Biological Journal of the Linnean Society, 2018, **XX**, 1–12. With 4 figures.

Life-history trade-offs result in evolutionary optimization of feather quality

YOSEF KIAT*, and NIR SAPIR

Animal Flight Laboratory, Department of Evolutionary and Environmental Biology and the Institute of Evolution, University of Haifa, Haifa 3498838, Israel

Received 16 July 2018; revised 14 August 2018; accepted for publication 19 August 2018

Resource allocation for body tissues is under strong selection pressures because allocating too many resources may waste both energy and essential nutrients, and allocating too few resources can result in functional disability. We thus hypothesized that feather quality is the outcome of life-history trade-offs that determine feather resource allocation and that these trade-offs are determined by species-specific annual routine and life-history attributes. We accordingly predicted that certain species will develop a more durable plumage when this plumage needs to function over a longer period as compared with species that replace their feathers soon after their creation. We tested this prediction using plumage quality indices and moult timing data of nest-grown juvenile feathers from 49 passerine species. By using feather length, mass and melanization measurements, we found that the lifespan of nest-grown feathers until projected replacement during the next moult is a strong predictor of feather quality. This was found in both an inter-specific analysis and when comparing different feathers of an individual. We suggest that the maintenance of functional feathers throughout the lifespan of a bird while avoiding excessive deposition of resources in feathers that are replaced soon after their growth represents an evolutionary process of resource allocation optimization.

ADDITIONAL KEYWORDS: annual routine processes – feather melanization – feather growth – feather structural durability – post-juvenile moult – resource allocation.

INTRODUCTION

The evolution of all organisms involves the optimization of resource allocation for different purposes such as growth and reproduction (Kozłowski & Wiegert, 1986; Watt, 1986; Stearns, 1992) with implications for individual development and long-term fitness (Monaghan, 2003). In addition, resource allocation for different organs and tissues of the body is under natural selection such that this investment reflects the importance of this tissue or organ for the organism's fitness (Johnson, 1985; Perrin, 1992; Perrin & Sibly, 1993). Allocating too many resources to a certain tissue or organ may waste both energy and essential nutrients that may be better utilized through investment in other tissues, whereas allocating too few resources may result in functional disability of specific tissues and organs. Consequently, current resource allocation patterns probably represent trade-offs between energy and nutrient conservation and tissue functionality that are the outcome of an evolutionary optimization process. Yet, this theoretically sound idea has not been rigorously tested (Glazier, 2009), and only anecdotal findings supporting it have been described (e.g. the regression of the wings in flightless birds and the disappearance of the eyes in animals that are found in total darkness within caves where there is no fitness advantage for having developed wings and eyes, respectively).

During juvenile development, the individual allocates resources to build its organs and tissues, and thus this process is critically important as its consequences may carry over for a long period of time, up to the entire lifespan of the individual (Silva *et al.*, 2007; Krause *et al.*, 2009). Nutritional deficits during this crucial stage may consequently result in functional disabilities. For example, food-deprived birds grow poor quality feathers (Murphy *et al.*, 1988) that may wear quickly after growth, hampering flight performance. The feathers of most juvenile passerines are grown before fledging while they are still in their nests, and

---

*Corresponding author. E-mail: yosefkiat@gmail.com

suitable resource allocation during this period may ensure that the feathers will function properly to insulate the birds and, upon fledging, to enable flight.

In addition to resource allocation by juveniles, breeding birds may have high motivation to reduce the cost of reproduction, including food provisioning to their young (Pianka, 1976) because reproduction constitutes one of the most energy-demanding processes during the annual cycle of the organism (Randolph *et al.*, 1977; Oftedal & Gittleman, 1989; Obeso, 2002). Parental investment reaches its peak at the post-hatching nest attendance period, during which juvenile development is rapid and requires high rates of food provisioning (Ricklefs, 1974; Bryant, 1979; Hails & Bryant, 1979; Drent & Daan, 1980). In light of the huge parental investment which may bear long-term consequences on both the nestlings and their parents (Conrad & Robertson, 1992; Sanz & Tinbergen, 1999), the evolution of resource allocation for feather growth in juvenile birds may be adjusted to the functional requirements of their plumage (Podlaszczuk *et al.*, 2016). Specifically, the allotment of resources that are required during juvenile plumage growth in the nest may be optimized by natural selection according to the duration for which a feather is required to function after the bird has departed from the nest.

Feathers become abraded and worn over time, and their renewal is therefore necessary to ensure their functionality for insulating the body, maintaining specific patterns of camouflage or ornamental display, and attaining aerodynamic capacities for flight performance and efficiency (Ginn & Melville, 1983; Jenni & Winkler, 1994; Swaddle *et al.*, 1996; Bridge, 2008). Consequently, all adult passerines moult their entire plumage at least once per year, presumably because a longer time interval between consecutive moults is disadvantageous. The timing of feather moult of juvenile passerines is known to vary greatly between different species. In general, juvenile passerines may undertake their first complete moult during either of the following three optional moult cycles: (1) post-juvenile moult (1–3 months after fledging), (2) pre-breeding moult (5–8 months after fledging) or (3) the first post-breeding moult (12–14 months after fledging). Some species undertake another partial moult during the first year of their life. For example, juveniles of species for which their first complete moult is post-breeding, 12–14 months after fledging, may perform a partial post-juvenile moult, a partial pre-breeding moult or both (Ginn & Melville, 1983; Jenni & Winkler, 1994; Newton, 2009; Kiat & Izhaki, 2016).

Moult timing may affect other important properties of this process such as moult duration and extent because these processes are limited by the time available for their completion. Limited moult duration may have severe consequences for feather quality. For example, feathers that grew over a short period were shorter (Hall & Fransson, 2000), showed more fault bars (Vágási *et al.*, 2012) and exhibited deterioration of structural and pigment-based colours compared to feathers that grew over a longer period (Dawson *et al.*, 2000; Serra *et al.*, 2007; Griggio *et al.*, 2009). This suggests an overall negative correlation between feather growth rate and quality, which in turn may affect reproductive success due to both low attractiveness and worse flight performance (Nilsson & Svensson, 1996). Notably, the time available for moult to take place may also affect the extent of moult (Ginn & Melville, 1983; Gargallo & Clarabuch, 1995; Kiat & Izhaki, 2016). When time is limited, moult extent may be restricted, possibly incurring costs related to the deteriorated performance of abraded feathers that have not been replaced (Bridge, 2008). In general, while extensive moult may improve plumage performance due to better functionality of fresh feathers, it may also involve high energetic costs (Walsberg, 1983; Jenni & Winkler, 1994). One may consequently conclude that species-specific life-history trade-offs affect the evolution of feather moult and determine various properties of the moult process (Jenni & Winkler, 1994; Svensson & Hedenström, 1999; Kiat & Sapir, 2017). An important property of the moult process is the quality of the feathers that are generated during this process. In the present study we specifically focus on juvenile plumage quality and how it may be affected by moult timing.

