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Research

Large-scale longitudinal climate gradient across the Palearctic region affects passerine feather moult extent

Yosef Kiat, Batmunkh Davaasuren, Tuvshinjargal Erdenechimeg, David Troupin and Nir Sapir

Y. Kiat (<https://orcid.org/0000-0002-3485-3517>) ✉ (yosefkiat@gmail.com), D. Troupin and N. Sapir (<https://orcid.org/0000-0002-2477-0515>), *Animal Flight Laboratory, Dept of Evolutionary and Environmental Biology and the Inst. of Evolution, Univ. of Haifa, Haifa, Israel.* – B. Davaasuren and T. Erdenechimeg, *Wildlife Science and Conservation Center of Mongolia, Ulaanbaatar, Mongolia.*

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Large-scale spatial gradients of environmental conditions shape organisms, populations and ecosystems. Even though environmental gradients are a key research theme in macro-ecology and biogeography, the effects of large-scale, east–west, environmental gradients are largely overlooked compared with north–south gradients. Our study focused on feather moult, an important and energy demanding process in birds. By comparing Western and Eastern Palearctic populations of 21 species, we found that juvenile passerines in the Western and Eastern Palearctic differ in the number of feathers moulted as part of their post-juvenile moult. This difference is most likely the result of a large-scale climatic gradient in cold season duration and consequent differences in the time available for moulting. Eastern populations were characterized by a limited extent of feather moult that was additionally affected by migration distance and body mass. The longer migration distance in the Eastern Palearctic caused a generally less extensive moult while high body mass was correlated with a low difference in moult extent between the Western and Eastern Palearctic regions. These results highlight the importance of linking annual cycle processes at the organismal level to the specific environmental conditions within the distribution range of each species.

Keywords: annual-routine process scheduling, continental-scale climate gradients, Eastern Palearctic, environmental effects on phenology, life-history transitions, migration timing

Introduction

Environmental conditions are not equal on Earth. In many cases, a gradient of environmental conditions exists over various geographical ranges. For example, elevational (Roy et al. 1998, Hodkinson 2005) or latitudinal gradients (Lawson and Weir 2014) or the distance from the ocean (Makarieva et al. 2009) may cause a gradient of environmental conditions due to differences in solar radiation and the intensity of oceanic moisture flux. These environmental gradients shape ecosystems and biodiversity at various levels, and hence, many studies have examined their effects across different ranges (Gaston 1996, Petru et al. 2006, Alexander et al. 2011, Pellissier et al. 2018). In addition, various ecological patterns and biological rules have been found when describing the impact of



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environmental conditions on organisms and biological systems across different gradients. Such patterns represent one of the key research themes to macro-ecologists and biogeographers (Gaston 2000, Ricklefs 2004, Steudel et al. 2012) and include the latitudinal diversity gradient (Mittelbach et al. 2007, Condamine et al. 2012), Bergmann's rule (Olson et al. 2009, Osorio-Canadas et al. 2016) and Allen's rule (Allen 1877).

Due to the seasonal variation in environmental conditions, constraints imposed by the environment on animal ecology and physiology are released during specific time windows throughout the year. This allows organisms to engage in crucial season-dependent processes such as breeding at the most appropriate time. Consequently, scheduling of different annual processes and life-history traits are expected to vary over spatial gradients of environmental conditions. This is because the time windows in which season-dependent processes can occur change in relation to local environmental conditions. Additionally, differences in seasonality between regions may influence the scheduling of extended and demanding events and processes along the annual cycle, such as reproduction, growth, moult and migration, which do not overlap among most bird species (Hemborg et al. 2001).

Rapid ecological and seasonal transitions across elevational and latitudinal gradients resulted in distinct life history differences across ecoregions and these differences in diversity, life history variation and community assemblage drew the attention of naturalists and researchers for decades. Thus, the ecological and biological impacts of various constraints arising from environmental conditions that vary across spatial gradients have been widely described for elevational (across the earth surface's height axis; Colwell and Lees 2000, Altshuler

and Dudley 2006) and latitudinal (across the equator–poles axis; Mittelbach et al. 2007, McKinnon et al. 2010, Lawson and Weir 2014) gradients, but, surprisingly, are much scarcer and limited in their geographic extent for longitudinal (across the east–west axis; but see Murray et al. 2004, Meiri et al. 2005, Han et al. 2011) gradients. This overlooked change in environmental conditions across longitudinal gradients is surprising due to the extreme change in climatic conditions over this axis in many parts of the world, for example, in the Eurasian Palearctic biogeographic zone (Seebohm 1901, Walter et al. 1975). The spatial climatic gradient of the Palearctic region is characterized mainly by the duration of the cold season and its intensity (longer duration and colder temperatures in the east than in the west for a given latitude; Fig. 1). This gradient may affect the annual cycle scheduling of fundamental seasonal processes, the time available for growth and development and the nature of various constraints on organisms, populations, species and ecosystems. Yet, to the best of our knowledge, no empirical data have demonstrated this effect throughout the entire Palearctic region, to date.

