

Age-Dependent Modulation of Songbird Summer Feather Molt by Temporal and Functional Constraints

Yosef Kiat^{1,*} and Nir Sapir²

1. Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, Edmond J. Safra Campus, Hebrew University of Jerusalem, Jerusalem 91904, Israel; 2. Animal Flight Laboratory, Department of Evolutionary and Environmental Biology, University of Haifa, Haifa 3498838, Israel

Submitted June 26, 2016; Accepted October 12, 2016; Electronically published December 20, 2016

Dryad data: <http://dx.doi.org/10.5061/dryad.q31s0>.

ABSTRACT: Time constraints influence various ecological, life-history, and demographic properties of individuals and populations of many species throughout the annual cycle. Feather molt is a timely undertaking that is considered among the three most energy-demanding processes in the life cycle of birds. To deal with time pressure, passerines may shorten their molt duration, using three non-mutually exclusive mechanisms: (1) replacing only part of the plumage, (2) increasing the speed of molt, and (3) postponing the renewal of some or all the plumage to a later season (i.e., from the summer to the overwintering period). We used a comparative approach by measuring 12,349 individuals from 134 passerine species to explore how feather molt of juvenile and adult passerines is evolutionarily modulated under time constraints. The results indicate that breeding at northern latitudes and long-distance migration limit the time available for molt and that the consequences of time constraints were age dependent. While the duration of adult summer molt decreased, the extent, rather than the duration, of juvenile molt declined under time constraints. This study highlights the importance of considering time constraints in order to enhance the understanding of selective forces that shape life-history processes and their consequences throughout the annual routine.

Keywords: annual routine, bird migration, breeding distribution, passerines, time constraints, wing feathers.

Introduction

In an environment that changes periodically over the year, the properties of major energy-demanding processes in an organism's life such as breeding, long-range movement, and the replacement of old skin, fur, feathers, or shell may have large effects on the organism's survival and reproduction. Specifically, the timing along the yearly cycle and the duration and scheduling of each process with re-

gard to other major processes are subject to natural selection, with implications for physiology, behavior, and, ultimately, animal fitness (McNamara et al. 1998; Houston and McNamara 1999; McNamara and Houston 2008). These life-history transitions throughout the annual routine may depend on the outcome of events that took place in previous seasons (Harrison et al. 2011; van den Heuvel et al. 2013), and such carryover effects were documented in various organisms under diverse ecological settings (O'Connor et al. 2014). Life-history transitions are further influenced by time constraints due to environmental seasonality, especially in high latitudes, where the seasonal cycle is strong and hence its consequences for different organisms could be severe (Gotthard et al. 1999; Wingfield 2008; Varpe 2012). Since many organisms are characterized by morphological, behavioral, and physiological differences between juvenile and adult life stages (e.g., Wingfield 2008; Marshall and Morgan 2011) and because of differences in carryover effects between different life stages (e.g., Rauset et al. 2015), selection pressures may vary between age groups (McNamara and Houston 1996; English et al. 2014), resulting in age-related differences of seasonality-driven life-history transitions (e.g., Marshall and Morgan 2011).

One of the most important life-history transitions for birds is feather molt (Barta et al. 2008). Renewal of feathers is essential for their function because they get worn with time as a result of exposure to ultraviolet radiation and other environmental factors. Consequently, passerine birds molt all of their flight feathers at least once per year (Jenni and Winkler 1994). Molt is considered one of the three most energy-demanding processes in the life cycle of birds (Newton 2009), and consequently molt does not usually overlap with breeding and migration, the two other most energy-demanding processes. The timing of molt is generally more variable within the annual cycle than that of breeding or migration because, unlike the latter two processes, molt may take place at different times throughout

* Corresponding author; e-mail: yosefkiat@gmail.com.

the year (Ginn and Melville 1983; Newton 2009). Long-distance migration is known to strongly influence the timing of molt by delaying the molt from the summer to the overwintering period (Jenni and Winkler 1994; Svensson and Hedenström 1999; Hall and Tullberg 2004). This delay likely results from the high costs involved in overlapping breeding and molt among long-distance migrants (Svensson and Nilsen 1997; Echeverry-Galvis and Hau 2013; Saino et al. 2014), especially for large bird species (Langston and Rohwer 1996). It is noteworthy that there appears to be an interplay between migration and molt, since although migration constitutes an important factor that limits the time available for molt and consequently affects molt strategy, molt timing may also affect migration timing (Kiat and Izhaki 2016a).

Feather molt may entail aerodynamic (Haukioja 1971; Jenni and Winkler 1994; Hedenström and Sunada 1999; Hedenström 2003) and thermoregulatory (Jenni and Winkler 1994; but see Schieltz and Murphy 1997) costs to birds. In addition, feather synthesis requires energy as well as specific nutrients whose acquisition may bear additional metabolic expenses (Murphy and King 1992; Lindström et al. 1993; Jenni and Winkler 1994). Yet the importance of these factors may vary between different species. Notably, the energetic costs of feather synthesis are high for small birds but substantially decrease with increasing body size (Murphy and King 1992; Lindström et al. 1993). To minimize these costs, the molt process usually occurs over a long period of time, such that the associated energy demands are not elevated to a degree that may impair the survival of the bird (Ginn and Melville 1983; Jenni and Winkler 1994). Thus, when the time period available for feather molt is limited, properties of the molt process may be affected (Barta et al. 2006, 2008; Hedenström 2008). Autumnal bird migration may limit the time available for molt because of its high metabolic demands that typically span over a long period of time soon after breeding. Moreover, low temperatures and the decrease of daylight hours with the progress of the autumn may lower food availability during this period, especially at northern latitudes (Jenni and Winkler 1994). Consequently, because birds will have less time for molting as the breeding latitude is higher (Haukioja 1971) and the migration distance increases (Kjellén 1994; de la Hera et al. 2009a), there may be benefits from shortening the postbreeding molt (Ginn and Melville 1983; Jenni and Winkler 1994).

To shorten molt duration in passerines, natural selection may lead to three main, non-mutually exclusive, mechanisms: (1) replacing only part of the plumage, (2) increasing the speed of molt, and (3) postponing some or all plumage renewal from the summer until the overwintering period, after the end of the autumn migration (Haukioja 1971; Ginn and Melville 1983; Jenni and Winkler 1994;

Rymkevich and Bojarinova 1996; Bojarinova et al. 1999; Hedenström 2008; Newton 2009; de la Hera et al. 2012). Yet adult birds cannot usually avoid replacing part of their plumage, as their plumage may become too worn if not renewed at least once per year (Jenni and Winkler 1994; Newton 2009). Thus, adults under time constraints may only increase the speed of molt or postpone their molt such that it will take place during the overwintering period. In contrast, for juveniles, increasing the speed of molt cannot usually be accomplished because of their inability to attain the high food intake that is necessary to meet the elevated energetic demands of this process so soon after fledging (Marchetti and Price 1989). In addition, juveniles fledge with fresh plumage that may enable them to forgo replacing part or all of their plumage during their first year of life.

