Feather moult and bird appearance are correlated with global warming over the last 200 years

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Global warming alters various avian phenological processes, including advanced reproduction and migration schedules. In birds, individual appearance is largely determined by plumage, influencing, for example, bird attractiveness, social status and camouflage. Juveniles of most passerine species replace their nest-grown plumage during the first months of life, a process that is called post-juvenile feather moult. Using data from ten natural history collections, we show that the extent of the post-juvenile moult has increased significantly over the last 212 years (1805–2016), a trend that is positively correlated with the temperature of the environment. Therefore, it seems that birds replaced more feathers under warmer conditions, causing juveniles to appear more similar to adult birds. Moreover, in several species, we describe a male–female switch in the extent of moult, with females currently replacing more feathers than males compared to the past. These results demonstrate different biological responses to climate warming by different phenotypes.
Global warming alters various phenological processes and consequently may disrupt phenological matches in many populations, species and ecosystems1–5. However, due to incomplete knowledge of the mechanisms linking temperature change and ecological responses, life-history alterations and evolutionary adaptations, predicting future responses of biological systems to global warming is still a major challenge1,5–7.

Feather moult is one of the most important and energy-demanding life history processes in the avian annual cycle8. Feather renewal is essential for maintaining plumage utility, because feathers accumulate wear and tear, and consequently their functionality in thermoregulation, aerodynamics and ornamentation deteriorates with time. In most passerine species, juveniles that replace their nest-grown feathers gain the appearance of adult plumage following their first feather moult. However, not all juvenile feathers are replaced at this stage, with the extent of partial moult depending mainly on available time and resources for moult, and may affect the extent of moult and its duration9,10. In spite of demonstrated effects of global warming on avian biology,1,3,14,15 and numerous studies revealing differences in thermoregulation16,17 and behaviour18,19 between females and males, whether the warming climate influences feather molting and whether the two sexes respond similarly are still open questions. To date, only two single-species and relatively short-term studies (33 and 11 years) demonstrated how feather moult advanced in response to climate warming4,20, with no reported effects on moult extent or differences between female and male birds. In this study, we show that the extent of the post-juvenile moult has increased significantly over the past 212 years (1805–2016), a trend that is positively correlated with the temperature of the environment. This suggests that birds replaced more feathers under warmer conditions, and causing juveniles to appear more similar to adult birds. Moreover, in several species, we find a male–female switch in moult extent, with females currently replacing more feathers than males compared to the past.

Results

Feather moult extent and climate warming. We measured the extent of feather moult in 19 passerine bird species that breed in the Western Palearctic ecozone and that have various migration strategies (n = 4012 individuals; Supplementary Table 1 and Supplementary Fig. 1) using skin specimens stored in ten natural-history museum collections, and additionally field measured live individuals in several countries (see details in Supplementary Table 2). We found that over the past 212 years (1805–2016), partial moult of juveniles became more extensive, correlating with global temperature increase [global mean temperature anomalies (GMTA); see Methods; Figs. 1a and 2a]. In 16 out of the 19 species examined, our models show a positive effect of GMTA on moult extent [Akaike information criterion, modified for small sample sizes (AICc); ΔAICc ≥ 2.10; Supplementary Table 3, see also Supplementary Table 4 for the effect of the year]. By applying phylogenetic generalised least square (PGLS) regression using global bird phylogeny21, we found that bird response to GMTA is indistinguishable between species exhibiting short- (n = 12 species) and long-distance (n = 7 species) migration, as well as between species with pre-migration moult (in the breeding areas; n = 15 species) and post-migration moult (after arrival to the tropical wintering areas; n = 4 species; Supplementary Table 5).

Sex-dependent response to climate warming. Among 10 sexually dichromatic species, we found a stronger response of females to GMTA than that of males in four species (Fig. 1b and Supplementary Table 3). In these species, the model that best explained the variation in moult extent included GMTA, individual sex and their interaction (ΔAICc ≥ 3.80). In these four species, the stronger response of females to warmer conditions than that of males caused a switch in the extent of feather moult between females and males, with females replacing more feathers than males from ~1990 onwards. In six other species, males and females did not differ in their response to GMTA (Supplementary Table 3). In the remaining nine species, males and females could not be distinguished and consequently the effect of bird sex could not be examined.

The effect of sexual-dichromatism level. We furthermore found that in the 10 sexually dichromatic species, the level of sexual-dichromatism in plumage ornamentation affects the magnitude of the difference in their sex-dependent response to GMTA. In species that are characterised by more ornamented male feathers compared with female feathers (e.g., Desert Wheatear Oenanthe deserti and Collared Flycatcher), the response of females to GMTA is stronger (r² = 0.41, F₁,₈ = 5.50, P = 0.047, λ = 0.00; PGLS), while in species with relatively weak sexual dichromatism, the response of males and females to GMTA was similar such that their moult extent increased similarly for the two sexes with increasing GMTA (Fig. 3).

