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Determinants of wing-feather moult speed in songbirds

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Abstract Wing morphology is known to strongly affect flight performance by affecting lift and drag during flight. Performance may consequently deteriorate during feather moult due to the creation of feather gaps in the wing. Since wing gap size may directly affect the extent of reduced flight capacity, rapid moult involving the creation of large feather gaps is expected to substantially impair flight compared with the small gaps induced by a slower moult. To examine the factors affecting wing-feather moult speed, we studied adults of nineteen resident or very short-distance migrant passerine species during their post-breeding moult using a model-selection framework following a phylogenetically controlled analysis. We examined the speed of wing-feather moult in relation to each species' flight distance index that was estimated based on local foraging movements rather than on longer flights (e.g., migration), assessed by the Delphi technique of expert evaluation. Moult speed was also examined with respect to six morphometric variables: body mass, wing loading, the feather comprising the tip of the wing, aspect ratio, wing span, and wing area. Our results suggest that flight distance index is the most important factor determining the speed of wing-feather moult in songbirds. Species that regularly fly a shorter distance were found to moult quickly, and those that take relatively longer flights moult slowly. These results suggest that the aerodynamic cost of wing area reduction due to feather moult shapes the evolution of annual routine processes by dictating a slower moult speed (resulting in small wing gaps) for species that regularly fly long distances and consequently may be affected more substantially by large wing gaps compared with short distance flyers.

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Introduction

A key function of bird flight feathers is their biomechanical role, as wing and tail feathers form the surface over which lift is generated to facilitate flight (Rayner 1988; Pennycuick 2008). To ensure their utility, feathers must be renewed on a regular basis because they are subject to constant wear and stochastic damage due to accidents (e.g., fast collision of the wing with branches). These processes may degrade the bird's flight feathers to an extent that can substantially impair its flight performance (Jenni and Winkler 1994). Feather degradation depends on bird habits and habitat, prevailing environmental conditions and parasite identity and load. In addition, physical contact with vegetation, the nest and predators may incur substantial feather damage (Ginn and Melville 1983; Jenni and Winkler 1994; Flinks and Salewski 2012).

Fully grown feathers are dead structures consisting mainly of avian keratin. Keratin is one of the most durable biological materials, with great strength, flexibility and resistance to hydrolytic protein-digesting enzymes and bacteria (Jenni and Winkler 1994). However, unlike other keratin structures, such as hair and claws, feathers cannot be renewed continuously from their base and are hence replaced only following the shedding of old feathers. This shedding occurs before new feathers that will grow in their place are fully developed, and this time lag between feather shedding and the full growth of the new feather creates a feather gap. Because several adjacent feathers may be shed during a short time interval, feather gaps of various widths and lengths are created during the moult process (Ginn and Melville 1983; Jenni and Winkler 1994; Swaddle and Witter 1997). The size of the feather gap is determined by the number of feathers that have been shed simultaneously or within a short time interval and by the feather growth rate, with the former factor being more important than the latter (Rohwer and Rohwer 2013).

Moult-related feather gaps may substantially hamper flight performance and increase flight metabolism during an extended period (Haukioja 1971; Green and Summers 1975; Francis et al. 1991; Lindström et al. 1994; Hedenström and Sunada 1999; see also a review by Hedenström 2003). The findings of experiments performed on moulting birds suggest a reduction in flight speed (Swaddle and Witter 1997), takeoff angle (Swaddle et al. 1999; Swaddle and Witter 1997; Williams and Swaddle 2003) and lift (Lind 2001; Lind and Jakobsson 2001; Bauchinger and Biebach 2006). In addition, the mass-specific metabolic cost of flight is higher for moulting birds compared with non-moulting birds (Chai 1997; Chai and Dudley 1999). Hedenström and Sunada (1999) suggested that gap size is important as large gaps have a more substantial effect on flight performance than small ones. In addition, several bird species were found to modify their behaviour by reducing their flight activity during moult, presumably due to their moult-related, impaired flight performance and elevated flight metabolism (Newton 1966; Bell 1970). Furthermore, birds were found to decrease their body mass during primary feather moult, presumably in order to compensate for the moult-induced reduction of weight support by the wings due to the loss of wing area (Chai 1997).