The plumage of juvenile passerines that is grown before fledging differs from that of adults in two ways: (1) it is usually weaker and looser in texture, and (2) in many species, its coloration is different from that of adults (Newton, 1966; Fogden, 1972; Jenni & Winkler, 1994; Butler *et al.*, 2008; Kiat & Izhaki, 2016). One to 3 months after fledging, most juvenile passerines undertake their post-juvenile moult that is of variable extent, ranging from only a few body feathers in some species to as much as the whole plumage in other species (Stresemann & Stresemann, 1966; Ginn & Melville, 1983; Jenni & Winkler, 1994). Thus, the extent of this moult varies substantially between different species. A notable consequence of a partial post-juvenile moult is the wide variation in the lifespan of different feathers between different parts of the plumage of the same individual.

To this end, we hypothesize that the quality of feathers grown before fledging may represent a resource allocation trade-off between tissue functionality and energy and nutrient conservation, to optimize bird fitness. Species that replace their feathers shortly after fledging are expected to develop poor quality plumage in the nest whereas those that moult a long time after leaving their nest are expected to grow durable feathers that will serve them for an extended duration. We consequently predict an inter-specific positive relationship between the lifespan of a species' nest-grown primaries and rectrices, determined by the timing of the first complete moult, and the quality of that species' nest-grown plumage. In addition, we predict a within-individual negative relationship between the moulting probability of a particular feather during the bird's post-juvenile moult that takes place in the breeding grounds (1–3 months after fledging) and that feather's durability. This prediction suggests that feathers that are likely to be replaced during this period will be of poorer quality than those that are likely to be retained for a longer time period. To test these two predictions we used a comparative framework by studying passerines from the Western Palearctic, combining measurements of moult timing with three informative measures of feather quality.

MATERIAL AND METHODS

Estimation of moult timing and extent

We used data from published literature to estimate the timing of the first complete moult for each study species (Ginn & Melville, 1983; Svensson, 1992; Cramp & Perrins, 1994; Jenni & Winkler, 1994). The timing of this complete moult falls into three categories (Fig. 1): (1) post-juvenile moult (1–3 months after fledging), (2) pre-breeding moult (5–8 months after fledging) and (3) first post-breeding moult (12–14 months after fledging), which is fixed for each of our study species. To quantify the probability of moult of specific feathers in species characterized by partial post-juvenile moult (a moult that takes place 1–3 months after fledging) we used a large database of passerine moult from individuals trapped by mist-nets from 2011 to 2015 in different sites in Israel, mostly in the Beit-Shean Valley (32°29′N, 35°31′E), Judean Desert (31°32′N, 35°23′E), Mt Hermon (33°19′N, 35°46′E), Soreq Valley (31°46′N, 34°55′E) and Jerusalem (31°46′N, 35°12′E). Additional data were obtained from bird specimens stored at the Steinhardt National Collections of Natural History at the Zoological Museum of Tel-Aviv University, Israel, and the Natural History Museum at Tring, UK. Using a score of 0 (non-moulted feather) or 1 (moulted feather) for six specific wing and tail feathers, we calculated moult probability for each feather by dividing the number of individuals whose specific feather was replaced during the post-juvenile moult by the total number of individuals from each species that were examined. These measurements were made only for individuals in which the moult process has already ended. The following feathers were examined: (1) fourth greater covert (GC_4), (2) first primary covert (PC_1), (3) middle tertial (T_8), (4) fifth secondary (S_5), (5) fourth primary (P_4) and (6) fourth rectrix (R_4) (Fig. 2). These feathers represent six important feather tracts among passerines that have a constant number of feathers. Selection of these specific feathers from each feather tract was due to their highly variable moult probability during the post-juvenile moult.

Feather quality measures

We quantitatively characterized the nest-grown feathers in relation to the feathers of the post-juvenile plumage (adult plumage) by defining ΔP_q, as follows:

$$\Delta \mathrm{P}_\mathrm{q} = \frac{\left(AP_q - JP_q\right)}{AP_q} \qquad (1)$$

where AP_q is a quality measure of the feathers following the first complete moult of these feathers (1–14 months after fledging, depending on species; see below), and JP_q is a quality measure of the nest-grown, juvenile primaries and rectrices. We applied the same method to examine the effect of the moulting probability of a particular wing and tail feather during the bird's partial post-juvenile moult (1–3 months after fledging) and of that feather's quality.

We used three different measures to estimate nest-grown plumage quality: (1) the melanization of the primaries, (2) feather length and (3) feather mass (standardized by feather length). The first calculated feather quality measure involves a measurement of feather melanization of the primary feathers of bird skins obtained from the Steinhardt National Collections of Natural History, Zoological Museum, Tel Aviv University. Because melanic feather keratin is composed of twisted β-sheet keratin rather than the α-helix keratin found in non-melanic keratin, melanic keratin is more capable of resisting abrasive wear than non-melanic keratin (Bonser, 1995, 1996). Consequently, higher feather melanin content provides better durability and hence reduced wear over time but may nonetheless incur higher metabolic costs during feather synthesis (Burtt, 1986). We used spectrometry (X-Rite i1Pro spectrometer, range 380–730 nm) to estimate a proxy of feather melanin content (Vortman *et al.*, 2011) by measuring feather colour at three random points on the primaries. These measurements were carried out directly on the folded wing of the bird specimen. We then converted the wavelength output of the spectrometer to sRGB (red–green–blue) colour space using Bruce Justin Lindbloom's spectral calculator spreadsheet (see http://www.brucelindbloom.com/). Because the primary feathers' chromatic elements are characterized