To this end, we hypothesize that in order to overcome time constraints, adults will increase their speed of molt or postpone their molt until the overwintering period, whereas juveniles will replace only part of their plumage or, similar to adults, will postpone their molt. We consequently predict that (1) breeding latitude and migration distance will affect molt patterns by imposing higher time constraints on passerine birds; (2) all adult passerines will renew all of their plumage at least once per year and, when under time constraints, will increase the speed of molt or postpone their molt; and (3) juveniles will postpone their molt and molt only part of their plumage under time constraints. Limited molt extent will hence be more common in juveniles than in adults.

Methods

Study Species and Sites

We measured wing and tail feather molt in a total of 134 passerine species. Both postjuvenile molt, which is the first molt occurring immediately after fledging at the breeding grounds, and postbreeding molt of adult birds were recorded. From 2011 to 2015, we sampled live birds from 100 species at different sites across Israel, mostly in the Beit-Shean Valley (32°29'N, 35°31'E), in the Judean Desert (31°32'N, 35°23'E), on Mount Hermon (33°19'N, 35°46'E), in the Soreq Valley (31°46'N, 34°55'E), and in 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, United Kingdom. We also used data from published literature (see details in tables S1–S3 in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.q31s0>; Kiat and Sapir 2017).

Molt Extent and Duration

Molt extent was determined by documenting the molt of the wing and tail feathers with a score of 0 (nonmolted feather) or 1 (molted feather). A total of 47 feathers for each individual were documented with this method, as follows: greater coverts (GC_{1-10}), carpal covert (CC), alulae (Al_{1-3}), primary coverts (PC_{1-9}), primaries (P_{1-9}), secondaries (S_{1-6}), tertials (T_{7-9}), and rectrices (R_{1-6}). We averaged the scores of individual feathers across all measured feathers for each individual in order to obtain an average value for each individual and then averaged this value across all the individuals of a specific species in order to calculate an average species-specific molt-extent value.

Active molt of primary feathers was recorded for birds in the field with a primary-score method that describes 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 one-third the length of a fully grown feather; 3 = a new feather with a length between one-third and two-thirds that 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. Molt duration in species where the primary-score method could not be applied was estimated with a model (Underhill and Zucchini 1988) implemented in the R package “moult” (Erni et al. 2012). This model was used to estimate postbreeding molt duration in 13 species and postjuvenile molt duration in 11 species. We additionally used data from published literature that contained information on the postbreeding molt duration of 67 species and the postjuvenile molt duration of 17 species (see details in table S2 in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.q31s0>; Kiat and Sapir 2017). To describe molt strategies, we used the terminology of Jenni and Winkler (Jenni and Winkler 1994). Since body mass is known to strongly affect molt duration (Carrascal and Polo 2006; de la Hera et al. 2009a; Rohwer et al. 2009), we added body mass as a predictor in all of the models. Information about body masses was obtained from Dunning (1992) as well as from our database (see table S1 in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.q31s0>; Kiat and Sapir 2017).

Migration Distance and Breeding Latitude

We considered breeding latitude and migration distance as factors that may limit the time available for molt after the breeding period. The mid-breeding latitude and the mid-overwintering latitude data for each species (in de-

grees) were calculated with BirdLife distribution maps (BirdLife International and NatureServe 2014). The mean migration distance (in kilometers) was calculated with Google Earth as the distance between these two latitudes. The breeding and the overwintering grounds of many species have a very wide range and also vary between years, making our estimates crude. To deal with this uncertainty and to account for within-species variation in breeding and overwintering localities (by including most of the breeding and overwintering localities of different populations of each species), we classified migration distance and breeding latitude into specific, wide-range, categories such that each species was assigned to one of three breeding-latitude categories— 25° – 40° N, 40° – 55° N, and $>55^{\circ}$ N—as well as to one of three migration distance categories: 0–2,500, 2,500–5,000, and $>5,000$ km.

Statistical Analysis

We used one-way ANOVAs to explore the effects of migration distance and mid-breeding latitude on molt extent and duration and selected models based on the lowest calculated Akaike information criterion, modified for small sample sizes (AICc; Burnham and Anderson 2002). In juveniles, in which high variation in the extent of postjuvenile molt exists between different species, the number of molted feathers may affect the duration of molt, as more time may be required to replace more feathers. To examine whether the extent of molt, migration distance, and breeding latitude affect molt duration, we used regression, one-way ANOVA, two-way ANOVA, and ANCOVA models and selected the best model on the basis of AICc. We selected a specific model only if it exhibited a $\Delta AICc > 2$ compared to other models (Burnham and Anderson 2002). Because adults molted all of their feathers in nearly all species (see “Results”), no models explaining molt extent in adults were used.

Since species-specific traits are known to be phylogenetically conserved, closely related species cannot be considered statistically independent from each other. To account for relatedness, we repeated the analysis, following the independent-comparisons method, which identifies evolutionarily independent comparisons (Felsenstein 1985). To account for phylogenetic nonindependence, for all analyses we used phylogenetic generalized least squares regression (Freckleton et al. 2002). We examined the strength of phylogenetic nonindependence by 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; it provides the best fit of the Brownian motion model to the tip data and ranges between 0 (no phylogenetic signal) and 1 (phylogenetic signal that depends

on branch lengths, as in the 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 relevant comparative methods and their use in ecological studies, see Mason (2010). We followed the phylogeny outlined by Jetz et al. (2012), using BirdTree.org (Rubolini et al. 2015); see figure A1. Analyses (two-tailed, critical $\alpha = 0.05$) were performed with R (ver. 3.2.2).

Results

We obtained molt data from 12,349 individuals of 134 passerine species belonging to 57 genera (tables S2, S3 in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.q31s0>; Kiat and Sapir 2017). All adults of all but one species we examined underwent a complete postbreeding molt that took place either before or after the autumn migration in the breeding or overwintering grounds, respectively, or split their molt such that it took place in both the breeding and the overwintering areas (fig. 1). In the latter scenario, birds arrested their molt during migration. The only species in which some individuals performed an extensive partial postbreeding molt rather than a complete molt was *Phylloscopus trochilus*. In contrast, among juveniles, only 35.3% of the species ($n = 36$ out of 102 species) went through a complete molt of their wing and tail feathers during their first year of life, while 64.7% ($n = 66$ out of 102 species) performed only a partial molt.

