

**WHY RENEW FRESH FEATHERS? ADVANTAGES AND CONDITIONS
FOR THE EVOLUTION OF COMPLETE POST-JUVENILE MOULT**

YOSEF KIAT¹ & IDO IZHAKI²

¹Israeli Bird Ringing Center, Society for the Protection of Nature in Israel. Bercha,
Doar-Naa Lev-Hashomron POB 257, 44835, Israel.

²Department of Evolutionary and Environmental Biology, University of Haifa, Haifa
3498838, Israel.

Corresponding author: Yosef Kiat, Israeli Bird Ringing Center, Society for the
Protection of Nature in Israel. Bercha, Doar-Naa Lev-Hashomron POB 257, 44835,
Israel. Email: yosefkiat@gmail.com.

Decision date: 10-Jun-2015

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/jav.00717].

SUMMARY

Juveniles of several passerine species renew all of their fresh juvenile feathers immediately after fledging (complete post-juvenile moult), in contrast to the majority, which perform a partial post-juvenile moult. To understand the adaptive roles of this phenomenon we compared the quality of juvenile plumage in species that perform a complete post-juvenile moult with that of species which perform a partial post-juvenile moult; we similarly compared juveniles and adults in each of these groups. The quality of feathers was measured by mass of primaries, colour, and length. In species which perform a complete post-juvenile moult the plumage quality of second-year individuals, in their first breeding season, is similar to the plumage quality of adults, unlike those species that perform a partial post-juvenile moult. In species which perform complete post-juvenile moult, the quality of the feathers grown in the nest is lower than the quality of adult post-breeding feathers. In contrast, in species which perform partial post-juvenile moult the quality of the feathers grown in the nest is similar to that of adult post-breeding feathers. We found that a complete post-juvenile moult strategy is much more common (1) in residents and short-distance migrants than in long-distance migrants, (2) in southern latitudes, (3) in species with medium body mass and (4) in omnivores and granivores. Our results indicate two adaptive roles of the complete post-juvenile moult strategy: (I) achieving high quality plumage in the first year which may increase individual survival probability and fitness and (II) allocating fewer resources to nestling plumage and more to nestling development, which enables the nestlings to leave the nest earlier, thus reducing the probability of encountering nest predators. We suggest that the complete post-juvenile moult, immediately after fledging, is an optimal strategy in favourable habitats and under low time constraints, as in some tropical ecosystems.

Key Words: post-juvenile moult, annual cycle, plumage quality, migration distance

INTRODUCTION

The renewal of flight and body feathers is necessary to ensure future survival because old feathers are abraded and worn due to behavioural activities, exposure to sunshine, and from other environmental factors. All adult passerines moult all of their flight feathers at least once each year. This moult occurs after breeding at the breeding grounds, or in some long-distance migrants, it is delayed and occurs in the tropical wintering areas, when the plumage is at its most abraded stage (Jenni & Winkler 1994, Newton 2009).

Newton (1966) noted that juvenile body feathers differ from those of adult in that they are weaker, looser in texture, and of a different colour. Jenni & Winkler (1994) also noted that juvenile body feathers are looser in texture than adult plumage; the juvenile feathers are lighter in colour than in adults, and in a few species, the juvenile body feathers are of relatively looser texture than those of juveniles of most other species. Whether juvenile remiges of Western Palaearctic passerines are also more loosely textured than those of adults has not thoroughly been studied, but visual inspection showed no conspicuous differences (Jenni & Winkler 1994). Fogden (1972) reported that in the tropical zone (Borneo), in contrast to European passerines, the entire plumage of juveniles of many species appeared to be of poorer quality than that of adults. Individual remiges and rectrices of juveniles were found to be as much as 30% lighter than corresponding feathers in adults. The juveniles' primaries are also slightly shorter on average than adults' primaries, with the exception of the juvenile outermost primary which in many species is longer than in adults; hence juveniles' wings are

often slightly more rounded than those of adults (Stewart 1963, Alatalo et al. 1983, Jenni & Winkler 1994).

Feather keratin is composed of twisted β -sheet rather than α -helix keratin. Melanic keratin has properties that make it more capable of resisting abrasive wear than non-melanic keratin (Bonser 1996). An increase in melanin is associated with a reduction of feather wear due to abrasion (Burt 1986). Kose & Moller (1999) found that white spots of *Hirundo rustica* tail feathers, lacking melanin, were more often found to be the site of feather breakage than the melanic parts of feathers of similar widths. In addition, the white tail spots were the preferred feeding site of the feather-eating lice, Mallophaga.

The juveniles of most passerines species replace their juvenile plumage sometime between a few weeks and a few months after fledging. The first renewal of the plumage is a post-juvenile moult which is of variable extent and may include only some body feathers. In most Western Palaearctic species, this moult includes coverts, tertials, and tail feathers and is defined as a partial post-juvenile moult (Stresemann & Stresemann 1966, Ginn & Melville 1983, Jenni & Winkler, 1994). In this moult strategy, the juvenile remiges are kept either for about a year, until the first post-breeding moult, or in long-distance migrants moulting in tropical wintering grounds, for about six months, until the first pre-breeding moult.

The less frequent strategy in the Western Palaearctic zone is a complete post-juvenile moult soon after fledging (Ginn & Melville 1983, Svensson 1992, Jenni & Winkler, 1994). Here the birds renew all plumage one to three months after fledging, during the summer/autumn, in the breeding area or nearby (Gauci & Sultana 1979, Ginn &

Melville 1983, Jenni & Winkler 1994). Jenni & Winkler (1994) noted that it is not clear why some species perform a complete post-juvenile moult. They also noted that this strategy appears to stem from phylogenetic relationships, and all European species of the Alaudidae, Passeridae, Sturnidae, Timaliidae and Aegithalidae perform it.

Fogden (1972) associated the lighter and poorer quality of juvenile plumage of species that perform a complete post-juvenile with the juvenile moult strategy in species breeding in the Borneo tropical zone. He suggested that nestlings presumably need less food to grow such feathers, and this might reduce the nestling period. Rapid nestling developmental rates and early nest leaving are probably the outcome of selective predation pressure. Thus, a slight shortening of the time spent in the nest might be adaptive in light of the very high rate of nest predation. The poorer quality of juvenile plumage necessitates a complete moult soon after the juvenile leaves the nest, presumably because such feathers are too weak to last a full year. Nevertheless, it has still not been shown whether the juvenile remiges are really less durable than those of adults, and whether the juvenile plumage's remiges of species with a complete post-juvenile moult are less durable than those of species with a partial moult strategy (Jenni & Winkler 1994). Therefore, here we compare the plumage quality of juveniles versus adults of the same species and of juveniles of species which perform a complete post-juvenile moult with those of species which perform a partial post-juvenile moult and undergo their first complete moult only after the first autumn migration or first breeding season.

