ORIGINAL ARTICLE

Low asymmetry of primary moult in Dunlins *Calidris alpina alpina* migrating to wintering grounds

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Abstract

The Dunlin is one of very few wader species that moults primaries when migrating to its wintering grounds. In our study, a total of 68.2% of immatures and 26.6 of adults underwent their primary moult when passing through the southern Baltic in autumn. More than 30% of moulting birds revealed differences in moult scores of left and right wings. However, 13% of Dunlins showed differences between the left and right wing not greater than 1%, and 50% of individuals showed differences between the two wings that were lower than 3% of the total mass of all primaries. The probability of asymmetry during the primary moult increased over time and decreased with the advancement of the primary moult. Sex and age of birds had no significant effect on the occurrence of moult asymmetry. The level of asymmetry in the primary moult increased in the following days of autumn migration and with the advancement of the primary moult. The mean index of primary moult asymmetry (the absolute value of the difference in moult advancement between the left and right wing) was lower in immature Dunlins than in adults, and in females compared to males. Hence, sex (males) and age classes (adults) that spend a longer time on the breeding grounds revealed a higher index of primary moult asymmetry, most probably as a result of higher levels of physiological stress. However, the low proportion of birds showing large asymmetry suggests that this is strongly constrained by selection for aerodynamic efficiency, as asymmetry in primaries affects aerodynamic stability, take-off costs, manoeuvrability and agility in birds with flapping flight.

Keywords Wing asymmetry · Fluctuating asymmetry · Stress · Waders · Aerodynamic efficiency

Zusammenfassung

Geringe Asymmetrie in der Handschwingenmauser von Alpenstrandläufern *Calidris alpina alpina* auf dem Zug ins Winterquartier

Der Alpenstrandläufer ist eine von sehr wenigen Limikolenarten, die ihre Handschwingen auf dem Zug ins Winterquartier mausern. In unserer Studie mauserten insgesamt 68,2% der Immaturen und 26,6% der Altvögel ihre Handschwingen, während sie im Herbst durch das südliche Baltikum zogen. Über 30% der mausernden Vögel zeigten Unterschiede in den Mauserwerten der beiden Flügel. Bei 13% der Alpenstrandläufer waren die Unterschiede jedoch nicht größer als 1% und bei 50% der Individuen geringer als 3% des Gesamtgewichts aller Handschwingen. Die Wahrscheinlichkeit einer asymmetrischen Handschwingenmauser nahm über die Zugzeit zu und mit dem Fortschreiten der Mauser ab. Geschlecht und Alter der Tiere hatten keinen signifikanten Einfluss auf das Auftreten von Mauserasymmetrie. Das Ausmaß der Asymmetrie in der Handschwingenmauser nahm in den folgenden Tagen des Herbstzuges und mit dem Fortschreiten der Handschwingenmauser zu. Der mittlere Index der Handschwingenmauser-Asymmetrie (die absolute Differenz im Fortschreiten der Mauser zwischen linkem und rechtem Flügel) war bei immaturen Alpenstrandläufern geringer als bei Altvögeln und bei Weibchen geringer als bei Männchen. Daher wies das Geschlecht (Männchen) bzw. die Altersklasse (Altvögel), die länger im Brutgebiet blieb, einen höheren Index der Handschwingenmauser-Asymmetrie auf, wahrscheinlich aufgrund von stärkerem physiologischen Stress. Insgesamt deutet der geringe Anteil von Vögeln mit starker Asymmetrie jedoch darauf hin, dass solche Asymmetrie

stark durch die Selektion für aerodynamische Effizienz begrenzt ist, da Handschwingen-Asymmetrie die aerodynamische Stabilität, die Energiekosten des Startens, die Manövrierfähigkeit und die Agilität von Vögeln mit Schlagflug beeinflusst.

