

The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines

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ABSTRACT

Although feathers are the unifying characteristic of all birds, our understanding of the causes, mechanisms, patterns and consequences of the feather moult process lags behind that of other major avian life-history phenomena such as reproduction and long-distance migration. Migration, which evolved in many species of the temperate and arctic zones, requires high energy expenditure to endure long-distance journeys. About a third of Western-Palearctic passerines perform long-distance migrations of thousands of kilometres each year using various morphological, physiological, biomechanical, behavioural and life-history adaptations. The need to include the largely non-overlapping breeding, long-distance migration and feather moult processes within the annual cycle imposes a substantial constraint on the time over which the moult process can take place. Here, we review four feather-moult-related adaptations which, likely due to time constraints, evolved among long-distance Western-Palearctic migrants: (i) increased moult speed; (ii) increased overlap between moult and breeding or migration; (iii) decreased extent of plumage moult; and (iv) moult of part or all of the plumage during the over-wintering period in the tropics rather than in the breeding areas. We suggest that long-distance migration shaped the evolution of moult strategies and increased the diversity of these strategies among migratory passerines. In contrast to this variation, all resident passerines in the Western Palearctic moult immediately after breeding by renewing the entire plumage of adults and in some species also juveniles, while in other species juvenile moult is partial. We identify important gaps in our current understanding of the moult process that should be addressed in the future. Notably, previous studies suggested that the ancestral moult strategy is a post-breeding summer moult in the Western Palearctic breeding areas and that moult during the winter evolved due to the scheduling of long-distance migration immediately after breeding. We offer an alternative hypothesis based on the notion of southern ancestry, proposing that the ancestral moult strategy was a complete moult during the ‘northern winter’ in the Afro-tropical region in these species, for both adults and juveniles. An important aspect of the observed variation in moult strategies relates to their control mechanisms and we suggest that there is insufficient knowledge regarding the physiological mechanisms that are involved, and whether they are genetically fixed or shaped by environmental factors. Finally, research effort is needed on how global climate changes may influence avian annual routines by altering the scheduling of major processes such as long-distance migration and feather moult.

Key words: adaptations, aerodynamic costs, annual cycle, bird migration, climate change, feather synthesis, life-history transitions, time stress.

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I. INTRODUCTION

The renewal of flight and body feathers is essential for their function because feathers become worn or lost with time due to exposure to radiation, parasites, physical abrasion and other environmental factors (Payne, 1972; Lindström & Nilsson, 1988; Flinks & Salewski, 2012). The performance of old and abraded plumage is poor (Bridge, 2008) and the cost of avoiding plumage renewal is high (Swaddle *et al.*, 1996). Thus, moult is a necessary process during the avian life cycle. Consequently, all passerines moult all of their flight feathers at least once per year (Stresemann & Stresemann, 1966), but they may do so either during a single moult period, or by dividing the moult cycle into several distinct periods in each of which only part of the plumage is replaced (Jenni & Winkler, 1994).

Feather moult may entail aerodynamic (Haukioja, 1971; Swaddle & Witter, 1997*b*; Hedenström & Sunada, 1999; Hedenström, 2003; Bridge, 2008; Achache, Sapir & Elimelech, 2018) and thermoregulatory (Newton, 1968; Lustick, 1970; King, 1980; Walsberg, 1983) costs. In addition, feather synthesis requires energy as well as specific nutrients whose acquisition may involve additional metabolic costs (Murphy & King, 1992; Lindström, Visser & Daan, 1993*b*). To accommodate these considerable costs, the moult process usually occurs over a period of time such that the associated energy demands are not elevated to a degree that could impair the bird's survival (Fogden, 1972; Kiat, Izhaki & Sapir, 2016 but see Rohwer *et al.*, 2009). In addition, the lower aerodynamic performance of wings that have feather gaps due to moult could affect bird survival. For example, Lind (2001) suggested a higher risk of predation due to moult as a consequence of reduced escape ability during take-off. Unfortunately, no empirical data are available regarding how moult affects bird survival in the wild.

The annual cycle of most migratory passerines is made up of a sequence of major life-history stages: breeding, moult and migration. Each stage has evolved to occur for the most effective duration and at the most appropriate time in relation

to bird fitness (Barta *et al.*, 2008; Dawson, 2008; Kiat *et al.*, 2016). Nonetheless, there is huge variation in the properties of the annual cycle among different bird species. These include the timing and duration of different life-history stages, their sequence and their degree of overlap (Newton, 2011). The moult strategy comprises the timing, extent and duration of plumage renewal within the annual cycle, as well as its degree of overlap with other major life-history stages and the environment in which the moult process takes place. As such, it varies greatly among populations, species, functional groups and size classes (Hall & Tullberg, 2004; Kennerley & Pearson, 2010; Kiat & Sapir, 2017). The moult strategy is shaped by the time available for moult during the annual cycle, which is affected by the scheduling of reproduction and long-distance migration during the year (Barta *et al.*, 2008; Newton, 2009; Kiat & Sapir, 2017). For example, the timing of gonadal regression after breeding affects moult onset and may also affect its duration (Dawson, 2008). Bird feather moult is further influenced by food-resource acquisition (Rymkevich & Bojarinova, 1996; Kiat & Izhaki, 2016*b*) because this dictates the availability of feather substances and consequently the rate of feather renewal. In addition, body size and mass may also affect the duration and extent of moult, and it is generally accepted that the longer time required to grow a larger feather constrains the moult of large bird species (de la Hera *et al.*, 2009; Rohwer *et al.*, 2009; Kiat & Izhaki, 2016*b*).

Long-distance migration is believed to have evolved, in most cases, as a strategy to maximize fitness in seasonal environments, and its occurrence and extent depend on a multitude of factors (Alerstam, Hedenström & Åkesson, 2003; Newton, 2010). In the present context of moult strategies, we classified bird species that breed in the Western-Palearctic region as long-distance migrants if their breeding distribution does not include the tropics and at least part of the population winters in the latter zone. Over-wintering may take place in equatorial Asia, sub-Saharan Africa or further south (south of 23°N which defines the northern limit of the tropics).

For animals living in a seasonal environment, the management of time in relation to ecological conditions and annual

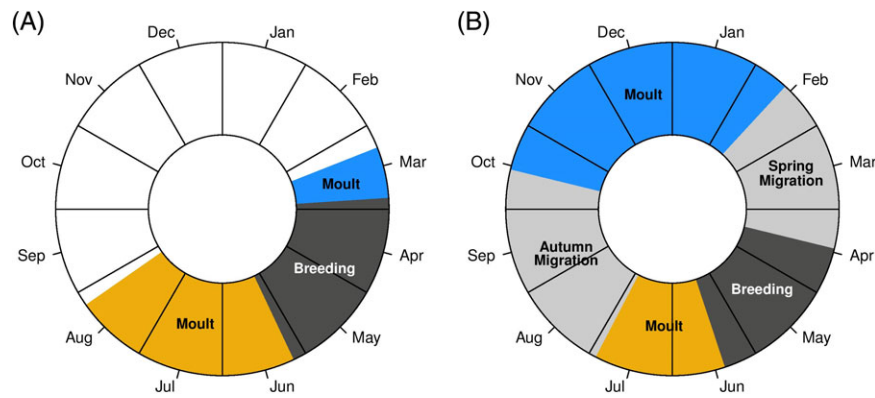


Fig. 1. A schematic representation of major annual processes in resident (A) and long-distance migrant (B) birds.

cycle processes is crucial. The time required for reproduction leaves a limited amount of time for other activities including migration (Alerstam *et al.*, 2003). Among long-distance migrants, breeding at high latitudes in the Western-Palaearctic region imposes severe time constraints, which is a probable explanation for the existence of behavioural, physiological and morphological adaptations connected with time limitations in these areas (Hedenström, 2008). There are two important effects of long-distance migration on bird moult strategies: (i) the scheduling of migration and the pre-migration fattening period places substantial limitations on the time available for moulting in the important, post-breeding, moulting period in the breeding area; and (ii) The suitable environmental conditions in most parts of the Afro-tropical and Indo-Malayan areas during the northern winter, characterized by longer daylight hours and warmer weather, allow for a relatively long moult period that is not available for species that spend the winter in or near their breeding areas in the northern parts of the Western-Palaearctic region (Hall & Tullberg, 2004; Hedenström, 2008; Newton, 2009, 2010) (Fig. 1). We note that these two effects are probably not based on differences in food availability between different locations that are usually unknown.

The annual routine of migratory birds differs substantially from that of resident birds (see Fig. 1), and the scheduling of autumn and spring migrations within the annual cycles have far-reaching consequences for other major, energy-demanding, processes such as breeding and feather moult (McNamara, Welham & Houston, 1998; Barta *et al.*, 2008). Consequently, the evolution of moult strategies in general as well as specific attributes of the moult process have likely been shaped by the properties of these major processes (e.g. Kiat & Sapir, 2017). Herein we discuss the adaptations of migrant passerines of the Western-Palaearctic region to moulting under the high time constraints imposed by long-distance migration. By reviewing the literature on the effects of long-distance migration on passerine feather moult, we aim to enhance knowledge about the interactions between the important and highly energy-demanding processes of moult and migration in order to advance our understanding of avian ecology and evolution. We highlight four different adaptations that have evolved among migratory passerines

that moult their feathers under time stresses imposed by long-distance migration: (i) increased moult speed; (ii) overlap between moult and breeding or migration; (iii) decreased extent of plumage moult; and (iv) moult of part or all the plumage during the over-wintering period in the tropics. We discuss the empirical evidence available for each of these adaptations within the context of the annual routine and specifically in relation to time constraints on feather moult in the breeding areas. We then discuss the consequences of over-wintering in the Afro-tropical or Indo-Malayan regions on the moult strategies of passerines by reviewing moult extent in the wintering areas in adult and juvenile birds.