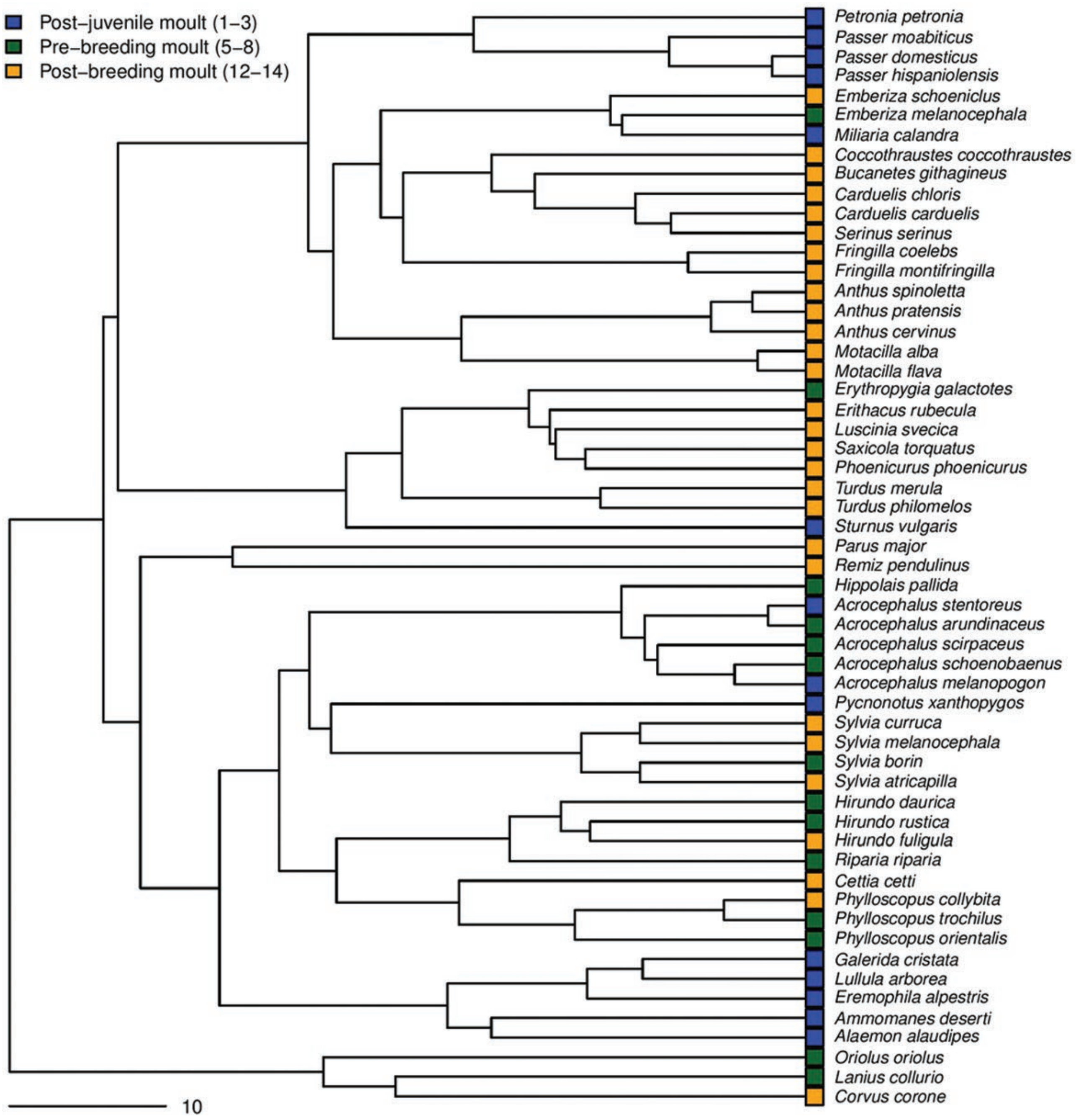

Figure 1. Phylogenetic tree for the 49 species examined in the study, based on Jetz *et al.* (2012), with data obtained from BirdTree.org (Rubolini *et al.*, 2015). The colours of the tips indicate the categories of the timing of the juvenile's first complete moult. The number of months over which the birds retained their juvenile plumage in each category is provided in parentheses. The scale (bottom left) represents 10 million years.

mainly by the RG (red–green) colour space (Kiat & Izhaki, 2016), we used the average value of these colours. Although melanin is biochemically highly stable, there are detectable differences in melanin-based colorations between museum specimens and wild birds that are mainly related to the collection time (Riley, 1997; Doucet & Hill, 2009). As expected, in our sample there is an effect of the year on bird wing colour measurements (multiple-species linear model, independent variable: year of collection, random variable: species; $P < 0.001$, slope = −9.86e-04 ± 2.12e-04, $R^2 = 0.067$; $N = 305$ individuals). Consequently, we corrected our

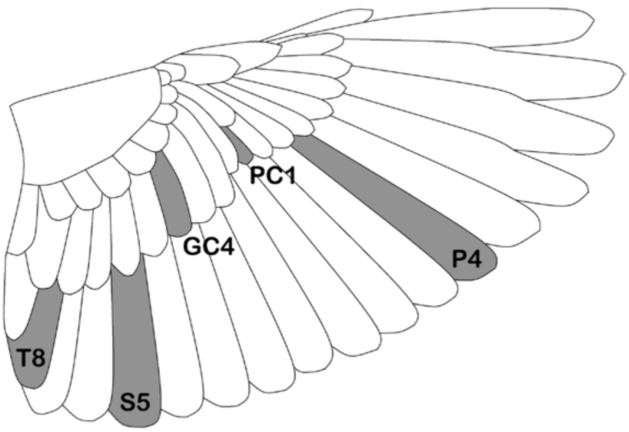

Figure 2. The wing feathers used for testing the effects of moult probability on juvenile plumage quality during the post-juvenile moult: (1) fourth greater covert (GC_4), (2) first primary covert (PC_1), (3) middle tertial (T_8), (4) fifth secondary (S_5), (5) fourth primary (P_4) and (6) fourth rectrix (R_4, not included in the figure).

data before the analysis by subtracting the slope value (−9.86e-04) multiplied by the number of years that passed from the year of collection to the latest year of feather collection in our sample (2013), as follows:

$$\mathit{Corrected\,Value} = \mathit{Calculated\,Value} - (9.86 \times 10^{-4}) \times (2013 - \mathit{Year\,of\,collection}), \text{ for each specimen.}$$

The second calculated feather quality measure consists of the wing chord length and tail length, measured using a ruler with an accuracy of 0.5 mm. We compared data from juvenile wings and tails that grew in the nest as well as those of individuals that had completed their post-juvenile moult and those of adult birds. This comparison was done using a large dataset of biometric data from the Israel Bird Ringing Center (IBRC) of birds that were ringed and measured in Israel during 1980–2015. Although wing chord is measured from the carpal joint to the tip of the longest primary feather and, as such, also includes non-feather tissues, the main component, and the main source of variation, of this measurement is the length of the longest primary feather. Similarly, tail length measurement is primarily related to the length of the longest rectrix (Svensson, 1992).

