



Short communication

Body mass and latitude both correlate with primary moult duration in shorebirds

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We investigated the effects of body mass and latitude on primary moult duration from published data of migrating shorebirds that moult exclusively on the wintering grounds. Non-phylogenetic and phylogenetic models demonstrated that body mass and latitude correlate with moult duration in a non-additive way: the models predict different latitudinal relationships for smaller and larger shorebirds, and in the northern hemisphere, primary moult duration increased allometrically with body mass (exponent = 0.17), whereas in the southern hemisphere, primary moult duration was not correlated with body mass. If birds optimize feather quality and if slower moult yields sturdier feathers, the fast primary moult of northerly wintering shorebirds indicates additional selection pressures at work.

Keywords: allometry, comparative analysis, feathers, latitudinal effects, tissue repair, waders.

Moult is an important phase of the life-cycle during which birds replace worn feathers, restore or adjust the insulation of the plumage, and may change plumage colours (Jenni & Winkler 1994, Hedenström 2006, Ginn & Melville 2007, Buehler & Piersma 2008). Moult dura-

tion and primary growth rate increase with body mass, and in the largest birds the replacement of all flight feathers may occur over several years (Hedenström 2006, Rohwer *et al.* 2009).

In many long-distance migrant shorebirds, the primary moult following reproduction takes place on the wintering grounds (Remisiewicz 2011). In some taxa, moult starts on the breeding grounds, is suspended during subsequent migration and resumes on the wintering grounds (Underhill 2003, Ginn & Melville 2007). In shorebirds moulting exclusively on the wintering grounds, the duration of primary moult varies with latitude, being shorter at northern than at southern latitudes (Morrison 1976, Summers *et al.* 1989, Marks 1993, Underhill 2003, Serra *et al.* 2006, Remisiewicz 2011). This latitudinal effect was found in interspecific and intraspecific comparisons, and has been related to the harsher winter conditions at northern latitudes, forcing northern wintering populations of shorebirds to complete moult before the onset of winter. Dietz *et al.* (2013) suggested that in north-temperate wintering Red Knot *Calidris canutus islandica* the onset of harsher weather conditions in October may be an important selection pressure determining the timing of primary moult termination, and hence moult duration, although changes in food availability and the arrival of aerial predators could also be involved.

The relationship between primary moult duration and latitude in migratory shorebirds is well established, but previous studies have not considered the effects of differing body masses. As moult duration increases with body mass, the latitudinal effect may differ between large and small species, i.e. larger species may reach minimal moult duration at more southern latitudes than smaller species, which will affect the relationship between moult duration and latitude. Using data from the literature, we assessed whether the latitudinal effect on primary moult duration in long-distance migrant shorebirds is robust and, in particular, whether body mass affects this relationship. In addition, if harsher winter conditions are an important factor limiting moult duration in northern latitudes, it may be that shorebirds moulting at southern latitudes with more benign wintering conditions are able to maximize moult duration, which may affect the relationship between moult duration and body mass. Therefore we also assessed whether this relationship differed between hemispheres.

METHODS

To avoid bias, we used only primary moult duration data determined in adult free-living migratory shorebirds following the method of Underhill and Zucchini (1988) and Underhill *et al.* (1990). We selected studies on taxa that exclusively moult on the wintering grounds, and excluded birds with suspended moult and birds with

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other non-continuous and abnormal moult patterns. All species included breed in northern latitudes, the majority at high latitudes. When body mass was not given, body mass during moult was taken from other published or unpublished sources. When latitude was not given, it was estimated from catching location. In total we assembled data on 27 shorebird populations of 11 species (Table S1).