Suspended moult and split-moult are two strategies in which the moult begins in the breeding areas after breeding and is then paused and recommences after the autumn migration. While regularly in split-moult most of the moult takes place in the breeding grounds, in suspended moult most of the feathers are replaced in the wintering areas and some feathers can be moulted twice. We argue that the extent to which suspended and split moults differ is unclear, despite their being treated as two independent moult strategies in the literature. We furthermore suggest that suspended and split moults are an adaptation to cope with limited time and resource availability during the main moult period for long-distance migratory species. Finally, we argue that moult physiology should receive more attention in the future, and that the moult strategies of migratory birds have important implications on aerodynamics, sexual selection and the effects of climate changes on migratory bird species. Our main aim herein is to improve our understanding of the causes, mechanisms, patterns and consequences of avian feather moult in migratory passerines.

II. THE EFFECTS OF TIME CONSTRAINTS ON FEATHER MOULT IN THE BREEDING AREAS

The main period available for moult for resident and migratory Western-Palaearctic passerines is after breeding and before the beginning of autumn migration or before the beginning of the cold season (Figs 1 and 2). There

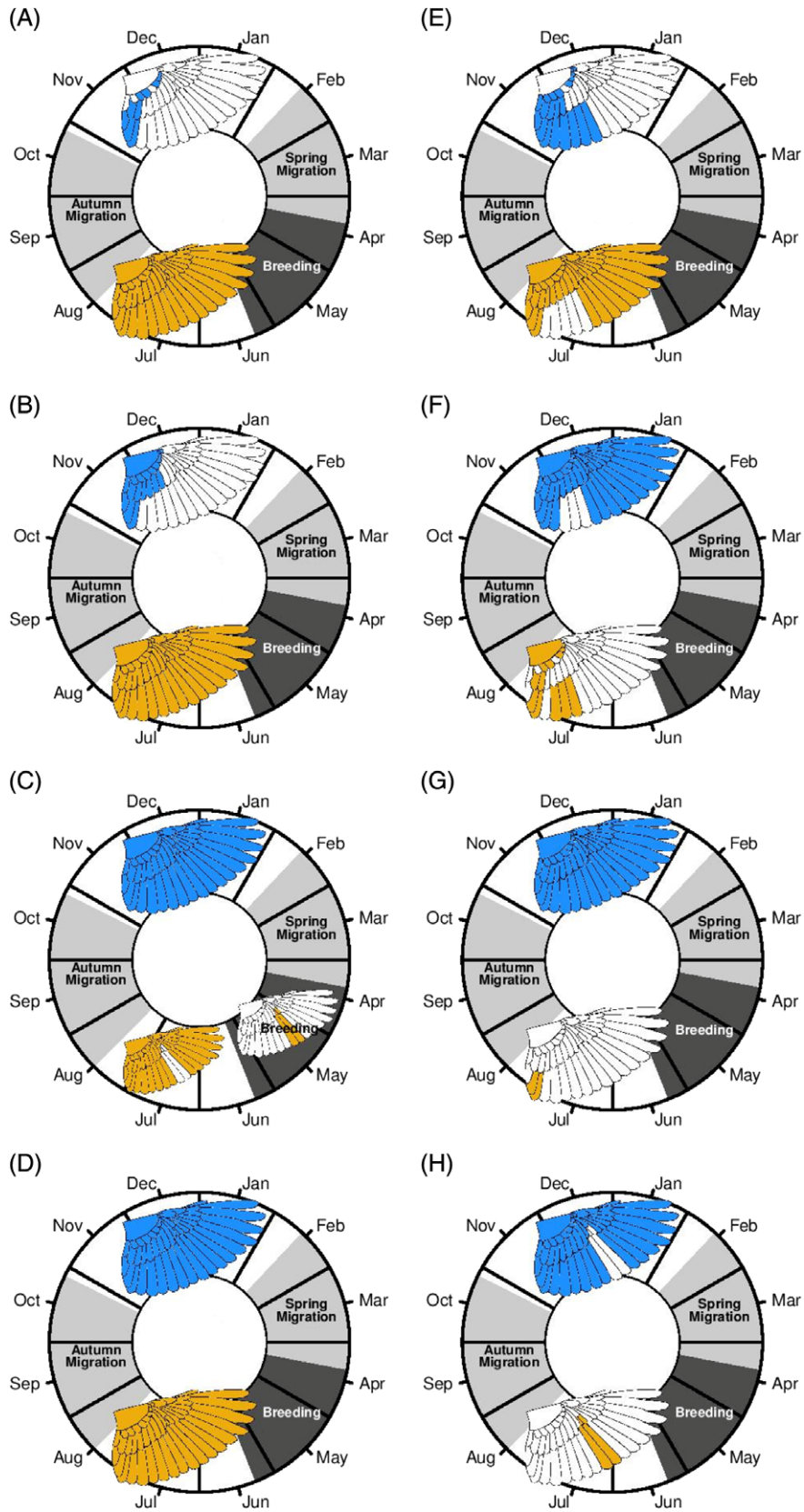


Fig. 2. Legend on nextpage.

are several advantages to undertaking the moult process during this period: (i) the plumage becomes worn following intense food-provisioning activity during breeding (Vágási *et al.*, 2011), making plumage renewal important; (ii) food resources are usually available during this relatively warm period of the year; (iii) because the birds are familiar with their breeding areas, their food resources during this period are usually known and are relatively predictable; (iv) adults have no other major conflicting challenges (e.g. food provisioning for young) during this period and hence can allocate time and energy to moult; and (v) plumage renewal during this period may increase the functional suitability of the plumage for the survival challenges of the autumn migration, for which wing surface integrity is critical (Holmgren & Hedenström, 1995), or for the cold winter for non-migrants, in which additional thermal insulation is necessary (Jenni & Winkler, 1994). Due to time limitations imposed by long-distance migration, migrants substantially shorten this moult period because they must allocate time and energy to fattening before migration, as well as for undertaking the actual migration which usually includes prolonged stopovers (Wikelski *et al.*, 2003). Hence,

there is a trade-off between the time allocated to moult and to migration, as these processes do not usually overlap since each necessitates a significant time and energy expenditure in the annual cycle (Newton, 2010). To overcome the time constraints imposed by migration, long-distance migrants may shorten the duration of their feather moult using one or more of four adaptations: (i) increased moult speed; (ii) overlap between moult and breeding or migration; (iii) decreased extent of plumage moult; and (iv) moult of part or all of the plumage during the over-wintering period in the tropics rather than in the breeding areas (Ginn & Melville, 1983; Jenni & Winkler, 1994; Newton, 2009; Kiat & Sapir, 2017). We note that sometimes points iii and iv are related because if moult extent after breeding is reduced it must usually be completed later, in this case in the over-wintering areas.

(1) Increased moult speed

The rate at which feathers grow is physiologically limited (Rohwer *et al.*, 2009). The materials used to synthesize a feather must be conducted through a collar of cells

Fig. 2. Sequences of annual cycle events and moult strategies among adult long-distance migrant passerines in the Western-Palearctic region (feathers coloured in orange are moulted in the breeding areas and feathers in blue are moulted in the non-breeding areas; modified from Newton (2009)). (A) Complete moult in the breeding areas and occasionally a limited partial moult before spring migration which usually includes only body feathers. This is a typical strategy among species that winter in the Western-Palearctic region as well as species that winter in the northern part of the Afro-tropical region. Examples: Bluethroat (*Luscinia svecica*), Northern Wheatear (*Oenanthe oenanthe*), Isabelline Wheatear (*Oenanthe isabellina*), Asian Desert Warbler (*Sylvia nana*) and Common Chiffchaff (*Phylloscopus collybita*). (B) Complete moult in the breeding areas and a partial moult before spring migration which regularly includes a few wing coverts and tertials. This is a typical strategy among species that winter further south. Examples: Tree Pipit (*Anthus trivialis*), Western Yellow Wagtail (*Motacilla flava*), Whinchat (*Saxicola rubetra*), Pied Flycatcher (*Ficedula hypoleuca*) and Cretzschmar's Bunting (*Emberiza caesia*). (C) Suspended moult during the breeding period, including initiation of the summer moult during the incubation period, suspension of the moult during nestling food provisioning and continuation of the moult process after the end of the breeding season from the point at which it was suspended. This strategy is regular among some Willow Warbler (*Phylloscopus trochilus*; which also includes a complete winter moult) populations in north-eastern England, Scandinavia and north-western Russia and is also rarely and irregularly found in other extremely long-distance migrants, e.g. Tree Pipit (*Anthus trivialis*). (D) Biannual moult, which includes two complete moults, occurring at the breeding and wintering areas. This strategy occurs among most populations of Willow Warbler (*Phylloscopus trochilus*; ~70%) and also among some Savi's Warbler (*Locustella luscinioides*) populations. (E) Split-moult that includes an extensive partial moult in the breeding areas and another extensive partial moult after arrival at the over-wintering areas. The moult in winter includes mainly secondaries and wing coverts. This strategy occasionally includes another limited partial moult before spring migration. It is a typical strategy among species that breed in the southern parts of the Western-Palearctic region and winter in the sub-Saharan Sahel and the northern Afro-tropical region. Examples: White-throated Robin (*Irania gutturalis*), Barred Warbler (*Sylvia nisoria*), Common Whitethroat (*Sylvia communis*), Woodchat Shrike (*Lanius senator*) and Ortolan Bunting (*Emberiza hortulana*). (F) Split-moult that includes an extensive partial moult in the breeding areas and another extensive partial moult after arrival at the over-wintering areas. The moult in the summer includes mainly secondaries and wing coverts. It is an opposite pattern to (E) and a rare strategy among species that undertake a complete moult in the winter, but it is regularly found in Eurasian Golden Oriole (*Oriolus oriolus*). Examples: Garden Warbler (*Sylvia borin*) and Western Bonelli's Warbler (*Phylloscopus bonelli*). (G) Limited partial moult in the breeding areas, which usually includes only body feathers, and a complete moult after arrival at the over-wintering areas in the tropics, which may be suspended within the tropics. This is a typical strategy among species that winter further south and in cases of food scarcity during moult in the breeding areas or with high time constraints during the post-breeding period as in swallows (Hirundinidae). Examples: Rufous-tailed Scrub-robin (*Cercotrichas galactotes*), Great Reed Warbler (*Acrocephalus arundinaceus*), Lesser Grey Shrike (*Lanius minor*), Spotted Flycatcher (*Muscicapa striata*) and Black-headed Bunting (*Emberiza melanocephala*). (H) Suspended moult, which occasionally occurs among species that perform a complete moult in the non-breeding areas (G). In this case the moult begins in the breeding areas, then becomes suspended and continues from the same point only after arrival at the over-wintering grounds. It is a typical strategy when time is short after breeding, e.g. among southern populations of Western-Palearctic breeding migrants. Examples: Sand Martin (*Riparia riparia*), Barn Swallow (*Hirundo rustica*), Eurasian Reed Warbler (*Acrocephalus scirpaceus*), Eastern Common Whitethroat (*Sylvia communis icterops*), and Masked Shrike (*Lanius nubicus*).