In this study, we test a continental longitudinal effect across the Palearctic biogeographic zone, which stretches over Eurasia, on wing–feather moult, an important process in the yearly cycle of passerine birds (Jenni and Winkler 1994). Among passerine species, moult strategies are shaped mainly by time constraints during the annual cycle, in which long periods of breeding, migration and feather moulting take place (Barta et al. 2006, 2008, Kiat et al. 2019a). The scheduling of these extended and energetically demanding activities is determined by environmental conditions and the timing of the other annual cycle events during the year, as these activities usually do not overlap

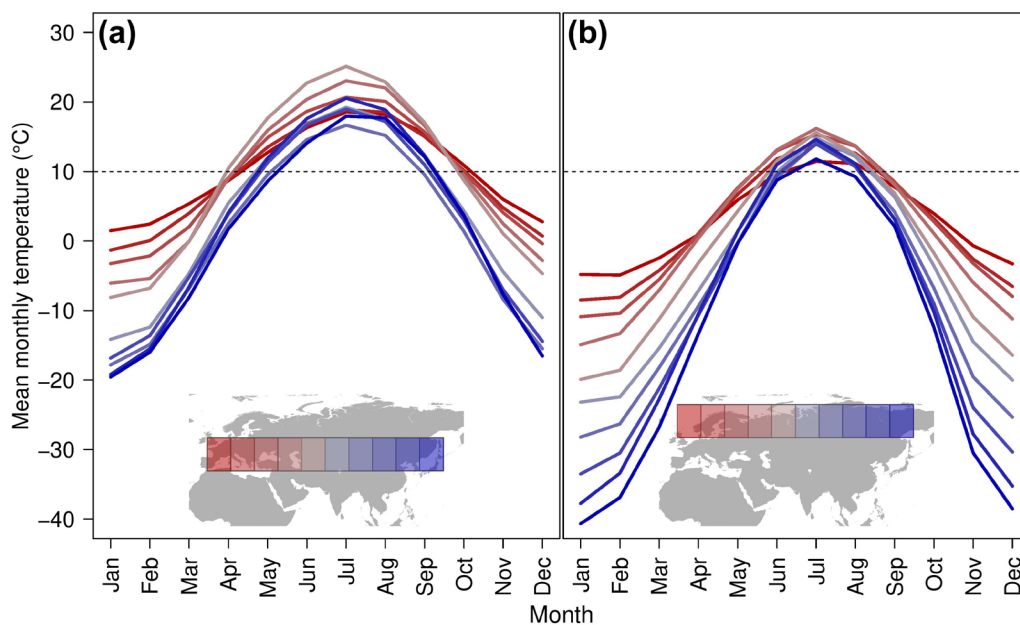


Figure 1. Mean monthly temperature (°C) in ten polygons across the longitudinal axis in the south (a) and north (b) of the Palearctic biogeographic zone. Mean monthly temperature data (spatial resolution of 30 s) were based on WorldClim ver. 2.1 climate data for 1970–2000 (Fick and Hijmans 2017). Data processing and calculations were performed using the R package ‘raster’ (Hijmans and van Etten 2016) and indicating a longer and colder winter in the Eastern Palearctic than in the Western Palearctic.

among passerines. For example, in migratory passerines, breeding takes place after spring migration is completed, and feather moult starts typically only after breeding (Jenni and Winkler 1994). In addition, the start time of each activity is also influenced by its overall duration along the yearly cycle. We specifically note that variation in the duration of feather moulting may affect additional properties of the moult process, such as its extent and sequence (Kiat et al. 2019a).

Among passerine species, one of the common strategies for dealing with time constraints is a reduction in moult extent (number of moulted feathers) during the first year of life (Bojarinova et al. 1999, Kiat and Sapir 2017). First-year birds are known to be particularly sensitive to time constraints (Marchetti and Price 1989, Hanson and Coss 1997), and consequently, partial moult is common among first-year individuals (Jenni and Winkler 1994, Kiat and Sapir 2017). Generally in passerines, the moult during the first year of life is intended to replace poor-quality nest-grown feathers with higher-quality feathers. Further, in many species, feather moulting changes the plumage of the bird such that it gains an adult-like appearance (Jenni and Winkler 1994, Kiat and Izhaki 2016; but see Kiat and Sapir 2018). Therefore, reduced moult extent at this stage of the bird's life could affect plumage functionality, including its appearance (Kiat et al. 2019b), and consequently bird attractiveness, as well as the bird's flight capacity (Bridge 2008). All of these are expected to have implications for future survival and reproduction (Senar et al. 1998, Minias and Iciek 2013, Crates et al. 2015).