We analysed the overall relationship between primary moult duration, and body mass and latitude by non-phylogenetic and phylogenetically informed analyses. Northern latitudes were given a negative sign (e.g. 45°N = -45) and southern latitudes a positive sign (e.g. 45°S = +45) in the analyses. We used the phylogenetic supertree of shorebirds (Thomas *et al.* 2004) to compute contrasts, which was trimmed in MESQUITE 2.74 (Maddison & Maddison 2010) to include only species for which data were available (Figure S1). Data on several populations or subspecies of a species were included by adding them as polytomies (as in Gutiérrez *et al.* 2012). Branch lengths were specified by Pagel's (1992) arbitrary method. We calculated the phylogenetic signal (*K* statistic; Blomberg *et al.* 2003) for latitude, log moult duration and log body mass using the MATLAB program PHYSIG_LL.m. *K* indicates the amount of signal in a trait relative to what would be expected for the specified phylogenetic tree given a Brownian motion model of evolution. If *K* = 1, then that trait has exactly the amount of signal expected for that given phylogenetic tree, whereas values > 1 indicate more signal than expected and values < 1 indicate less signal than expected (Blomberg *et al.* 2003).

Because there was no *a priori* assumption as to the nature of the relationship between moult duration on the one hand and body mass and latitude on the other, we estimated the overall effect of body mass and latitude on primary moult duration with linear and quadratic models using a non-phylogenetic conventional ordinary least squares regression (OLS) and a phylogenetic generalized least square regression (PGLS) in R 3.0.2. For the PGLS models we used a Brownian motion correlation

structure (corBrownian), applying the packages *ape* (phylogeny) and *nlme* (fitting of linear and non-linear models using generalized least squares; functions *gls* and *gls*). For the linear models, we ran a series of four models with log(moult duration) as the dependent variable and log(body mass), latitude, log(body mass) and latitude; or log(body mass), latitude and their interaction term as independent variables. For the quadratic models, we ran a series of three models using the same independent variables (a quadratic model with log(body mass) and latitude without an interaction term was not possible). Model selection was based on the Akaike information criterion corrected for small sample sizes (AICc). A model was considered to describe the data significantly better when it had the lowest AICc or when it differed < 2 AICc points from the model with lowest AICc.

Means are presented with standard error (se) and compared with ANOVA (SPSS Statistics 20). Because sample size per hemisphere was small, *n* = 13 for the northern and *n* = 14 for the southern hemisphere, we used conventional allometric regression and univariate analysis of variance with log(moult duration) as the dependent variable, log(body mass) as a covariate and hemisphere as fixed factor, to assess whether the allometric relationship between moult duration and body mass differed between hemispheres.

RESULTS

In the moult data used (Table S1), body mass and primary moult duration had a significant phylogenetic signal (Table 1), suggesting that these physiological traits are affected by their evolutionary history. Latitude, however, did not exhibit a significant phylogenetic signal (Table 1), indicating that related species were not statistically more likely to winter (and moult) at similar latitudes than would be expected at random.

Primary moult duration of adult shorebirds was not directly correlated with body mass (Fig. 1a, Table 2). Moult duration increased with latitude from north to

Table 1. Statistics for randomization tests for significance of the phylogenetic signal for latitude, moult duration and body mass calculated from a tree with branch lengths set according to Pagel's (1992) arbitrary method. The tip data and phylogenetic tree are shown in Table S1 and Figure S1, respectively. Log-transformed data were used for moult duration and body mass. Significant results for the randomization test of the mean squared error (MSE; lower values indicate better fit of tree to data) on the phylogenetic tree indicate the presence of phylogenetic signal for all traits. *K* statistics indicate the amount of phylogenetic signal relative to a Brownian motion expectation (Blomberg *et al.* 2003).

Trait	Expected MSE ₀ /MSE	Observed MSE ₀ /MSE	<i>K</i>	MSE _{candidate}	MSE _{star}	<i>P</i>	ln ML _{candidate}	ln ML _{star}
Latitude	2.61	0.60	0.23	2385.07	1413.02	0.40	-135.72	-142.791
Moult duration	2.61	1.18	0.44	0.02	0.02	0.003	18.46	16.731
Body mass	2.61	4.30	1.65	0.04	0.11	< 0.001	8.77	-7.540

ML, maximum likelihood; MSE, mean squared error. The 'candidate' is the observed tree topology, whereas the 'star' is a tree with internal branch lengths set to 0.