In addition, we measured the length of six feathers from six different feather tracts (GC_4, PC_1, T_8, S_5, P_4 and R_4; Fig. 2) that were collected from 16 individuals (eight juveniles before their post-juvenile moult and eight adults after their post-breeding moulting period) per species, in a total of 16 passerines species. We collected, measured and weighed a total of 1536 feathers. The third calculated feather quality measure is length-standardized feather mass of the six wing and tail feathers mentioned above (GC_4, PC_1, T_8, S_5, P_4 and R_4). We weighed each feather using an analytical digital balance (Ohaus Pioneer PA-64) with an accuracy of 0.1 mg and measured the length of each feather using a ruler with a resolution of 0.5 mm. We standardized feather mass by dividing it by feather length. It has been shown that higher length-standardized feather mass values indicate a wider rachis and a greater density of barbs (De La Hera *et al.*, 2010) and, consequently, higher feather mass values are likely to reflect higher feather bending stiffness and resistance to wear (Dawson *et al.*, 2000; Muñoz *et al.*, 2011). Feather collection was performed under a permit from the Israel Nature and Parks Authority (NPA permit 2015/40723).

STATISTICAL ANALYSIS

Because species traits are known to be phylogenetically conserved and thus data from closely related species are not statistically independent, we performed the analysis to account for phylogenetic non-independence (Felsenstein, 1985). We therefore 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). Using PGLS regression we explored the effects of the timing of the birds' first complete moult (independent categorical variable of three categories: post-juvenile moult, pre-breeding moult and first post-breeding moult) on the ΔP_q value that we quantified using measurements from primary feather melanization and wing and tail feather length (dependent variables). In addition, we used PGLS regression to explore the effect of the probability of moulting a certain feather during the post-juvenile moult (independent variable) on the ΔP_q values of feather length and mass (dependent variables). The phylogenetic tree (Fig. 1) was obtained from an analysis of global bird diversity (Jetz *et al.*, 2012) using 10 000 trees gained from BirdTree.org (Rubolini *et al.*, 2015). The consensus tree was built using BEAST (v.1.8.4). The analyses (two-tailed, critical $\alpha = 0.05$) were performed using R (v.3.2.2) and SPSS (v.22).

RESULTS

EFFECTS OF THE TIMING OF JUVENILE COMPLETE MOULT ON FEATHER QUALITY

We obtained data from 49 passerine species regarding the timing of the first complete moult since fledging in juveniles. In addition, we measured the melanization of primary feathers in 305 museum skins belonging to 26 species. We used wing length data from 18 175 individuals belonging to 42 species and tail length data from 12 768 individuals belonging to 29 species (Table S1).

Using PGLS regressions we found that all juvenile quality measures of nest-grown primaries and rectrices were significantly related to the timing of the juvenile's first complete moult in these species (post-juvenile, pre-breeding or post-breeding). This was found when examining the primary feather melanization ($F_{2,23} = 31.47$, $R^2 = 0.732$, $P < 0.001$, $N = 26$ species; Fig. 3A), wing length ($F_{2,39} = 37.33$, $R^2 = 0.657$, $P < 0.001$, $N = 42$ species; Fig. 3B) and tail length ($F_{2,26} = 38.98$, $R^2 = 0.750$, $P < 0.001$, $N = 29$ species; Fig. 3C). Overall, a late complete moult of juvenile birds was a good predictor for high-quality nest-grown primaries and rectrices, while a relatively early complete moult was associated with lower quality feathers grown prior to fledging. The Pearson correlation coefficient (r) between the ΔP_q values that were calculated from feather melanization and wing length was 0.71 ($P < 0.01$, $N = 19$ species), and that between ΔP_q values calculated from feather melanization and tail length was 0.83 ($P < 0.001$, $N = 17$ species). We also found a significant correlation between ΔP_q values calculated from wing and tail lengths ($r = 0.83$, $P < 0.001$, $N = 29$ species).

EFFECTS OF MOULT LIKELIHOOD OF SPECIFIC FEATHERS DURING POST-JUVENILE MOULT ON FEATHER QUALITY

We explored the effect of the calculated moult probabilities on the ΔP_q value of a specific feather 1–3 months post-fledging using moult data from 3120 individuals from the 16 tested species (Supporting Information, Table S2).

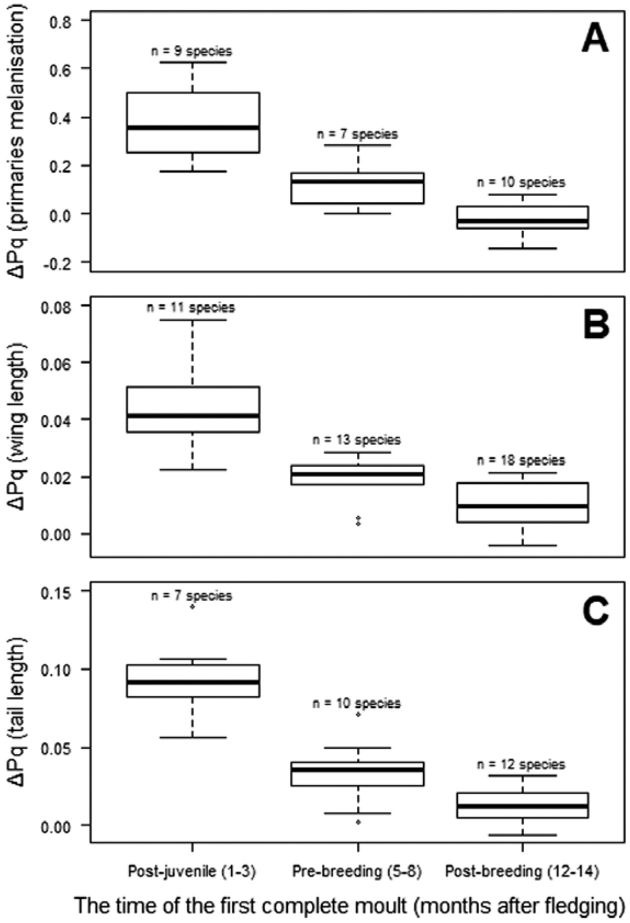

Figure 3. Effects of the timing of the first complete moult on the quality of nest-grown juvenile feathers based on feather melanization and length. ΔP_q is a quality measure of feathers that grew in the nest in relation to those of adult birds of the same species. A, primary feather melanization in 26 passerine species. B, wing chord length in 42 passerine species. C, tail length in 29 passerine species. The boxplots display the 5th percentile, 1st quartile, median, 3rd quartile and 95th percentile of the data in each category. The results of statistical analyses are reported in Table 1.