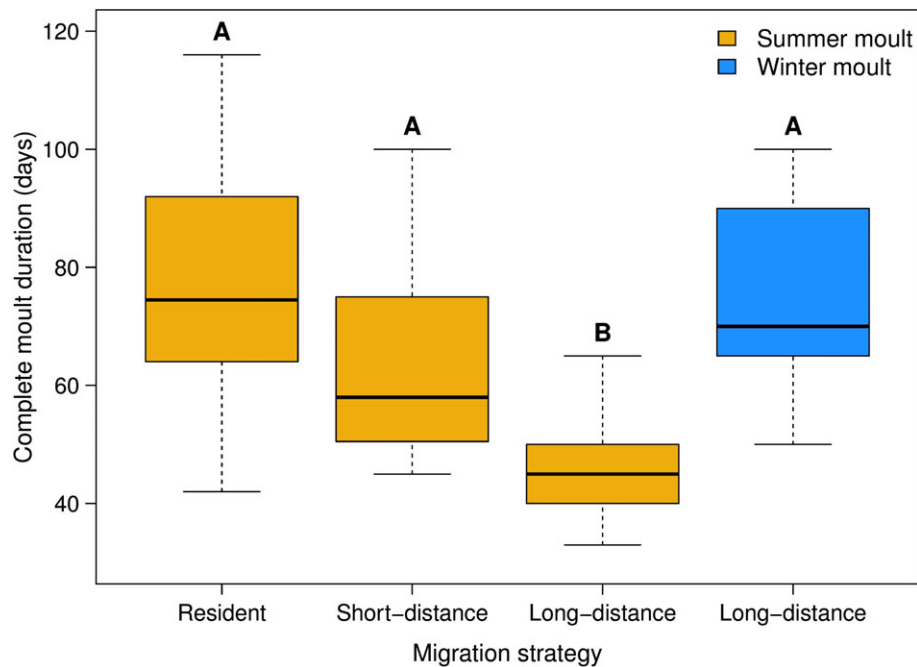


Fig. 3. Variation in complete moult duration between groups of species that have different migratory strategies and moult timing (summer or winter, based on de la Hera *et al.*, 2009; de La Hera *et al.*, 2010b; Kiat & Sapir, 2017). The analysis includes 90 Western-Palaearctic passerines. Data on moult duration are from published literature (Ginn & Melville, 1983; Bensch *et al.*, 1991; Shirihai *et al.*, 2001; de la Hera *et al.*, 2009, 2010b; Kennerley & Pearson, 2010; Kiat & Sapir, 2017) (see online Supporting information, Table S1). The difference in moult duration among the four groups is significant (ANOVA, $F_{3,87} = 11.612$, $P < 0.001$; phylogenetic generalized least-squares model, $\lambda = 0.75$, $P = 0.005$). Different letters above the columns indicate a significant difference ($P < 0.05$) based on Tukey *post-hoc* comparisons. The results indicate that summer moult among long-distance migrants ($N = 21$ species) is significantly shorter than among residents ($N = 38$ species) or short-distance migrants ($N = 19$ species), as well as winter-moulting species ($N = 13$ species). The boxplots display the minimum, 1st and 3rd quartile, median and maximum values of each category.

surrounding the base of the feather follicle, thus limiting feather growth rate. The rate of feather synthesis increases with bird body mass to the power of 0.171 (Rohwer *et al.*, 2009). Consequently, there is little difference in feather growth rate (keratin synthesis) across species ranging in mass from a few grams to several kilograms (Rohwer *et al.*, 2009; Bridge, 2011). Hence, an increase of feather moult speed cannot be achieved by increasing the growth rate of individual feathers.

Long-distance migrants whose main moult takes place immediately after breeding and before the autumn migration (Fig. 2A–E) frequently increase moult speed to reduce moult duration. The duration of this relatively rapid complete moult is affected by migration distance such that long-distance migrants complete their moult in a much shorter time than resident species or short-distance migrants (Hedenström, 2008; de la Hera *et al.*, 2009; Kiat & Sapir, 2017) (Fig. 3). To increase moult speed, migrant species can reduce the intervals between the shedding of successive feathers and increase the number of feathers that are grown simultaneously (Berger, 1967; Haukioja, 1971). Such a rapid moult may impair flight performance and in extreme cases may even cause flightlessness due to aerodynamic failure (Haukioja, 1971). Only species that can cope with impaired flight performance

for a short period of time can increase their moult speed through this strategy. For example, thrushes (Turdidae) and warblers (Sylviidae) can survive with smaller wing surface areas for short periods because they can still perform the short flight bouts that are required for foraging in their bushy habitat (Williamson, 1957; Gaston, 1976). By contrast, the aerial feeding of swallows (Hirundinidae) requires elaborate manoeuvres, and these species cannot tolerate the substantial flight impairment and associated reduced wing performance (Achache *et al.*, 2018) caused by increasing their moult speed in this way (Kiat *et al.*, 2016).

High moult speed determined by the number of feathers grown simultaneously (Rohwer & Rohwer, 2013) is associated with lower quality and thus less-durable plumage (Serra, 2001), consequently decreasing bird survival and reproductive success (Nilsson & Svensson, 1996; Morales *et al.*, 2007) and likely reducing subsequent migration speed (Hedenström, 2008). This strategy, however, is necessary to overcome the time constraints imposed by long-distance migration in many species. Experimentally time-stressed Lesser Whitethroats (*Sylvia curruca*) and European Starlings (*Sturnus vulgaris*) sped up moult and grew shorter, less-durable primary feathers (Dawson *et al.*, 2000; Hall & Fransson, 2000). In addition, time-stressed Blue Tits (*Cyanistes caeruleus*)

and House Sparrows (*Passer domesticus*), which are resident species, developed body feathers with lower insulation capacity (Nilsson & Svensson, 1996; Vágási *et al.*, 2012). Migratory Blackcaps (*Sylvia atricapilla*) preferentially allocate available resources to wing feathers at the expense of tail feathers, which are presumably less important when undertaking migratory flights, resulting in wing feathers of higher quality compared to those of resident individuals (de la Hera *et al.*, 2010a). These results suggest a trade-off between feather moult speed and feather quality. Willow Warblers (*Phylloscopus trochilus*) perform a biannual, complete moult (Fig. 2D), in which the post-breeding first moult is rapid and occurs before the autumn migration and the second is longer and occurs in the wintering areas (Underhill *et al.*, 1992). The feathers that grow during the winter are of better quality than those that grow before the autumn migration (de La Hera, Pérez-Tris & Tellería, 2010b). Furthermore, experimentally time-stressed individuals with accelerated moult speed showed degraded pigment-based and structural colours compared to their unmanipulated counterparts (Serra *et al.*, 2007; Griggio *et al.*, 2009). Thus, another cost of rapid moult can be the impairment of feather colouration, which may have negative consequences for attractiveness and consequently reproductive success.