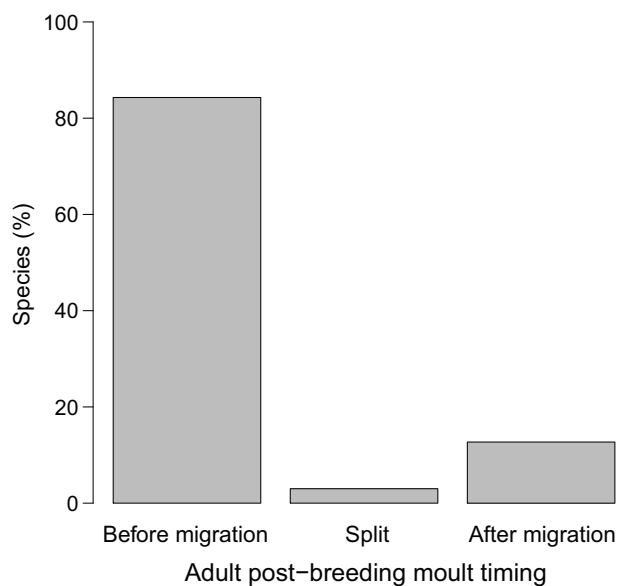


Figure 1: Timing of adult postbreeding molt (% of species, $n = 134$ species).

About half of the species whose juveniles performed a complete wing and tail molt delayed this molt to the overwintering period (47.2%, $n = 17$ out of 36 species).

We found that the two selected models ($\Delta\text{AICc} < 8.60$) explaining the variation in adult postbreeding molt duration included the independent variables migration distance and breeding latitude, with ($F_{4,75} = 17.02$, $R^2 = 0.45$, $P < .001$) and without ($F_{3,76} = 20.89$, $R^2 = 0.43$, $P < .001$) their interaction (table 1). Species characterized by northern breeding latitudes and long migration distances were found to molt relatively quickly (fig. 2). The two selected models ($\Delta\text{AICc} < 2.77$) explaining the variation in the extent of postjuvenile molt included a model with the independent variable migration distance ($F_{2,94} = 23.95$, $R^2 = 0.32$, $P < .001$) and a model that included the independent variables migration distance and breeding latitude, together with their interaction ($F_{4,92} = 13.33$, $R^2 = 0.34$, $P < .001$). This indicates a significant negative effect of these factors on the extent of postjuvenile feather molt (table 1). Short-distance migrants and southern species were found to molt a greater proportion of their wing and tail feathers than long-distance migrants and northern species, likely as a result of the less constrained period over which their molt process can be carried out (fig. 3). The selected model ($\Delta\text{AICc} = 2.06$) explaining the variation in postjuvenile molt duration is a model that included the extent of molt, indicating a significant positive effect of molt extent on molt duration (table 1). Species characterized by an extensive molt replaced their feathers over a relatively long period of time ($F_{2,25} = 10.62$, $R^2 = 0.42$, $P < .001$; fig. 4).

The results of the analysis suggest a high phylogenetic signal in the data (average of maximum likelihood value of $\lambda = 0.83$; see details in table 1). All of the analyses were corrected for the effects of phylogenetic relatedness by use of the maximum value of λ . The Pearson correlation coefficient (r) between migration distance and breeding latitude was 0.41 ($t = 3.93$, $df = 78$, $P < .001$, $n = 134$ species).

Discussion

The seasonal environments where many organisms live impose time and energy constraints on different life-history properties, including litter and clutch size, development rate, and body size (for example Rowe et al. 1994; Abrams et al. 1996; Gotthard et al. 1999; Wingfield 2008; Varpe 2012). The response of organisms to these constraints is often age dependent, because these limiting factors may operate differently on adult and young organisms (McNamara and Houston 1996; English et al. 2014). Our results suggest that the summer molt of both adult and ju-

Table 1: AICc and phylogenetic signal (λ) of models explaining the duration and extent of summer feather molt in passerines

Explanatory variables in the model	<i>F</i> (df)	<i>R</i> ²	<i>P</i>	λ	AICc	Δ AICc
Adult postbreeding molt duration:						
Body mass + migration distance \times breeding latitude	17.02 (4, 75)	.45	<.001	1.00	685.42	...
Body mass + migration distance + breeding latitude	20.89 (3, 76)	.43	<.001	1.00	687.00	1.58
Body mass + breeding latitude	23.20 (2, 77)	.36	<.001	.98	694.02	8.60
Body mass + migration distance	8.82 (2, 77)	.17	<.001	1.00	715.35	29.93
Postjuvenile molt extent:						
Body mass + migration distance	23.95 (2, 94)	.32	<.001	.82	12.50	...
Body mass + migration distance \times breeding latitude	13.33 (4, 92)	.34	<.001	.78	13.19	.69
Body mass + migration distance + breeding latitude	15.97 (3, 93)	.32	<.001	.80	15.27	2.77
Body mass + breeding latitude	4.94 (2, 94)	.08	.009	.73	42.97	30.47
Postjuvenile molt duration:						
Body mass + molt extent	10.62 (2, 25)	.42	<.001	1.00	271.70	...
Body mass + molt extent + breeding latitude	7.40 (3, 24)	.42	.001	.99	273.76	2.06
Body mass + migration distance	8.98 (2, 25)	.37	.001	1.00	273.76	2.06
Body mass + breeding latitude	12.15 (2, 25)	.45	<.001	.00	274.69	2.99
Body mass + migration distance + breeding latitude	6.78 (3, 24)	.39	.002	.96	274.77	3.07
Body mass + molt extent + migration distance	6.81 (3, 24)	.39	.002	1.00	274.93	3.23
Body mass + migration distance \times breeding latitude	7.54 (4, 23)	.49	<.001	.00	275.51	3.81
Body mass + molt extent \times breeding latitude	5.29 (4, 23)	.39	.004	.98	275.72	4.02
Body mass + molt extent \times migration distance	5.16 (4, 23)	.38	.004	1.00	276.25	4.55
Body mass + molt extent + migration distance + breeding latitude	5.34 (4, 23)	.39	.003	.98	277.41	5.71

Note: AICc = Akaike information criterion, modified for small sample sizes. Selected models (Δ AICc < 2) are shown in boldface.

venile passerines may be severely constrained by other major energy-demanding processes in the annual cycle, namely, breeding and migration. The limited time available for molt is an important consequence of the birds' breeding and overwintering distribution ranges, such that northerly breeding species and long-distance migrants are considerably more stressed for time after breeding (Kiat and Izhaki 2016b; Kiat et al. 2016). To overcome the limited time available for molt, different mechanisms have evolved in juveniles and adults, depending on the life-history time constraints of each age group. In the case of adults, molt may start only after the end of the highly demanding food-provisioning period in which the birds intensively forage to provide large quantities of food for their young (Jenni and Winkler 1994; Siikamäki et al. 1994; Hemborg and Lundberg 1998). The duration of adult molt is negatively affected by breeding latitude and migration distance, which apparently limit the time available for molt, thereby strongly affecting molt patterns. Similarly, the extent, rather than the duration, of juvenile molt is affected by these two factors, suggesting that juveniles are affected by these factors in a different way than adults are. Yet despite the similar timing of molt onset and the apparently similar effects of the aforementioned time stressors, adult and juvenile birds developed very different strategies of molt under time constraints.