Discussion

Among most Western Palearctic passerines, the main moulting period occurs immediately after the end of the breeding season, usually near the breeding grounds. Consequently, the birds have sufficient time to complete the moult process before food is depleted during the winter. Other birds, consisting several long-distance migrant species, moult later, such that the replacement of their feathers occurs immediately after their arrival to the tropical wintering areas. Four important phenological changes in the avian annual cycle were reported as widespread responses to global warming: (I) Earlier spring arrival to the breeding grounds among both short- and long-distance migratory passerines4,22, (II) earlier breeding timing (e.g., egg-laying and fledging) among residents as well as short- and long-distance migratory passerines,4,4; (III) delayed onset of autumn migration, mainly among short-distance migratory passerines, which might be caused by reduced migration distance15,22,23; and (IV) earlier autumn migration mainly among long-distance migratory passerines15. These changes affect the scheduling of breeding, moulting and migration—all highly energy-demanding annual cycle processes2,24,25.

Delayed autumn migration or earlier breeding may result in a longer pre-migration moult period by advancing the moult onset1 and, likely, also delaying its termination. This extension of the moult period could be advantageous to birds that moult before migration (short- or long-distance migrants; Fig. 2b), allowing the birds to replace more feathers and hence to increase their moult extent. For long-distance migrants that moult in the tropical wintering areas, the advancement of the autumn migration15 and the earlier migration onset may result in an earlier arrival to the tropical wintering areas, which might prolong the time available for moult immediately after the autumn migration (Fig. 2b). Moreover, earlier moult after the autumn migration in the northern tropics which are characterised by summer rains could be advantageous due to the higher food abundance in this region in early autumn, which nonetheless declines soon afterwards26,27. The earlier arrival and overall extension of the time available for
moult, as well as the more abundant food resources during the moult period, may allow the birds to moult more feathers, resulting in a more extensive moult, with potential advantages for flight efficiency, thermoregulation and ornamentation.

How feather moult affects bird appearance and thereby sexual interactions is a largely overlooked aspect of avian biology. Unlike adults of most passerine species, which moult their whole plumage, juveniles of most Western Palearctic passerines, stressed by time and limited by their overall inferior physiological condition and foraging competency, only partially moult after fledging. As a result, juveniles are often easily identified by their partial moult and nest-grown feathers, signalling youth and associated with low competitive ability. A more extensive partial moult by juveniles may result in plumage that is more adult-like. This may positively affect bird fitness through sexual selection, though birds that underwent their post-juvenile moult and consequently have a more adult-like appearance and increased attractiveness may also be subject to more aggressive behaviour from competing adults.
example during territorial disputes\textsuperscript{12}. We note that, in general, females have higher nesting and post-fledging parental investment than males\textsuperscript{32–34}, likely exposing the females’ plumage to higher mechanical strain that may lead to higher feather abrasion during the breeding period\textsuperscript{35}. Moreover, the onset of the post-breeding moult, which follows the post-juvenile moult, is later among females than among males\textsuperscript{36–39}. Thus, plumage of females that moulted extensively during their post-juvenile period may be more durable in the breeding period. Thereby, an extensive post-juvenile moult may positively affect bird fitness, also among females.

Males and females differ in several behavioural, physiological, ecological, morphological and chromatical characteristics: e.g., thermoregulation\textsuperscript{16,17}, migration distance\textsuperscript{19} and colourfulness\textsuperscript{40}, which are predicted to interact differentially with climatic conditions. Our results demonstrate a stronger response of females than males in moult extent under climate warming in four species out of 10 sexually dichromatic species, and in no species males moulted significantly more extensively than females (Fig. 1b and Supplementary Table 3). In these four species, GMTA, sex and their interaction affected moult extent. We note that the response of females to GMTA is stronger in highly sexual-dichromatic species as oppose to species in which males and females have similar ornamentation (Fig. 3). It is not clear why the response to GMTA is influenced by sexual-dichromatism, and we speculate that two factors may be involved: (1) feather durability and (2) ornamentation plumage cost. Feathers characterised by blackish and melanin-rich colour are more durable than non-melanic feathers\textsuperscript{41,42}, and hence, to overcome their larger feather wear, females may benefit from a more extensive moult compared with males, but only in species in which females have lighter and therefore less durable plumage than males. The other explanation is based on the costs and benefits of ornamented feathers of males. While these ornaments could provide mating advantages, they may also induce a cost, for example, if sex-biased mortality or a more aggressive behaviour occurs as a result of a more ornamented male plumage\textsuperscript{12,43,44}. We note that our results regarding the differences between males and females in the response to GMTA in relation to their sexual-dichromatism level are based on a rather small sample size (10 species), and
published bird photos for species in which it was possible to identify moulted and non-moulted feathers from photos, e.g., from the Internet Bird Collection (IBC; https://www.hbw.com/IBC). The age of each bird was identified using unique published characteristics for each species. Moreover, regularly, juvenile nest-grown feathers are poorer in texture, duller and characterised by higher abrasion level than that of feathers growing during the post-juvenile moult or by adults. Using all these plumage characteristics, each individual was aged as either a first-year (post-juvenile) or an adult bird (always older than first-year). We identified post-juvenile individuals as those which had completed their partial feather renewal but had not yet begun their first complete adult moult. Each wing and tail feather of first-year individuals was classified as being moulted or non-moulted. Moult extent was determined by documenting the moult of the wing and tail feathers using a score of 0 (non-moulted feather) or 1 (moulted feather). A total of two feather tracts and 48 feathers were documented using this method for each individual, as follows: lesser-coverts (LC; proportion), median-coverts (MC; proportion), greater-coverts (GC; proportion), carpal-covert (CC), alula (A1), primary covert (PC), secondary (S2), tertials (T2–3) and rectrices (R1–6). For two feather tracts with numerous small and difficult to distinguish feathers (lesser- and median-coverts) we only estimated the moult proportion. Then, we calculated the species-specific mean area of each tested feather tract (mm²) using photos that were taken in the field on live birds or on bird skins in the museums. We measured feather tract area using Adobe Photoshop version 6.0.1.3a (Supplementary Table 7 and Supplementary Fig. 2). Then, based on the moult data, we calculated the area of the moulted plumage area in the wing and the tail of each individual.