(2) Overlap between moult and breeding or migration

Usually, moult does not overlap with other highly demanding energetic annual cycle events, such as breeding and migration (Jenni & Winkler, 1994; Newton, 2009). This is because feather synthesis during the moult period requires high energy expenditure (Dolnik & Gavrilo, 1979; Murphy & King, 1992; Lindström *et al.*, 1993b; Klaassen, 1995; Cyr, Wikelski & Romero, 2008). In addition, moulting increases thermoregulation costs and substantially hampers flight performance such that the energy expended to sustain flight increases (Haukioja, 1971; Lindström *et al.*, 1993b; Hedenström & Sunada, 1999; Hedenström, 2003; Tomotani *et al.*, 2018a). Due to these high demands, there is no complete overlap between moult and breeding or migration in passerines. However, long-distance migrants that have only a short window of time available for moult before embarking on their autumn migration may initiate their moult before the end of the breeding period and may finish their moult after migration starts (Evans, 1966; Haukioja, 1971; Neto & Gosler, 2006). An overlap between flight feather moult and active migration was documented in Sand Martins (*Riparia riparia*) during autumn migration in Israel where 7.2% of examined adults showed active moult of the primaries ($N = 19$ of 265 individuals; Y. Kiat, unpublished data). Although a moult–migration overlap is rare, an overlap between moult and pre-migration deposition of subcutaneous lipids may be rather common (Jenni-Eiermann & Jenni, 1996; Merilä, 1997; Pilastro, Spina & Micheloni, 1998; Rubolini, Massi & Spina, 2002). Among captive adult male Bluethroats (*Luscinia svecica*), a group of individuals that were experimentally time-shifted by photoperiodic

manipulation to 1 month later than the natural light regime at their moulting grounds at 66°N started to deposit lipids in the middle of the moult process whereas individuals in the control group first started to deposit fat only after moult was complete, as in free-living individuals. Also, while the speed of moult did not differ between the two groups, lipid deposition rate following completion of the moult was higher in the time-shifted group (Lindström, Daan & Visser, 1994).

A moult–breeding overlap is more common in males than females, suggesting that males are less constrained during this period compared to females (Hemborg & Merilä, 1998; Hemborg, 1999; Neto & Gosler, 2006; Mumme, 2018). This probably reflects a lower parental investment than that of females (Hemborg, Lundberg & Siikamäki, 1998; Jahn *et al.*, 2017), allowing them to meet the demands of breeding and moult simultaneously. However, the consequences of this overlap may be substantial as shown by experiments with the Pied Flycatcher (*Ficedula hypoleuca*), a long-distance migrant. In these experiments the two innermost primary feathers were removed in free-living individuals, imitating the natural loss of these feathers during the early stages of the moult process (Slagsvold & Dale, 1996; Hemborg *et al.*, 1998). Both males and females undergoing this manipulation, and their fledglings, showed lower body condition. In addition, the survival of manipulated adult males was lower than that of males in the control group. Interestingly, a study in wild populations of this species showed that females with a moult–breeding overlap were characterized by a higher body mass and lower stress levels [measured as levels of the stress protein heat shock protein 60 (HSP60)] at the end of the breeding season compared with females without a moult–breeding overlap. Furthermore, a higher proportion of females with a moult–breeding overlap returned to the breeding grounds the following year compared with females that did not overlap breeding with feather moult, possibly indicating a higher survival of these birds. Nevertheless, females characterized by a moult–breeding overlap had a lower reproductive output in terms of lower hatchling and fledgling numbers (Morales *et al.*, 2007). Therefore, there seems to be a trade-off between investment in reproduction and survival that is expressed in the moult strategy of the individual. A comparison of the moult–breeding overlap between different Pied Flycatcher populations indicated that, among males but not females, the proportion of moulting individuals increased with increasing latitude. This may suggest that a moult–breeding overlap strategy is used to a greater extent by Pied Flycatcher males that have a shorter breeding season in more northerly regions of the Western-Palaearctic (Hemborg, Sanz & Lundberg, 2001), possibly suggesting that the time available for moult (shorter in higher latitudes) modulates this trade-off.

Foraging effort is not evenly distributed across the breeding season. The incubation period is characterized by a relatively low frequency of foraging activity in comparison with the nestling-feeding period when parents forage intensively to provide food for their young (see also Merkle & Barclay, 1996; Slagsvold & Johansen, 1998). Although an uncommon

strategy, a few migrant species initiate their summer moult during the incubation period, suspend the moult during the nestling food-provisioning period, and then continue the moulting process after the breeding season from the point at which it was suspended (Fig. 2C). This pattern is known for some Willow Warbler populations in north-eastern England, Sweden, Finland and north-western Russia (Tiainen, 1981; Bensch *et al.*, 1985; Lapshin, 1988; Underhill *et al.*, 1992; Norman, 1998). In north-eastern England, more than 30% of individuals use this strategy (Norman, 1998). The breeding of Willow Warbler at high latitudes coupled with very long-distance migration imposes extreme time constraints which probably selected for this unusual adaptation. This rare pattern is also reported in other high-latitude breeding species such as the Tree Pipit (*Anthus trivialis*) (Jenni & Winkler, 1994).

(3) Decreased extent of plumage moult

Species that winter in the Afro-tropical and Indo-Malayan regions have much more time available for moult during the winter than in their Western-Palaearctic breeding areas. Thus, many of these species perform an extensive winter moult and can dramatically shorten the duration of their summer moult (Kiat & Sapir, 2017). For example, adults of some northern populations of Willow Warbler may delay replacement of part of their plumage, retaining it during the summer moult and later performing a complete second moult in their Afro-tropical wintering area (Fig. 2D). In Sweden, 34% of Willow Warbler adults still retained a few old and abraded flight feathers during their autumn migration, following the completion of their summer moult (Hedenström, Lindström & Pettersson, 1995). In some species, feathers not moulted during a partial summer moult are renewed as part of a second partial moult in winter. This moult strategy is known as 'split-moult' (Hasselquist *et al.*, 1988; Norman, 1991; Lindström *et al.*, 1993a) (Fig. 2E) (see Section III.4 for distinguishing between split-moult and suspended moult). Typically, feathers that are replaced during the second stage in split-moulters are those that constitute the last stage of the regular moult sequence in species that undergo a single complete moult (Fig. 2E, F). These include the innermost secondaries, alula and rectrices. Retaining their secondaries allows split-moulters to allocate resources preferentially to primary feather synthesis (see also Kiat & Izhaki, 2017).

This phenomenon creates an irregular moult strategy among many long-distance migrant species that split their moult. Among Willow Warblers in Sweden, females showed a significantly higher incidence of non-moulted feathers. Among females, 44% of individuals retained their old secondaries, twice as many as in males. The average number of retained old secondaries in individuals with at least one unmoulted secondary feather was 2.3 for males and 2.8 for females (Hedenström *et al.*, 1995). This may be explained by the lower investment in breeding activities by males, allowing them to invest more time and energy to moulting, resulting in their higher proportion of moulted

feathers compared to females (see also Section II.2). In the Common Whitethroat (*Sylvia communis*), moult strategies are not fixed and vary substantially among different populations, probably reflecting different selective pressures resulting from differences in environmental conditions and life-history strategies. This variability includes most of the strategies employed by long-distance migrants, i.e. complete summer moult (Fig. 2A), complete winter moult (Fig. 2G), split-moult (Fig. 2E), etc. (Jenni & Winkler, 1994; Shirihai, Gargallo & Helbig, 2001; Waldenström & Ottosson, 2002).

Juveniles begin their life with fresh feathers in the same period that adult plumage is the most worn. The complete moult that juveniles of a few species (e.g. Eurasian Skylark *Alauda arvensis*, Bearded Reedling *Panurus biarmicus* and Eurasian Tree Sparrow *Passer montanus*) undergo 1–3 months after leaving the nest may be an ancestral juvenile moult strategy in habitats with long periods of favourable environmental conditions after the breeding season, such as those in some tropical areas (Fogden, 1972; Kiat & Izhaki, 2016b). However, in the breeding areas of many long-distance migrants there is only a very short time window available for moult before migration. Consequently, there are only two known long-distance migrant species, Greater Short-toed Lark (*Calandrella brachydactyla*) and Bimaculated Lark (*Melanocorypha bimaculata*), which exhibit a complete juvenile summer moult before migration (Kiat & Izhaki, 2016b). The fresh plumage of recently fledged juveniles allows them to avoid replacing part or all of their plumage before the autumn migration or before the beginning of winter, thus saving energy and time (Kiat & Sapir, 2017). Avoiding the need to replace part of the plumage before the autumn migration may also be necessary due to the limited ability of juveniles to allocate sufficient resources to moulting in this early stage of their life due to their relatively low foraging success compared with adults (Marchetti & Price, 1989; Wunderle, 1991). Several long-distance migrant species delay their first complete juvenile moult until reaching the over-wintering areas (e.g. Melodious Warbler *Hippolais polyglotta*, Lesser Grey Shrike *Lanius minor* and Black-headed Bunting *Emberiza melanocephala*), whereas others do not replace most of the wing and tail feathers during their first year of life (e.g. Thrush Nightingale *Luscinia luscinia*, Northern Wheatear *Oenanthe oenanthe* and Red-breasted Flycatcher *Ficedula parva*) (Jenni & Winkler, 1994; Kiat & Sapir, 2017).