The duration of moult in passerines is highly variable among species and may last from 5 weeks in warblers and northern latitude species to 25 weeks in some swallows and

tropical species (Fogden 1972; Ginn and Melville 1983; Jenni and Winkler 1994). Several studies described how time limitations during specific seasons may affect moult duration (Fogden 1972; Hall and Fransson 2000; de la Hera et al. 2011), but other factors that determine the speed and duration of feather moult have been thus far largely overlooked. Feather moult duration may covary with bird flight ecology, and it has been suggested that the relatively slow moult of the starling (*Sturnus vulgaris*) during which only small feather gaps are created in the wings is linked to the bird's necessity to maintain high flight capacities throughout the moult process (Rayner and Swaddle 2000). Nevertheless, the relationship between feather moult speed and bird size, morphology and flight performance has not yet been empirically examined using a rigorous, interspecific, comparative approach.

We hypothesized that the aerodynamic cost of wing moult will modulate the speed of moult and predicted a negative relationship between the species' flight performance in the form of bird flight distance range and its speed of moult. Specifically, we predicted that natural selection will favour slow wing-feather moult in species that frequently fly long distances and which, as such, may be subject to high aerodynamic costs if their wing-feather gaps are large. In species that tend to fly for short distances, no substantial aerodynamic costs are expected, even when rapid feather moult may result in large wing gaps. For these latter species, we predicted a relatively fast moult and hence a short overall moult duration. To test this hypothesis, we examined the relationship between wing-feather moult speed and an important flight performance variable (flight distance) in nineteen passerine species, using a flight distance index based on expert assessment by undertaking a phylogenetically controlled comparative analysis. We additionally tested the role of morphology and body size on moult speed using six different morphometric variables, namely wing aspect ratio, wing span, the flight feather comprising the tip of the wing (indicative of wing shape), wing area, wing loading and body mass.

Methods

We used mist nets to trap songbirds, and measured the size, wing morphology and wing flight feather moult of adult birds of both sexes. The data were collected from nineteen resident and short-distance (<500 km) migrant species with body mass of 6–80 g in different sites in Israel, mostly in the Beit-Shean Valley (32°29′N, 35°31′E), the Judean Desert (31°32′N, 35°23′E), on Mt. Hermon (33°19′N, 35°46′E), the Soreq Valley Ringing Station (31°46′N, 34°55′E), the Jerusalem Bird Observatory (31°46′N, 35°12′E) and the Eilat Ringing Station (29°34′N, 34°58′E). One of these species, the barn swallow, has two morphologically distinct subspecies occurring in the country, and the individuals examined in our work belonged to the *transitiva* subspecies which resides and moults in Israel and not to the *rustica* subspecies which breeds in Europe and moults in sub-Saharan Africa.

Moult speed quantification

We used the primary score (PS) method to describe the state of each primary feather on a scale of 0–5 (Ginn and Melville 1983), as follows: 0: a remaining old feather, 1: a missing old feather or a new feather that is found completely within its pin, 2: a new feather just emerging from its sheath up to the length of a one-third of a fully grown feather, 3: a new feather with a length between one and two-thirds of a fully grown feather, 4: a new feather

that is more than two-thirds the length of a fully grown feather and with remains of waxy sheath at its base, and 5: a new, fully developed feather with no traces of remaining waxy sheath at its base. To estimate the moult speed of each individual, we used the residual raggedness value (RRV) method (Bensch and Grahn 1993). This method estimates the size of the feather gap in the wing that is created by moult, and is also strongly and negatively correlated with moult duration (Rohwer et al. 2009). The RRV is the inverse value of PS for each of the wing's nine primary feathers (P_1–P_9), counted outward, such that when PS = 1, RRV = 4, and when PS = 2, RRV = 3, etc., but for PS = 0, RRV = 0 as well because there is no gap when the feather is in both the PS = 0 and PS = 5 stages during which old and new, fully grown feathers respectively, are found in the wing. To reliably study birds during active primary moult, we calculated the RRV only for individuals with a fully grown P_1 (PS = 5) and an old P_9 (PS = 0). We did so by summing the RRV from all of the primary feathers. This was done to avoid calculating a biased estimate of the primary moult speed in cases where the feather gap is not confined within the surface of the wing that consists of all of the primaries. This estimate is independent of bird size and morphology, controls for the stage of wing feather moult stage and allows for reliable cross-species comparison (Bensch and Grahn 1993).