However, we suggest that the early nest leaving is not the only adaptive role of the complete post-juvenile moult. We hypothesize that an important adaptive role of the complete post-juvenile moult strategy is to reduce the disparity between the juvenile and adult plumage quality in the cold season and in the breeding season. The juveniles which belong to species which utilize this strategy produce more efficient plumage in the first pre-breeding period by renewal of the whole plumage concurrent with adults performing their post-breeding moult. Achieving high quality plumage in the first year may decrease the differences of remige quality between adults and juveniles, and thus, may increase juvenile survival probability and fitness. In previous studies the difference between juveniles and adults in remige quality was not measured but described only by human eye (Jenni & Winkler 1994). Here we measured this difference. We posited that the difference between juvenile plumage and adult plumage in remige quality must be more significant in species which perform complete post-juvenile moult than in species that perform partial post-juvenile moult. But, after the complete post-juvenile/breeding moult, in winter and pre-breeding period, the difference between first year individual plumage and adult plumage in remige quality must be more significant in species which perform partial post-juvenile moult than in species that perform complete post-juvenile moult. The difference would be characterized by the remiges' melanic keratin rate, the remiges' mass, and the primaries' lengths.

We expected that the complete post-juvenile moult strategy evolved only in environments/regions with conditions that support a long moult period after the breeding season. We thus tested the conditions that affected the time available for adults to complete their post-breeding moult. Previous studies showed that long

migration distance and/or low body mass result in a relatively short moult duration (Jenni & Winkler 1994, de la Hera et al. 2009). In the current paper we examine the main constraints on time availability for moult including migration strategy, breeding latitude, body mass, and diet.

We expected to find the complete post-juvenile moult more common in residents or short-distance migratory species than in long-distance migrants. Species that breed in northern latitudes have only a short time to moult owing to low food availability and short daylight hours for feeding (Ginn & Melville 1983). Accordingly, we expected to find the complete post-juvenile moult strategy to be more common in southern latitude regions with longer summers and less extreme winters. Carrascal & Polo (2006) and de la Hera et al. (2009) noted that body mass has an independent effect on moult duration. Accordingly, passerines with high body mass need more time to moult than species with low body mass. We expected that the complete post-juvenile moult would be more common in species with a relatively low body mass. Mead, mentioned in Ginn & Melville (1983), noted that for British species, a complete post-juvenile moult occurs in species whose young are largely fed on a vegetarian diet such as the Corn Bunting, *Emberiza calandra*. He suggested that such a diet may be deficient in amino-acids essential for the development of strong plumage. However, the majority of those species were actually largely found to feed their nestlings arthropods (Ginn & Melville 1983). Lastly, time availability for moult also depends on food quality during the breeding period. For example, arthropod availability decreases earlier than vegetarian food items like seeds. Thus, we expected a complete post-juvenile moult strategy to be more common in granivores than in insectivores.

Taking into the account that (I) time is the main constraint for the evolution of the complete post-juvenile moult strategy, and (II) in most species which perform a partial post-juvenile moult, the adults perform a complete post-breeding moult in same period; we predict that adults will perform moulting at a higher speed than juveniles. Thus, for many species, the time available for adults to undertake a complete post-breeding moult is not long enough for juvenile to perform a complete moult. Therefore, we compared the moulting speed between adults and juveniles to demonstrate the difference in time needed for juveniles and adults to complete their moult, in species which perform a complete post-juvenile moult.

Here we address two main questions: (I) What is the benefit of a complete post-juvenile moult strategy compared to a partial post-juvenile moult? (II) Assuming that a complete post-juvenile moult is an adaptive attribute, why is this moult strategy not more widespread among other bird species? To answer this question we examined the conditions in which this strategy has an advantage and fitness benefits over the partial post-juvenile moult strategy. We intend to demonstrate that (I) the result of the renewal of whole juvenile plumage after leaving the nest is high quality plumage, and (II) time constraints limit the evolution of this moult strategy to only a few passerine species in the Western Palaearctic zone.

METHODS

Relationship between juvenile moult strategy and primaries worn away in the pre-breeding period

Worn feathers fade and lose their colours. The relationship between juvenile moult strategy and primaries worn away in the pre-breeding period was measured by spectrometer (X-Rite II Pro spectrometer, range 380-730 nm), as described by Vortman et al. (2011), on bird skins in the Steinhardt National Collections of Natural History, Zoological Museum, Tel Aviv University. To improve sampling, for each skin we measured the colour at three random points on the primaries. Our colour scoring was based on the RGB (red-green-blue value) colour space. When feathers' chromatic elements were scored on the RG (red-green) average, the flight feathers were characterized by these colours (Vortman et al. 2011). Although our aim here was to compare feather quality between juveniles and adults, there is no way to distinguish between juveniles and adults of the complete moult in the pre-breeding period. Therefore we randomly sampled individuals of nine resident or short-distance species of both moult strategies in the pre-breeding period (February to April) such that both ages (juveniles and adults) were likely included in the sample. The partial post-juvenile moult species were *Oenanthe lugens* (n = 9), *Lanius excubitor* (n = 16), *Onychognathus tristramii* (n = 17) and *Carduelis carduelis* (n = 18); the complete post-juvenile moult species were *Galerida cristata* (n = 18), *Ammomanes deserti* (n = 24), *Pycnonotus xanthopygos* (n = 23), *Passer domesticus* (n = 23) and *Emberiza calandra* (n = 19).

Because the spectrum of feather colour is different between species we used the coefficient of variation (CV) to standardized and make the colour values comparable

among species. Because sample size affects the CV we randomly selected the same number of individuals ($n = 9$) from each species sample. This number was chosen because this was the minimum sample size of one of the species (*Oenanthe lugens*).

Comparison of plumage quality for each of the two moult strategies

The change in plumage quality from juvenile to post-juvenile was defined as Δ -plumage, calculated as:

$$\Delta p = \frac{(A_p - J_p)}{A_p}$$

Where J_p is juvenile plumage grown in the nest before fledgling and A_p is a feather which grows during post-juvenile moult or later (adult plumage). Δ -plumage (Δp) was calculated for three different parameters related to plumage quality: primaries' lengths, mass and colours. All feathers were sampled within one month of the end of their growth. Juvenile feathers were sampled immediately after nest leaving and post-juvenile feathers were sampled immediately after the end of the complete moult.

Primaries' lengths

We measured the maximum wing length in ringing sessions in Israel during 2006-2014. Maximum wing length measurements were taken by flattening the camber and straightening the lateral curvature of wing, with precision of 0.5 mm. The main component of the wing length is the primaries' lengths. The lengthening of the wing after leaving the nest, is caused only by the replacement of shorter primaries with longer primaries (Ginn & Melville 1983).