(4) Delay of part or all of the moult until winter

As opposed to breeding and migration, which are constrained to take place during specific periods of the year, moult can be delayed to a later season to alleviate time constraints on long-distance migrants (Alerstam *et al.*, 2003; Barta *et al.*, 2008). There is a general negative correlation between the breeding and wintering latitudes of migratory species such that the winter quarters are situated in reverse latitudinal sequence to the breeding sites, a pattern called a 'leap-frog migration' (Palmén, 1874; Salomonsen, 1955). Species and populations that breed at more northerly latitudes in the Western-Palaearctic region thus have less time available for

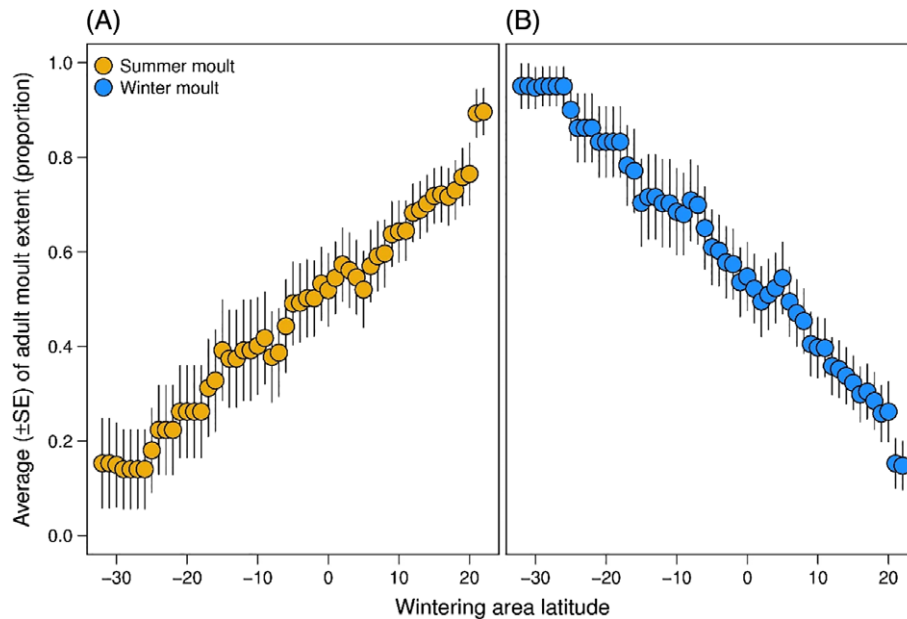


Fig. 4. Extent of adult moult (mean \pm S.E.; proportion of feathers moulted) for (A) summer moult in breeding areas, and (B) winter moult in non-breeding areas in relation to wintering latitudes for 74 long-distance migrant species that over-winter in the Afro-tropical region (22°N to 32°S, Table S2). The distribution data are based on BirdLife distribution maps (BirdLife International and NatureServe, 2014) and moult extent data are based on our own data (Y. Kiat, unpublished data) as well as published literature (Pearson, 1973; Cramp, 1977; Ginn & Melville, 1983; Aidley & Wilkinson, 1987; Svensson, 1992; Shirihai *et al.*, 2001; Kennerley & Pearson, 2010). There is a significant positive correlation (Spearman $r_s = 0.991$, $P < 0.001$) in (A) and a significant negative correlation (Spearman $r_s = -0.993$, $P < 0.001$) in (B) between the latitude of the species' over-wintering area and the extent of summer or winter moults, respectively.

moulting in their breeding areas compared with species and populations that breed at more southerly latitudes due to the earlier onset of the cold season and their longer migration distance. Species that winter within the Western-Palaearctic region (i.e. at relatively northern latitudes) also have less time available for moult due to the early onset of the cold season compared with species that winter further south due to the favourable conditions that prevail in the Afro-tropical and Indo-Malayan regions during the northern winter. This relaxation of time constraints in the tropics during winter, together with the leap-frog migration pattern, leads to a negative correlation between the time available for moulting in the breeding and in the wintering areas (Fig. 4). Consequently, an extensive moult during the over-wintering period (Fig. 2C–H) uniquely characterises long-distance migrants. Species that undertake this moult strategy are characterized by a short post-breeding time window before migration must commence, during which an extensive moult cannot take place (Fig. 1). Because of its importance, this strategy is considered in more detail in Section III.

III. MOULT IN THE WINTERING AREAS

(1) Extensive partial winter moult

A partial winter moult is common among resident and migratory Western-Palaearctic passerines during late

winter or early spring. This moult strategy usually includes renewal of body feathers, tertials, a few wing coverts and occasionally some flight feathers (Fig. 2A, B). These feathers are often highly abrading over time (Jenni & Winkler, 1994). A partial winter moult is more common and extensive among long-distance migrants that winter in the Afro-tropical or Indo-Malayan regions than in species that winter in the Western-Palaearctic region (Figuerola & Jovani, 2001). It may be the case that the plumage of long-distance migrants is subject to greater likelihood of damage than the plumage of residents as a consequence of their longer flights during migration. The more extensive winter moult in long-distance migrants, which also includes the renewal of the flight feathers, may therefore function to ensure that the birds embark on spring migration with new wing feathers that have better aerodynamic capacities (Bridge, 2008) and thus may lower the metabolic costs of flight. An additional advantage to a partial winter moult among long-distance migrants is that moult can take place more slowly in the Afro-tropical and Indo-Malayan wintering areas, as opposed to a time-limited post-breeding moult before the autumn migration (Lindström *et al.*, 1994; Kiat & Sapir, 2017). We note that there are no empirical data with which to assess these suggestions, and it is likely to be extremely difficult to determine which selection forces underlie the evolution of bird feather moult timing. In some long-distance migrants, the extensive partial winter moult produces a more colourful mating plumage [e.g. some wagtails (*Motacilla*)

and flycatchers (*Ficedula*)], with clear implications for sexual selection (Hill, 1991; Johnsen *et al.*, 1998; Figuerola & Jovani, 2001; Siefferman & Hill, 2003). A change in colour can take place either by moulting or by the abrasion of cryptic feather fringes, a process which takes a relatively long time (Tökölyi, Bokony & Barta, 2008). Figuerola & Jovani (2001) found that species with larger changes in sexual dichromatism between seasons tend to undertake the most extensive moult before the start of the breeding season (pre-migration), presumably in order to arrive at the breeding areas in new, attractive, breeding plumage. An extensive winter moult is a typical strategy in long-distance migrants, but less so in residents in which mating plumage is more likely to be associated with the abrasion of feathers grown during the post-breeding moult, or by a limited-extent partial moult before breeding (Tökölyi *et al.*, 2008).

(2) Split-moult

The ancestral moult strategy among Western-Palearctic passerines is thought to be a complete moult after breeding in the breeding areas (Svensson & Hedenström, 1999; Hall & Tullberg, 2004) (Fig. 2A, B). For some species, however, the time available for moult is limited in both their temperate breeding areas and tropical wintering grounds. Insufficient time for the completion of an entire moult cycle in either the Western-Palearctic breeding areas or the Afro-tropical wintering areas presumably caused a split in the moult of several migrant species between two different geographic areas and periods of the year. These species do not perform a complete moult in either the summer or the winter moult cycles but all of their plumage is annually renewed over the two moult periods (Stresemann & Stresemann, 1966; Hasselquist *et al.*, 1988; Nikolaus & Pearson, 1991; Hedenström *et al.*, 1992) (see Fig. 2E, F; to distinguish between split-moult and suspended moult, see Section III.4). This moult strategy is typical of long-distance migrants which breed in relatively southern parts of the Western-Palearctic region and winter in sub-Saharan Africa. Migrants arrive in the northern tropics at the end of the summer rains when food is abundant, but soon afterwards, it starts to decline (Hogg, Dare & Rintoul, 1984; Aidley & Wilkinson, 1987; Bensch *et al.*, 1991; Trierweiler *et al.*, 2013). Hence, the time available for moult may also be limited in this part of the tropics. The split-moult strategy is therefore probably an adaptation to conditions in which the time available for moulting is limited in both the Western-Palearctic breeding and Afro-tropical over-wintering areas.

The split-moult strategy represents a deviation from the common moult strategy as species performing a split-moult do not undertake a single complete moult at any point in the annual cycle. Svensson & Hedenström (1999) used a phylogenetic analysis to show that the split-moult of Barred Warbler (*Sylvia nisoria*) and Orphean Warbler (*Sylvia hortensis*) evolved from an ancestral state of summer moult. They also suggested that this rare split-moult pattern might represent an evolutionary transition between summer and winter moults (Norman, 1997; Svensson & Hedenström,

1999) and that this intermediate step is unlikely to persist due to strong directional or disruptive selection favouring either winter or summer moult (Svensson & Hedenström, 1999). However, it is also possible that split-moult evolved in response to time stress and food-resource shortage during the original moult period (summer or winter). The occurrence of this strategy among species whose main moulting period is the summer (e.g. Orphean Warbler; Fig. 2E) and also among species whose main moulting period is the winter (e.g. Eurasian Golden Oriole *Oriolus oriolus*; see Fig. 2F) may contradict the suggestion of Svensson & Hedenström (1999) that this strategy represents an evolutionary transition between summer and winter moults. In addition, captive Orphean Warblers that were experimentally prevented from breeding moulted a few weeks earlier than control individuals, and, as a result, completed their entire moult before the autumn migration (Berthold & Querner, 1982b). Clearly, the split-moult of Orphean Warbler is not strictly endogenously controlled and fixed but can be modulated by individual state and possibly by environmental conditions. This suggests that this species' moult strategy is a complete summer moult that usually cannot be completed due to time and resource-availability constraints. Consequently, it cannot be considered an evolutionarily transitional strategy (Mead & Watmough, 1976; Norman, 1991; Svensson & Hedenström, 1999). The split-moult found in this species may be facultative, presumably to facilitate migration when the moult has not yet been completed (Berthold & Querner, 1982b).