Using PGLS regressions, we found that feather moult likelihood 1–3 months post-fledging predicts length-standardized masses of each of the six examined feathers. For three out of the six feathers (GC_4, S_5 and R_4, but not PC_1, T_8 or P_4), the same was also found for feather length (Table 1). Therefore, the feathers that grew in the nest are of higher quality when their probability of renewal soon after fledging is low (Fig. 4). In specific feathers, low renewal probabilities 1–3 months post-fledging were associated with longer feathers. In some species, nest-grown feathers were even more durable (higher length-standardized mass) than those of adult birds (i.e. their ΔP_q values were negative, see Table S2), especially for bird species that carry out their first complete moult only 12–14 months after departing from the nest, following their first breeding season (e.g. *Motacilla flava* and *Parus major*).

DISCUSSION

We studied how the properties of juvenile plumage of different species may expose the trade-offs involved in the process of resource allocation by exploring how changes in the duration for which the feathers need to function may affect the quality of the plumage when grown. Using three different measures of feather quality (melanization, length and mass), we found that projected juvenile feather lifespan is a strong predictor of its quality. In species undertaking a complete post-juvenile moult soon after fledgling, the quality of the plumage grown in the nest was poorer than that of species that moulted their feathers during the winter (first pre-breeding moult) or those that replaced their feathers only after their first breeding season (first post-breeding moult), 12–14 months after departing from the nest. In addition, we found that the quality of a specific feather grown in the nest is related to the probability of that feather being replaced during the post-juvenile moult such that feathers that are seldom replaced during this period are of higher quality, probably because they need to function over a long period of time. The positive and significant correlation between ΔP_q values that were calculated from feather melanization and length, as well as values that were calculated from wing and tail fathers (lengths) may indicate that quality measures are correlated for different traits (length and melanization) and between different parts of the body, suggesting that they reliably reflect different aspects of feather quality in the different species. These results may imply that species-specific resource allocation for feather growth prior to fledging probably evolved in relation to the expected duration over which the plumage needs to function, as reflected in the timing of complete feather moult in these species.

In contrast to studies suggesting that plumage quality influences the extent of feather moult (Fogden, 1972; Guallar & Figuerola, 2016), we suggest that projected moult timing and extent affect the quality of juvenile wing and tail feathers based on evolutionary inferences regarding resource allocation. Our findings indicate that optimization of resource allocation through natural selection results in higher allocation of resources for feathers that need to function over a longer period of time (see also Howell, 2001, 2010). In species in which the feathers are replaced relatively quickly after they have been produced, the quality of nest-grown feathers is reduced, presumably to save valuable resources in the form of nutrients and energy.

Complete post-juvenile moult on the breeding grounds is probably an optimal moult strategy in habitats with favourable environmental conditions where birds may have a long time to complete their moult after the end of the breeding season and before the beginning of autumn migration. Indeed, complete post-juvenile moult has been described in species that inhabit some sub-tropical and tropical areas (Fogden, 1972; Kiat & Izhaki, 2016). In our study, species that are characterized by durable nest-grown juvenile plumage and relatively late first complete moult (12–14 months after fledging) are mainly residents or short-distance migrants that usually breed in northern latitudes (e.g. *Fringilla* sp., *Carduelis* sp., *Motacilla alba* and *Parus major*). Species that are characterized by poorer nest-grown juvenile plumage and earlier first complete moult are mainly long-distance migrants (e.g. *Emberiza melanocephala* and *Acrocephalus scirpaceus*) or residents which breed in relative southern latitudes (e.g. *Pycnonotus xanthopygos* and *Ammomanes deserti*). We suggest that the geographical distribution of the breeding range and the migration distance of different species, which affect the time available for the moult process (Noskov & Rymkevich, 2010; Kiat & Sapir, 2017), may affect the optimization of resource allocation throughout the development period of nestlings.

Relatively longer-distance migrants and higher-latitude breeders that are challenged by time constraints consequently either perform a less extensive moult of their juvenile plumage soon after fledgling (Ginn & Melville, 1983; Jenni & Winkler, 1994; Gargallo & Clarabuch, 1995; Kiat & Sapir, 2017) or avoid renewing wing and tail feathers in their first year of life (Jenni & Winkler, 1994; Kiat & Izhaki, 2016). Consequently, these species developed alternative pathways to maintain functional plumage, and we propose that the growth of higher quality plumage in the nest constitutes an important mechanism to maintain functional plumage under high

Table 1. Statistical results of PGLS regressions that tested the effects of the time of the first complete moult and moult probability of specific feathers during post-juvenile moult on ΔP_q, quantified by feather melanization, mass and length as feather quality measures; significant results are given in bold font