We hypothesize that feather moult duration and, assuming a similar speed of moult, its extent, are affected by climatic conditions across a longitudinal axis within a species (Kiat and Sapir 2017). The time available for moulting is longer in the Western Palearctic compared to the Eastern Palearctic due to east–west differences in the duration and intensity of the cold season (longer and colder in the east than in the west, for a given latitude; Fig. 1). In addition, longer migration distances in species and populations that breed in the Eastern Palearctic may reduce the time available for moulting by further shortening the time available for moult in the breeding areas (Kiat et al. 2019a, Briedis et al. 2020). We thus predict that within a species, post-juvenile moult extent will be greater among western populations than among eastern ones. Finally, we propose that additional factors that affect the moulting process, such as latitude, which was found to negatively affect moult extent (moult is more extensive in southern than in northern latitudes; Kiat and Sapir 2017), or body mass, which is positively correlated with moulting speed (de la Hera et al. 2009, Rohwer et al. 2009, Kiat and Izhaki 2016), may modulate this longitudinal effect.

Methods

Study species and feather moult data collection

The study included 21 Palearctic passerine species from the families Motacillidae (5 species), Cinclidae (1 species),

Muscicapidae (5 species), Turdidae (2 species), Paridae (2 species), Sittidae (1 species), Laniidae (1 species), Fringillidae (3 species) and Emberizidae (1 species), which are characterized by a wide distribution range across the Palearctic biogeographic zone. For these species, we sampled the extent of feather moult in Western and Eastern Palearctic populations. The border between these populations was defined as the eastern border of European Russia, the Ural Mountains and the Caspian Sea (Sclater 1858, Tutin et al. 1964, Roselaar 2006). We included species for which we were able to measure at least 10 individuals from each population (Supplementary material Appendix 1 Table A1).

Data were obtained from bird skins stored in the collections of nine natural history museums: 1) Natural History Museum (Tring; UK), 2) Muséum National d'Histoire Naturelle (Paris, France), 3) National History Museum of Denmark (Copenhagen, Denmark), 4) Museum für Naturkunde (Berlin, Germany), 5) Museo Nacional de Ciencias Naturales (Madrid, Spain), 6) Naturhistoriska Riksmuseet (Stockholm, Sweden), 7) Natural History Museum Vienna (Vienna, Austria), 8) Steinhardt Museum of Natural History, Tel-Aviv University (Tel-Aviv, Israel) and 9) the Finnish Museum of Natural History (Helsinki, Finland). We included bird skins only if collected within the species' breeding areas, in stopover sites within the Palearctic region, or rarely in southern non-breeding areas (only if the bird's origin, east or west, could be identified for certain as described below). Additionally, we used moult data that were collected during bird ringing activities in Israel (several sites, mainly the Jerusalem Bird Observatory, 31.78°N, 35.21°E, and Beit She'an Valley, 32.45°N, 35.54°E) and Mongolia (Khurkh Bird Ringing Station, Khurkh River Valley, Khentii, 48.28°N, 110.49°E). The moult region (Western or Eastern Palearctic) of the individuals that were examined in the study was determined by the collection or sampling location or by plumage and other morphological characteristics (according to published information) (Del Hoyo et al. 2019). This information was used to assign individuals to a specific subspecies, which is confined to a certain breeding distribution range (Supplementary material Appendix 1 Table A1).

The age of each bird was determined using published plumage characteristics for passerine species (Jenni and Winkler 1994). Juvenile, nest-grown feathers are poorer in texture, duller and characterized by higher abrasion than those grown during the post-juvenile moult (by juveniles) or the post-breeding moult (by adults). Using these plumage characteristics, each individual was aged as either a first-/second-calendar year bird or an adult. We used specimens of all first-/second-calendar year individuals that had completed their partial, post-juvenile moult but had not yet begun their first complete moult. Therefore, data from late autumn (of the first calendar year) to early summer (of the second calendar year) was included in the analysis, with the exception of the spotted flycatcher *Muscicapa striata* and Motacillidae species (genera *Anthus* and *Motacilla*) that undergo an extensive wing moult during their first winter (following a partial post-juvenile moult, as in other tested species). Consequently,

data for these species were collected only from autumn to early winter. Even though the examined specimens were collected at different dates within the sampling period, there is no expected impact of the date of collection on the recorded moult since an additional moult in these birds takes place only in the following autumn (or in winter in the spotted flycatchers and Motacillidae species). All the specimens that were included in this work were collected in the Palearctic region in the years 1806–2019. All data were collected by the first author during 2012–2020.