In general, the molt of adults takes place either before or after the autumn migration or is split between these two periods (Jenni and Winkler 1994). Adults of almost all of the passerine species examined in our study exhibited a complete wing and tail molt. In the single exceptional species (*Phylloscopus trochilus*), about 30% of the individuals we sampled did not complete their postbreeding molt. This rather odd pattern likely evolved as a consequence of the unique second annual molt (prebreeding molt) in this species that takes place in the overwintering areas, allowing some individuals to forgo molting several feathers in the postbreeding molt (Underhill et al. 1992). Adults must molt their entire plumage at least once a year to ensure its functionality; thus, adults under time constraints may only increase the speed of molt or postpone their molt to a more convenient period during winter (figs. 1, 2; table 1). Each of these two responses may bear certain associated consequences. For example, postponing molt until the overwintering period may result in the undertaking of the autumn migration with old, abraded flight feathers (Holmgren and Hedenström 1995), while high molt speed may cause the growth of poor-quality feathers (Hall and Fransson 2000; de La Hera et al. 2009b), which may lead to decreased survival and low future reproductive success (Dawson et al. 2000). Furthermore, molting before the autumn migration may overlap with breeding to some

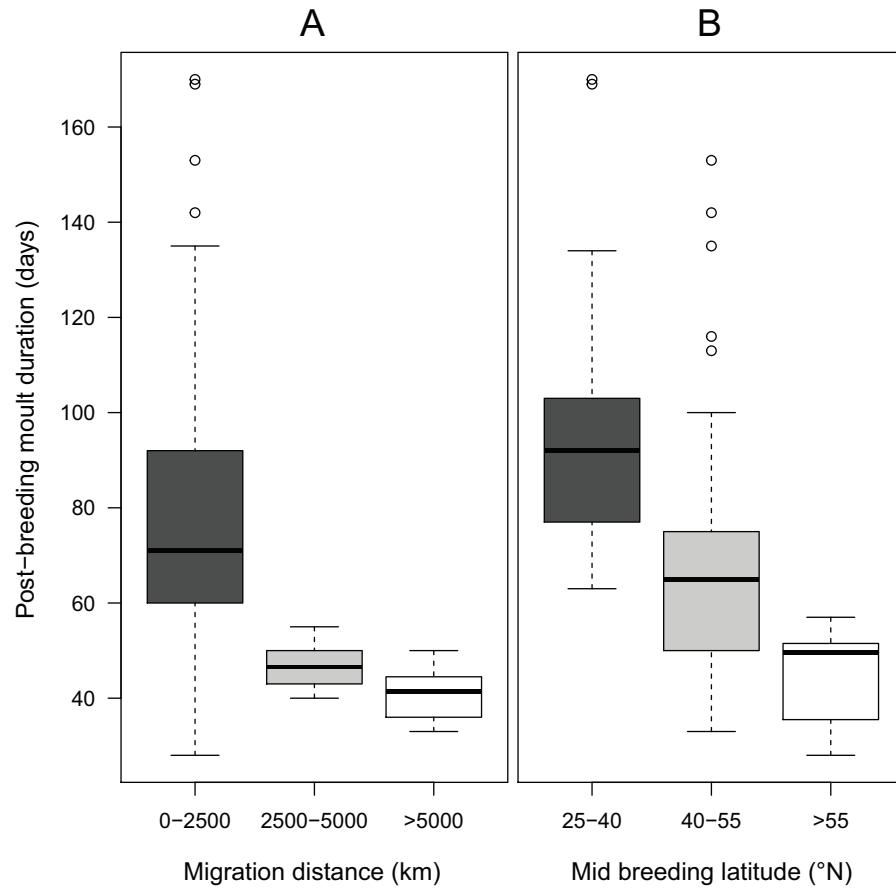


Figure 2: Effects of migration distance (A) and breeding latitude (B) on the duration of adult postbreeding molt. The box plots display the fifth, twenty-fifth, fiftieth (median), seventy-fifth, and ninety-fifth percentiles of the data of each category.

degree, which could also reduce fitness (Svensson and Nilsen 1997; Hemborg and Lundberg 1998; Hemborg et al. 1998).

We note that, in contrast to adult birds, juveniles probably cannot obtain the high food quantities required to boost their molt speed, likely because of their overall limited foraging capabilities (Marchetti and Price 1989). Juveniles start their life with fresh plumage, such that they may forgo replacing part of their plumage during their first year of life. Indeed, our results suggest that under time constraints, juveniles molt fewer feathers, replacing only part of their plumage in order to shorten their molt duration (fig. 3; table 1). Our findings further suggest that for juveniles, complete (postjuvenile) molt is probably an optimal molt strategy in habitats with favorable environmental conditions, where birds would have a long time to complete their molt after the end of the breeding season and in which food is readily available. Indeed, this has been described in some tropical and subtropical areas

(Fogden 1972; Kiat and Izhaki 2016b). We propose that partial postjuvenile molt has evolved in long-distance migrant species under conditions of limited time for molt. This partial molt has probably been made possible only because nest-grown juvenile feathers may last for a relatively long period by being structurally durable, allowing the birds to replace only part of their plumage. We consequently predict more-durable nest-grown juvenile feathers in species characterized by time-limited postjuvenile molt, as more-durable juvenile plumage at fledging may enable a less extensive and overall shorter postjuvenile molt. However, among many species, for example, those that renew their entire plumage soon after fledging, juvenile plumage is not structurally durable (Kiat and Izhaki 2016b). In addition, the quality of the juvenile plumage is affected by the overall duration that the young spend in the nest (e.g., Rohwer et al. 2005). Therefore, we propose that future exploration of the relationship between the extent of postjuvenile molt and juvenile feather durability may