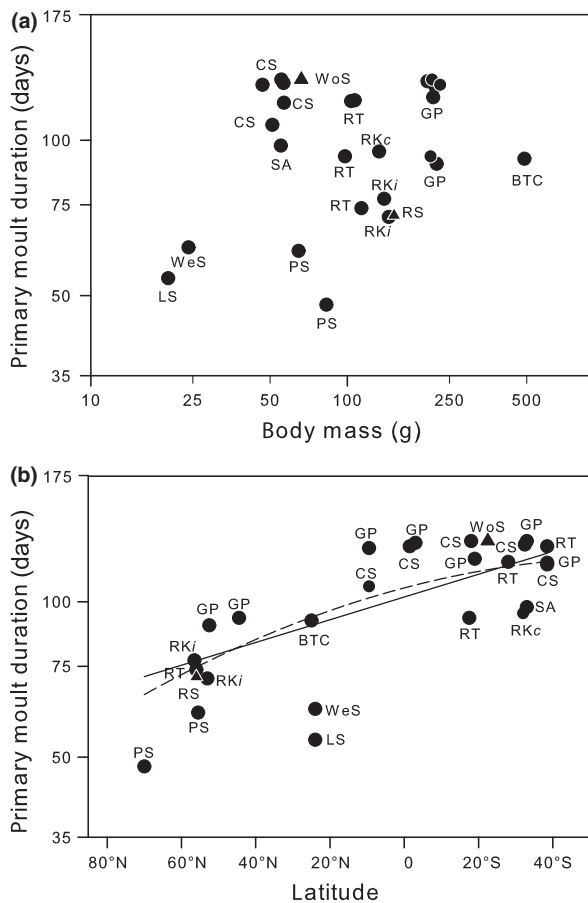


Figure 1. (a) The allometric relationship between primary moult duration in adult shorebirds that moult on their wintering grounds and body mass at the moulting area (raw data). Body mass was derived from another source when not given with moult duration. (b) The relationship between primary moult duration and latitude of the moulting site (raw data). The lines represent the PGLS linear model (solid line) and the equally well supported PGLS quadratic model (dashed line, see Table 2). Symbols: circle, coastal species; triangle up, inland species. See Table S1 for species abbreviations and sources.

south, as indicated by the support for the linear and quadratic models including latitude (Fig. 1b, Table 2). The best supported models to describe the data were quadratic OLS and PGLS models that included body mass, latitude and their interaction (Table 2). The non-phylogenetic and phylogenetic analyses yielded similar best models. The best models with the lowest AICc had AICc weights that were higher (0.53 for the OLS and 0.28 for the PGLS) than the weight of the next-best model (PGLS including only latitude, $\Delta\text{AICc} = 4.01$, weight = 0.07). This indicates that in migrating shorebirds, body mass and latitude correlate with moult duration in a complex manner.

DISCUSSION

In contrast to what has been found in birds generally (Hedenström 2006, Rohwer *et al.* 2009), primary moult duration in shorebirds was not directly correlated with body mass, but body mass was correlated with primary moult duration when taking latitude into account. This suggests that body mass may affect the relationship between latitude and primary moult duration and vice versa.

Latitude can affect the relationship between body mass and moult duration through different latitudinal relationships for smaller and larger shorebirds, and/or a difference in the allometric relationship between northern and southern hemispheres. To demonstrate the effect of body mass on the latitudinal relationship, we calculated primary moult duration for a small (25 g) and a large (250 g) shorebird using the parameter estimates of the best, most extended quadratic OLS model (Table 2). The results show that the decrease in moult duration from south to north differs between small and large shorebirds, and that large shorebirds indeed reach minimal moult duration at more southern latitudes than small shorebirds (Fig. 2a). Due to the quadratic nature of the model, primary moult duration increases again after reaching this minimum, while it is more likely that, in reality, moult duration remains stable thereafter.