Dependent variable	Independent variable		N (species)	Slope ± SE	t	F_{df}	R^2	λ	P		Figure
ΔP_q (primary feather melanization)	Time of first complete moult	Post-juvenile	9	0.371 ± 0.045	8.293	$31.47_{2,23}$	0.732	0.263	**<0.001**	**<0.001**	3A
		Pre-breeding	7	0.123 ± 0.045	2.720				**0.012**		
		Post-breeding	10	0.043 ± 0.044	−0.993				0.331		
ΔP_q (wing length)	Time of first complete moult	Post-juvenile	11	0.044 ± 0.003	13.240	$37.33_{2,39}$	0.657	0.054	**<0.001**	**<0.001**	3B
		Pre-breeding	13	0.018 ± 0.003	5.716				**<0.001**		
		Post-breeding	18	0.010 ± 0.003	3.721				**<0.001**		
ΔP_q (tail length)	Time of first complete moult	Post-juvenile	7	0.089 ± 0.011	8.140	$38.98_{2,26}$	0.750	0.809	**<0.001**	**<0.001**	3C
		Pre-breeding	10	0.028 ± 0.010	2.787				**0.010**		
		Post-breeding	12	0.008 ± 0.011	0.749				0.461		
ΔP_q (P_4 mass)	P_4 moult probability		16	4.186 ± 0.583	7.174	$51.47_{1,14}$	0.786	0.000		**<0.001**	4A
ΔP_q (S_5 mass)	S_5 moult probability			4.083 ± 0.859	4.751	$22.57_{1,14}$	0.617	0.000		**<0.001**	
ΔP_q (T_8 mass)	T_8 moult probability			2.865 ± 0.928	3.089	$9.54_{1,14}$	0.405	0.000		**0.008**	
ΔP_q (GC_4 mass)	GC_4 moult probability			2.726 ± 0.768	3.550	$12.60_{1,14}$	0.474	0.000		**0.003**	
ΔP_q (PC_1 mass)	PC_1 moult probability			3.181 ± 1.148	2.771	$7.68_{1,14}$	0.354	0.000		**0.015**	
ΔP_q (R_4 mass)	R_4 moult probability			4.242 ± 0.835	5.079	$25.80_{1,14}$	0.648	0.000		**<0.001**	
ΔP_q (P_4 length)	P_4 moult probability		16	5.933 ± 3.741	1.586	$2.52_{1,14}$	0.152	0.000		0.135	4B
ΔP_q (S_5 length)	S_5 moult probability			11.202 ± 4.199	2.668	$7.12_{1,14}$	0.337	0.000		**0.018**	
ΔP_q (T_8 length)	T_8 moult probability			2.778 ± 1.763	1.575	$2.48_{1,14}$	0.151	0.000		0.138	
ΔP_q (GC_4 length)	GC_4 moult probability			8.141 ± 1.660	4.903	$24.04_{1,14}$	0.632	0.992		**<0.001**	
ΔP_q (PC_1 length)	PC_1 moult probability			3.462 ± 1.946	1.779	$3.16_{1,14}$	0.184	0.000		0.097	
ΔP_q (R_4 length)	R_4 moult probability			4.632 ± 2.037	2.274	$5.17_{1,14}$	0.270	0.000		**0.039**	

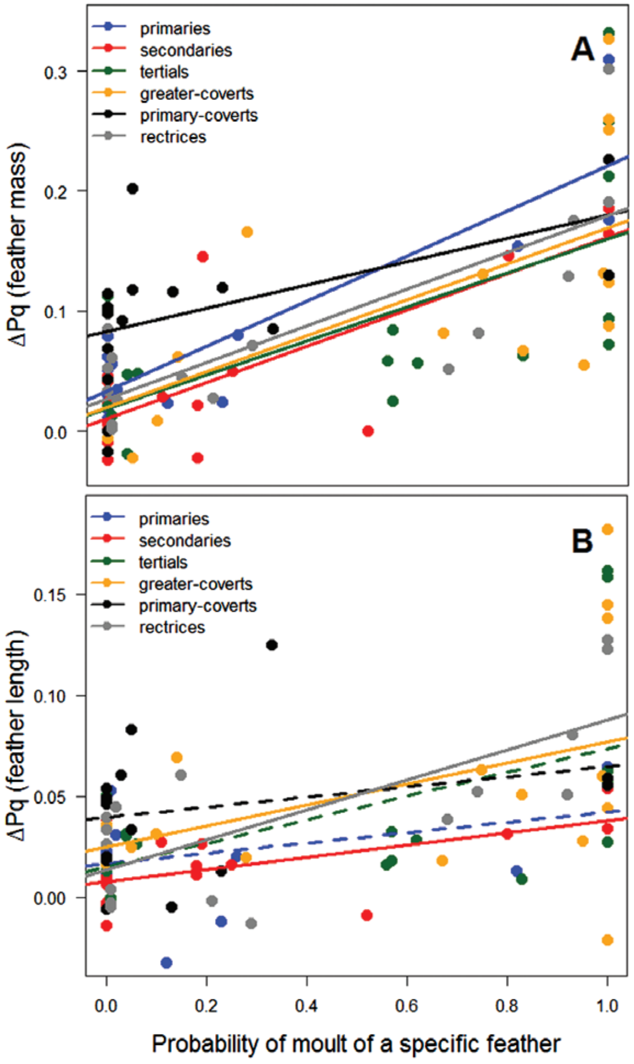

Figure 4. Effects of moult probability on feather quality of specific feathers during post-juvenile moult in six feathers from the wing and the tail of 16 species, using ΔP_q – a quality measure of feathers that grew in the nest in relation to those of adult birds of the same species. A, length-standardized feather mass. B, feather length. Note that statistically significant effects were found for GC_4, S_5 and R_4 (solid lines), but not for PC_1, T_8 or P_4 (dashed lines). The results of statistical analyses are reported in Table 1.

time constraints. De La Hera *et al.* (2010) suggested that rapid development of the juvenile plumage is an adaptation aimed at reducing the likelihood of nest predation and mortality of the young, and this could minimize the importance of migration-related time constraints in dictating plumage properties. Our findings nevertheless suggest that time constraints imposed by breeding and moulting in northern latitudes and by long-distance migration, which affect the juvenile's moult timing and extent (Ginn & Melville, 1983; Jenni & Winkler, 1994; Gargallo & Clarabuch, 1995; Kiat & Izhaki, 2016), influence the quality of the juvenile's plumage. These results are further compatible with the finding that the quality of the juvenile's plumage is affected by the overall duration that the juvenile spends in the nest (Rohwer *et al.*, 2005; Butler *et al.*, 2008). The shorter duration that the juvenile spends in the nest correlates with poorer plumage quality but nevertheless may reduce the likelihood of nest predation.

Partial post-juvenile moult creates differences in the lifespan of different feathers of juvenile birds. Our findings suggest that resource allocation considerations modulated the investment in these specific feathers such that their quality is related to their expected lifespan. In this study we tested only the juvenile's nest-grown feathers, but similar relationships between feather lifespan and quality could also be found in adults. For example, feathers of species that undergo a biannual complete moult (e.g. *Phylloscopus trochilus*; Underhill *et al.*, 1992), such that their feathers are replaced twice a year, are expected to be of lower quality than those of species that have only a single annual moult, such that their feathers must function over a longer period (see also Pap *et al.*, 2015).