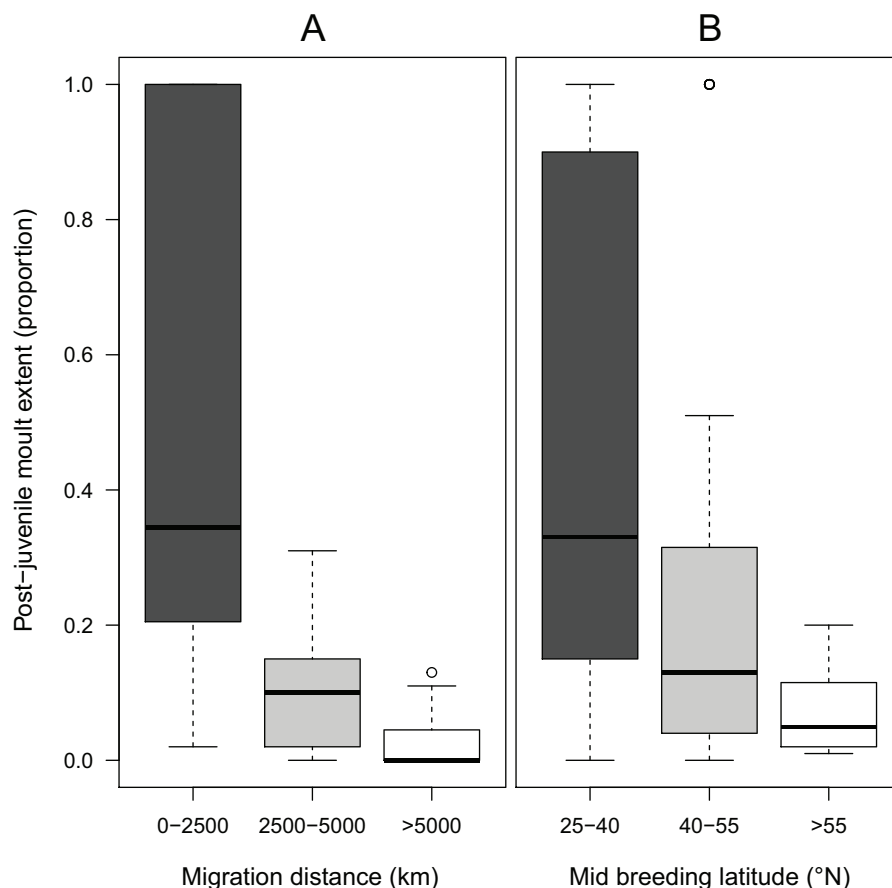


Figure 3: Effects of migration distance (A) and breeding latitude (B) on the extent of postjuvenile molt. The box plots display the fifth, twenty-fifth, fiftieth (median), seventy-fifth, and ninety-fifth percentiles of the data of each category.

enhance the understanding of structural, functional, and life-history trade-offs in birds.

Time constraints, which may be caused by various biotic and abiotic factors, represent an important ecological burden for many organisms (Dunbar et al. 2009). They may affect life-history traits, annual-routine timing, and animal behaviors such as foraging patterns (Lewis et al. 2004), sexual selection (Backwell and Passmore 1996), parental care (Rauter and Moore 2004), and body growth rate (De Block and Stoks 2004) as well as body size, maturation age, and willingness to take risks (Johansson and Rowe 1999). Here, we suggest that passerines developed specific adaptations to deal with time constraints on a major life-history process, namely, the summer feather molt. These adaptations include the shortening of molt duration, the postponement of the molt, and the execution of only a partial, rather than a complete, molt. The implications of these adaptations could be substantial. For example, rapid molt by adults may promote risk-taking behavior during foraging to meet the elevated metabolic demands of the

molt process. Moreover, the energy cost of flight may be additionally increased because of the larger feather gaps that are created during a fast molt (Haukioja 1971; Hedenström and Sunada 1999; Bridge 2003; Hedenström 2003; but see Chai 1997).

A different consequence of time constraints on the feather molt process is related to the allocation of resources in the synthesis of newly grown feathers. It has been found that molt under time stress, in which feathers grow more rapidly, results in low-quality feathers, compared to those grown over a relatively longer time period (Dawson et al. 2000; Hall and Fransson 2000; Serra 2001; Dawson 2004; Serra et al. 2007). This may affect feather functionality and, in extreme cases, may even necessitate undertaking another molt cycle, as in *P. trochilus* (de la Hera et al. 2010). It appears that there is a limit on the rate at which birds can grow individual feathers, and there is surprisingly little variation across species of different size with regard to feather growth rate, which implies that most birds generate feather tissue as fast as they possibly can (Rohwer et al.

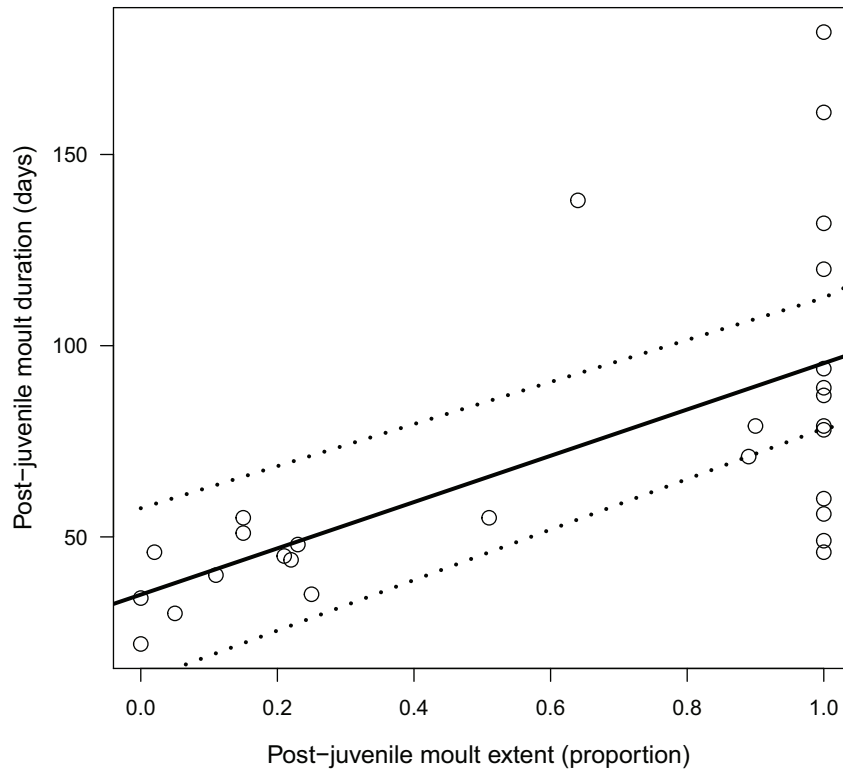


Figure 4: Effect of the extent of molt on the duration of postjuvenile molt ($n = 28$ species; $P < .001$). Dashed curves represent the 95% confidence interval of the linear regression.