Primaries' lengths were measured for 25 resident or short-distance migrant species in Israel of both moult strategies. We measured 14 species with partial post-juvenile

moult strategy: *Anthus pratensis* (n = 623), *Motacilla alba* (n = 1186), *Erithacus rubecula* (n = 222), *Luscinia svecica* (n = 1085), *Saxicola torquata* (n = 162), *Turdus philomelos* (n = 146), *Turdus merula* (n = 259), *Cettia cetti* (n = 592), *Phylloscopus collybita* (n = 1359), *Parus major* (n = 173), *Remiz pendulinus* (n = 103), *Fringilla coelebs* (n = 1393), *Fringilla montifringilla* (n = 50) and *Serinus serinus* (n = 115) and 11 species with a complete post-juvenile moult strategy: *Galerida cristata* (n = 82), *Ammomanes deserti* (n = 96), *Lullula arborea* (n = 32), *Pycnonotus xanthopygos* (n = 533), *Acrocephalus stentoreus* (n = 155), *Acrocephalus melanopogon* (n = 77), *Petronia petronia* (n = 129), *Passer domesticus* (n = 84), *Passer hispaniolensis* (n = 182), *Passer moabiticus* (n = 84) and *Emberiza calandra* (n = 125).

Feather mass

We collected one primary (P₆) from 128 juvenile and 117 post-juvenile/breeding plumage individuals of six resident species in Israel. Three of them use a partial post-juvenile moult strategy, *Turdus merula* (n = 38), *Cettia cetti* (n = 57) and *Parus major* (n = 27), and the other three, *Pycnonotus xanthopygos* (n = 43), *Acrocephalus stentoreus* (n = 42, and *Passer domesticus* (n = 38), have a complete post-juvenile moult strategy. We weighed the feathers using an analytical digital balance (Ohaus Pioneer PA-64) with precision of 0.1 mg. We normalized feather mass by dividing the mass by feather length.

Primaries' colour

The primaries' colour measurements were also taken on bird skins by the spectrometer method as detailed above. This parameter was measured for 19 species resident to Israel or that were short-distance migrants. Colour was measured in ten species with a

partial post-juvenile moult strategy, *Anthus pratensis* (n = 10), *Motacilla alba* (n = 11), *Luscinia svecica* (n = 10), *Turdus philomelos* (n = 10), *Turdus merula* (n = 10), *Parus major* (n = 10), *Serinus serinus* (n = 10), *Carduelis carduelis* (n = 10), *Carduelis chloris* (n = 11) and *Emberiza schoeniclus* (n = 10), and in nine species with a complete post-juvenile moult strategy, *Galerida cristata* (n = 17), *Lullula arborea* (n = 12), *Eremophila alpestris* (n = 14), *Alaemon alaudipes* (n = 10), *Pycnonotus xanthopygos* (n = 11), *Sturnus vulgaris* (n = 12), *Passer domesticus* (n = 14), *Passer moabiticus* (n = 12) and *Emberiza calandra* (n = 13).

Moult speed

The data of an active primaries moult were collected during the post-breeding/post-juvenile moult. We used the primary score (PS) method to describe the state of each primary on a scale of 0 to 5 (Ginn & 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 the sheath up to the length of one third of a fully grown feather, 3 - a new feather with a length between one and two thirds of a fully grown feather, 4 - a new feather that is more than two thirds the length of a fully grown feather and with remains of waxy sheath at its base, and 5 - a new, fully developed feather with no traces of remaining waxy sheath at its base. To estimate the moult speed of each individual, we used the residual raggedness value (RRV) method (Bensch & Grahn 1993). This method estimates the size of the feather gap in the wing that is created by moult, and respectively the individual moult speed. The RRV is the inverse value of PS for each of the wing's nine primaries (P₁-P₉), such that when PS = 1, RRV = 4, and when PS = 2, RRV = 3, etc., but for PS = 0, RRV = 0 as well (because there is no gap when the feather is in both the PS = 0 and PS = 5 stages). To

reliably study birds during active primary moult, we calculated the RRV only for individuals with a fully grown P_1 ($PS = 5$) and an old P_9 ($PS = 0$). We did so by summing up the RRV from all of the primary feathers. This was done to avoid calculating a biased estimate of the primary moult speed in cases where the feather gap is not confined within the surface of the wing that consist all of the primaries. This estimate is consequently independent of bird size and morphology and allows for reliable cross-species comparison (Bensch & Grahn 1993).

We collected active moult data on 10 species which performed a complete post-juvenile moult in Israel during 2006 - 2014: *Hirundo rustica transitiva* (n = 502 juveniles, 137 adults), *Ammomanes deserti* (n = 13 juveniles, 26 adults), *Pycnonotus xanthopygos* (n = 114 juveniles, 14 adults), *Prinia gracilis* (n = 85 juveniles, 11 adults), *Acrocephalus stentoreus* (n = 47 juveniles, 16 adults), *Nectarinia osea* (n = 25 juveniles, 5 adults), *Passer domesticus* (n = 24 juveniles, 21 adults), *Passer moabiticus* (n = 76 juveniles, 21 adults), *Carduelis carduelis* (n = 9 juveniles, 18 adults) and *Carduelis cannabina* (n = 8 juveniles, 43 adults).

Juvenile moult strategy with regard to migration distance, breeding latitude, body mass and diet

We evaluated the conditions that may limit time availability for the adults to complete post-breeding moult in 269 species that breed in the Western Palaearctic zone. Information on migration distance, breeding latitude, body mass and diet, together with the juvenile moult strategy, was drawn from published literature (Ginn & Melville 1983, Cramp et al. 1988-1994, Jenni & Winkler 1994, Shirihai et al. 2001, Dunning 2008, Kennerley & Pearson 2010).

We categorized each species as either a complete or partial post-juvenile moult, as a resident, short-distance or long-distance migrant, and also by its main diet as herbivorous/granivorous, insectivorous or omnivorous. For each species we noted the average body mass and the entire latitudinal breeding distribution range. The percentage of species that perform complete post-juvenile moult was calculated for every latitude.

Phylogenetic analysis

Species traits are known to be phylogenetically conserved (Felsenstein 1985). To account for phylogenetic non-independence we conducted all relevant analyses using phylogenetic generalized least square (PGLS) regression (Freckleton et al. 2002). All phylogenetically controlled analyses were performed in R (v. 3.1.3; R Development Core Team 2014). We corrected the branch lengths of the phylogenetic tree using the maximum likelihood value of the scaling parameter λ (Pagel 1997) implemented in the R package 'caper' (Orme 2013).