Compared with non-passerines, the basic moult sequence (the order of feather replacement during the moult process) of passerines is rather uniform among species (Ginn & Melville, 1983). In the split-moult strategy, the flight feathers that are retained after the main moult period has ended are the secondaries, usually S_{1-5} (Fig. 2E, F), and less often, the alula or rectrices. These feathers (secondaries, alula and rectrices) are the last to be replaced during a complete moult (Ginn & Melville, 1983; Norman, 1991). Retaining these feathers may therefore indicate that the bird did not have enough time to complete the entire moult sequence, possibly due to time stress caused by migration onset (Berthold & Querner, 1982b). Consequently, the split-moult pattern cannot be considered as a fully endogenously controlled moult strategy (Mead & Watmough, 1976; Berthold & Querner, 1982b; Norman, 1991), but rather a derived variant of the complete moult, modulated by individual state and environmental conditions. We note, however, that some studies have suggested that split-moult is an endogenously controlled moult strategy (Hedenström *et al.*, 1992; Lindström *et al.*, 1993a). We propose that current data do not favour the latter explanation, but further analyses are clearly required.

(3) Complete moult in the wintering areas

A complete moult in the over-wintering areas occurs only among long-distance migrants (Jenni & Winkler, 1994; Svensson & Hedenström, 1999) (Fig. 2G). This complete winter moult is considered to be an adaptation for

long-distance migration that evolved from the ancestral summer moult strategy (Svensson & Hedenström, 1999). Complete moult in the wintering areas occurs in species that are found in habitats with a short period of high food availability during the summer and high resource abundance at their Afro-tropical and Indo-Malayan wintering grounds (Barta *et al.*, 2008).

There are some advantages to moulting in the over-wintering rather than the breeding areas: (i) saving time after breeding may allow earlier arrival to the tropics, possibly facilitating the occupancy of higher quality territories (Price, 1981); (ii) In most cases, time is less limited in the tropics during winter compared with the post-breeding period in the breeding areas, allowing a slower moult (Fig. 3) and minimizing its impact on flight performance (Pearson, 1973; de La Hera *et al.*, 2009; but see Bensch *et al.*, 1991). In addition, feathers that grow at a slower rate are longer (Dawson *et al.*, 2000; Hall & Fransson, 2000; Saino *et al.*, 2004; de La Hera *et al.*, 2010b) and more durable than feathers that grow quickly (Serra, 2001; Serra *et al.*, 2007; Griggio *et al.*, 2009) which may have substantial implications for the feathers' morphological integrity and consequently their function; (iii) Migrant species can avoid a costly moult–breeding overlap that could interfere with parental care and pre-migration fuel deposition (Svensson & Nilsen, 1997; Svensson & Hedenström, 1999; Mumme, 2018); (iv) Moulting in winter enables the utilization of abundant food resources in the tropical wintering areas, as opposed to declining food resources in the Western Palearctic after breeding (Svensson & Hedenström, 1999); and (v) Renewal of the plumage before spring migration and hence just before the breeding season may facilitate higher breeding success as the sexual-attraction function of plumage is most conspicuous following moult (Pearson, 1973) and the cost of long-distance flight may be lower with recently renewed flight feathers, as opposed to old abraded feathers (Bridge, 2008) (see also Section II.4). This strategy would carry the disadvantage of undertaking the autumn migration with abraded flight feathers, but it is possible that such species could compensate for their impaired flight performance during autumn by migrating earlier or more slowly than species migrating with fresh feathers (Fransson, 1995; Kiat & Izhaki, 2016a). In addition, the higher durability of winter-grown feathers (point ii above) may mean that these feathers have accumulated less damage by the autumn migration. Further study is required to assess these suggestions.

A good food supply is necessary for feather regeneration, and consequently the moult process may depend strongly on seasonal changes in food abundance (Ginn & Melville, 1983). A low availability of food is probably the main factor affecting moult timing, given the high nutritional and metabolic demands of this process (Murphy, 1996). This applies not only to migrants that moult following breeding in the Western Palearctic but also to species that moult in the Afro-tropical wintering areas (Barta *et al.*, 2008). Empirical evidence for changes in moult timing due to food availability is rare and

additional studies are needed to corroborate the relationship between food availability and moult timing (but see Hahn, 1995). In addition, environmental conditions may affect the structural properties and colour of feathers generated during a moult (Swaddle & Witter, 1997a), suggesting that food availability may influence a variety of features of the moult process.

Many species migrate to the northern sub-Saharan region in the early autumn, taking advantage of the region's high food abundance during this period (Jones, 1995). Some migratory species, including Eastern Bonelli's Warbler (*Phylloscopus orientalis*), Great Reed Warbler (*Acrocephalus arundinaceus*) and eastern populations of Common Whitethroat begin their post-breeding migration very early, in June or July, when food is still abundant in their Western-Palearctic breeding habitats. Moreau (1972) suggested that late arrival to the northern parts of the sub-Saharan region may affect moulting due to the progressive depletion of food resources in this area after the end of the wet summer season (Jones, 1995), but empirical studies indicate food-resource depletion in this region only from October (Morel, 1973; Trierweiler *et al.*, 2013) and throughout the winter period (Schlaich *et al.*, 2016).

Species migrating to sub-Saharan Africa tend to follow the rains as they move south during late autumn and winter. Consequently, some of these species have two moult periods, one in autumn somewhere in the northern sub-Saharan region and a second in late winter, in the southern part of Africa (Pearson & Backhurst, 1983; Pearson & Lack, 1992; Kennerley & Pearson, 2010). Thus, these species, which are usually considered to undergo a complete moult in their wintering areas, actually divide their moult into two temporally and geographically separate phases by suspending the moult process within the wintering period. The moult starts relatively rapidly on reaching the northern sub-Saharan regions, is suspended upon commencement of the within-Africa southern migration, and then resumes after arrival at the southern wintering grounds. This strategy may occur, for example, in Sedge Warblers (*Acrocephalus schoenobaenus*) and Savi's Warblers (*Locustella luscinioides*). Among some species, there is another partial moult in late winter following their earlier complete moult in winter (e.g. Common Whitethroat and Olivaceous Warbler *Iduna pallida*) (Gaston, 1976; Pearson & Backhurst, 1983; Bensch *et al.*, 1991; Shirihai *et al.*, 2001; Salewski *et al.*, 2004).

(4) Suspended moult

Suspended moult differs from split-moult mainly in the extent of moult in each of the two moult periods. While split-moult includes an extensive first moult and a more minor second moult that involves all the feathers that were not moulted in the first moult phase (but see below), the first phase of suspended moult includes a limited flight feather moult with the main bulk of this moult taking place during the second phase of the moult. Furthermore, split-moult usually includes several feathers that are moulted twice, whereas suspended moult typically represents one complete

moult which is divided into two distinct periods (usually also in two different geographical regions; Fig. 2H, but see Section II.2 and Fig. 2C) and no feathers are moulted twice. Nevertheless, although often treated as two different moult strategies, it is not clear if the mechanisms that control the split-moult strategy differ from that of suspended moult. We suggest that both patterns evolved in long-distance migrants to cope with time and possibly food-availability constraints during the main moult period, just after breeding. Herein, we maintain the separation between these two strategies following previous authors (Hasselquist *et al.*, 1988; Norman, 1991; Lindström *et al.*, 1993a; but see Mead & Watmough, 1976; Hall & Tullberg, 2004).

Some individuals of several species that usually complete their moult during winter in the Afro-tropical or Indo-Malayan regions start the moult process in the north, within the Western-Palearctic region. These individuals may be subject to less time constraints, possibly because they bred in a relatively southern part of the breeding range or had a failed breeding attempt. These individuals operate opportunistically by utilizing the available resources in their Western-Palearctic breeding habitats to initiate the moult process earlier than their conspecifics. In these individuals, the moult is suspended during migration and then continues from the point at which it was suspended after arrival at the wintering grounds (Stresemann & Stresemann, 1966; Svensson, 1992) (Fig. 2H). This suspended moult does not constitute a regular strategy for any species, although in some species it can be relatively common. For example, in Barn Swallows (*Hirundo rustica*), suspended moult has been documented in 2.6–19.0% of all adults at several sites in central and southern Europe (Pimm, 1970; Kasperek, 1976; Pilastro *et al.*, 1998). This pattern also occurs among other migratory hirundinids, including Eurasian Crag Martin (*Phyonoprogne rupestris*), Sand Martin, Red-rumped Swallow (*Cecropis daurica*) and Northern House Martin (*Delichon urbicum*) (Elkins & Etheridge, 1977; Ginn & Melville, 1983). The high prevalence of this moult type in the swallow family is probably a result of the slow moult rate required by these aerial insectivores to maintain their aerodynamic abilities (Kiat *et al.*, 2016) necessitating a long period to accomplish their moult. Beginning the moult process in the north may represent a substantial advantage, since the long duration of the moult (up to 185 days; Ginn & Melville, 1983) would otherwise impact the scheduling of other processes within their annual routine. This strategy also occurs among long-distance migratory non-passerines (e.g. Common Quail (*Coturnix coturnix*), European Turtle Dove (*Streptopelia turtur*) and European Bee-eater (*Merops apiaster*); Mead & Watmough, 1976) which also moult over a relatively long duration (de la Hera *et al.*, 2009). We note that the frequency of suspended moult may be related to differences in the timing and location of breeding among different populations. For example, it may be more common in southern populations within the Western-Palearctic region because they will have more time while food is still abundant in the breeding areas before commencing their migration.