To demonstrate the effect of latitude on the relationship between primary moult duration and body mass, we calculated allometric relationships for northern and southern moulting shorebirds separately. Northern and southern hemisphere moulting shorebirds did not differ in body mass (149 ± 34 vs. 117 ± 18 g, respectively; ANOVA, $F_{1,25} = 0.68$, $P = 0.42$), but note that the variation was larger in the northern than southern hemisphere (coefficient of variation (CV) = 83 and 60%, respectively). Geographical moulting location (hemisphere) had a strong effect on the relationship between moult duration and body mass (UNIVARIATE ANALYSIS OF VARIANCE; $\log(\text{body mass})$ $P = 0.05$; hemisphere $P < 0.001$). The allometric regression was significant for shorebirds moulting at northern latitudes (Fig. 2b), but not at southern latitudes (Fig. 2c). Although we cannot exclude that the difference in variation in body mass may have affected these results, the analysis as well as the smaller variation in moult duration in the southern hemisphere (CV = 12 vs. 28% in the northern hemisphere) suggest that southern hemisphere shorebirds may have maximized primary moult duration, and that in these shorebirds, primary moult duration is not correlated with body mass but rather with the maximal time available for moult.

The allometric exponent of the northern hemisphere shorebirds (0.17) was comparable to those of 0.19 found

Table 2. Comparison of various models relating moult duration (days, log-transformed) and body mass (M_b , grams, log transformed), latitude (lat, in degrees) and their interaction in shorebirds. Ordinary least squares (OLS) and phylogenetically informed generalized least squared (PGLS) models are ranked according to their AICc weights. PGLS analyses for linear and quadratic models (PGLS_L and PGLS_Q, respectively) were conducted using a Brownian motion correlation structure. The best supported models are highlighted in bold.

Model	Intercept	M_b	M_b^2	Lat	Latitude ²	$M_b \times \text{Lat}$	Intercept P	$M_b P$	$M_b^2 P$	Lat P	Lat ² P	$M_b \times \text{Lat } P$	AICc	ΔAICc	w_i^a
OLS_Q	0.6432 (0.3952)	1.3418 (0.4104)	-0.3080 (0.1022)	0.0065 (0.0027)	-0.00005 (0.00001)	-0.0025 (0.0013)	0.1185	0.0037	0.0066	0.0263	0.0012	0.0714	-66.33	0.00	0.53
PGLS_Q	0.8996 (0.4768)	1.1666597 (0.5074)	-0.2877 (0.1321)	0.0048 (0.0026)	-0.00003 (0.00001)	-0.0016 (0.0012)	0.0731	0.0319	0.0410	0.0777	0.0065	0.2038	-65.02	1.31	0.28
PGLS _L	2.0092 (0.0652)	—	—	0.0022 (0.0003)	—	—	< 0.0001	—	—	< 0.0001	—	—	-62.32	4.01	0.07
PGLS _Q	2.0268 (0.0653)	—	—	0.0019 (0.0003)	-0.000015 (0.00001)	—	< 0.0001	—	—	< 0.0001	0.1779	—	-61.63	4.70	0.05
PGLS _L	1.8739 (0.1812)	0.0621 (0.0775)	—	0.0022 (0.0003)	—	—	< 0.0001	0.4312	—	< 0.0001	—	—	-60.25	6.08	0.03
PGLS _L	2.0004 (0.1924)	0.0008 (0.0842)	—	0.0067 (0.0028)	—	-0.0022 (0.0014)	< 0.0001	0.9925	—	0.0264	—	0.1214	-60.09	6.24	0.02
OLS _L	1.7952 (0.0925)	0.1009 (0.0458)	—	0.0095 (0.0033)	—	-0.0033 (0.0016)	< 0.0001	0.0380	—	0.0081	—	0.0530	-58.64	7.69	0.01
OLS _L	1.7246 (0.0912)	0.1374 (0.0449)	—	0.0029 (0.0004)	—	—	< 0.0001	0.0054	—	< 0.0001	—	—	-57.19	9.14	0.01
OLS _L	2.0002 (0.0168)	—	—	0.0028 (0.0004)	—	—	< 0.0001	—	—	< 0.0001	—	—	-51.06	15.27	0.00
OLS _Q	2.0288 (0.0276)	—	—	0.0022 (0.0006)	-0.00002 (0.00002)	—	< 0.0001	—	—	0.0012	0.2083	—	-50.11	16.22	0.00
PGLS _Q	0.2292 (0.805)	2.0523 (0.8871)	-0.5572 (0.2392)	—	—	—	0.7785	0.0296	0.0286	—	—	—	-31.83	34.50	0.00
PGLS _L	1.9647 (0.3322)	0.0092 (0.1418)	—	—	—	—	< 0.0001	0.9488	—	—	—	—	-29.10	37.23	0.00
OLS _L	1.7649 (0.1608)	0.1079 (0.0790)	—	—	—	—	< 0.0001	0.1842	—	—	—	—	-28.14	38.19	0.00
OLS _Q	0.9195 (0.7498)	0.9879 (0.7666)	-0.2230 (0.1932)	—	—	—	0.2319	0.2098	0.2599	—	—	—	-26.82	39.51	0.00