Introduction

Moulting of flight feathers is one of the most important processes in the avian annual cycle (Kjellén 1994; Barta et al. 2008). It incurs not only costs of feather synthesis, but also energetic expenses associated with increased flight costs as a consequence of gaps in wing area and increased predation risk due to lower manoeuvrability (Lindström et al. 1993; Swaddle et al. 1999; Lind 2001). As moult-related feather gaps seriously hinder flight performance and also increase flight metabolism (Tucker 1991; Chai 1997; Hedenström and Sunada 1999; Kiat et al. 2016), the cost of a decrease in wing area interplays with the timing of major annual life cycle events, such as migration and breeding (Kiat et al. 2016). Therefore, moulting strategies, and particularly the primary moult, are often investigated in studies on life history and trade-offs, due to their interactions with environmental conditions (De la Hera et al. 2009; Remisiewicz et al. 2009; Rohwer et al. 2011; Barshep et al. 2013).

Variations in the seasonality of food supply on breeding and wintering grounds drive the timing of flight feather moult with respect to migration (Barta et al. 2008). The majority of small and medium-sized migratory birds moult flight feathers after breeding before their autumn migration, or after migration on the wintering grounds. Some species begin the primary moult on the breeding grounds, suspend it during migration and complete the process on the wintering grounds, whereas others replace all primaries during the post-migration period (Cramp and Simmons 1986; Jenni and Winkler 1994; Holmgren and Hedenström 1995; Barta et al. 2008). As both the flight feather moult and breeding are energy-demanding processes, the overlap between them is costly (Holmgren and Hedenström 1995; Hemborg and Lundberg 1998). Hence, such an overlap is quite rare, and in waders breeding in the Northern Hemisphere it has only been found in short- or medium-distance migrants (Pienkowski et al. 1976; Walters 1984). Although a moult-breeding overlap leads to costs, it may also be an adaptive strategy (Barta et al. 2006; Bridge 2006; Morales et al. 2007).

Asymmetry during the primary moult has been described both in wild (Rasmussen 1988; Polo and Carrascal 1999; Hall and Franson 2001; Freed and Cann 2012; Zuberogoitia et al. 2013) and captive, non-manipulated birds (Mallet-Rodrigues 2012). As the moult takes place simultaneously on both wings, asymmetry in moulting of corresponding feathers on the right and left wings, defined as a random deviation from perfect symmetry in bilateral traits, may be used in studies on fluctuating asymmetry (Palmer 1994). It is widely accepted that fluctuating asymmetry reflects an animal's ability to cope with the sum of challenges that affect it during the growth period (Palmer and Strobeck 1986; Møller and Swaddle 1997). Primaries and other large feathers are suitable morphological traits for the study of fluctuating asymmetry, since they are replaced regularly and their morphogenesis may be studied under different environmental pressures (Polo and Carrascal 1999; Aparicio and Bonal 2002). Although much emphasis has been put on evaluating the influence of food limitation or ectoparasitism on the extent of asymmetry in flight feathers and how such asymmetry affects flight performance (e.g. Brown and Brown 1998; Swaddle and Witter 1994, 1998; Hambly et al. 2004), studies on species that replace primaries during migration are scarce and concern individuals with an interrupted moult (Hall and Franson 2001), or describe asymmetry in the moult pattern in individual birds (Cannell et al. 1983).

The Dunlin *Calidris alpina* is one of very few wader species that moults primaries when migrating towards its wintering grounds (Gromadzka 1989). Numerous birds from nominative subspecies that pass through the Baltic region in autumn originate from the vast area between Scandinavia and Central Siberia (Gromadzka 1985; Gromadzka and Ryabitsev 1998) up to the Taimyr Peninsula (Soloviev et al. 2012). Individuals at all stages of primary feather replacement are found among these birds (Gromadzka 1989; Holmgren et al. 1993), which makes this species a perfect choice for studies on the extent of fluctuating asymmetry in primaries growing during migration. Moreover, Dunlins in their second calendar year of life (immatures) migrate to their breeding grounds, which is rare among Arctic waders (Soikkeli 1967; Gratto and Morrison 1981; Hockey et al. 1998; Tavera et al. 2016). This provides an opportunity to search for age- and sex-dependent differences in many aspects of their migratory behaviour.