Bird size and morphology measurements

To examine the impact of wing morphology and bird size on primary moult speed, we measured the wing area (the area of both wings) and the wing span of live birds in the field and used bird body mass data from our database of ringed birds in Israel during 2006–2016 (Table 1). Wing and body mass data were recorded throughout the entire year, with the exception of the feather moult period over which wing area and body mass are known to decrease to various extents (e.g., Chai 1997; Carrascal and Polo 2006). From these measurements, we calculated the mean aspect ratio (AR) and wing loading (WL) of each species. The AR was calculated as the square of the wing span (WS) divided by the wing area (WA):

$$AR = \frac{WS^2}{WA}, \tag{1}$$

and wing loading (WL) was calculated as the ratio of bird body mass (m_b) to wing area (WA):

$$WL = \frac{m_b}{WA}. \tag{2}$$

Additionally, for each individual, we determined the primary wing feather comprising the tip of the wing. The tip of the wing was measured in bird skins that did not have moulted wing feathers at the time of their collection and that were stored at the Steinhardt National Collections of Natural History, Zoological Museum, Tel-Aviv University (Table 1).

Flight distance index

We examined the role of bird flight behaviour on the speed of wing-primary moult using a bird flight distance index. We defined the flight distance index as the characteristic flight bout in the bird's life, typically representing local foraging flights, apart from migration and other long distance movements such as natal dispersal. Bird flight distance was

Table 1 Moult speed [residual raggedness value (RRV)], flight distance category (A: 1–25 m, B: 25–200 m, and C: >200 m), and six morphometric traits of nineteen passerine species (sample sizes in parentheses)

Species	Moult speed RRV	Flying distance	Aspect ratio	Wing span (m)	Tip of wing (primary feather no.)	Wing area (m^2)	Wing loading (kg m^{-2})	Body mass (kg)
Barn swallow	3.708	C	6.364	0.317	8.889	0.016	1.203	0.019
Hirundo rustica	(137)	(15)		(22)	(27)	(22)		(1408)
Rock martin	4.190	C	6.593	0.295	9.000	0.130	1.167	0.015
Hirundo fuligula	(21)	(15)		(6)	(9)	(6)		(66)
Desert lark	6.769	B	4.065	0.276	6.800	0.019	1.112	0.020
Ammomanes deserti	(26)	(15)		(12)	(15)	(12)		(50)
Common bulbul	5.733	A	3.704	0.289	5.861	0.023	1.693	0.037
Pycnonotus xanthopygos	(15)	(15)		(21)	(18)	(21)		(559)
Blackbird	5.867	B	3.987	0.354	6.868	0.031	2.600	0.080
Turdus merula	(30)	(15)		(18)	(19)	(18)		(338)
Graceful prinia	5.667	A	3.448	0.134	5.875	0.005	1.327	0.007
Prinia gracilis	(15)	(15)		(20)	(12)	(20)		(869)
Cetti's warbler	8.000	A	3.564	0.180	6.375	0.009	1.484	0.013
Cettia cetti	(18)	(15)		(20)	(12)	(20)		(2159)
Clamorous reed-warbler	6.632	A	3.939	0.239	7.441	0.015	1.648	0.023
Acrocephalus stentoreus	(19)	(15)		(21)	(17)	(21)		(338)
Sardinian warbler	7.375	A	3.817	0.169	7.000	0.007	1.387	0.010
Sylvia melanocephala	(8)	(15)		(17)	(20)	(17)		(271)
Palestine sunbird	7.400	A	3.682	0.155	6.450	0.007	0.985	0.006
Nectarinia osea	(5)	(15)		(9)	(10)	(9)		(65)
Great grey shrike	4.308	B	4.527	0.317	7.722	0.022	2.730	0.060
Lanius excubitor	(13)	(15)		(6)	(18)	(6)		(63)
Rock nuthatch	5.000	B	3.650	0.236	7.167	0.015	1.824	0.027
Sitta neumayer	(11)	(15)		(10)	(6)	(10)		(34)
House sparrow	4.864	B	4.139	0.239	7.778	0.014	2.051	0.028
Passer domesticus	(22)	(15)		(21)	(18)	(21)		(90)
Dead-sea sparrow	5.952	B	4.005	0.179	7.458	0.008	1.775	0.013
Passer moabiticus	(21)	(15)		(8)	(12)	(8)		(185)
Syrian serin	5.608	B	4.432	0.222	7.938	0.011	1.180	0.013
Serinus syriacus	(158)	(15)		(10)	(8)	(10)		(65)
Goldfinch	5.190	B	4.599	0.219	7.875	0.010	1.462	0.015
Carduelis carduelis	(21)	(15)		(21)	(16)	(21)		(81)
Linnet	4.851	B	4.725	0.226	8.147	0.011	1.602	0.017
Carduelis cannabina	(47)	(15)		(21)	(17)	(21)		(261)
Striolated bunting	7.000	B	4.046	0.219	7.813	0.012	1.068	0.012
Emberiza striolata	(29)	(15)		(11)	(8)	(11)		(102)
Rock bunting	4.941	B	3.788	0.231	6.875	0.014	1.688	0.024
Emberiza cia	(34)	(15)		(16)	(12)	(16)		(65)