Thus, these individuals are subject to a lower level of time stress, consequently allowing them a more advanced moult in their breeding areas than individuals that breed in more northerly regions of the Western-Palearctic (Swann & Baillie, 1979). However, this trade-off will also depend on the extent to which individuals of southern populations are able to devote more time to breeding, for example by increasing their number of broods and breeding attempts. In conclusion, suspended moult probably represents an adaptation by long-duration moulters that may enable them to complete the moult under less time pressure.

(5) Extensive moult in the first year of life

Juveniles have a lower foraging success in comparison with adults (Marchetti & Price, 1989; Wunderle, 1991). While adult passerines moult their entire plumage at least once a year, in some species of Western-Palearctic passerines, juveniles do not renew their flight feathers during their first year of life but undertake their first complete moult after their first breeding season when they are about 12–14 months old (e.g. Northern Wheatear, Eurasian Nuthatch *Sitta europaea* and Siberian Tit *Poecile cinctus*) (Kiat & Sapir, 2017). However, it is likely that under favourable environmental conditions during the post-breeding period, such as in some tropical areas, the renewal of the whole plumage by juveniles is probably an optimal moult strategy (Kiat & Izhaki, 2016b). Renewal of juvenile plumage during winter is probably advantageous over postponing it to the first post-breeding season because the birds will begin their first breeding season with fresh adult plumage, which may benefit their breeding success both in terms of the aerodynamic advantages of flying with recently renewed plumage (Rohwer *et al.*, 2005; Bridge, 2008; Kiat & Izhaki, 2016b) and of attracting a mate. Of all Western-Palearctic passerines, both residents and migrants, only 20% of juveniles perform a complete moult in the breeding areas following fledging (Kiat & Izhaki, 2016b) (Fig. 5). This group of species includes only two long-distance migrants (Greater Short-toed Lark and Bimaculated Lark). The relative rarity of this moult strategy among juvenile migrants presumably reflects substantial time constraints on juvenile migrants. Wintering in the Afro-tropical and Indo-Malayan regions allows juveniles of long-distance migrants to renew their plumage under less time constraint during winter (Svensson & Hedenström, 1999; Hall & Tullberg, 2004; Newton, 2009; Kennerley & Pearson, 2010). Hence, in many Western Palearctic passerine species, juveniles moult extensively during the first winter (Fig. 5).

IV. DIRECTIONS FOR FUTURE STUDY

Following the above review of moult strategies and the effects of long-distance migration on feather moult in Western-Palearctic passerines, we now propose several research directions that may substantially advance our

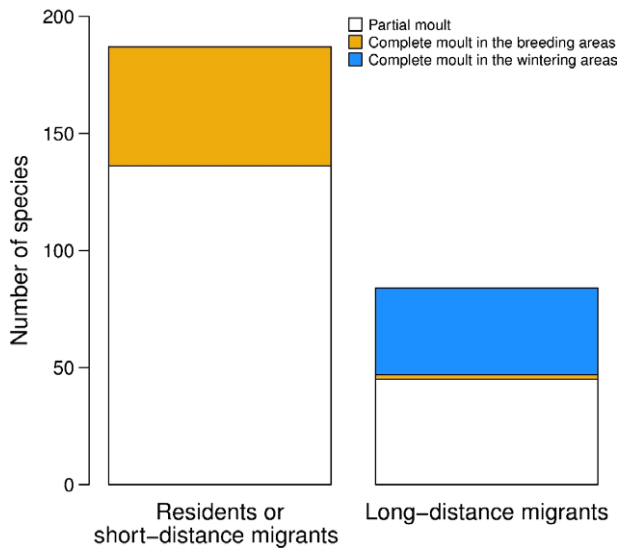


Fig. 5. The moult strategy of 271 Western-Paleartic passerine species during the first year of life in relation to migration strategy.

understanding of moult in migratory birds. We suggest a focus on the evolution of moult strategies and exploring the implications of moult-related adaptations that have evolved in relation to long-distance migration. In addition, our knowledge of the genetic and physiological basis of feather moult and its modulation by environmental factors is still very limited. Understanding patterns of consistency and diversity in moult patterns in migratory individuals, populations and species may provide important information about natural variation and the functional significance of feather moult. Lastly, whether migratory birds will be able to adapt and adjust their moult patterns in response to climate change is still an open question.

(1) The evolution of moult strategies

An important knowledge gap that currently hinders our understanding of moult patterns in migratory birds is the characteristics of moult outside the Western-Paleartic region, in the Afro-Tropical and Indo-Malayan regions, including the timing, location, sequence, speed and degree of variation of the moult process. Bridging this knowledge gap is vital for understanding the origin and evolution of moult strategies and how they may be shaped by environmental conditions (Figuerola & Jovani, 2001; de la Hera *et al.*, 2009; Newton, 2009; Bridge, 2011).

It has been generally accepted that the ancestral moult strategy is a complete post-breeding summer moult in the Western Palearctic breeding areas (Fig. 2A, B) and that moulting during the winter period (Fig. 2G) constitutes an adaptation that evolved later among long-distance migrants wintering in the Afro-tropical and Indo-Malayan regions (Svensson & Hedenström, 1999; Hall & Tullberg, 2004) (Fig. 6). Although this approach is supported by phylogenetic analyses, these analyses are limited for three main reasons:

(i) observational studies reveal that the timing of moult may change rapidly within a lineage (e.g. Shirihai *et al.*, 2001; Waldenström & Ottosson, 2002), which may violate the assumptions of these evolutionary analyses; (ii) These studies did not take into account the moult strategy during the first year of life, which is an integral part of the moult strategy of each species and thus did not include a key component for understanding the evolution of moult strategies among Western-Paleartic passerines, both resident and migratory (Kiat & Sapir, 2017); and (iii) The analyses used data from Western-Paleartic species from genera in which many species are resident in the tropical zone (e.g. *Hirundo*, *Acrocephalus* and *Phylloscopus*). Yet, tropical members of these genera were not included in the analyses, despite their close phylogenetic relationship with Western-Paleartic migrants that were included in the analyses. We therefore suggest that the conclusions of the above-mentioned phylogenetic analyses should be treated with caution. Future phylogenetic analyses should include data from a larger set of species, including tropical residents, to reflect better the phylogenetic relationships that may explain the moult strategies of Western-Paleartic migrants.

In this section we consider the four different moult strategies that are generally used by Western Palearctic passerines (strategies I-IV in Table 1; see also Fig. 6). The complete and simultaneous moult of adults and juveniles of the same species during either the post-breeding period or the over-wintering period by most Western-Paleartic passerines (strategy II: resident species that moult immediately after breeding or strategy IV: long-distance migrants that moult after arriving at the over-wintering areas, respectively; Jenni & Winkler, 1994; Kiat & Izhaki, 2016b) may suggest a link between these strategies. By contrast, partial moult only among juveniles of northern breeding species (strategy I), constituting an exceptional trait in comparison to the other moult strategies, might have evolved as an adaptation for breeding in the north where the time to complete the moult after fledging is limited (Kiat & Sapir, 2017). According to the ‘southern home’ or ‘southern ancestry’ hypothesis and a new evolutionary analysis, the origin and the ancestral region of most long-distance migratory species in the Western-Paleartic is the Afro-tropical region (Rappole, 1995; Safriel, 1995; Claramunt & Cracraft, 2015). We consequently offer an alternative to the notion that the ancestral moult strategy was a complete post-breeding moult in Western Palearctic breeding areas. We propose that the ancestral moult strategy was a complete post-breeding moult that took place in tropical regions (occurs during the northern winter; strategy IV), which would likely have been the breeding areas before migration evolved. This scenario of complete post-breeding and post-juvenile moults immediately after breeding in the breeding areas is similar to the pattern shown by resident passerines in tropical zones (strategy III; Fogden, 1972; Kennerley & Pearson, 2010). We thus suggest that the complete moult of adults and juveniles of some species immediately after breeding in the Western-Paleartic region (strategy II) is a strategy