In this study, we examined whether the occurrence and extent of asymmetry in the primary moult might be linked to age, sex, moult advancement, day of the season or amount of energetic reserves in Dunlins migrating through the southern Baltic towards their wintering grounds. We hypothesize that the extent of asymmetry may reflect the overlap of energetically costly activities such as breeding, migration and primary moult. From this hypothesis we predict that moult asymmetry may be strongly constrained

by selection for aerodynamic efficiency, which is crucial for birds during migration; as a consequence of this, large asymmetry should be avoided.

Methods

Bird catching

Dunlins were caught using walk-in traps (Busse and Meissner 2015) at the mouth of the Vistula River on the Baltic coast of Poland (54°21′N, 18°57′E) between 2009 and 2015. Each year, daily trapping started around 10 July and finished around mid-September. This period covers almost the whole migration of non-juvenile Dunlins in this area (Meissner and Sikora 1995; Meissner et al. 2009).

Wing length (rule with an accuracy of 1 mm), total head length and bill length (callipers with an accuracy of 0.1 mm) of each trapped Dunlin were measured (Busse and Meissner 2015). Birds were also weighed with an electronic balance with an accuracy of 1 g. The age of captured birds was determined according to the description given by Meissner and Skakuj (2009), which allows distinguishing two age classes among non-juvenile Dunlins: immatures (birds in the second calendar year) and adults (older than 2 years). The group of 515 birds that could not be aged due to the lack of diagnostic feathers was excluded from the analyses. Dunlins were sexed according to a discriminant function based on the bill and wing lengths derived for birds older than 1 year migrating through the Baltic (Meissner and Pilacka 2008). In total, data on 7729 Dunlins were analysed in this study, including 3294 immatures and 4435 adults. Division of the time period into successive 10-day periods followed Berthold (1973).

Moult scoring

In the field, we used a standard moult formula, where the moult stage for each of ten primaries of both wings was recorded as a score between 0 (old feather) and 5 (new, full grown feather) (Ashmole 1962). The sum of moult scores for each of ten primaries on one wing of each bird gave the primary moult score (PMS), ranging from 0 (moult had yet to begin) to 50 (moult completed). These scores from both wings were summed and used as an index of primary moult advancement (IPMA), where 0 indicates a bird that has not yet started primary moult and 100 indicates a bird that has finished the primary moult in both wings. To transform the distribution of PMSs to a linear form, the standard moult formula of each bird was transformed into the proportion of feather mass grown (PFMG), where feathers that had moult scores of 1, 2, 3, 4 and 5 were given a corresponding moult index of 0.125, 0.375, 0.625, 0.875 and 1, respectively, to represent the proportion of feather mass grown (Underhill and Summers 1993). The mean relative mass of each primary, which is needed for this transformation, was calculated from feathers dried to constant mass, obtained from three birds found dead near the study area (Table 1). Due to the small intraspecific variation in relative masses of primaries (Underhill and Joubert 1995), a sample of three sets of primaries was sufficient, especially given that the coefficient of variation in each case was not greater than 3%. The absolute difference between PFMG of the left and right wing was used as an index of primary moult asymmetry.

To check if asymmetry in the primary moult is related to the amount of energetic stores, the scaled mass index (SMI) (Peig and Green 2009) was used as a proxy of body condition. It was calculated as:

$$SMI = BM \left[\frac{BL_0}{BL} \right]^b,$$

where BM and BL are body mass and bill length of an individual, BL_0 is the arithmetic mean value of bill length of the whole Dunlin sample and b is the scaling exponent estimated from the standardized major axis regression of body mass and bill length calculated by dividing the slope of the ordinary linear square regression of lnBM and lnBL by Pearson's correlation coefficient (Peig and Green 2009). Among all linear body measurements, we used bill length, because it is the best predictor of the overall body size in Dunlins (Davidson 1983; Goede and Nieboer 1983; Piersma and van Brederode 1990).