classified to the following three flight distance categories: A: 1–25 m, B: 25–200 m and C: more than 200 m. To determine the flight distance index for all of the studied species, we used the Delphi technique (Riggs 1983; Blair 1996) based on the assessments of fifteen experienced birdwatchers. The selected class for each species was determined by the majority of votes (Table S1).

Statistical analysis

We used linear models to explore the effects of flight distance index, bird size and morphometrics on RRV and selected the best model based on its lowest calculated Akaike information criterion, modified for small sample sizes (AIC_c; Burnham and Anderson 2002). We utilized a one-way ANOVA to examine the effect of flight distance index (independent categorical variable) on RRV and used the Holm adjustment for post hoc comparisons (Holm 1979) between the three flight distance index categories. We applied linear regressions to test the effects of bird body mass, wing span, wing area, aspect ratio, wing tip and wing loading (independent continuous variables) on RRV and used the Bonferroni correction to control for the inflated likelihood of error when performing multiple statistical tests such that we considered the results to be significant only if $p < 0.05/28 = 1.79 \times 10^{-3}$. Because closely related species are not statistically independent and species traits are known to be phylogenetically conserved, we repeated the analysis following the independent contrasts method, which identifies evolutionarily independent comparisons (Felsenstein 1985). To account for phylogenetic non-independence, we conducted all analyses using phylogenetic generalized least square (PGLS) regression (Freckleton et al. 2002). We examined the strength of phylogenetic non-independence using the maximum likelihood value of the scaling parameter λ (Pagel 1997) implemented in the R package 'Caper' (Orme 2013). Pagel's λ is a multiplier of the off-diagonal elements of the variance–covariance matrix, which provides the best fit of the Brownian motion model to the tip data, and ranges between zero (no phylogenetic signal) and one (phylogenetic signal that depends on branch lengths as in analysis of phylogenetically-independent contrasts). We then corrected for the effects of shared ancestry using the maximum value of λ. For a comprehensive review of comparative methods and their use in ecological studies see Mason (2010). The phylogenetic tree (Fig. S1) was obtained from an analysis of global bird diversity (Jetz et al. 2012) using BirdTree.org (Rubolini et al. 2015). For an expanded account of these methods see Jetz et al. (2012, Supplementary Methods Sect. 1.1.1).

We used Pearson correlation to determine the relationship among the six morphological parameters and Spearman correlation to calculate the correlations between bird flight distance index and the six morphological parameters (Table S2). All statistical analyses were performed in R (v. 3.1.3; R Development Core Team 2014), and all tests were two-tailed, tested with a Bonferroni-corrected critical α of 1.79×10^{-3} (as specified above). Data are presented as mean values ±1 SD.

Results

We recorded primary feather moult during the post-breeding moult period (June–November, see Fig. S2), in 650 individuals of nineteen songbird species during 2012–2015 in their breeding areas. All nineteen species in this study are residents or very short

distance migrants (<500 km) that do not moult under substantial time constraints (Ginn and Melville 1983; Jenni and Winkler 1994; Barta et al. 2006). Bird wing morphology was measured in 290 individuals during 2013–2014, and average species body mass was determined from 7069 individuals that were ringed in Israel during 2006–2016 (Table 1).

Here we present the results from only single or two factors analyses because the AIC_c values for analyses >2 factors were higher (Table 2) and therefore these models were not selected. We found that the best model for explaining the variation in RRV is the model that included the categorical variable flight distance index, indicating a significant negative effect of flight distance on RRV ($p < 0.001$; Table 2). All of the post hoc comparisons between the three flight distance index categories were statistically significant (Fig. 1; $p = 0.004$ for the 0–25 m versus 25–200 m comparison, $p = 0.001$ for the 0–25 m versus

Table 2 AIC_c and phylogenetic signal (λ) of models explaining the variation in moult speed (residual raggedness value) in relation to flight distance and six morphometric variables in nineteen passerine species (all models above the line are significant with a critical α of $<1.79 \times 10^{-3}$ following a Bonferroni correction for multiple tests)