^a w_i , Akaike weight of model.

by Hedenström (2006) and of 0.14 by Rohwer *et al.* (2009), and similar to the exponent of 0.17 for primary feather growth rate (Rohwer *et al.* 2009). This correspondence may seem remarkable, but for his analysis, Hedenström (2006) used 60 species from Ginn and Melville (1983 edition). These authors included only species that breed or undergo a major moult in Britain, in the northern hemisphere. Also, the majority of the 43 species used by Rohwer *et al.* (2009) moult in the

northern hemisphere. It may be worthwhile to assess whether moult duration differs between northern and southern hemisphere in birds in general.

The latitude of destination of these migrant shorebirds thus seems a major determinant of their primary moult duration, even affecting the allometric relationship with body mass. Disentangling the effects of latitude and migration distance is difficult with our dataset, as the vast majority of the populations in the analysis breed at high northern latitudes so that migration distance and moult latitude are closely correlated. However, the latitudinal effect is also apparent in the much shorter (~22%) moult duration of adult northern wintering Red Knots and Grey Plovers *Pluvialis squatarola* compared with non-breeding over-summering second-year birds or captive adults (Serra *et al.* 2006, Dietz *et al.* 2013). If migration distance had more impact on primary moult duration than latitude, one would expect that primary moult duration increases with migration distance because feather quality is expected to increase with moult duration (see below) and feathers are expected to wear more when flying longer distances. This effect is present in the current dataset, where in most taxa, migration distance increases when moulting further south, and primary moult duration increases from north to south. Yet the non-migrating Red Knots and Grey Plovers had a longer moult duration than the migrating adults, which indicates that in shorebirds it is the environment, represented by latitude, that has a major impact on moult duration, rather than migration distance.

It is well known that the timing, rate and extent of moult are flexible (Jenni & Winkler 1994, Ginn & Melville 2007, Wingfield 2008), enabling birds to solve part of the problem of fitting all life-cycle stages into 1 year by varying the duration of moult (Helm & Gwinner 2006). If birds maximize feather quality and if slower moult leads to higher quality feathers (Dawson *et al.* 2000, Hall & Fransson 2000, Serra 2001, Dawson 2004,