Statistical analysis

A general linear model (GLM) was applied to check for the differences in primary moult advancement between immatures and adults, and in the following 10-day periods. We

Table 1 Mean relative mass (%) of primaries of two adult and one juvenile Dunlin found dead in the mouth of the Vistula in autumn

Primary no.	1	2	3	4	5	6	7	8	9	10
Mean	4.22	4.80	5.76	6.82	8.46	10.18	11.76	13.78	15.74	18.48
SD	0.129	0.126	0.183	0.126	0.171	0.129	0.058	0.310	0.096	0.486
CV	2.3	2.4	2.6	2.2	2.4	1.0	0.5	2.8	0.6	3.0

Primaries were numbered from the innermost to outermost

CV Coefficient of variation

used a generalised linear model (GLZ) with binomial distribution and logit link function or logarithm link function and normal error distribution (McCullagh and Nelder 1983) to account simultaneously for the effects of all independent variables on the occurrence of asymmetrical primary moult and the index of primary moult asymmetry, respectively. In this analysis, only birds with asymmetrical moult (the index of primary moult asymmetry greater than 0) were taken into account. Dependent variables in GLZ analyses were related separately to sex, age, date of capture (day number in a year), an index of primary moult advancement and SMI. The Wald χ^2-statistic was used to test for significant differences between groups. A stepwise backward selection was applied to include significant variables ($p < 0.05$) in the model. All statistical procedures were performed using Statistica 12 software (StatSoft 2014).

Results

Between the first half of July and the second half of August, the proportion of individuals in active primary moult increased from 33 to 94% in immatures and from 8 to 32% in adults (Fig. 1). In total, 68.2% of immatures moulted primaries, whereas only 26.6% of adults were in the primary moult.

In both age classes, the vast majority of birds had PFMG lower than 30% and only 2.1% of adults and 3.0% of immatures exceeded 50% of the grown primary feather mass (Fig. 2). Immatures were more advanced in the primary moult than adults (GLM, $F_{5,3403} = 36.31$, $p < 0.001$; Fig. 3), and the mean index of primary moult advancement increased in the following 10-day periods (GLM, $F_{5,3403} = 113.89$, $p < 0.001$; Fig. 3).

Data from all years were pooled, as we found no statistically significant differences between the proportion of individuals showing moult asymmetry among birds caught in subsequent years, either in immatures (G-test, $G = 4.24$, $df = 6$, $p = 0.643$) or adults (G-test, $G = 9.96$, $df = 6$; $p = 0.126$). Among birds moulting primaries, there were significantly more cases of asymmetrical moult in adults (37.7% of 2248 individuals) than in immatures (32.5% of 1178 individuals) (G-test, $G = 9.98$, $df = 1$, $p = 0.003$).

Difference in PMS and PFMG between left and right wings did not differ significantly from zero either in adults or immatures (one-sample t-test, $p > 0.252$ in all cases). Median difference in PMS between the left and right wing primaries was two points and 2.9% in PFMG. In a few extreme cases, these differences reached from ten to 15 points (seven individuals) and 12–20% in PMS and PFMG (14 individuals), respectively (Fig. 4). About 34% of birds revealed only a slightly asymmetrical primary moult (one-point difference in PMS between both wings), whereas half of them showed
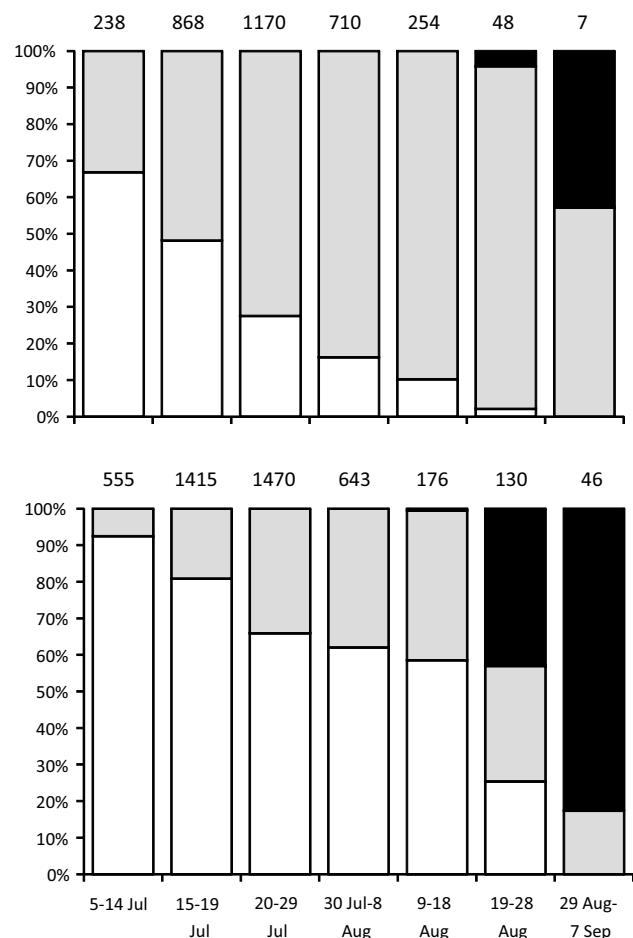