To quantify moult extent, each wing feather of each individual was classified as being either moulted or non-moulted in the post-juvenile moult. In this study, we included only individuals whose moult has ended, confirmed by the absence of signs of moult upon visual inspection of each feather. Indications of active feather moult include the presence of feathers that are short in length and those with protective peripheral sheath remains. Moult extent was determined by documenting the moult of the wing feathers using a score of 0 (non-moulted feather) or 1 (moulted feather). A total of 42 feathers were documented using this method in each individual, as follows: greater-coverts (GC_{1-10}), carpal-covert (CC), alula (Al_{1-3}), primary coverts (PC_{1-9}), primaries (P_{1-10}), secondaries (S_{1-6}) and tertials (T_{7-9}). In addition, we measured the proportion of moulted feathers in two feather tracts, the lesser-coverts (LC) and the median-coverts (MC). These two feather tracts are characterized by numerous small and difficult to distinguish feathers, for which we estimated the proportion of the area moulted.

For each species, we calculated the mean migration distance in each region, Western or Eastern Palearctic, and the mid-breeding (and hence mid-moulting) latitude using published distribution maps (BirdLife International and NatureServe 2014, Del Hoyo et al. 2019). The mid-breeding latitude (and mid-wintering latitude, see below) was calculated separately for each region as the average of the northernmost latitude and the southernmost latitudes of a species' distribution range, and the mean migration distance was the distance between the mid-breeding and mid-wintering distribution areas. Due to the inaccuracy of these maps, we calculated the migration distance to the nearest 1000 km. We also incorporated published data of the species' mean body mass (Dunning 2007; Supplementary material Appendix 1 Table A1).

Statistical analysis

We used generalized linear modelling (GLM; family = Gamma; $g(\mu) = 1/\mu$; R package 'lme4'; Bates et al. 2012; gamma distribution was selected using the R package 'fitdistrplus'; Delignette-Muller and Dutang 2015) to explore the effects of longitude (east or west) on the extent of moult. We also tested the possible effects of the moulting year as an independent variable due to changes in climate conditions over time (Kiat et al. 2019b). A model that included an interaction between the effects of longitude and year was also tested. Each species was tested separately, and we selected the

best model based on the Akaike information criterion, modified for small sample sizes (AICc; Akaike 1987). A specific model was selected only if it exhibited a $\Delta AICc > 2.00$ compared to other models. Model selection was performed using the R package 'MuMIn' (Barton and Barton 2019) and r^2 was calculated using the R package 'rsq' (Zhang 2018).

In addition, we used a comparative approach to test the effects of three independent variables that may affect bird moulting properties (de la Hera et al. 2009, Kiat and Sapir 2017, Kiat et al. 2019a). These variables included the difference in migration distance between Western and Eastern Palearctic, the species-specific mid moulting latitude and body mass. We specifically tested their effects on the intensity of the relationship between the longitudinal effect and moult extent (dependent variable), calculated as the difference (Δ) in the extent of passerine wing moult between the Western and Eastern Palearctic. Because species traits are known to be phylogenetically conserved, and thus data from closely related species are not statistically independent, we repeated the analysis following the independent contrasts method which identifies evolutionarily independent comparisons (Felsenstein 1985). To account for phylogenetic non-independence, we conducted this analysis using phylogenetic generalized least square (PGLS) regression (Freckleton et al. 2002). We examined the strength of phylogenetic non-independence using the maximum likelihood value of the scaling parameter Pagel's λ (Pagel 1997) implemented in the R package 'caper' (Orme 2013). Pagel's λ is a multiplier of the off-diagonal elements of the variance-covariance matrix, which provides the best fit of the Brownian motion model to the tip data and ranges between zero (no phylogenetic signal) and one (phylogenetic signal that depends on branch lengths as in the analysis of phylogenetically independent contrasts). We then corrected for the effects of shared ancestry using the maximum likelihood value of λ . The phylogenetic tree (Fig. 2) was obtained from an analysis of global bird diversity (Jetz et al. 2012) using 10 000 trees that were generated from BirdTree.org (Rubolini et al. 2015). The consensus tree was built using BEAST ver. 1.8.4. Analyses (two-tailed, critical $\alpha = 0.05$) were performed using R (ver. 3.6.2; R Development Core Team).

Results

We found that partial post-juvenile moult is more extensive in the Western Palearctic than in the Eastern Palearctic region (Fig. 3 and Supplementary material Appendix 1 Fig. A1). In 13 of the 21 species examined ($n = 3126$ individuals), the selected models showed a longitudinal effect on moult extent ($\Delta AICc > 2.00$); in the remaining eight species, a model that included the longitudinal effect was not selected over the other models ($\Delta AICc < 2.00$; Supplementary material Appendix 1 Table A2).