Optimization of resource allocation is a major factor affecting the evolution of life-history traits in all organisms (Charnov, 1976; Pianka, 1976; Caraco, 1980; Kozłowski & Wiegert, 1986; McNamara & Houston, 1986; Hall *et al.*, 1992; Giudice *et al.*, 2015). Most studies dealing with resource allocation have focused on growth and reproduction (Kozłowski & Wiegert, 1986; Watt, 1986; Stearns, 1992) or resource allocation to immune responses (e.g. Rauw 2012). Very few studies have dealt with how organisms allocate resources to different organs and tissues of the body (Johnson, 1985; Perrin, 1992; Perrin & Sibly, 1993; Pap *et al.*, 2015). To the best of our knowledge, our results represent the first evidence for optimization of resource allocation by natural selection following a comparative analysis. The optimization of resource allocation during the nesting period is probably a result of the energy-demanding avian reproduction process, which may be modulated by different temporal constraints and other factors (e.g. predation risk). The high energetic demands of avian breeding provides strong motivation for shortening the nesting period and minimizing parental food provision to a level that will still ensure appropriate plumage function. This may further allow energy to be allocated to other tissues, sensory systems and immune function, presumably leading to a higher survival rate of the juveniles.

ACKNOWLEDGEMENTS

We would like to thank Hein van Grouw and Mark Adams from the Natural History Museum at Tring (UK) and Daniel Berkowic, Amos Belmaker and Roi Dor from the Steinhardt Museum of Natural History, Tel-Aviv University (Israel), for facilitating the measurements of museum specimens. We thank Peter Pyle and two anonymous reviewers for their constructive comments that substantially improved our work. Finally, we are indebted to the ringers and ornithologists who obtained the data used in this study.

REFERENCES

Bonser RHC. 1995. Melanin and the abrasion resistance of feathers. *Condor* **97:** 590–591.

Bonser RHC. 1996. The mechanical properties of feather keratin. *Journal of Zoology* **239:** 477–484.

Bridge ES. 2008. How does imping affect wing performance? *Journal of Wildlife Rehabilitation* **29:** 4–9.

Bryant DM. 1979. Reproductive costs in the house martin (*Delichon urbica*). *Journal of Animal Ecology* **48:** 655–675.

Burtt EH. 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithological Monographs* **38:** 1–126.

Butler LK, Rohwer S, Speidel MG. 2008. Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. *Journal of Avian Biology* **39:** 629–639.

Caraco T. 1980. On foraging time allocation in a stochastic environment. *Ecology* **61:** 119–128.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9:** 129–136.

Conrad KF, Robertson RJ. 1992. Intraseasonal effects of clutch manipulation on parental provisioning and residual reproductive value of Eastern phoebes (*Sayornis phoebe*). *Oecologia* **89:** 356–364.

Cramp S, Perrins CM. 1994. *Birds of the Western Palearctic: handbook of the birds of Europe, the Middle East and North Africa.* NewYork: Oxford University Press.

Dawson A, Hinsley SA, Ferns PN, Bonser RHC, Eccleston L. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society of London B: Biological Sciences* **267:** 2093–2098.

De La Hera I, Hedenström A, Pérez-Tris J, Tellería JL. 2010. Variation in the mechanical properties of flight feathers of the blackcap *Sylvia atricapilla* in relation to migration. *Journal of Avian Biology* **41:** 342–347.

Doucet SM, Hill GE. 2009. Do museum specimens accurately represent wild birds? A case study of carotenoid, melanin, and structural colours in long-tailed manakins *Chiroxiphia linearis*. *Journal of Avian Biology* **40:** 146–156.

Drent RH, Daan S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68:** 225–252.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125:** 1–15.

Fogden MPL. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* **114:** 307–343.

Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* **160:** 712–726.

Gargallo G, Clarabuch O. 1995. Extensive moult and ageing in six species of passerines. *Ringing & Migration* **16:** 178–189.

Ginn HB, Melville DS. 1983. *Moult in birds. BTO guide19*. Thetford: British Trust for Ornithology.

Giudice DM, Gangestad SW, Kaplan HS. 2015. Life history theory and evolutionary psychology. In: Buss DM, ed. *The handbook of evolutionary psychology.* NewYork: Wiley, 68–95.

Glazier DS. 2009. Resource allocation patterns. In: Rauw WM, ed. *Resource allocation theory applied to farm animal production*. Wallingford: CABI, 22–43.

Griggio M, Serra L, Licheri D, Campomori C, Pilastro A. 2009. Moult speed affects structural feather ornaments in the blue tit. *Journal of Evolutionary Biology* **22:** 782–792.

Guallar S, Figuerola J. 2016. Factors influencing the evolution of moult in the non-breeding season: insights from the family Motacillidae. *Biological Journal of the Linnean Society* **118:** 774–785.

Hails CJ, Bryant DM. 1979. Reproductive energetics of a free-living bird. *Journal of Animal Ecology* **48:** 471–482.

Hall KSS, Fransson T. 2000. Lesser whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. *Journal of Avian Biology* **31:** 583–587.

Hall CAS, Stanford JA, Hauer FR. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. *Oikos* **65:** 377–390.

Howell SNG. 2001. Feather bleaching in gulls. *Birders Journal* **10:** 198–208.

Howell SNG. 2010. *Peterson reference guide to molt in North American birds (Peterson Reference Guides).* Boston: Houghton Mifflin Harcourt.

Jenni L, Winkler R. 1994. *Moult and ageing of European passerines.* London: A&C Black.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature* **491:** 444–448.

Johnson IR. 1985. A model of the partitioning of growth between the shoots and roots of vegetative plants. *Annals of Botany* **55:** 421–431.

Kiat Y, Izhaki I. 2016. Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. *Journal of Avian Biology* **47:** 47–56.

Kiat Y, Sapir N. 2017. Age-dependent modulation of songbird summer feather moult by temporal and functional constraints. *American Naturalist* **189:** 184–195.

Kozłowski J, Wiegert RG. 1986. Optimal allocation of energy to growth and reproduction. *Theoretical Population Biology* **29:** 16–37.

Krause ET, Honarmand M, Wetzel J, Naguib M. 2009. Early fasting is long lasting: differences in early nutritional conditions reappear under stressful conditions in adult female zebra finches. *PLoS One* **4:** e5015.

McNamara JM, Houston AI. 1986. The common currency for behavioral decisions. *American Naturalist* **127:** 358–378.

Monaghan P. 2003. Resource allocation and life history strategies in birds. *Acta Zoologica Sinica* **50:** 942–947.

Muñoz A, Aparicio JM, Bonal R. 2011. Male barn swallows use different signalling rules to produce ornamental tail feathers. *Evolutionary Ecology* **25:** 1217–1230.