Fig. 1 Percentage of Dunlins at different primary moult stages. White Birds that have not yet started primary moult, grey birds in primary moult, black birds with all new primaries (moult finished in both wings). Top Immatures, bottom adults. Sample sizes are given above the bars

a difference of less than two PMS points. When taking into account PFMG, 13% of Dunlins showed a difference between the left and right wing that was not greater than 1%, and 50% of individuals showed a difference between the two wings that was lower than 3% of the total mass of primaries.

Among all independent variables, only day number in a year and the index of primary moult advancement had significant influences on the occurrence of moult asymmetry. The probability of asymmetry in the primary moult increased over time and decreased with the advancement of the moult (Table 2). Sex and age of birds had no significant effects on the occurrence of moult asymmetry (efficient score statistics from stepwise GLZ were 0.020 and 0.195 for sex and age, respectively, and $p > 0.66$ in both cases).

The backward stepwise GLZ procedure selected a model with the day number in a year, index of moult advancement, sex and age, which had a significant influence on the IPMA. The asymmetry in the primary moult
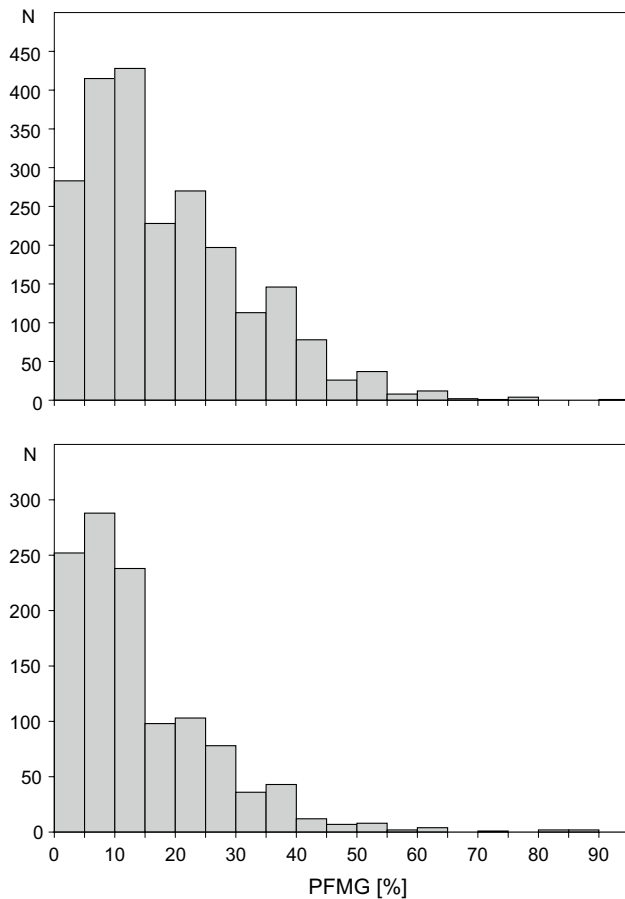
Fig. 2 Distribution of mean primary feather mass grown (PFMG) for both wings in immature (top) and adult (bottom) Dunlins
