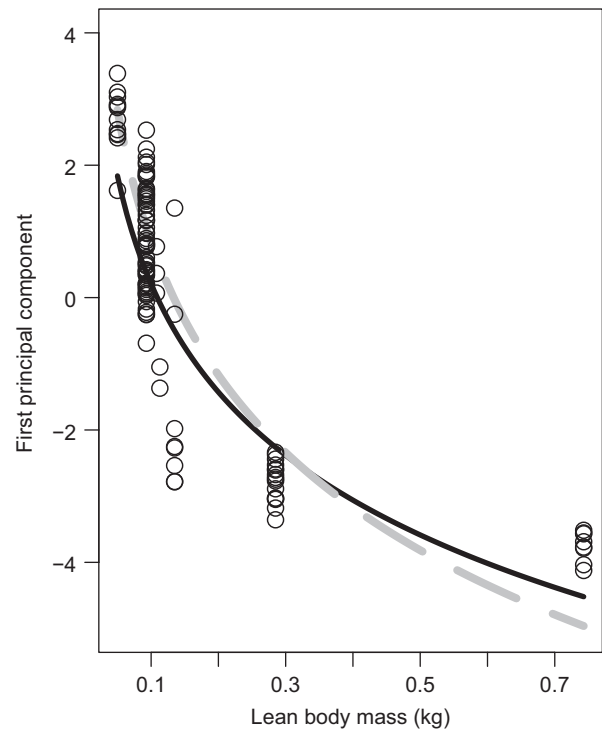| Migration variables	PC1	PC2	PC3
1) Migration speed	**0.41**	–0.05	0.33
2) Total staging duration	–0.43	0.09	**0.52**
3) Total migration duration	–0.43	–0.02	**0.56**
4) Migration distance	0.09	**–0.77**	0.03
5) Step length	–0.27	**–0.61**	–0.12
6) Departure date	**0.46**	0.04	0.21
7) Arrival date	0.41	–0.16	**0.49**
Proportion of variance	0.58	0.22	0.11
Cumulative proportion	0.58	0.80	0.91

Figure 4. Relationships between the first principal component of the principal component analysis performed on seven migration variables and lean body mass for seven sandpiper species migrating northward along the East Asian-Australasian Flyway towards their breeding grounds. The first principal component correlated positively with migration speed, departure date and arrival date, explaining 58% of the variance in the seven migration variables (Table 3). Grey dashed line is drawn according to the back-transformation of equations presented in Table 2, estimated from MCMCglmm.

a major and general relationship between size and migratory speed and migration timing.

Partial migration speed declined with lean body mass proportional to mass$^{-0.51}$ and mass$^{-0.56}$ with or without correcting for phylogeny, respectively. This decline was more pronounced than both mass$^{-0.15}$ using data presented in Watanabe (2016), and the predicted mass$^{-0.19}$ and mass$^{-0.14}$ by Hedenström (2003) and Lindström (1991), respectively. Statistical support for this decline was also strong with an R^2 of 0.48 and 0.65, with and without correcting for phylogeny, respectively. These values are much higher than the 0.14 found in Watanabe (2016). The much more pronounced decline of migration speed with lean body mass in our empirical data could potentially be attributed to our specific study design, which focussed on one family of birds widely ranging in size but with comparable ecological responses migrating along a single flyway. Although non-significant, traditional and overall migration speed also tended to decline with size, especially after correcting for phylogeny. As earlier explained and as confirmed by our results, traditional migration speed suffers from an overestimate of migration speed, whereas overall migration speed estimates involve correction with a

species rather than an individual-specific pre-migratory staging duration. Nevertheless, the non-significant patterns with size in these alternative estimates of migration speed corroborate the partial migration speed results of a decline in migration speed with size.

Neither total staging duration 2) nor total migration duration 3) scaled with size, with or without corrections for phylogeny. Although inconsistent with prediction, these results confirm other empirical data (Watanabe 2016). Also contrary to prediction and earlier findings that migration distance 4) decreases with size (within species: Hein et al. 2012, Gray et al. 2014, Jones and Witt 2014, across species: Martell et al. 2014, Watanabe 2016), we did not find a decline in migration distance, despite the largest species, Far Eastern curlew, covering a much shorter distance than most of the smaller species. Bar-tailed godwit appeared the noticeable outlier (Fig. 2,4), although excluding this species from analysis did not change the (insignificant) result.