Explanatory variables in the model	R^2	F	P	λ	AIC_c
Flight distance	0.59	24.14	<0.001	0.00	48.19
Flight distance, wing loading	0.64	14.43	<0.001	0.00	48.24
Aspect ratio, wing loading	0.64	14.21	<0.001	0.00	48.43
Flight distance, wing span	0.63	13.79	<0.001	0.00	48.79
Flight distance, wing area	0.62	13.05	<0.001	0.00	49.45
Flight distance, body mass	0.62	13.00	<0.001	0.00	49.49
Flight distance, tip of wing	0.61	12.53	0.001	0.00	49.92
Flight distance, aspect ratio	0.59	11.70	0.001	0.00	50.70
Aspect ratio, body mass	0.54	9.50	0.002	0.00	52.95
Wing span, wing area	0.53	9.01	0.002	0.00	53.50
Aspect ratio	0.44	13.55	0.002	0.00	53.84
Aspect ratio, wing span	0.52	8.55	0.003	0.00	54.01
Aspect ratio, wing area	0.51	8.28	0.003	0.00	54.33
Wing span, tip of wing	0.48	7.36	0.005	0.00	55.44
Aspect ratio, tip of wing	0.44	6.39	0.009	0.00	56.67
Tip of wing, wing loading	0.44	6.16	0.010	0.00	56.98
Tip of wing, wing area	0.43	6.07	0.011	0.00	57.10
Tip of wing, body mass	0.43	6.02	0.011	0.00	57.17
Wing span	0.33	8.27	0.010	0.00	57.45
Tip of wing	0.32	7.99	0.012	0.00	57.66
Wing span, body mass	0.38	4.83	0.023	0.00	58.85
Wing span, wing loading	0.33	3.95	0.040	0.00	60.21
Wing loading	0.21	4.56	0.048	1.00	62.06
Wing area	0.10	1.92	0.183	0.00	62.94
Body mass	0.12	2.35	0.144	0.91	63.81
Wing area, body mass	0.14	1.27	0.307	1.00	64.62
Wing loading, wing area	0.22	2.30	0.133	1.00	64.63
Wing loading, body mass	0.21	2.15	0.149	1.00	64.90
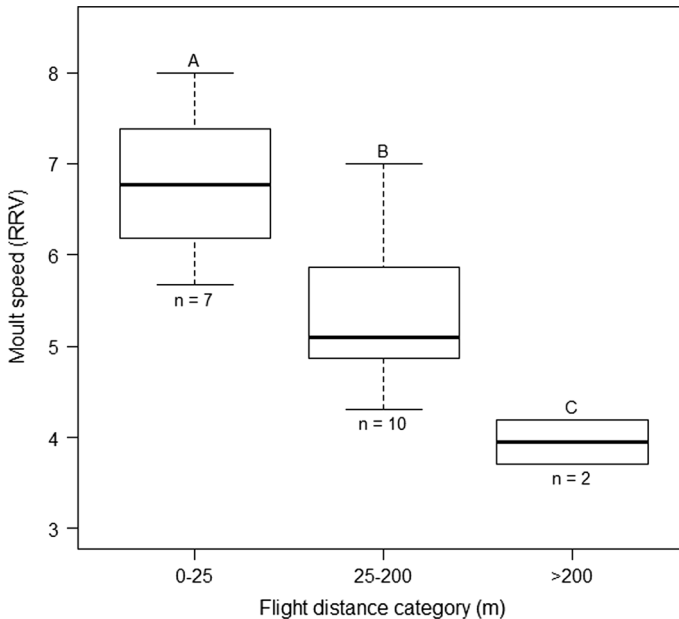
Fig. 1 The effect of flight distance on wing-feather moult speed [residual raggedness value (RRV)] in nineteen passerine species (One-way ANOVA; df = 17, F = 24.14, $R^2 = 0.59$, $p < 0.001$). The *boxplots* display the minimum, first and third quartiles, median and maximum values of each category. There was no phylogenetic signal in the data (maximum likelihood value of $\lambda = 0$). *Different letters above the bars* indicate a statistically significant difference ($p < 0.05$ by the Holm multiple comparisons test)

>200 m comparison, and $p = 0.035$ for the 25–200 m versus >200 m comparison). Species characterized by long flight distance were found to moult slowly, and hence, their wing-feather gap was relatively small (Fig. 1). The results also indicate that there was no phylogenetic signal in the data (maximum likelihood value of $\lambda = 0$) (see Fig. S1).