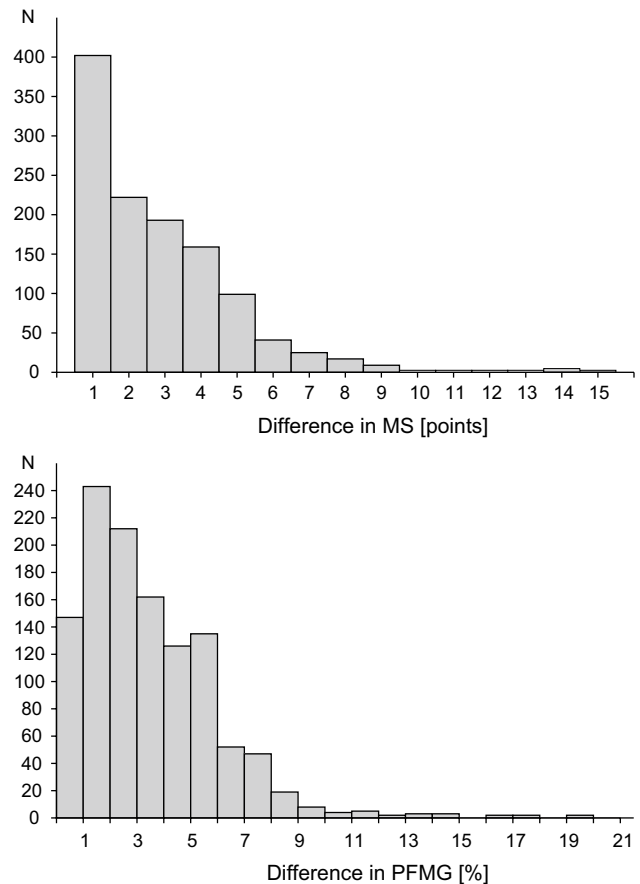
Fig. 4 Distribution of differences in primary moult scores (MS; top) and primary feathers mass grown (PFMG; bottom) between left and right wings of Dunlins showing asymmetrical moult (both age groups combined)
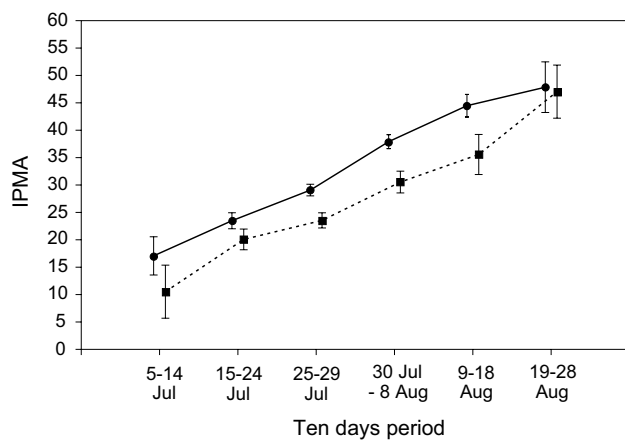
Fig. 3 Mean index of primary moult advancement (IPMA) of immature (dots, solid line) and adult (squares, dashed line) Dunlins in the following 10-day periods. Only birds undergoing active primary moult were taken into account. Whiskers show 95% confidence interval. Data from the period after 28 August were omitted due to small sample size

Table 2 Selected generalised linear model (GLZ) model with binomial distribution and logit link function for the occurrence of asymmetrical primary moult in Dunlins as the response variable and day number in a year (*Day*) and index of primary moult advancement as covariates

Explanatory variable	Coefficient	SE	Wald χ^2	p
Constant	-4.376	0.819	28.58	<0.0001
Day	0.022	0.004	29.29	<0.0001
Index of moult advancement	-0.031	0.002	178.84	<0.0001

increased in the following days of autumn migration and with the advancement of the primary moult. Also, the mean IPMA was lower in immature Dunlins than in adults, and in females compared to males (Table 3). Finally, no significant interaction was found between age and sex in the GLZ model (GLZ, Wald statistic = 1.64, $p = 0.20$).