By applying phylogenetic generalized least square (PGLS) regression using global bird phylogeny (Jetz et al. 2012), we found that the difference between moult extent in the

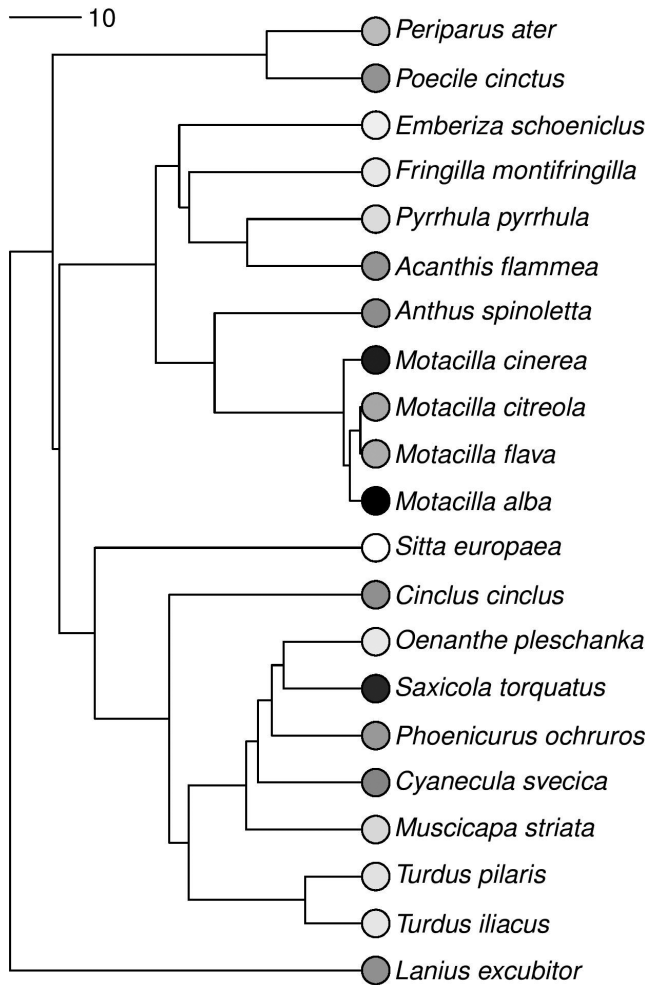


Figure 2. The phylogenetic tree of the 21 species included in the phylogenetic generalized least square (PGLS) analysis. The tree is based on an analysis of global bird diversity (Jetz et al. 2012) using 10 000 trees obtained from BirdTree.org (Rubolini et al. 2015). The consensus tree was built using BEAST ver. 1.8.4. The tip colour represents the difference in (Δ) moult extent between the Eastern and the Western Palearctic samples (black = maximum Δ , white = minimum Δ). The scale (top left) represents 10 million years.

Western and Eastern Palearctic regions is affected by species-specific differences in migration distance (between Western and Eastern Palearctic populations of each species) and body mass, but not by moult latitude (Fig. 4, Table 1). The longer migration distance in the Eastern Palearctic, probably as a result of the longer and colder winter in this region (Fig. 1), caused a generally less extensive moult among passerines. In addition, high body mass was correlated with a low difference in moult extent between the Western and Eastern Palearctic regions. We conclude that these two factors differently affect the extent of moult in the Western and Eastern Palearctic; while the difference in migration distance increases the longitudinal difference in post-juvenile moult extent, body mass decreases the difference so that heavier species have a weaker longitudinal effect (i.e. the moult extent of species

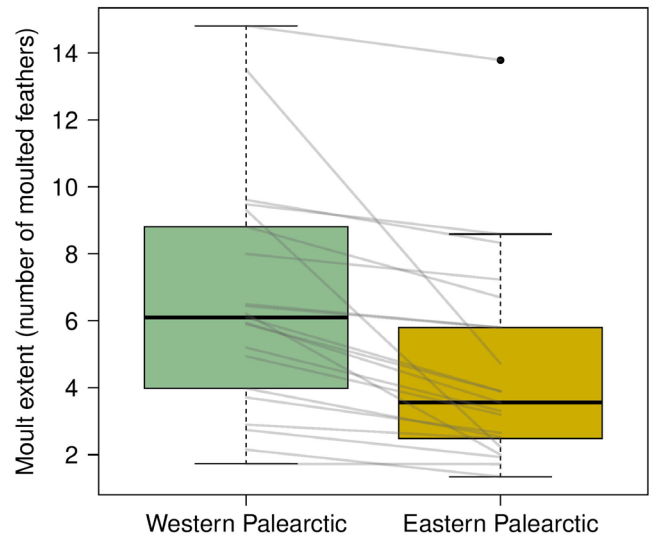


Figure 3. The difference in mean moult extent (number of moulted feathers) between the Western and Eastern Palearctic ($n = 21$ passerine species). The results indicate that moult extent among western populations is greater than among eastern populations of the same species. The boxplots display the minimum, 1st and 3rd quartiles, median and maximum of each tested region.