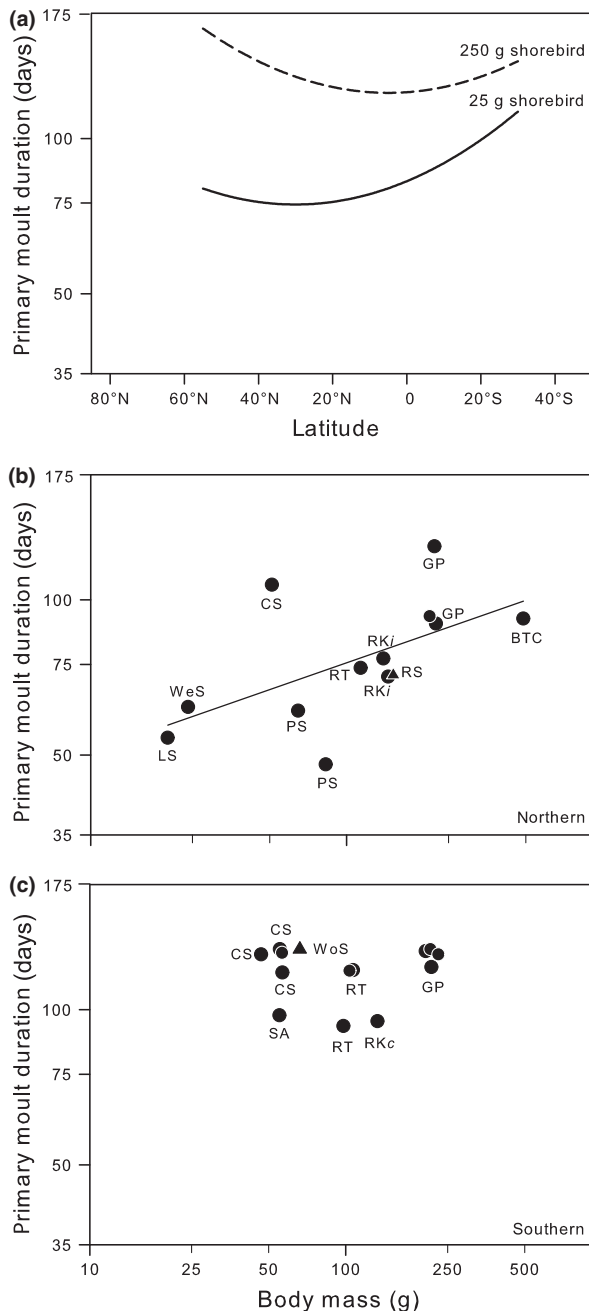


Figure 2. (a) The predicted relationship between primary moult duration and latitude of moulting for a small (25 g, solid line) and large (250 g, dashed line) shorebird. The best model, the most extended quadratic OLS (see Table 2), was used to calculate the predicted moult duration. (b) The allometric relationship between primary moult duration in adult shorebirds that moult in the northern hemisphere and body mass at the moulting area. The linear regression equation (solid line) is: $\log(\text{moult duration}) = 1.53 (\pm 0.154) + 0.17 (\pm 0.08) \log(\text{body mass})$ ($n = 13$, $P < 0.05$, $R^2 = 0.33$). (c) The allometric relationship between primary moult duration in adult shorebirds that moult in the southern hemisphere and body mass at the moulting area ($n = 14$, $P = 0.79$, $R^2 = 0.01$). Symbols: circle, coastal species; triangle up, inland species. See Table S1 for species abbreviations and sources.

de la Hera *et al.* 2009, 2010), longer moult duration is the better option (Hall & Fransson 2000, Serra 2001). This suggests that for reasons other than feather quality, primary moult is accelerated in northerly areas, an acceleration that comes with costs. Apart from a decrease in feather quality (both a decrease in mechanical quality and resistance to wear), accelerated moult may increase daily energy costs for moult, flight and thermoregulation, and decrease flight abilities, resulting in increased predation danger (Jenni & Winkler 1994, Kjellén 1994, Nilsson & Svensson 1996).

Flight feather quality must be essential to shorebirds that make nonstop migration flights of several thousands of kilometres. In Grey Plovers, wing length loss after a year varied between 0.7 and 3.3% of the original length (Serra 2001). Primary moult duration was the key factor determining feather durability, as it explained 59% of the variation in annual rates of primary abrasion, whereas migration distance explained only 14% (Serra 2001). Even though migration flights were probably considerably shorter in northerly than in southerly wintering shorebirds (most of them bred at high northern latitudes), the effect of moult duration on flight feather quality is likely to have an impact on flight costs and predation-evading flight abilities (van den Hout *et al.* 2010). In addition to this disadvantage, northerly wintering shorebirds may endure increased thermoregulatory costs due to decreased quality of their plumage (Nilsson & Svensson 1996). How northern wintering shorebirds deal with these issues remains unknown.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Additional information of the species used in Figure 1. Presented are species name and the abbreviation used in Figure 1, mean latitude of capture location, body mass, primary moult duration, and the sources from which the data were obtained.

Figure S1. The phylogenetic tree used to generate phylogenetically independent contrasts in log body mass and latitude for 12 shorebird species. The phylogenetic tree is based on Thomas *et al.* (2004) with the original untransformed branch lengths. See *Methods* for details.