Table 3 Effects of day number in a year (*Day*), index of primary moult advancement (*IPMA*), age and sex on index of primary moult asymmetry among Dunlins captured in Puck Bay during autumn migration, according to the selected GLZ model

Explanatory variable	Coefficient	SE	Wald χ^2	p
Constant	−4.721	0.458	106.09	<0.0001
Day	0.006	0.002	6.21	0.0127
IPMA	0.007	0.001	27.70	<0.0001
Age (immature)	−0.058	0.021	7.43	0.0064
Sex (female)	−0.059	0.022	6.96	0.0083

Estimated regression coefficients are set to zero for baseline categories of categorical variables (age—adult, sex—male)

Discussion

Asymmetry in primaries affects aerodynamic stability and thus flight efficiency, take-off cost, manoeuvrability and agility in birds with flapping flight (Thomas 1993; Swaddle 1997; Swaddle and Witter 1998). That is why asymmetry in primaries, which are used for propulsion during flight, is always lower than in secondaries or rectrices (Stiles 1995; Polo and Carrascal 1999; Brommer et al. 2003; Arroyo et al. 2004), and migratory birds have more symmetrical wings than others (Balmford et al. 1993). Indeed, half of Dunlins with an asymmetrical primary moult had slight differences between both wings that were not greater than two PMS points and not greater than 3% of PFMG. This suggests that the extent of fluctuating asymmetry in the primary moult of migrating Dunlins could be strongly constrained, e.g. by selection for aerodynamic efficiency, and thus possibly represents a fitness cost to birds passing the southern Baltic, as asymmetry in primaries may reduce the probability of survival, as shown in the Ural Owl *Strix uralensis* and Cliff Swallow *Petrochelidon pyrrhonota* (Brown and Brown 1998; Brommer et al. 2003).

Deviations from bilateral symmetry correlate with fitness differences and are treated as indicators of environmental stress (Møller and Swaddle 1997). It is widely accepted that actual environmental conditions, particularly food limitation during the growth period, may disturb the process of feather synthesis and consequently affect the level of asymmetry of growing feathers (Swaddle and Witter 1994; Møller 1996; Freed and Cann 2012). In general, individuals that are in worse body condition or are nutritionally stressed show higher levels of asymmetry, especially in traits directly affecting locomotion (Thomas 1993; Swaddle and Witter 1994; Polo and Carrascal 1999; Nosil and Reimchen 2001). However, in this study, we found no relationship between a proxy of body condition (scaled mass index) and the index of primary moult asymmetry. It should be borne in mind that sandy coasts of the southern Baltic do not offer good feeding conditions for waders due to the lack of tides (Kube

1994; Meissner 2007) and that the vast majority of non-juvenile arctic waders stopping here arrive with low energetic reserves, usually remain for a few days only and reveal only a slight body mass increase during this time (Meissner 1998, 2007; Meissner and Górecki 2006). Moreover, very few individuals are retrapped in subsequent migratory seasons (Waterbird Research Group KULING, unpublished data), which suggests that the Gulf of Gdańsk is an emergency feeding site for these birds rather than a regular stopover.

The rough estimation of primary moult duration in Dunlin populations breeding in Siberia east of the Yamal Peninsula is about 48 days, and the mean mass growth of primaries was estimated as 2.08% of primary mass per day (Holmgren et al. 2001). Hence, birds that started to moult before their arrival at the study area must have commenced this on the breeding ground or during the first stage of their autumn migration. Data from museum skins analysed by Greenwood (1983) and Gromadzka (1989), as well as data from birds caught on nests in different parts of Eurasian breeding areas of the Dunlin (Kania 1990; Holmgren et al. 2001), indicate that only birds breeding east of the Ural Mountains initiate their primary moult when incubating eggs. The residence time of non-juvenile Dunlins in Siberian breeding areas after chick rearing remains unknown, but the timing and dynamics of their migration in Baydaratskaya Bay (southern Yamal Peninsula) and in the Baltic are very similar, with a migration peak of non-juvenile birds being only 5–6 days later in the Gulf of Gdańsk (southern Baltic) than in Yamal (Chernichko et al. 1998; Meissner and Strzałkowska 2006). This suggests that these birds depart from the breeding grounds shortly after breeding. Hence, in moulting birds caught in the study area, the causes of asymmetry in the primary moult were probably mostly connected with conditions on the breeding grounds rather than those at the previous stopover sites.