RESULTS

Relationship between juvenile moult strategy and primaries worn away in the pre-breeding period

We measured the primaries' red/green value as an index for colour that displayed the wear difference between the juvenile primaries, in partial post-juvenile and complete post-juvenile moulters, in the pre-breeding period. In four species which perform a partial post-juvenile moult, the range of coefficients of variation (CV) of the wear value was 18.3% - 25.2%, more than three times higher than the five species which perform a complete post-juvenile moult (5.0% - 7.6%, Fig. 1). The results indicate that there is no phylogenetic signal in the data (maximum likelihood value of $\lambda = 0$). In all species which perform a partial post-juvenile moult ($n = 4$) the juveniles' primaries were significantly ($P < 0.05$) more worn than the adults' primaries in the pre-breeding period (Fig. 2). We could not compare juveniles and adults in species that perform a complete post-juvenile moult because age cannot be determined after the post-juvenile and post-breeding moults.

Comparison of plumage quality for each of the two moult strategies

We analyzed the Δp for species which perform a partial versus complete post-juvenile moult, considering three parameters: primaries' mass, primaries' colour and primaries' length which can describe the plumage quality (Fig. 3A-C). For primaries' mass and primaries' colour we found that the mean value is different from zero only for the complete post-juvenile moult species group. For primaries' length in both groups of post-juvenile moult strategy, the value is different from zero, but in complete post-juvenile moult strategy group, the value was significantly higher than that of the

groups of species with a partial post-juvenile moult. The results indicate that there is no phylogenetic signal in the data (maximum likelihood value of $\lambda = 0$).

Moult speed

The moult speed in 10 species which perform a complete post-juvenile moult was significantly different between juveniles and adults (Paired t-test, $t_9 = -3.77$, $P = 0.004$), with juveniles moulting more slowly than adults (Fig. 4).

Characteristics of species with complete post-juvenile moult strategy

We carried out analyses to detect correlations between migration distance, breeding latitude, body mass and diet. These analyses did not show any high correlations between these variables (Table S1), such that we analyzed each variable separately.

Migration distance

Only 53 species (19.7%) that breed in the Western Palaearctic zone perform a complete post-juvenile moult. Of these, 81.1% were residents and 18.9% were short-distance migrants. None of the long-distance migratory species perform a complete post-juvenile moult (Fig. 5).

Breeding Latitude

A complete post-juvenile moult strategy in the Western Palaearctic zone is more common in southern than in northern latitudes. For example, north of 55°N fewer than 10% of breeding species perform complete post-juvenile moult, while south of 34°N more than 25% of breeding species use this strategy (Fig. 6A-B).

Body mass

Complete post-juvenile moult strategy is less common in species with low body mass than in those with high body mass. Only 23.2% (n = 125 out of 189 resident or short-distance migrant species) of the species with body mass < 30 g perform a complete post-juvenile moult, whereas 54.5% of the species with body mass of 31-60 g (n = 33 species) and 45.5% with body mass of 61-90 g (n = 11 species) perform this strategy. There are no species with body mass higher than 90 gr. (n = 19 species) whose juveniles perform a complete post-juvenile moult (Fig. 7A).

Diet

Complete post-juvenile moult strategy was related to the bird's diet. In granivores (n = 77 species out of 189 resident or short-distance migrant species), 45.5% perform a complete post-juvenile moult, in omnivores (n = 26 species), 38.5% did so, and in insectivores (n = 86 species), only 9.3% perform complete post-juvenile moult (Fig. 7B).

DISCUSSION

In regions where the annual cycle is weak and there is less of a time limit on moulting in the post-breeding period, such as in the tropics, the complete post-juvenile moult is the most common moult strategy for juveniles (Fogden 1972). In regions with strong seasonal cycles, this moult strategy is possible only if time is not a main constraint. In this paper, we evaluated the adaptive roles of a complete post-juvenile moult and associated this moult strategy with migration strategies, geographic location, body mass and diet among Western Palaearctic passerines. From our results, the answer to

the question "why juveniles renew fresh feathers?" is because there is time, and if there is a time, the renewal of feathers can improve survival and fitness.

Plumage quality

Our results support the hypothesis that a complete post-juvenile moult produces high quality plumage in the first winter and first breeding season, which can increase the individual survival probability during the first year and the reproductive success during the first breeding season. In all examined species whose post-juvenile moult is partial, the juveniles began their first breeding season with plumage that was about 10 months old, which was indeed more worn than that of the adults (Figs. 1-2). In species with a complete post-juvenile moult, adult and post-juvenile plumage quality did not differ, or at least not significantly. In these species, juveniles renew all of their plumage concurrent with adults performing their post-breeding moult, so adults and juveniles start the breeding season with a similar plumage status. This complete moult must be carried out soon after the fledging because all of these species winter in the north, and likely cannot perform the moult in the cold winter season.

Low resource allocation in the juvenile plumage brings about a short nesting period

In all species that perform a complete post-juvenile moult, the juvenile plumage was poorer and weaker than in species that perform partial post-juvenile moult (Fig. 3). In the complete post-juvenile moult species, the first moult occurred one to three months after fledging and encompassed all flight feathers. Hence these juveniles' flight feathers function for only two to four months. By contrast, the partial post-juvenile moult species did not renew their flight feathers in this moult. Hence in these species,

the juvenile flight feathers play an important role for more than a year, from fledging to the end of the first breeding season. Accordingly, resource allocation for the juvenile plumage in complete post-juvenile moult species is lower, and thus may result in a shorter nesting period. Early nest leaving and rapid nestling developmental rates are adaptive for coping with nest predators. Early nest leaving is less common in species with protected nests such as hole-nesting (Lack 1948, Ricklefs 1968, Bosque & Bosque 1995). In at least two partial post-juvenile moult species (*Cettia cetti* and *Parus major*), the juvenile flight feather quality was found to be higher than that of adult post-breeding flight feathers. This result indicates the long time these juveniles maintain their juvenile flight feathers (more than a year from fledging to first post-breeding moult) as compared with adults (a year, between the post-breeding moults). Plumage quality during breeding can have a marked effect on reproduction success. Ferns & Lang (2003) found that high quality plumage was associated with breeding success.

Conditions that enable a complete post-juvenile moult strategy

The main constraints on time availability for moult are migration, the cold season, body mass and diet. Our results show that in Western Palaearctic passerines, the time constraints on adult post-breeding moult also constrain the extent of juvenile moult. The low moulting rate of juveniles compared with adults (Fig. 4) emphasizes the high time constraint for juveniles. This result can also explain why juveniles of most species do not perform a complete post-juvenile moult, even though their adults do perform their annual complete moult in the same period. This result is probably due to low foraging success of juveniles compared with adults. Low foraging success can also influence the length of time available for moulting. The lower foraging success

by juvenile birds than by adults has been attested to by many studies and reviewed by Marchetti and Price (1989).