2009; Rohwer and Rohwer 2013). Birds can increase their overall rate of feather replacement by growing more feathers simultaneously, but it may be this fundamental limit on individual feather growth, along with the need to maintain enough wing surface for flight (Kiat et al. 2016), that determines the minimum molt period for many species. This idea is an alternative to the notion that molt is limited by constraints on resource acquisition.

Age-related differences in behavior, physiology, and life-history transitions may be the outcome of various selection pressures affecting movement patterns, responses to environmental variability, mortality, and reproduction (e.g., Holberton and Able 2000; Berkeley et al. 2004; Bowen et al. 2006; Descamps et al. 2006; Weladji et al. 2006; van den Hout et al. 2008). Time stressors, which affect juvenile and adult animals differently, may consequently modulate the properties of major annual routine processes in various organisms. Our findings highlight age-related differences in molt properties in songbirds, specifically suggesting that, as opposed to adults, time-constrained juveniles do not molt their entire plumage, likely because they cannot obtain sufficiently high food intake rates required to increase their speed of molt. Indeed, in species

that undertake a complete postjuvenile molt, juveniles molt relatively slowly, compared with adults that undergo a complete molt at an approximately similar time of year (Kiat and Izhaki 2016b). Energy budgets of animals are potentially limited by several factors, including the available feeding time and the metabolic capacity of the animal (Hammond and Diamond 1997). In our case, limits on energy budgets, probably resulting from poor foraging capabilities of juvenile birds, had a decisive role in shaping bird evolutionary response to time constraints in relation to feather molt. Our findings suggest that two different adaptations to mitigate time constraints have evolved in passerines and that they are employed according to bird age.

Acknowledgments

We thank M. Adams and H. van Grouw, from the Natural History Museum at Tring, and D. Berkowic, from the Steinhardt National Collections of Natural History, Zoological Museum, Tel-Aviv University, for facilitating the measurements of museum specimens, and S. Meiri for his help with phylogenetic analysis.

APPENDIX

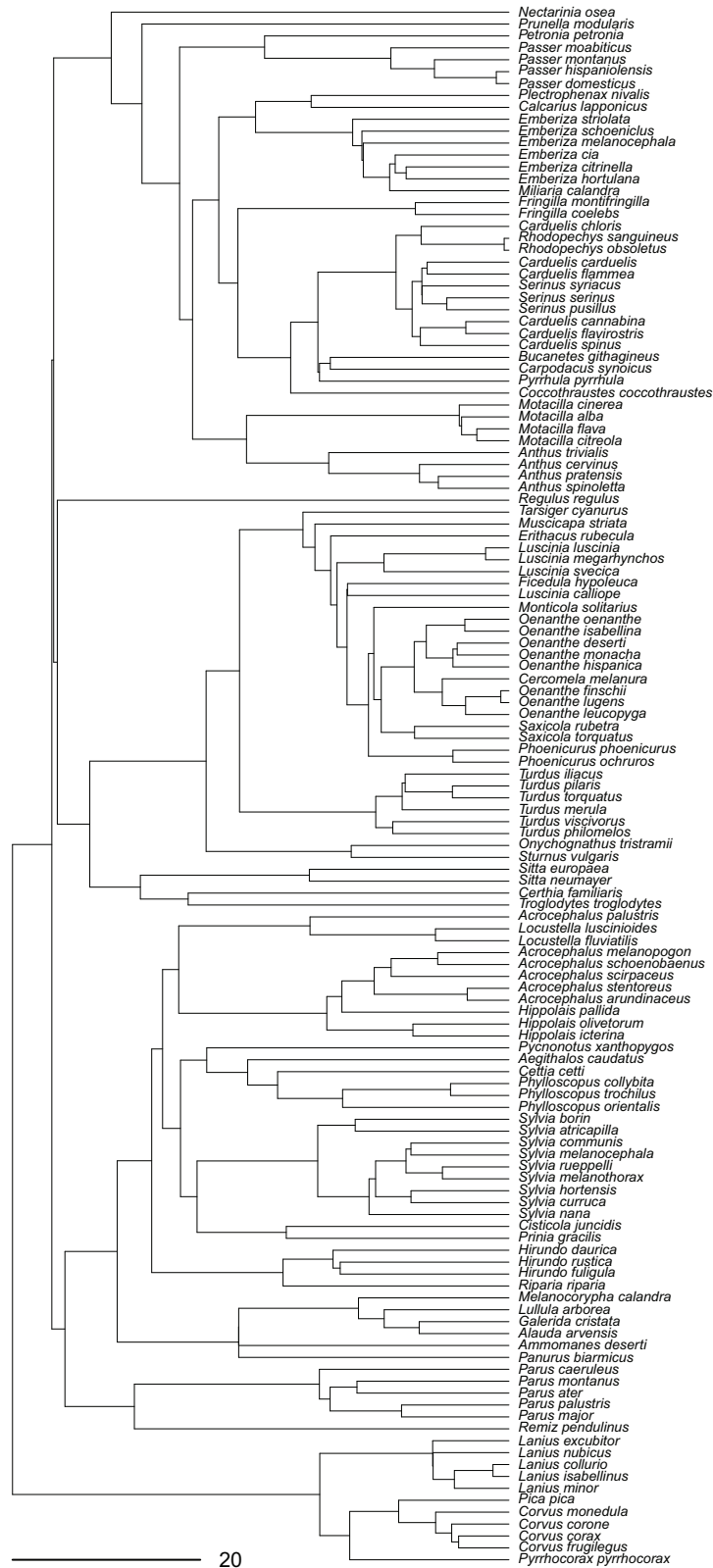


Figure A1: Phylogenetic tree for the 134 species included in the analysis.