There is not a single morphometric variable that significantly affected the RRV (Table 2 and Fig. 2, $p > 1.79 \times 10^{-3}$ which is the critical significance level following a Bonferroni correction) when it comprised the only explanatory variable in a statistical model, as opposed to the flight distance index (see Table 2). A high phylogenetic signal (maximum likelihood value of $\lambda > 0.9$) was found for wing loading, body mass and wing area (Table 2). We found a significant positive correlation (see Table S2 and Fig. 3) between flight distance index and aspect ratio ($p < 0.001$) and tip of wing ($p < 0.001$), but not for wing span ($p = 0.050$), wing area ($p = 0.286$), wing loading ($p = 0.590$) and body mass ($p = 0.303$).

Discussion

While previous studies that dealt with feather moult and flight mostly tackled the effects of moult on flight performance (for example, Chai and Dudley 1999; Williams and Swaddle 2003; Lind and Jakobsson 2001), the present study investigated the role of bird morphological traits and an important flight performance attribute (flight distance) in shaping the wing's feather moult speed which is an annual routine process with implications on bird
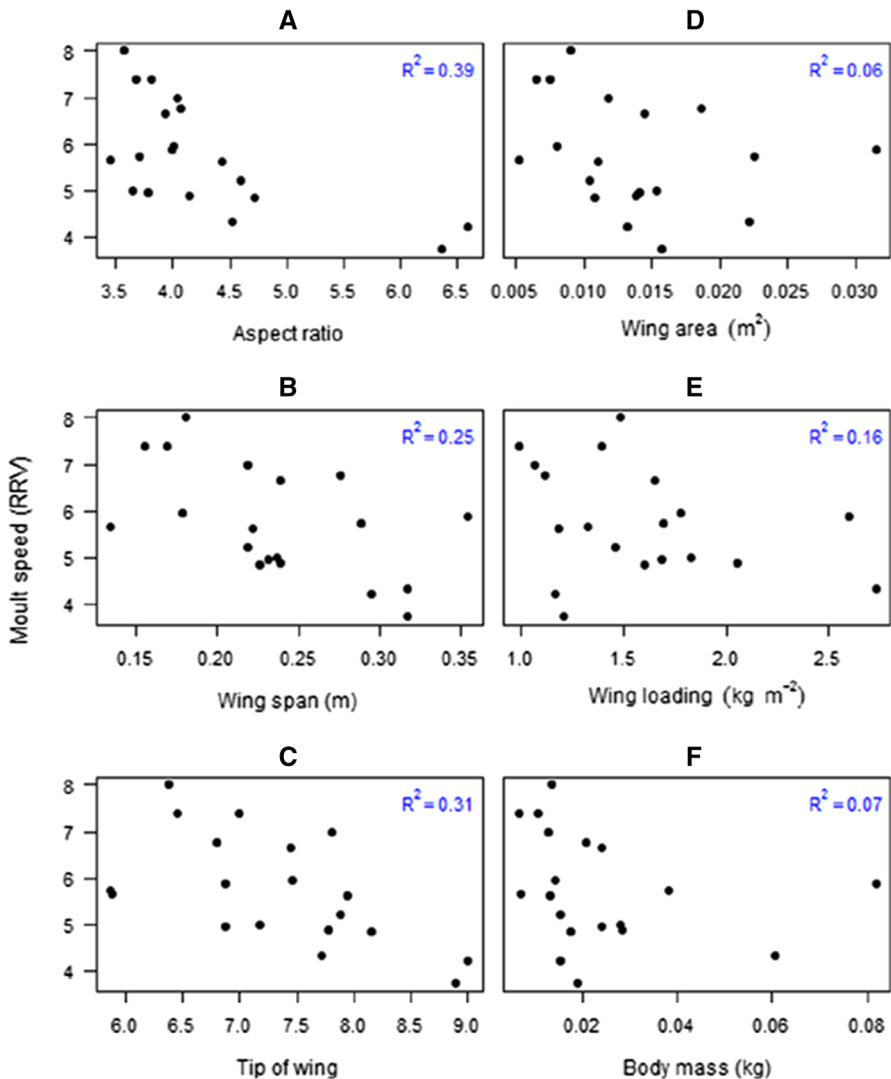
Fig. 2 The effects of bird size and wing morphology on moult speed [residual raggedness value (RRV)] in nineteen passerine species. The morphometric variables included in the analysis are: **a** aspect ratio, **b** wing span, **c** tip of the wing, **d** wing area, **e** wing loading and **f** body mass