Migration

In passerines of the Western Palearctic, the complete post-juvenile moult strategy occurs only in residents and short-distance migrants (Fig. 5). Not a single long-distance migrant species performs this moult strategy. Long-distance migration forms a significant time constraint, so time is insufficient for juveniles to renew all of their plumage. The adult long-distance migrants can complete their moult due to their high foraging efficiency as compared with their juveniles (Enoksson 1988, Desrochers 1992). In addition, moulting immediately after the breeding season is more necessary for adults because breeding activities cause high abrasion of plumage (Jenni & Winkler 1994). Either way, as a result of the time constraint, the adult long-distance migrants usually delay their moult until winter and also divide or suspend their complete moult (Jenni & Winkler 1994, Svensson & Hedenstrom 1999).

Species with more than one migration strategy also show several juvenile moult strategies. The juveniles of the residential subspecies perform a complete moult strategy whereas juveniles of the migratory subspecies perform a partial moult or delay their moult until arrival at their wintering grounds. This pattern can be found in two reed-warbler species (*Acrocephalus stentoreus* and *Acrocephalus melanopogon*) where the juveniles of the resident populations of both species perform a complete post-juvenile moult; the juveniles of the long-distance migratory populations (*Acrocephalus stentoreus brunnescens* and *Acrocephalus melanopogon mimicus*) delay the complete moult until arrival at tropical winter zones, like other long-distance migrant *Acrocephalus* warblers (Kennerley & Pearson 2010).

Breeding latitude

The passerines that breed in the northern hemisphere avoid an active moult in the winter, with its harsh environmental conditions such as low temperatures, food shortage and short daylight hours available for foraging (Ginn & Melville 1983, Jenni & Winkler 1994). This period is more extensive and longer in northern than in southern latitudes. Our results show a negative association between breeding location and the proportion of species that perform a complete post-juvenile moult (Fig. 6). We suggest that a complete post-juvenile moult strategy demands a relatively long post-juvenile period with favourable environmental conditions. Similarly, in some species which perform a partial post-juvenile moult, the extent of the partial moult is influenced by latitude. Thus juveniles in northern populations renew only limited parts of the plumage while in southern populations, the juveniles undertake a more extensive moult (Ginn & Melville 1983, Gargallo & Clarabuch 1995). In several species, some individuals perform a complete post-juvenile moult while others perform a partial post-juvenile moult. This pattern has been reported for *Sylvia melanocephala* and for some *Carduelis* species (Ginn & Melville 1983, Jenni & Winkler 1994, Shirihai et al. 2001). We suggest that this pattern may be the first stage of evolution toward the complete post-juvenile moult in populations that breed in the southern latitudes.

Body mass

Body mass has an independent effect on moult duration (de la Hera et al. 2009). Large passerines may benefit from slower moult because they depend more on flight capability to maintain feeding ability (Carrascal & Polo 2006) or to avoid predation

(Jenni & Winkler 1994, Williams & Swaddle 2003). Our results indicate that, as in adults, in juveniles, the body mass limits the possibility of species to perform a complete post-juvenile moult. Not a single species with average body mass higher than 85 gr. performs this moult strategy.

Diet

Although the highest percentage of the complete post-juvenile moult strategy was found in the 31-90 gr. groups (Fig. 7A), and not in the lowest body mass group, this result can be explained by the diet of this body mass group. Our results show that diet is also associated with moult strategies. The incidence of the complete post-juvenile moult in insectivores is lower than in granivores or omnivores (Fig. 7B). Most food sources are less available in winter; in contrast to vegetarian food like seeds or fruits, arthropods are not available earlier in autumn. In the temperate zone, the moulting season is limited by winter; the moult occurs before winter sets in, when food is still available (Ginn & Melville 1983). This difference in food availability in the post-breeding period also influences the length of time available for moulting.

The low incidence of the complete post-juvenile moult in the lowest body mass group (1-30 gr.) can be explained by their diet; the majority of species in this group (56%, $n = 126$ species) are insectivores, compared with a minority of species (23%, $n = 44$ species) in the 31-60 and 61-90 gr. groups. The incidence of the complete post-juvenile moult species in the lowest body mass group, without taking into account insectivores, is 40% ($n = 55$ species), close to the rates in the 31-60 and 61-90 gr. groups.

Moult speed

Our results indicate that the shortage of time availability is the main constrain for the evolution of a complete post-juvenile moult strategy. This moult strategy is adaptive only for those species which have a relatively long time period available after the breeding season. In most species which perform a partial post-juvenile moult, the adults perform a complete moult at the same time. Our results show that adults moult at a higher speed in comparison with juveniles. Thus, the time availability is sufficient for adults, but not for juveniles, to perform a complete moult.

To conclude, we suggest that the complete post-juvenile, immediately after the breeding season, is an optimal moult strategy in habitats with favourable environmental conditions with long period after the breeding season, such as those in some tropical areas.

ACKNOWLEDGEMENTS

We are grateful to Roi Dor and Daniel Berkowich from the Steinhardt National Collections of Natural History, Zoological Museum, Tel Aviv University for their help. We are grateful also to Nadav Israeli from the Hula Valley Birding Center for sharing the Mt. Hermon and Hula Valley ringing data, and to Ora Schwarz for help with mapping.

REFERENCES

Alatalo, R.V., Gustafsson, L. & Lundberg, A. 1983. Why do young passerine birds have shorter wings than older birds? *Ibis* 126: 410-415.

Bensch, S. & Grahn, M. 1993. A new method for estimating individual speed of molt. *Condor* 95: 305-315.

Bonser, R.H. 1996. The mechanical properties of feather keratin. *Journal of Zoology* 239: 477-484.

Bosque, C. & Bosque, M.T. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *American Naturalist* 145: 234-260.

Burt Jr, E.H. 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithological Monographs* 38: 1-126.

Carrascal, L.M. & Polo, V. 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.

Cramp, S., Perrins, C.M. & Brooks D.J. 1988-1994. *Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the western Palearctic*. Oxford University Press.

de la Hera, I., Diaz, J.A., Perez-Tris, J. & Telleria, L. 2009. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. *Journal of Avian Biology* 40: 461-465.

Desrochers, A. 1992. Age and foraging success in European Blackbirds: variation between and with individuals. *Animal Behaviour* 43: 885-894.

Dunning, J.B. 2008. *CRC Handbook of Avian Body Masses*, second edition. CRC Press. Cleveland. USA.

Enoksson, B. 1988. Age and sex differences in dominance and foraging behavior of Nuthatches (*Sitta europaea*). *Animal Behaviour* 36: 231-238.

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

Ferns, P.N. & Lang, A. 2003. The value of immaculate mates: relationships between plumage quality and breeding success in shelducks. *Ethology* 109: 521-532.

Fogden, M.P.L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114: 307-343.

Freckleton, R. P., Harvey, P. H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, 160: 712-726.

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

Gauci, C. & Sultana, J. 1979. Moult of the Sardinian Warbler. *II-Merill*. 20: 1-13.