Literature Cited

- Abrams, P. A., O. Leimar, S. Nylin, and C. Wiklund. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *American Naturalist* 381–395.
- Backwell, P. R. Y., and N. I. Passmore. 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behavioral Ecology and Sociobiology* 38:407–416.
- Barta, Z., A. I. Houston, J. M. McNamara, R. K. Welham, A. Hedenström, T. P. Weber, and O. Feró. 2006. Annual routines of non-migratory birds: optimal moult strategies. *Oikos* 112:580–593.
- Barta, Z., J. M. McNamara, A. I. Houston, T. P. Weber, A. Hedenström, and O. Feró. 2008. Optimal moult strategies in migratory birds. *Philosophical Transactions of the Royal Society B* 363:211–229.
- Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85:1258–1264.
- BirdLife International and NatureServe. 2014. Bird species distribution maps of the world. BirdLife International, Cambridge, and NatureServe, Arlington, VA.
- Bojarinova, J. G., E. Lehtikoinen, and T. Eeva. 1999. Dependence of postjuvenile moult on hatching date, condition and sex in the great tit. *Journal of Avian Biology* 30:437–446.
- Bowen, W. D., S. J. Iverson, J. I. McMillan, and D. J. Boness. 2006. Reproductive performance in grey seals: age-related improvement and senescence in a capital breeder. *Journal of Animal Ecology* 75:1340–1351.
- Bridge, E. S. 2003. Effects of simulated primary moult on pigeon flight. *Ornis Fennica* 80:121–129.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.
- Carrascal, L. M., and V. Polo. 2006. Effects of wing area reduction on winter body mass and foraging behaviour in coal tits: field and aviary experiments. *Animal Behaviour* 72:663–672.
- Chai, P. 1997. Hummingbird hovering energetics during moult of primary flight feathers. *Journal of Experimental Biology* 200:1527–1536.
- Dawson, A. 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in common starlings *Sturnus vulgaris*. *Ibis* 146:493–500.
- Dawson, A., S. A. Hinsley, P. N. Ferns, R. H. C. Bonser, and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society B* 267:2093–2098.
- De Block, M., and R. Stoks. 2004. Life-history variation in relation to time constraints in a damselfly. *Oecologia (Berlin)* 140:68–75.
- de la Hera, I., D. F. DeSante, and B. Milá. 2012. Feather growth rate and mass in Nearctic passerines with variable migratory behavior and molt pattern. *Auk* 129:222–230.
- de la Hera, I., J. A. Díaz, J. Pérez-Tris, and J. L. Tellería. 2009a. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. *Journal of Avian Biology* 40:461–465.
- de la Hera, I., J. Pérez-Tris, and J. L. Tellería. 2009b. Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. *Biological Journal of the Linnean Society* 97:98–105.
- . 2010. Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines. *Journal of Avian Biology* 41:609–614.
- Descamps, S., S. Boutin, D. Berteaux, and J.-M. Gaillard. 2006. Best squirrels trade a long life for an early reproduction. *Proceedings of the Royal Society B* 273:2369–2374.
- Dunbar, R. I. M., A. H. Korstjens, and J. Lehmann. 2009. Time as an ecological constraint. *Biological Reviews* 84:413–429.
- Dunning, J. B., Jr., ed. 1992. CRC handbook of avian body masses. CRC, Boca Raton, FL.
- Echeverry-Galvis, M. A., and M. Hau. 2013. Flight performance and feather quality: paying the price of overlapping moult and breeding in a tropical highland bird. *PLoS ONE* 8(5):e61106. doi:10.1371/journal.pone.0061106.
- English, S., A. W. Bateman, R. Mares, A. Ozgul, and T. H. Clutton-Brock. 2014. Maternal, social and abiotic environmental effects on growth vary across life stages in a cooperative mammal. *Journal of Animal Ecology* 83:332–342.
- Erni, B., B. T. Bonnevie, H.-D. Oschadleus, R. Altwegg, and L. G. Underhill. 2012. moult: an R package to analyse moult in birds. *Journal of Statistical Software* 52(8). doi:10.18637/jss.v052.i08.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114:307–343.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* 160:712–726.
- Ginn, H. B., and D. S. Melville. 1983. Moult in birds. BTO Guide, no. 19. British Trust for Ornithology, Tring.
- Gotthard, K., S. Nylin, and C. Wiklund. 1999. Seasonal plasticity in two satyrine butterflies: state-dependent decision making in relation to daylength. *Oikos* 84:453–462.
- Hall, K. S. S., and T. Fransson. 2000. Lesser whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. *Journal of Avian Biology* 31:583–587.
- Hall, K. S. S., and B. S. Tullberg. 2004. Phylogenetic analyses of the diversity of moult strategies in Sylviidae in relation to migration. *Evolutionary Ecology* 18:85–105.
- Hammond, K. A., and J. Diamond. 1997. Maximal sustained energy budgets in humans and animals. *Nature* 386:457–462.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18.
- Haukioja, E. 1971. Flightlessness in some moulting passerines in northern Europe. *Ornis Fennica* 48:101–116.
- Hedenström, A. 2003. Flying with holey wings. *Journal of Avian Biology* 34:324–327.
- . 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B* 363:287–299.
- Hedenström, A., and S. Sunada. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology* 202:67–76.
- Hemborg, C., and A. Lundberg. 1998. Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. *Behavioral Ecology and Sociobiology* 43:19–23.
- Hemborg, C., A. Lundberg, and P. Siikamäki. 1998. Trade-off between reproduction and moult—a comparison of three Fennoscandian pied flycatcher populations. *Oecologia (Berlin)* 117:374–380.