behavior and the scheduling of annual routine events, as well as on bird flight aerodynamics and energetics. In our analyses, we used the flight distance of the bird to describe a pertinent aspect of its flight performance. This index was estimated based on local foraging movements, rather than migratory and other long distance flights, as the set of species examined in the present analysis is made of resident and short-distance migrants. As such, migration, if it exists at all in their annual routine, is likely not a substantial process for these species (Barta et al. 2006). This is in contrast to other studies considering bird feather moult of long-distance migrants for which the migration journey comprises a critical event
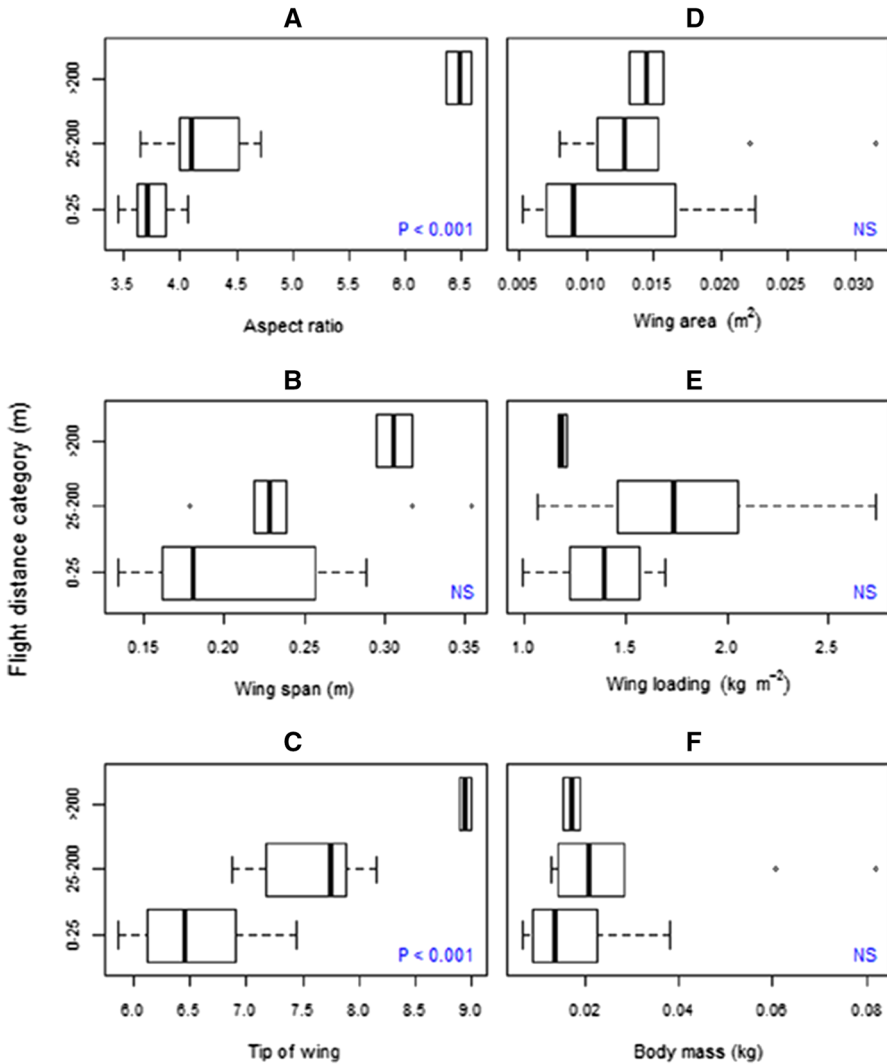
Fig. 3 The association between flight distance category and the morphometric variable (**a** aspect ratio, **b** wing span, **c** tip of wing, **d** wing area, **e** wing loading and **f** body mass) in nineteen songbird species

in the annual routine (e.g., Lindström et al. 1994; de la Hera et al. 2009). While our study used expert assessments to determine bird flight distances, a different measure of bird flight performance, which was used by Moreno and Carrascal (1993), is the time a bird spent flying. While various flight properties can be further explored, flight distance and duration are most likely correlated because as a bird flies further, its flight duration monotonically increases. To quantify the speed of wing feather moult, we used the RRV method (Bensch and Grahn 1993) that is based on the size of the feather gap in the wing that is created during moult. This measure is positively correlated with the number of feathers that have been shed simultaneously and it is negatively correlated with moult duration because as

speed is higher, more feathers are shed simultaneously and the overall duration of moult decreases (Rohwer et al. 2009; Rohwer and Rohwer 2013).