Ginn, H.B. & Melville, D.S. 1983. *Moult in birds (BTO guide)*. British Trust for Ornithology.

Jenni, L. & Winkler, R. 1994. Moults and Ageing of European Passerines. London: Academic.

Kennerley, P. & Pearson, D. 2010. Reed and bush warblers. A&C Black.

Kose, M. & Moller, A.P. 1999. Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the Barn Swallow (*Hirundo rustica*). *Behavioral Ecology and Sociobiology* 45: 430-436.

Lack, D. 1948. The significance of clutch-size. Part III. - Some Interspecific Comparisons. *Ibis* 90: 25-45.

Marchetti, K. & Price, T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological Reviews* 64: 51-70.

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

Newton, I. 2009. Moults and plumage. *Ringed & Migration* 24: 220-226.

Orme, D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. R package version, 5: 2.

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

R Development Core Team. 2014. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. (<http://www.R-project.org>).

Ricklefs, R.E. 1968. Patterns of growth in birds. *Ibis* 110: 419-451.

Shirihai, H., Gargallo, G. & Helbig, A.J. 2001. *Sylvia warblers*. Princeton. New Jersey: Princeton University Press.

Stewart, I.F. 1963. Variation of wing length with age. *Bird Study* 10: 1-9.

Stresemann, E. & Stresemann, V. 1966. *Die mauser der vögel*. Friedländer.

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

Svensson, L. 1992. *Identification Guide to European Passerines*.

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

Williams, E.V. & Swaddle, J.P. 2003. Moulting, flight performance and wingbeat kinematics during take-off in European Starlings *Sturnus vulgaris*. *Journal of Avian Biology* 34: 371-378.

Appendix

Table S1. Spearman correlation rank (r_s) between migration distance, breeding latitude, body mass and diet (n = 269 bird species).

*P < 0.05, **P < 0.001, ns - not significant

	Breeding latitude	Body mass	Diet
Migration strategy	0.39**	-0.25**	-0.30**
Breeding latitude	-	-0.04 ^{ns}	0.12*
Body mass	-	-	-0.34**

Figure legends

Fig. 1. Coefficient of variation (CV) of primaries' wear value in the pre-breeding period for juveniles with partial (4 species) versus complete moult (5 species) strategies. Sample size for each species is $n = 9$ individuals (*O.lug* - *Oenanthe lugens*, *L.exc* - *Lanius excubitor*, *O.tri* - *Onychognathus tristramii*, *C.car* - *Carduelis carduelis*, *G.cri* - *Galerida cristata*, *A.des* - *Ammomanes deserti*, *P.xan* - *Pycnonotus xanthopygos*, *P.dom* - *Passer domesticus* and *E.cal* - *Emberiza calandra*).

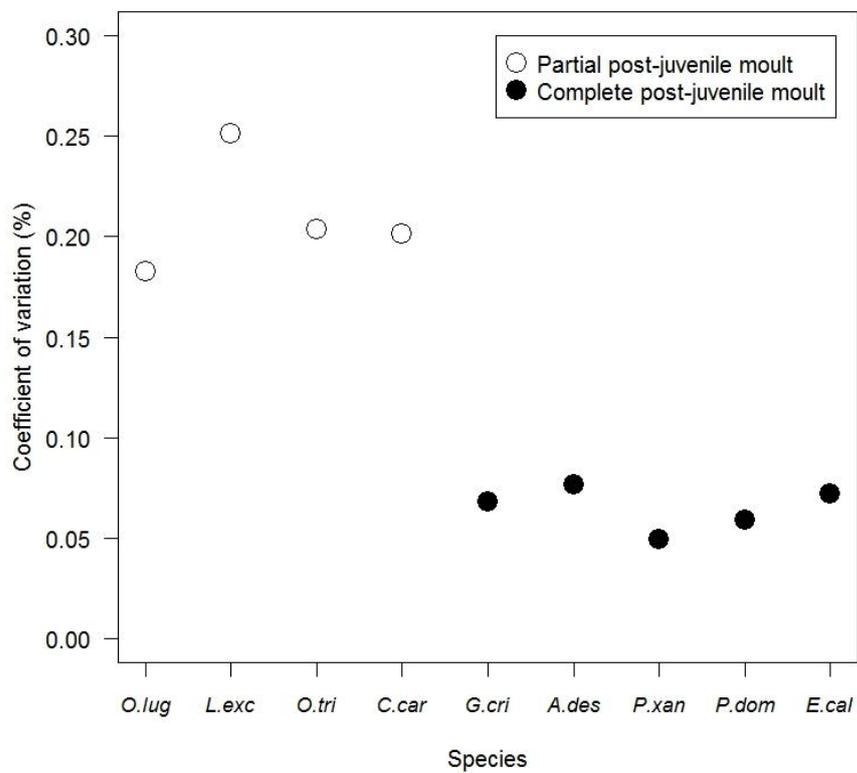


Fig. 2. Primaries' wear value (mean \pm SD) in the pre-breeding period, in partial post-juvenile moult species (n=4). The difference between juveniles and adults in each species was significant (Two sample t-tests, $P < 0.05$).