**Methods**

**Data collection.** Data were obtained from bird skins stored in the collections of 10 natural history museums: (I) Natural History Museum (Tring; UK), (II) Museum National d’Histoire Naturelle (Paris, France), (III) National History Museum of Denmark (Copenhagen, Denmark), (IV) Museum für Naturkunde (Berlin, Germany), (V) Museo Nacional de Ciencias Naturales (Madrid, Spain), (VI) Naturhistoriska Riksmuseet (Stockholm, Sweden), (VII) Natural History Museum Vienna (Vienna, Austria), (VIII) Steinhardt Museum of Natural History, Tel-Aviv University (Tel-Aviv, Israel), (IX) National Natural History Collections, the Hebrew University of Jerusalem (Jerusalem, Israel) and (X) Naturhistorisches Museum (Basel, Switzerland). Additionally, we used moult data that was collected during bird ringing activities in Spain, Italy, Switzerland and Israel. We also used

**Study species.** The study includes Western-Palaearctic species of the genera Turdus (Turdidae), Oenanthe (Muscicapidae), Monticola (Muscicapidae), Ficedula (Muscicapidae) and Lanius (Laniidae), of which we measured more than 100 individuals each (Supplementary Table 1). The identification of moulted versus non-moulted feathers in these species is straightforward (Supplementary Fig. 3), permitting each species, we collected data for all subspecies that are common in the Western-Palaearctic region (e.g., nilotica, senator and badia subspecies of Lanius senator; Supplementary Table 1). Since Lanius excubitor displays a markedly different moult strategy (including moult extent) between its northern subspecies (excubitor) and southern ones (aucheri, elegante and algeriensis; Supplementary Table 6), we considered this species in our analyses as two separate species: Lanius excubitor (excubitor; Great Grey Shrike) and Lanius (excubitor) aucheri (Southern Grey Shrike), as has been done in several previous studies.

**Moult timing and location.** The birds were tested after the end of their post-juvenile moult and before their first post-breeding moult. We determined that moult has ended since we visually inspected each feather and could not trace signs that the moult is still undergoing by recording feathers that are shorter in size and feathers with remains of their protective peripheral sheath. In species that moult before autumn migration, examined individuals were between ~3 and ~12 months old (approximately during September–June). In species that moult after the autumn migration, in the over-wintering areas, examined individuals were between ~7 and ~12 months old (approximately during January–June). In these periods, no additional moult is undertaken and no feathers are replaced (in the study species, a pre-breeding moult is rare and very limited or does not exist). Thus, examining birds that were collected or examined in the field during these periods reliably represent the extent of the post-juvenile moult that occurred earlier, either near the breeding areas or, in the case of post-migration moult, in the over-wintering areas. We note that several studies suggested that the extent of feather moult is affected by latitude: southern species were found to moult more extensively than northern ones. Due to the uncertainty involved with determining the geographic location of moult in birds that were collected throughout the year, often thousands of kilometers away from their natal, breeding and moultng areas, we could not include the latitudes of the mounting area in our analyses. Each museum collection used in the study consists specimens of various sources that were collected in different localities. By using data from 10 bird collections and from live birds that were examined in several countries (Supplementary Table 2), it can be assumed that we created a largely randomly sampled dataset.

**Global mean temperature anomalies.** We used the global mean temperature anomalies (GMTA) as a proxy for global temperature in our analyses. GMTA data for the period 1880–2016 were obtained from the National Aeronautics and Space Administration (NASA), Goddard Institute for Space Studies (https://data.giss.nasa.gov/gistemp/). These anomalies were calculated relative to the mean temperature of the 1951–1980 reference period. The reconstruction of GMTA data for the period 1801–1879 was obtained from published data that is based on glacier length fluctuations. We note that GMTA, by its nature, is an index that cannot capture small-scale variation over local spatial scales and within short-time scales (e.g., between different months). Therefore, the ecological relevance of this index is limited when inferring different biological processes that take place over smaller spatial and temporal scales in which fine-scale variation is important.
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