- Holberton, R. L., and K. P. Able. 2000. Differential migration and an endocrine response to stress in wintering dark-eyed juncos (*Junco hyemalis*). *Proceedings of the Royal Society B* 267:1889–1896.
- Holmgren, N., and A. Hedenström. 1995. The scheduling of molt in migratory birds. *Evolutionary Ecology* 9:354–368.
- Houston, A. I., and J. M. McNamara. 1999. *Models of adaptive behaviour: an approach based on state*. Cambridge University Press, Cambridge.
- Jenni, L., and R. Winkler. 1994. *Moult and ageing of European passerines*. A & C Black, London.
- Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. *Nature* 491:444–448.
- Johansson, F., and L. Rowe. 1999. Life history and behavioral responses to time constraints in a damselfly. *Ecology* 80:1242–1252.
- Kiat, Y., and I. Izhaki. 2016a. Moult strategies affect age differences in autumn migration timing in East Mediterranean migratory passerines. *PLoS ONE* 11(1):e0147471. doi:10.1371/journal.pone.0147471.
- . 2016b. Why renew fresh feathers? advantages and conditions for the evolution of complete post-juvenile moult. *Journal of Avian Biology* 47:47–56.
- Kiat, Y., I. Izhaki, and N. Sapir. 2016. Determinants of wing-feather moult speed in songbirds. *Evolutionary Ecology* 30:783–795.
- Kiat, Y., and N. Sapir. 2017. Data from: Age-dependent modulation of songbird summer feather molt by temporal and functional constraints. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.q31s0>.
- Kjellén, N. 1994. Moult in relation to migration in birds—a review. *Ornis Svecica* 4:1–24.
- Langston, N. E., and S. Rohwer. 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. *Oikos* 76:498–510.
- Lewis, S., E. A. Schreiber, F. Daunt, G. A. Schenk, S. Wanless, and K. C. Hamer. 2004. Flexible foraging patterns under different time constraints in tropical boobies. *Animal Behaviour* 68:1331–1337.
- Lindström, Å., G. H. Visser, and S. Daan. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiological Zoology* 66:490–510.
- Marchetti, K., and T. Price. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological Reviews* 64:51–70.
- Marshall, D. J., and S. G. Morgan. 2011. Ecological and evolutionary consequences of linked life-history stages in the sea. *Current Biology* 21:R718–R725.
- Mason, G. J. 2010. Species differences in responses to captivity: stress, welfare and the comparative method. *Trends in Ecology and Evolution* 25:713–721.
- McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. *Nature* 380:215–221.
- . 2008. Optimal annual routines: behaviour in the context of physiology and ecology. *Philosophical Transactions of the Royal Society B* 363:301–319.
- McNamara, J. M., R. K. Welham, and A. I. Houston. 1998. The timing of migration within the context of an annual routine. *Journal of Avian Biology* 29:416–423.
- Murphy, M. E., and J. R. King. 1992. Energy and nutrient use during moult by white-crowned sparrows *Zonotrichia leucophrys gambelii*. *Ornis Scandinavica* 23:304–313.
- Newton, I. 2009. Moult and plumage. *Ringing and Migration* 24: 220–226.
- O'Connor, C. M., D. R. Norris, G. T. Crossin, and S. J. Cooke. 2014. Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere* 5(3):28. doi:10.1890/ES13-00388.1.
- Orme, D. 2013. *caper: comparative analysis of phylogenetics and evolution in R*. R package, version 5. <http://caper.r-forge.r-project.org/>.
- Pagel, M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26:331–348.
- Rauset, G. R., M. Low, and J. Persson. 2015. Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. *Ecology* 96:3153–3164.
- Rauter, C. M., and A. J. Moore. 2004. Time constraints and trade-offs among parental care behaviours: effects of brood size, sex and loss of mate. *Animal Behaviour* 68:695–702.
- Rohwer, S., L. K. Butler, D. R. Froehlich, R. Greenberg, and P. P. Marra. 2005. Ecology and demography of east-west differences in molt scheduling of Neotropical migrant passerines. Pages 87–105 in R. Greenberg and P. P. Marra, eds. *Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins University Press, Baltimore.
- Rohwer, S., R. E. Ricklefs, V. G. Rohwer, and M. M. Copple. 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biology* 7(6):e1000132. doi:10.1371/journal.pbio.1000132.
- Rohwer, V. G., and S. Rohwer. 2013. How do birds adjust the time required to replace their flight feathers? *Auk* 130:699–707.
- Rowe, L., D. Ludwig, and D. Schluter. 1994. Time, condition, and the seasonal decline of avian clutch size. *American Naturalist* 143: 698–722.
- Rubolini, D., A. Liker, L. Z. Garamszegi, A. P. Møller, and N. Saino. 2015. Using the BirdTree.org website to obtain robust phylogenies for avian comparative studies: a primer. *Current Zoology* 61:959–965.
- Rymkevich, T. A., and J. G. Bojarinova. 1996. Variation in the extent of postjuvenile moult in the great tit near Lake Ladoga (Russia). *Bird Study* 43:47–59.
- Saino, N., M. Romano, D. Rubolini, R. Ambrosini, A. Romano, M. Caprioli, A. Costanzo, and G. Bazzi. 2014. A trade-off between reproduction and feather growth in the barn swallow (*Hirundo rustica*). *PLoS ONE* 9(5):e96428. doi:10.1371/journal.pone.0096428.
- Schieltz, P. C., and M. E. Murphy. 1997. The contribution of insulation changes to the energy cost of avian molt. *Canadian Journal of Zoology* 75:396–400.
- Serra, L. 2001. Duration of primary moult affects primary quality in grey plovers *Pluvialis squatarola*. *Journal of Avian Biology* 32: 377–380.
- Serra, L., M. Griggio, D. Licheri, and A. Pilastro. 2007. Moult speed constrains the expression of a carotenoid-based sexual ornament. *Journal of Evolutionary Biology* 20:2028–2034.
- Siikamäki, P., M. Hovi, and O. Rätti. 1994. A trade-off between current reproduction and moult in the pied flycatcher—an experiment. *Functional Ecology* 8:587–593.
- Svensson, E., and A. Hedenström. 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.
- Svensson, E., and J.-Å. Nilssen. 1997. The trade-off between molt and parental care: a sexual conflict in the blue tit? *Behavioral Ecology* 8:92–98.
- Underhill, L. G., R. P. Prys-Jones, R. J. Dowsett, P. Herroelen, D. N. Johnson, M. R. Lawn, S. C. Norman, D. J. Pearson, and A. J. Tree.

1992. The biannual primary moult of willow warblers *Phylloscopus trochilus* in Europe and Africa. *Ibis* 134:286–297.
- Underhill, L. G., and W. Zucchini. 1988. A model for avian primary moult. *Ibis* 130:358–372.
- van den Heuvel, J., M. Saastamoinen, P. M. Brakefield, T. B. L. Kirkwood, B. J. Zwaan, and D. P. Shanley. 2013. The predictive adaptive response: modeling the life-history evolution of the butterfly *Bicyclus anynana* in seasonal environments. *American Naturalist* 181:E28–E42.
- van den Hout, P. J., B. Spaans, and T. Piersma. 2008. Differential mortality of wintering shorebirds on the Banc d’Arguin, Mauritania, due to predation by large falcons. *Ibis* 150(suppl. 1):219–230.
- Varpe, Ø. 2012. Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. *Journal of Plankton Research* 34:267–276.
- Weladji, R. B., J.-M. Gaillard, N. G. Yoccoz, Ø. Holand, A. Mysterud, A. Loison, M. Nieminen, and N. C. Stenseth. 2006. Good reindeer mothers live longer and become better in raising offspring. *Proceedings of the Royal Society B* 273:1239–1244.
- Wingfield, J. C. 2008. Organization of vertebrate annual cycles: implications for control mechanisms. *Philosophical Transactions of the Royal Society B* 363:425–441.

Natural History Editor: Mark A. McPeck



Eurasian crimson-winged finch (*Rhodopechys sanguineus*): young male after partial postjuvenile molt. Photo credit: Yosef Kiat.