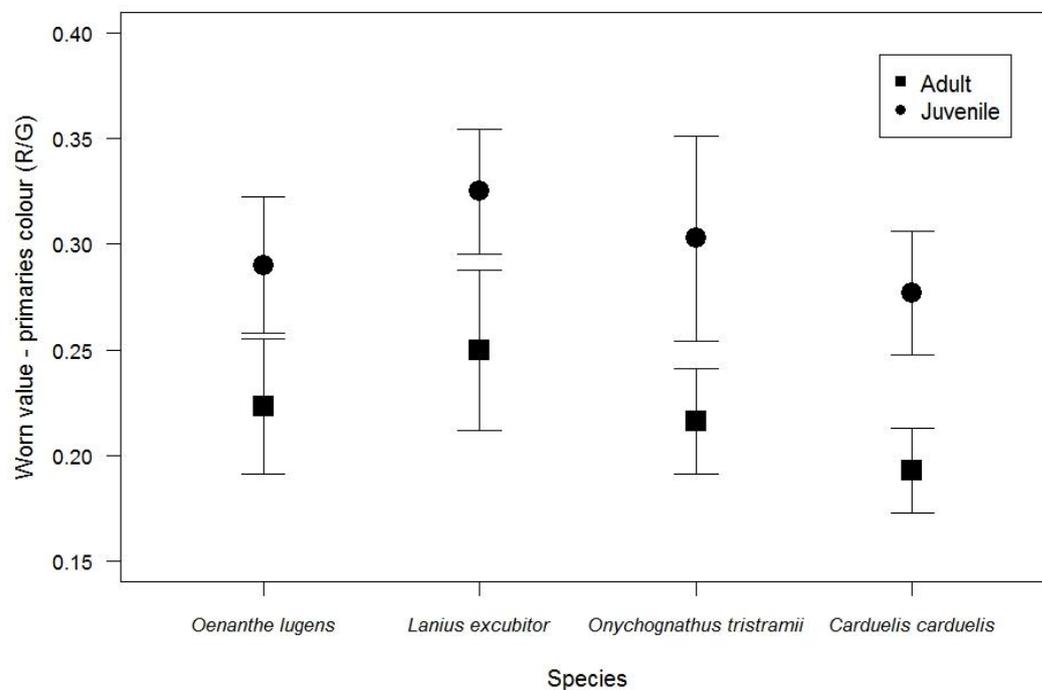


Fig. 3. A. Δp primaries mass of partial ($n = 3$ species) versus complete post-juvenile moult ($n = 3$ species). The mean value is different from zero only for the complete post-juvenile moult species group (One-sample t-test, $t_2 = 5.67$, $P < 0.05$). In the three species which perform partial post-juvenile moult, the Δp was not significantly different from zero (One-sample t-test, $t_2 = -0.45$, $P > 0.05$). **B.** Δp primaries colour (R/G) value of partial ($n = 10$ species) versus complete post-juvenile moult ($n = 9$ species). The mean value is different from zero only for the complete post-juvenile moult species group (One-sample t-test, $t_8 = 9.18$, $P < 0.001$). In ten species which perform a partial post-juvenile moult, the Δ -plumage was not significantly different from zero (One-sample t-test, $t_9 = -0.68$, $P > 0.05$). **C.** Δp primaries length of partial ($n = 14$ species) versus complete post-juvenile moult ($n = 11$ species). The mean value is different from zero for both groups of species (One-sample t-test, $P < 0.05$) with the mean value of the group of species with a complete post-juvenile moult strategy being significantly higher than that of the groups of species with a partial post-juvenile moult (Two-sample t-test, $t_{23} = 6.5$, $P < 0.001$).

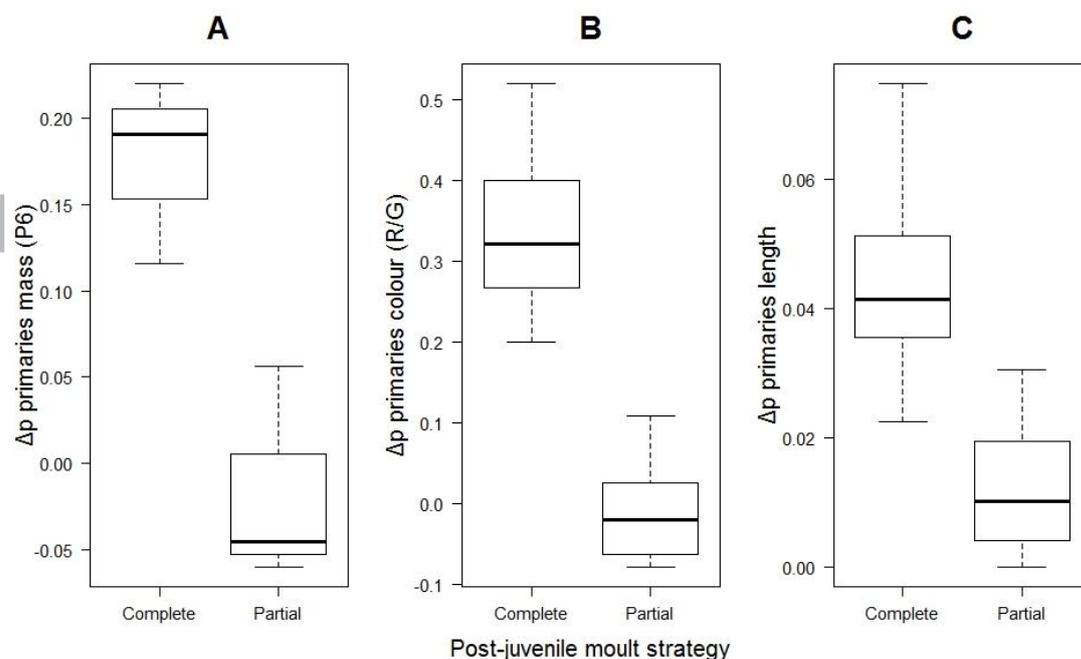


Fig. 4. Difference in moult speed (RRV) between juveniles and adults (n = 10 species, P-value < 0.05).

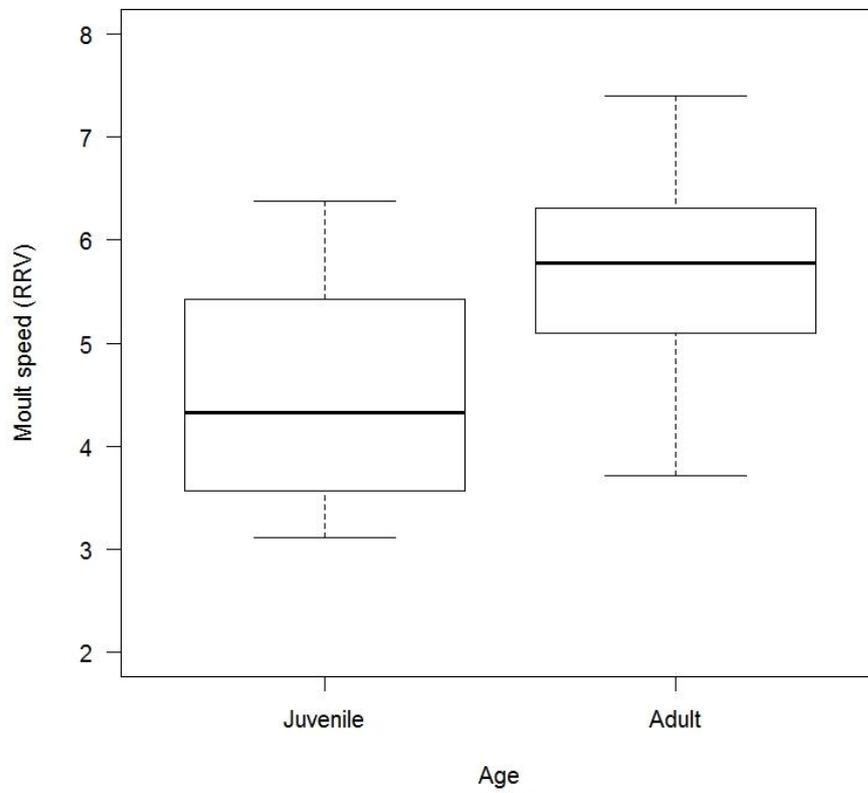


Fig. 5. The association between complete post-juvenile moult (% of species) and migration strategy (n = 269 species).