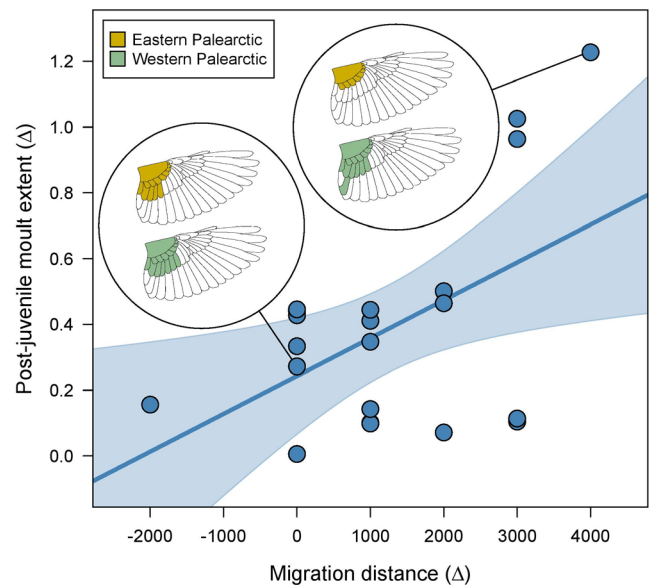


Figure 4. The effect of species-specific differences in (Δ) migration distance on the difference in (Δ) moult extent between Western and Eastern Palearctic passerines among the 21 examined species ($\pm 95\%$ confidence intervals). The results indicate a strong relationship between Δ migration distance and Δ moult extent: if an eastern population migrates a longer distance than the western population of the species, the extent of its moult decreases compared to the western population. The circled insets depict examples of Δ moult extent between Western and Eastern Palearctic regions in relation to the Δ migration distance for two species (right: coal tit *Periparus ater*, left: white wagtail *Motacilla alba*). The coloured wing areas depict the wing's moulted feathers while non-coloured areas represent non-moulted feathers.

Table 1. The effects of difference in (Δ) migration distance, mean latitude and body mass on the Δ moult extent (longitude difference between Western and Eastern Palearctic populations): list of statistical models (phylogenetic generalized least square (PGLS) regression), statistics and Akaike information criterion (AICc).

Model	λ	r^2	df	logLik	Δ migration distance coefficient (km)	Mean latitude coefficient ($^\circ$)	Body mass coefficient (g)	AICc	Δ AICc	Akaike weight
~ Δ migration distance+body mass	0.00	0.41	3	-0.44	1.41e-04 \pm 4.29e-05	NA	-5.44e-03 \pm 2.51e-03	8.29	0.00	0.55
~ Δ migration distance	0.00	0.26	2	-2.88	1.15e-04 \pm 4.51e-05	NA	NA	10.44	2.15	0.19
~ Δ migration distance+body mass+mean latitude	0.00	0.42	4	-0.23	1.44e-04 \pm 4.42e-05	-5.27e-03 \pm 9.10e-03	-5.43e-03 \pm 2.55e-03	10.97	2.68	0.15
~ Δ migration distance+mean latitude	0.00	0.27	3	-2.71	1.19e-04 \pm 4.65e-05	-5.43e-03 \pm 9.96e-03	NA	12.84	4.55	0.06
Null model	0.00	0.00	1	-5.97	NA	NA	NA	14.17	5.88	0.03
~ body mass	0.00	0.06	2	-5.35	NA	NA	-3.19e-03 \pm 2.96e-03	15.38	7.09	0.02
~ mean latitude	0.00	0.00	2	-5.96	NA	1.53e-03 \pm 0.01	NA	16.60	8.31	0.01
~ mean latitude+body mass	0.00	0.06	3	-5.35	NA	-9.51e-04 \pm 0.01	-3.18e-03 \pm 3.05e-03	18.11	9.82	0.00

with relatively high body mass were more similar in the two regions compared with species of low body mass).

Discussion

Large-scale spatial gradients in environmental conditions may affect organisms and ecosystems at different levels (Gaston 1996, 2000, Mittelbach et al. 2007, Steudel et al. 2012). In this study, we examined the effects of differences in climatic conditions that affect the timing and the duration of the breeding and the post-fledging moulting period at high latitudes (Fig. 1), on the extent of the post-juvenile moult, a critically important process in the avian yearly cycle, with implications for plumage performance. Our results suggest a reduced moult extent (number of moulted feathers) by juveniles of most of the tested species in the Eastern Palearctic compared to the Western Palearctic (Fig. 3, Supplementary material Appendix 1 Table A2, Fig. A1). In addition, we found that differences in moult extent between Western and Eastern Palearctic were modified by migration distance and body mass (Fig. 4, Table 1). For a given latitude, the cold season is longer and colder in the east than in the west (Seeböhm 1901, Walter et al. 1975, Fig. 1). Probably as a result of these harsher winter conditions, migration distance in the Eastern Palearctic is longer (Supplementary material Appendix 1 Table A1; see also Meiri et al. 2005). We note that migration distance may also depend on wintering sites availability, for example, land-masses and their climate (Newton 2010).