Murphy ME, King JR, Lu J. 1988. Malnutrition during the postnuptial molt of white-crowned sparrows: feather growth and quality. *Canadian Journal of Zoology* **66:** 1403–1413.

Newton I. 1966. The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* **108:** 41–67.

Newton I. 2009. Moult and plumage. *Ringing & Migration* **24:** 220–226.

Nilsson JA, Svensson E. 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London B*: *Biological Sciences* **263:** 711–714.

Noskov GA, Rymkevich TV. 2010. Regulation of annual cycle parameters and its role in the microevolutionary process in birds. *Uspekhi sovremennoi biologii* **130:** 346–359.

Obeso JR. 2002. The costs of reproduction in plants. *New Phytologist* **155:** 321–348.

Oftedal OT, Gittleman JL. 1989. Patterns of energy output during reproduction in carnivores. In: Gittleman JL, ed. *Carnivore behavior, ecology, and evolution*. Boston: Springer, 355–378.

Orme D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. *R Package* **5:** 1–36.

Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* **26:** 331–348.

Pap PL, Osváth G, Sándor K, Vincze O, Bărbos L, Marton A, Nudds RL, Vágási CI. 2015. Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat. *Functional Ecology* **29:** 746–757.

Perrin N. 1992. Optimal resource allocation and the marginal value of organs. *American Naturalist* **139:** 1344–1369.

Perrin N, Sibly RM. 1993. Dynamic models of energy allocation and investment. *Annual Review of Ecology and Systematics* **24:** 379–410.

Pianka ER. 1976. Natural selection of optimal reproductive tactics. *American Zoologist* **16:** 775–784.

Podlaszczuk P, Kamiński M, Włodarczyk R, Kaczmarek K, Janiszewski T, Minias P. 2016. Plumage quality mediates a life-history trade-off in a migratory bird. *Frontiers in Zoology* **13:** 47.

Randolph PA, Randolph JC, Mattingly K, Foster MM. 1977. Energy costs of reproduction in the cotton rat, *Sigmodon hispidus*. *Ecology* **58:** 31–45.

Rauw WM. 2012. Immune response from a resource allocation perspective. *Frontiers in Genetics* **3:** 267.

Ricklefs RE. 1974. The energetics of reproduction in birds. In: Paynter RA, ed. *Avian energetics*. Cambridge: Nuttall Ornithological Club, 152–292.

Riley PA. 1997. Melanin. *The International Journal of Biochemistry & Cell Biology* **29:** 1235–1239.

Rohwer S, Butler LK, Froehlich DR, Greenberg R, Marra PP. 2005. Ecology and demography of East–West differences in molt scheduling of neotropical migrant passerines. In: Greenberg R, Marra PP, eds. *Birds of two worlds: the ecology and evolution of migration*. Baltimore: Johns Hopkins University Press, 87–105.

Rubolini D, Liker A, Garamszegi LZ, Møller AP, Saino N. 2015. Using the BirdTree.org website to obtain robust phylogenies for avian comparative studies: a primer. *Current Zoology* **61:** 959–965.

Sanz JJ, Tinbergen JM. 1999. Energy expenditure, nestling age, and brood size: an experimental study of parental behavior in the great tit *Parus major*. *Behavioral Ecology* **10:** 598–606.

Serra L, Griggio M, Licheri D, Pilastro A. 2007. Moult speed constrains the expression of a carotenoid-based sexual ornament. *Journal of Evolutionary Biology* **20:** 2028–2034.

Silva MC, Boersma PD, Mackay S, Strange I. 2007. Egg size and parental quality in thin-billed prions, *Pachyptila belcheri*: effects on offspring fitness. *Animal Behaviour* **74:** 1403–1412.

Stearns SC. 1992. *The evolution of life histories.* Oxford: Oxford University Press.

Stresemann E, Stresemann V. 1966. Die mauser der vögel. *Journal of Ornithology* **107:** 1–448.

Svensson L. 1992. *Identification guide to European passerines.* Stockholm: Ugga.

Svensson E, Hedenström A. 1999. A phylogenetic analysis of the evolution of moult strategies in Western palearctic warblers (Aves: Sylviidae). *Biological Journal of the Linnean Society* **67:** 263–276.

Swaddle JP, Witter MS, Cuthill IC, Budden A, McCowen P. 1996. Plumage condition affects flight performance in common starlings: implications for developmental homeostasis, abrasion and moult. *Journal of Avian Biology* **27:** 103–111.

Underhill LG, Prys-Jones RP, Dowsett RJ, Herroelen P, Johnson DN, Lawn MR, Norman SC, Pearson DJ, Tree AJ. 1992. The biannual primary moult of Willow Warblers *Phylloscopus trochilus* in Europe and Africa. *Ibis* **134:** 286–297.

Vágási CI, Pap PL, Vincze O, Benko Z, Marton A, Barta Z. 2012. Haste makes waste but condition matters: molt rate-feather quality trade-off in a sedentary songbird. *PLoS ONE* **7:** e40651.

Vortman Y, Lotem A, Dor R, Lovette IJ, Safran RJ. 2011. The sexual signals of the East-Mediterranean barn swallow: a different swallow tale. *Behavioral Ecology* **22:** 1344–1352.

Walsberg GE. 1983. Avian ecological energetics. In: Farner DS, King JR, Parkes KC, eds. *Avian biology*. NewYork: Academic Press, 161–220.

Watt WB. 1986. Power and efficiency as indexes of fitness in metabolic organization. *American Naturalist* **127:** 629–653.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. ΔP_q data for the three analyses testing the effects of the timing of the first complete moult on juvenile plumage quality.

Table S2. Data used for analyses involving the length-standardized feather mass [ΔP_q (M)], feather length [ΔP_q (L)] and moult probability. The ΔP_q values were calculated from 16 individuals, eight adults and eight juveniles, from each species. Moult probability data were calculated from the following species (sample sizes): *Anthus cervinus* (85), *Motacilla flava* (438), *Luscinia svecica* (428), *Phoenicurus phoenicurus* (74), *Turdus merula* (110), *Cettia cetti* (72), *Acrocephalus stentoreus* (248), *Sylvia atricapilla* (413), *Sylvia curruca* (430), *Sylvia melanocephala* (116), *Phylloscopus collybita* (382), *Parus major* (67), *Corvus corone* (58), *Passer domesticus* (53), *Bucanetes githagineus* (74) and *Carduelis chloris* (72).