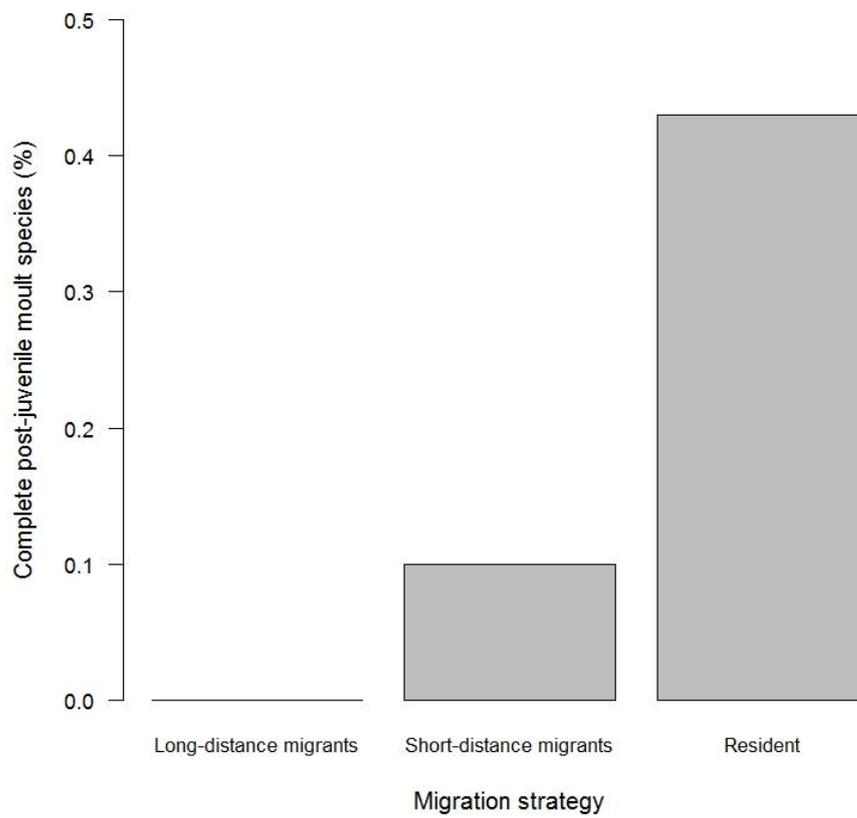


Fig. 6. Percentage of complete post-juvenile moult species (n = 269) in relation to (A) breeding latitude and (B) distribution in the Palaearctic region.

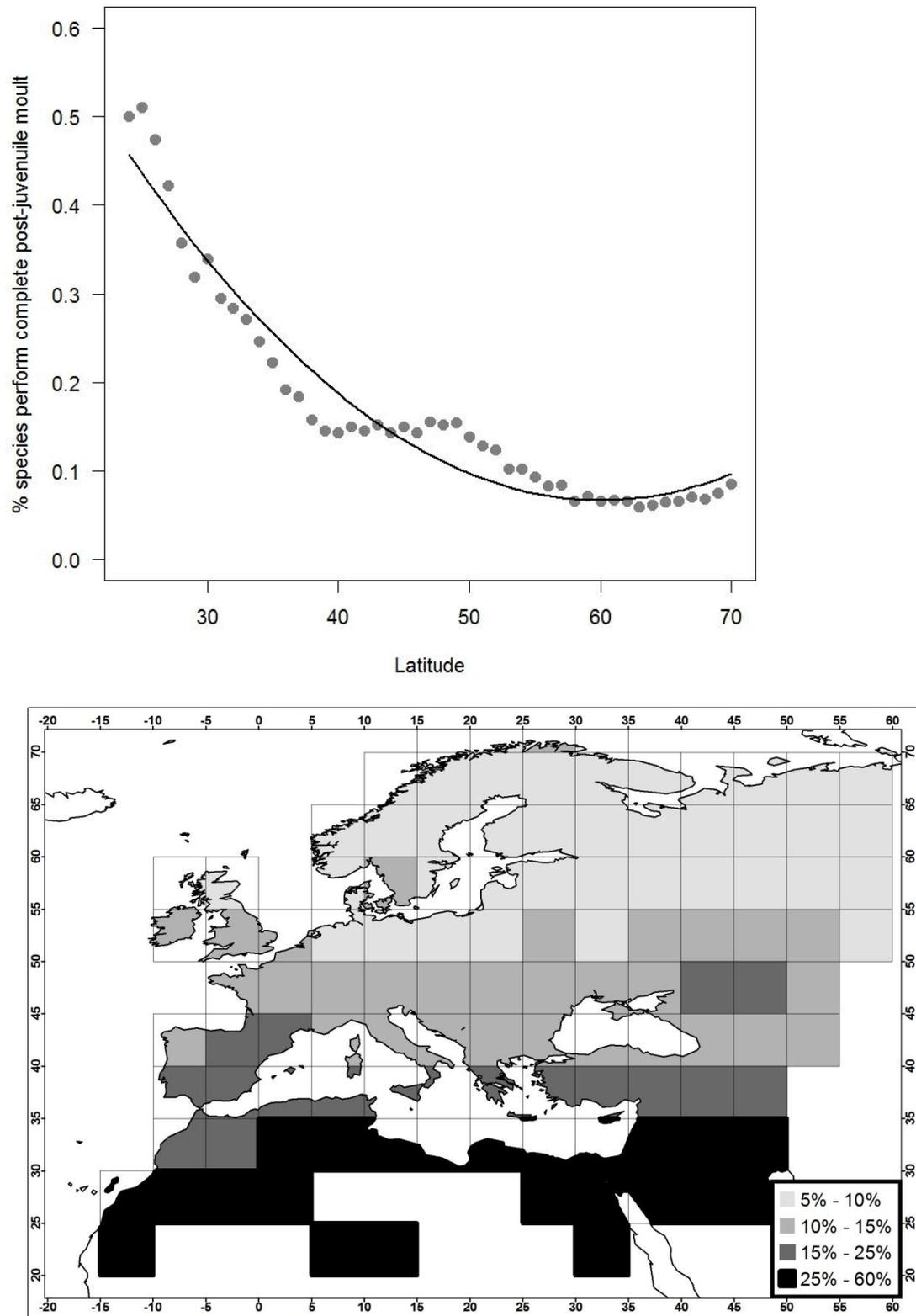


Fig. 7. A. Percentage of complete post-juvenile moult species (residents and short-distance migrants; $n = 189$) in body mass categories ($\chi^2 = 15.4$, $df = 3$, $P < 0.01$).

B. Percentage of complete post-juvenile moult species (residents and short-distance migrants; $n = 189$) in three diet categories. Chi-square goodness of fit test indicated that the observed frequencies of birds in each diet category were significantly different from the values expected at random (equal frequencies of birds in each diet category, $\chi^2 = 20.1$, $df = 2$, $P < 0.001$).