Among juvenile passerines, the extent of wing feather moult (remiges and wing-coverts) is known to be largely affected by time availability (Jenni and Winkler 1994, Bojarinova et al. 1999, Kiat and Izhaki 2016, Kiat and Sapir 2017). Importantly, breeding in the east may occur later in the spring than in the west. Consequently, the time that is available for moulting, which is determined by the difference between hatch date and the date in which migration

commences or when food becomes less abundant during fall for resident birds, is shorter in the Eastern than in the Western Palearctic (see example from species inhabiting each region in Fig. 5). Specifically, hatch date is known as one of the most important determinants of post-juvenile moult extent (Rymkevich and Bojarinova 1996, Bojarinova et al. 1999, Elrod et al. 2011). Since hatch date occurs later in the east than in the west, less time is available for moult in the east than in the west. This effect, which is primarily determined by climatic factors that affect the start of the breeding period, is likely carried-over from the breeding season to the moulting season. Thereby, it likely affects the extent of moult in hatch-year birds, potentially explaining our findings regarding differences in moult extent between Western and Eastern Palearctic populations. In addition, the time that is available for breeding is relatively longer in the west, such that multiple breeding cycles may take place and hence high variation in hatch dates likely characterizes many passerine species in this region compared with their conspecific populations from the Eastern Palearctic (Böhning-Gaese et al. 2000). In the east, the time available for breeding is shorter, there are less breeding cycles (usually only a single breeding cycle per year) and hence the variation in hatch dates is likely lower. We note that a spatial difference in feather moult timing between east and west populations was previously documented among Neotropical migrant passerines (Rohwer et al. 2005). This difference was attributed to differences in precipitation and climate over a spatial scale of \sim 3500 km. To the best of our knowledge, our work is the first to document a difference in a life-history process across the entire Palearctic biogeographic zone (\sim 7500 km).

Moulting latitude is known to be an important factor affecting moult extent (Jenni and Winkler 1994, Kiat and Izhaki 2016, Kiat and Sapir 2017). The moulting latitude is similar in the Eastern and Western Palearctic regions among the 21 species investigated in this study (Supplementary material Appendix 1 Fig. A2). Nevertheless, the exact moulting

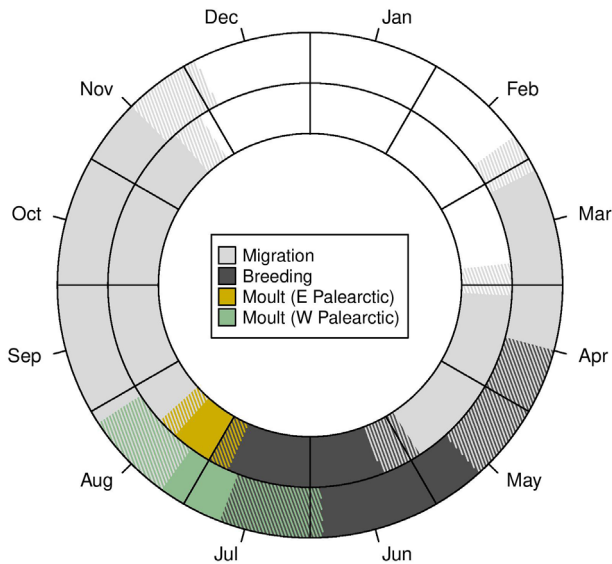


Figure 5. A schematic representation of major annual processes in Eastern (inner circle) and Western Paelearctic (outer circle) passerines based on data from species with distribution ranges restricted to each region (no data is available for different populations of species inhabiting both regions). The information is based on published data (Del Hoyo et al. 2019) and the authors' field experience (Supplementary material Appendix 1 Note 1) and suggests a likely delay of about one month in spring and summer but not autumn events in Eastern Paelearctic populations, causing a shorter post-juvenile moulting period compared to the Western Paelearctic. The overlap between migration, breeding and moulting is represented by colour combinations.

latitude of each of the examined individuals was unknown, potentially causing bias due to this knowledge gap. Similarly, the hatching date, which may substantially vary among individuals, specifically in Western Paelearctic populations, may also affect the extent of moulting (Bojarinova et al. 1999). A future study accounting for the exact moulting latitude and hatching date of each bird may refine the conclusions of our work.