In Dunlins on east European and Siberian breeding grounds, there is a clear tendency for increasing the overlap of the primary moult with egg incubation and chick attendance with latitude and longitude (Holmgren et al. 2001). As metabolisable energy requirements increase during the moult (Lustik 1970; Dietz et al. 1992; Hoye and Buttemer 2011), overlapping the primary moult with other energetically expensive activities, such as migration, is expected to result in significant trade-offs in energy allocation. Moreover, migratory birds have less time for moulting than sedentary birds and are forced to produce feathers faster (Jenni and Winkler 1994; Kjellén 1994), which may increase the level of physiological stress. Hence, it is supposed that birds from more eastern and northern parts of this vast breeding area, which started to breed and hence migrated towards the wintering grounds later in the season, revealed higher stress levels because they started the primary moult during incubation and continue this when rearing chicks (Gromadzka 1989; Holmgren et al. 2001).

Indeed in our study, the proportion of Dunlins showing an active primary moult increased throughout the season, and the index of primary moult asymmetry increased in the following days of the migration period and was greater in birds more advanced in primary replacement. A higher proportion of Common Whitethroats *Sylvia communis* with an asymmetrical number of newly grown primaries was recorded in the later part of the migration season, which was suggested to be a result of a high metabolic rate caused by the stress of moulting late in the season (Hall and Franson 2001). However, it should be remembered that the mass of primaries increases gradually from the innermost to the outermost feather and that P10 has over four times greater relative mass that P1 (see Table 1). The growth rate across primaries in waders seems to be similar (see Remisiewicz 2011 for a review), hence the progress through subsequent growth stages of an innermost primary seems to be four times faster than that of the outermost one, and this may an influence on the differences in scores between the inner and outer primaries. On the other hand, the probability of asymmetry in the primary moult in Dunlins decreased as the moult advanced (i.e. towards more outer primaries). Moreover, in Dunlins, the gap in the wing area due to not fully grown feathers generally decreased in later stages of the moult (Holmgren et al. 1993). It should be noted that the vast majority of Dunlins migrating through the Baltic during their active primary moult usually have no more than five or six new primaries (Holmgren et al. 1993; authors' unpublished data), so they are in the middle stage of primary replacement. All these findings suggest that birds avoid asymmetry, especially in the middle part of the wing, as this has a larger effect on increasing the energetic cost of flight than more distal gaps (Hedenström and Sunada 1999).

In the Dunlin, females attend broods for less time than males and usually depart during the first 10–12 days after the hatch (Soikkeli 1967; Jamieson 2011). Immatures that breed for the first time are less involved in breeding activities because they have a higher number of breeding failures than older, more experienced birds, and usually depart from the breeding grounds earlier (Meissner 2015). Hence, the higher index of primary moult asymmetry in adults than in immatures documented in this study, and in males compared to females, may reflect higher stress levels due to the longer period of involvement in breeding activities and consequently the longer overlap between the moult and breeding.

It seems that the extent of asymmetry in the primary moult in migrating Dunlins reflects the overlap of energetically costly activities such as breeding, migrating and flight feather replacement. The sex (males) and age class (adults) that spend more time on the breeding grounds revealed a higher index of primary moult asymmetry, most probably as a result of higher levels of physiological stress. However,

the low proportion of birds with large asymmetry suggests that such asymmetry is related to some costs that, generally, are avoided.

Compliance with ethical standards

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