For both total staging duration 2) and total migration duration 3), the Far Eastern curlew seemed to be the (downward) outlier (Fig. 2,2 and 2,3), which could potentially be explained by two non-exclusive factors. Firstly, the hypothesised time constraints on large species may possibly have a larger impact on their migration strategy than we initially expected, forcing large species like Far Eastern curlew to save even more time by cutting their migration short (Fig. 2,4) and opting to breed at more southern latitudes (between 42–52°N) than their smaller relatives (e.g. above 70°N for the smallest sanderling). Secondly, the Far Eastern curlew may have evolved to breed at more southerly locations where environmental conditions allow for longer breeding seasons. Across all species in our dataset this appears to be a general trend not exclusive to Far Eastern curlew, breeding latitude being negatively correlated with size across all species ($t_{7,12} = -4.05$, $p = 0.010$).

Inconsistent with the prediction that step length decreases with size (Hedenström 2006, 2008), we did not find any pattern in step length 5) with size (with or without correcting for phylogeny; Fig. 2,5). Also inconsistent with the predicted decline from aerodynamic theory was an earlier analysis of flight range using empirical data that found a positive rather than a negative relationship with size (Klaassen 2003). Rather than depending largely on size, step length may also be more context dependent and vary with weather conditions and notably wind assistance. In addition, geography may play a role, migrants being more likely to stop just before crossing large ecological barriers such as oceans and deserts (Weber and Houston 1997, Risely et al. 2015, Briedis et al. 2016) irrespective of the distance flown prior to reaching that barrier.

Limited sample size and limited spatial resolution may have an effect on the investigated trends and notably for staging duration, migration distance and step length with size. Sample size was notably low for medium sized species (i.e. 3 and 2 for grey-tailed tattler and red knot, respectively), leading to a reduced detection power in statistical analyses and a reduced detection probability in any potential trends.

Geolocation is known for varying and generally limited accuracy and precision in location estimates and exact timing of migration (Lisovski and Hahn 2012). However, light intensity data gathered from migratory shorebirds used in this study can be expected to be of high quality due to the habitat of these species (e.g. no effect of dense vegetation) and notably due to the relatively long step length that provides clear signals in sunrise and sunset times between disparate stopover locations (i.e. 99% of steps were longer than 500 km and 89% longer than 1000 km).

In addition to migration speed, departure date 6) and arrival date 7) also showed a clear relationship with size, both before and after correcting for phylogeny (Table 2, Fig. 2,6 and 2,7). Large birds generally need more time to complete their breeding cycle (Klaassen 2003, Hedenström 2006) and they therefore both departed from their wintering grounds and arrived at their breeding grounds ahead of their smaller relatives by as much as two months. The finding that large species arrived earlier at their breeding grounds was consistent with the observations in geese and swans (Klaassen et al. 2006), and also agrees with the finding that large shorebird species pass a stopover site earlier than small species (Zhou et al. 2016). If larger species breed at lower latitudes, as shown here, our findings also agree with observational data suggesting that shorebirds breeding at lower latitudes are the first to depart from their wintering grounds (within population: Newton 2003, Conklin et al. 2010, between populations: Piersma et al. 1990).

Together, migration speed, departure date and arrival date are all size dependent and are inter-related as shown in the correlation (Fig. 3) and PCA (Table 3) analyses. Although largely untested to date, migration speed and migration date varied with size in the a priori predicted fashion. The scaling of these migration behaviours with size is of great importance to our understanding of size-related migration adaptations and, next, the potential consequences of species' size-differences for their differential susceptibility to environmental changes along their flyways (Lindström et al. 2014). Migration comprises a series of behaviours that takes the birds from their wintering grounds via a chain of stopover sites to their breeding destination. Any habitat loss or deterioration, or inhospitable weather conditions along their flyway, can delay their departure and thus potentially affect their timely arrival at the breeding grounds and reduce reproductive success, ultimately affecting population size. This may mirror what has occurred with migrants around the globe (Kirby et al. 2008, Wilcove and Wikelski 2008) and particularly along the EAAF, where long-distance migratory shorebirds have experienced one of the greatest population declines (Nebel et al. 2008, Wilson et al. 2011, Wetlands International 2012). Along the EAAF, habitat deterioration and loss of major stopover sites, e.g. within the Yellow Sea, occur at an alarming rate (Murray et al. 2014, 2015), and are demonstrated to correlate highly with the shorebirds' population declines (Studds et al. 2017). Large birds in this case may be thought more vulnerable for such adverse effects, given their incapacity for a fast migration. However, in accordance with their

faster migration, small species have evolved to breed at high latitudes with a very narrow window for breeding, which again makes them more constrained in their flexibility and resilience to environmental change, despite their capacity for fast migration. Thus, despite here identified differential size constraints on migratory behaviour, the vulnerability of large and small species to environmental disturbances may be additionally shaped by other ecological and physiological constraints.

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