Our results may indicate that bird flight distance during routine foraging flights is an important predictor of the speed of moult in songbirds. We suggest that the speed of wing-feather moult is modulated by the aerodynamic costs of wing-feather gaps. Fast wing-feather moult, during which large feather gaps are created, induces high aerodynamic costs for birds that fly long distances. Consequently, selection against fast wing-feather moult likely took place in species that fly long distances, whereas aerodynamic costs are likely meagre in short distance flyers, permitting fast and extensive wing-feather moult. Rapidly moulting species are characterized by low aspect ratio, body mass and wing loading and their longest primary is closer to mid wing compared with species that moult slowly (Fig. 2). Slow moulting species are characterized by a high aspect ratio and the tip of the wing located near the leading edge, features associated with superior flight capacities (Pennycuick 1978). Our analysis suggests a major role of flight behavior over bird size and wing morphology, such that short distance flyers can afford having large pace of moult feathers gaps to rapidly complete their moult, while a slow inducing small wing gaps is evident in species that commonly fly over long distance, to avoid excessive aerodynamic costs.

We found that in swallows (*Hirundo rustica* and *Hirundo fuligula*), the speed of wing-feather moult was extremely slow. These birds spend most of their day in flight and trap insects on the wing. Maintaining high flight capabilities is therefore essential for them, and they apparently traded off rapid moult speed for flight performance. We note that these species are characterized by pointed wings (tip of the wing close to the leading edge, *H. rustica* = 8.89 and *H. fuligula* = 9.00 versus an average of 7.15 in other species), as well as very high aspect ratio (6.36 and 6.59, respectively, versus an average of 4.01 in the other species). Moult duration of *H. rustica* and *Riparia riparia*, another species with similar flight habits and morphometry, is 150 and 135 days, respectively, which are the longest among all European passerines (Ginn and Melville 1983).

Bird body mass and feather moult duration has been found to be positively related (de la Hera et al. 2009). This study proposed that species with high body mass moult relatively slowly compared with low body mass species. This finding is explained by the larger amount of keratin required for feather synthesis in large species. Our results, nonetheless, suggest that wing span better predicts wing-feather moult speed than body mass (Table 2; Fig. 2). This result, however, is compatible with the explanation regarding the amount of keratin required during moult because wing span is likely strongly correlated with the quantity of keratin required during moult, possibly more than with regard to bird body mass.

An important implication of extended moult duration is the requirement for high nutrient availability over a long period of time. It has been found that species over-wintering in temperate zones cannot moult during the winter due to the scarcity of food resources (Ginn and Melville 1983; Jenni and Winkler 1994). These species (e.g. *Calcarius lapponicus* and *Plectrophenax nivalis*) typically moult quickly after the end of their breeding period and before winter, and may completely lose their flight ability during their short moulting period (Haukioja 1971; Green and Summers 1975; Ginn and Melville 1983). This rather extreme moult strategy is obviously unsuitable for other species that must feed during flight and must maintain high flight capacities even during moult. For example, the European populations of all swallow species perform their complete moult in their African over-wintering quarters, where they are seemingly able to obtain enough sustenance for their moult (Ginn and Melville 1983; Jenni and Winkler 1994).

The implications of morphological wing deficits are multitudinous and may include impaired biomechanical performance and increased metabolism, bearing direct fitness consequences due to reduced foraging capabilities and increased daily metabolic costs (Tucker 1991; Hedenström and Sunada 1999; Hedenström 2003; Hambly et al. 2004; Carrascal and Polo 2006). Our work focused on a seldom studied aspect of bird feather moult, related to the evolution of annual routine processes and how they may be shaped by aerodynamic considerations. Our findings highlight the importance of linking animal form, function and fitness (Arnold 1983) by scrutinizing the factors affecting bird wing-feather moult speed. We propose that moult-related aerodynamic costs may be of lesser importance for species that fly for only short distances, as their flights may not bear substantial aerodynamic costs throughout their daily routines. Consequently, this work demonstrates the importance of biomechanical considerations in the evolution of annual routines, linking movement properties, morphology, and the pace of annual routine processes. As such, it exemplifies the importance of integrating ecological knowledge to more fully understand evolutionary processes (Schoener 2011).

Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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