The implications of partial moulting

Partial replacement of juvenile, nest-grown wing feathers during the first year of life is a common strategy among passerines due to constraints involving available time for moulting or food resources that must be acquired for this process (Jenni and Winkler 1994, Kiat and Izhaki 2016). These constraints may occur in extreme northern moulting areas (Kiat and Sapir 2017), as a result of long-distance migration (Kiat et al. 2019a), higher body mass (de la Hera et al. 2009, Kiat and Izhaki 2016) or late hatching dates (Bojarinova et al. 1999). These effects are more severe for juvenile than for adult birds due to the juveniles' lower foraging proficiencies (Marchetti and Price 1989) and anti-predator capabilities (Hanson and Coss 1997, Rajala et al. 2003).

Partial moulting affects bird appearance and thereby may affect sexual and social interactions. As a result, juveniles can

be easily identified by their partial moulting and nest-grown feathers that signal their low competitive abilities (Grant 1990). An extensive partial moulting may increase the attractiveness of males during the first breeding season and may positively affect bird fitness through sexual selection. However, individuals that moulting extensively and consequently have a more adult-like appearance may also be subjected to more aggressive behavior from competing adults (Senar et al. 1998).

The global warming analogy

Many studies have examined the influence of various environmental factors over large-scale biogeographic gradients. These include the influence of latitude (Mittelbach et al. 2007, Lawson and Weir 2014), elevation (Roy et al. 1998, Hodkinson 2005) or longitude (Füreder et al. 2005, Dunn et al. 2006, Finlay et al. 2011); however, large-scale longitudinal effects have only been rarely investigated thus far. Our results demonstrate the importance of considering longitudinal effects in studies of biological processes that depend on environmental conditions across biogeographic zones. Specifically, within the Paelearctic, there are substantial differences in the climatic conditions along a longitudinal axis which calls for further studies regarding the influences of this spatial climatic pattern.

We note that there are several similarities between the longitudinal effects that have been revealed in our work and those described in studies of global climate change. These similarities include earlier arrival to the warmer Western Paelearctic breeding areas compared to the colder Eastern Paelearctic ones, similar to the earlier arrival to breeding areas in recent, warmer years, compared to historic arrival dates (Møller et al. 2010, Tomotani et al. 2018). In addition, the extensive moulting of hatch-year passerines in Western Paelearctic populations, compared to Eastern Paelearctic populations that is described in the current study resembles the extensive moulting found in recent years compared to the past (Kiat et al. 2019b). Moreover, migration distance is shorter in the Western Paelearctic compared to the Eastern Paelearctic, and this distance even became shorter as a result of the global climate warming (Visser et al. 2009, Pulido and Berthold 2010). Therefore, understanding longitudinal and, more generally, large-scale spatial gradients of biological phenomena that result from climatic conditions may improve our understanding of various impacts of global climate change on avian life-history patterns and the evolution of the phenology of different activities within the annual routine (for example, migration, feather moulting and breeding).

Directions for future study

We propose future research directions to improve our understanding of the impact of the longitudinal environmental gradient across the Paelearctic region on organisms, populations, species, communities and ecosystems. We hypothesize that biogeographic and macro-ecological patterns that were

found over latitudinal gradients, for example, species diversity (Mittelbach et al. 2007, Condamine et al. 2012) and body size (Bergmann's rule; Olson et al. 2009), may also hold true across the Palearctic longitudinal gradient. Consequently, we call for a broad exploration of longitudinal gradients in a variety of taxonomic groups, communities, food-webs and ecosystems. Specifically, we hypothesize that this environmental gradient also affects key properties of breeding in birds (Wyndham 1986, Böhning-Gaese et al. 2000), and possibly additional taxa, as well as various properties of bird migration (Meiri et al. 2005, Briedis et al. 2020), including migration distance, direction, timing and over-wintering areas of different migratory populations and species across the Palearctic.

Conclusions

Environmental conditions on Earth have specific spatial and temporal attributes that can have immense influence on biological systems. Understanding how environmental gradients shape various biological processes can improve our understanding of organismal life-history and annual-routine scheduling of different activities such as migration, feather moult and breeding, as well as their evolutionary development. Furthermore, this improved understanding can also help us predict future responses to changes that may occur on the planet. In this study, we focused on moult, an important process in the avian yearly cycle, and how this process may be shaped by an environmental longitudinal gradient, a seldom studied, large-scale environmental factor. Our findings highlight the importance of linking the evolution of annual cycle processes at the organismal level to the environmental conditions to which the organism is exposed. We propose that moult extent decreases as a response to the more extensive and colder winter in the Eastern Palearctic compared with the Western Palearctic. Consequently, this work exemplifies the importance of integrating biogeography and climatology to enhance our understanding of biological patterns and their causes over large spatial scales.

Data availability statement

Data available from the Open Science Framework (OSF) – Center for Open Science: <<https://osf.io/2meax/>>.

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Supplementary material (available online as Appendix at <www.ecography.org/appendix/ecog-05287>). Appendix 1.