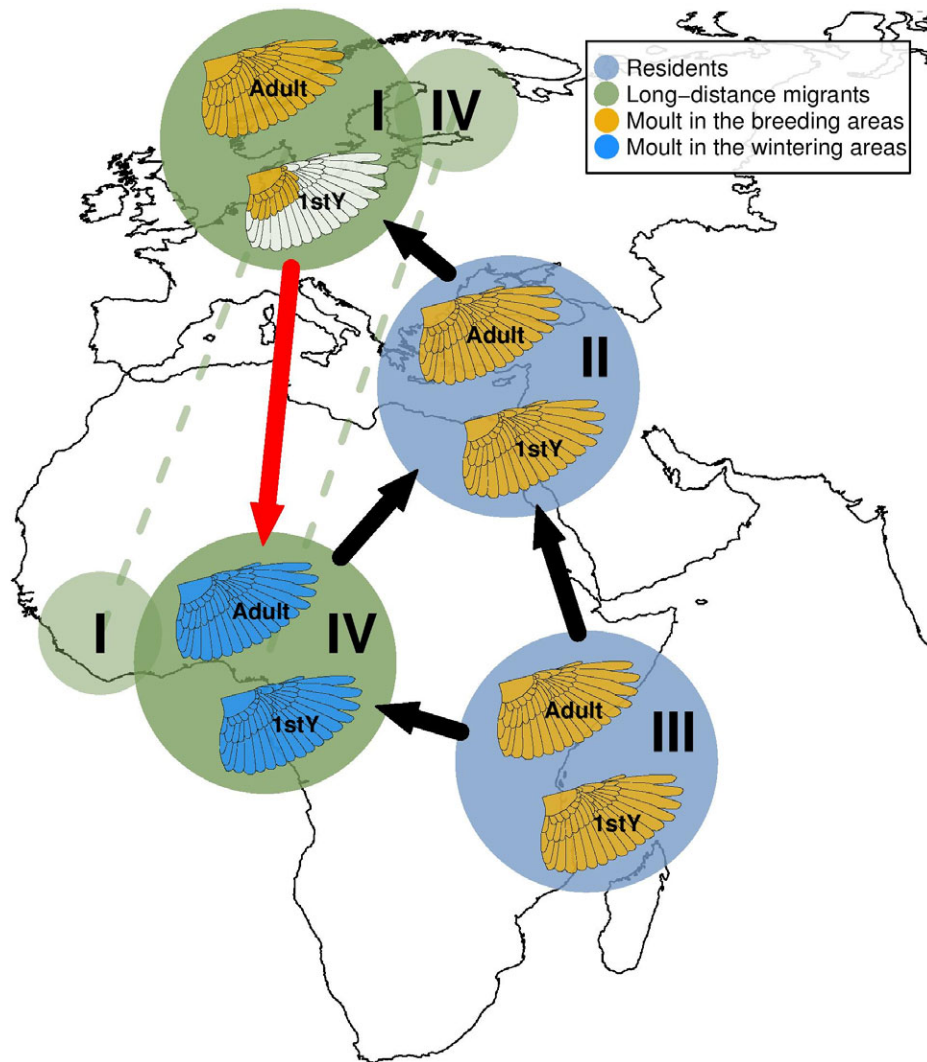


Fig. 6. Two possible routes for the evolution of moult strategies among Western-Palearctic passerines. Red arrow represent the hypothesis that the ancestral moult strategy was a summer moult in the breeding areas (I) while the postponement of the moult to the over-wintering, non-breeding areas (IV), is an adaptation that evolved later among long-distance migrants (Svensson & Hedenström, 1999; Hall & Tullberg, 2004). The black arrows represent our proposed hypothesis that the ancestral moult strategy took place within the Afro-tropical and Indo-Malayan regions for both adults and juveniles (III). Our hypothesis then suggests that the first evolutionary step was migration for breeding to the Western-Palearctic while retaining the ancestral moult timing in tropical regions (IV), or colonization of the Western-Palearctic region but retaining the ancestral trait of complete juvenile (depicted by 1stY) moult (II). Among some long-distance migrants that colonized the Western-Palearctic region, juvenile moult extent decreased (I) in the Western-Palearctic breeding areas, likely because a complete moult could not be usually completed under the environmental conditions prevailing in these areas during autumn (see also Table 1).

that was preserved after these lineages started to breed in the Western-Palearctic region. According to our theory, some migratory species that perform winter moult (strategy IV) maintained the scheduling of moulting in tropical regions even after the development of migration between the Afro-tropical and the Western-Palearctic regions. After the development of long-distance migration that included the geographic separation between Western-Palearctic breeding areas and Afro-tropical wintering areas, the moult of juveniles became less extensive as a result of time stresses prevailing in the north after the end of the breeding period (strategy I;

Fig. 6; Kiat & Sapir, 2017). Some support for this hypothesis is based on the fact that complete moult among some tropical resident species takes place during the equivalent of the northern winter (strategy III; Shirihai *et al.*, 2001; Kennerley & Pearson, 2010). However, among tropical resident species, the timing of moult is more variable than for species that moult in the Western-Palearctic region, indicating that the latter species are under much severer time stresses. According to our hypothesis, long-distance migrants that moult their plumage during northern winter (strategy IV) retained the ancestral moult timing and location (Table 1) despite

Table 1. Breeding area, migration strategy, moult extent, moult season and timing during the year and in relation to breeding and migration of Western Palearctic passerine species that are classified by the four general moult strategies outlined in Section IV.1 and Fig. 6^a.

Moult strategy (Fig. 6)	I	II	III	IV
Breeding area	○ Western-Palearctic region	○ Western-Palearctic region	● Afro-tropical and Indo-Malayan regions	○ Western-Palearctic region
Migration strategy	● Long-distance	● Resident	● Resident	● Long-distance
Moult extent	● Adult - complete 1stY - partial	○ Adult - complete 1stY - complete	○ Adult - complete 1stY - complete	○ Adult - complete 1stY - complete
Moult season	○ Summer (northern)	○ Summer (northern)	● Winter (northern)	● Winter (northern)
Moult timing	● Post-breeding	● Post-breeding	● Post-breeding	● Post-migration

^aThe colour scheme of the properties of the moult strategies match those in Fig. 6.

the geographic separation between breeding and moulting locations and the development of long-distance migration between breeding and moulting periods. Consequently, we propose that the complete summer moult of adults and the partial moult of juveniles in the Western-Palearctic breeding areas (strategy I) is a derived strategy, resulting from the development of a resident lifestyle or short-distance migration in many different bird lineages in this region. These northerly breeding species became subject to strong time pressures due to the strong seasonality of the climate at high latitudes, and we propose that the timing of major annual routine processes, including their moult, was optimized through natural selection (McNamara *et al.*, 1998; Barta *et al.*, 2008; Kiat & Sapir, 2018).

This discussion highlights the importance of considering the evolution of moult strategies in the context of major annual processes such as migration in order to explain the variability of moult patterns among migratory bird species. Indeed, flexibility in moult timing might be a prerequisite for the development of a migratory strategy (Hall & Tullberg, 2004). We suggest that attempts to understand the evolution of moult strategies will shed light on the evolution of bird migration. Although the factors that determine the timing of moult are becoming clearer (Holmgren & Hedenström, 1995; Barta *et al.*, 2008), we still do not understand fully why a particular species performs a particular type of moult. We propose that species distribution patterns may determine moult strategy, including its timing. For example, a split-moult strategy is more typical of long-distance migrants that breed in the southern parts of the Western-Palearctic region and winter in the northern parts of the Afro-tropical region (e.g. White-throated Robin *Irania gutturalis*, Orphean Warbler and Woodchat Shrike *Lanius senator*). Understanding the association between moult strategy and species distribution may help to explain other aspects of the evolution of moult timing.

The modelling framework of Barta *et al.* (2008) could be used to produce testable predictions regarding the evolution of moult strategies among individuals, populations and

species within the constraints imposed by breeding and migration (Figs 1 and 2). Such an approach may help in deciphering sex-related differences in moult patterns that could result from behavioural and physiological differences during breeding (e.g. parental investment in brooding and food provision). In addition, exploration of differences among populations that have extensive breeding ranges in the Western-Palearctic region and presumably experience different selective pressures such as climate, seasonal timing, and variation in food availability, could be explored using empirically derived food densities throughout the yearly cycle for each population. Barta *et al.* (2008) suggested that the sharp reduction in available food resources in the Western-Palearctic region at the end of summer could explain the evolution of winter moult, and also differences in moult strategies between Nearctic migrants and Western-Palearctic migrants. Furthermore, this framework may be used to investigate how future climatic changes may affect the availability of food resources and to explore how this might impact bird moult and migration timing.

(2) The implications of moult-related adaptations to long-distance migration

To overcome the time constraints imposed by migration, long-distance migrants can shorten the total duration of the moult process or boost moult speed by increasing the number of feathers that grow simultaneously (see Section II.1). However, a rapid moult is likely to impair flight performance and therefore affect foraging behaviour, diet, habitat preference, predation risk and movement (Haukioja, 1971; Lima & Dill, 1990). Both moult speed and also its timing are likely to have implications on flight performance during migration. Although the differences between autumn and spring migration strategies have been extensively discussed (Newton, 2010; Tøttrup *et al.*, 2011; Nilsson, Klaassen & Alerstam, 2013), differences in plumage quality between spring and autumn and the effects of migration and breeding on feather condition have received little attention (but

see Kiat & Izhaki, 2016a). In addition, different foraging techniques (e.g. aerial foraging or foraging within vegetation) may affect feather condition to different extents. It would be interesting to compare the costs of performing an autumn migration with abraded plumage *versus* the more common occurrence of migration after the renewal of flight feathers (Bridge, 2008). It would also be useful to study the implications of moult timing (and the consequent state of the plumage) on breeding success, specifically in the performance-related context of food provisioning to the young. We still do not know if recently renewed (in a winter moult) plumage is more advantageous in terms of reproductive success than plumage that was renewed in a post-breeding moult before the autumn migration.

If breeding with fresh plumage leads to higher reproductive success, we should be able to measure differences in fitness and life-history traits between summer and winter moulters with implications for the population dynamics of these species. In summer moulters, there is usually a large difference in plumage abrasion between adults and first-year individuals during breeding because the first complete moult usually occurs only after the first breeding season (12–14 months after fledging). Conversely, in winter moulters, the first complete juvenile moult usually occurs during the winter, meaning that first-year individuals and adults have similar plumage condition during the next breeding season. This possible age-related difference in plumage quality in summer compared to winter moulters may provide an opportunity to investigate differences in breeding success related to moult strategy.

(3) The physiology of moult

The biochemical and hormonal basis of bird feather moult and its metabolic consequences are not well understood and any differences between migratory and resident species and between species that are characterized by different moult strategies remain unknown. Many aspects of this process have not yet been explored, including gene expression that may indicate specific control mechanisms during moulting *versus* non-moulting periods and through different stages of the moult sequence. Consequently, future research should focus on the study of the physiological control mechanisms underlying feather moult that are entrained by environmental factors such as day length (Jenni & Schaub, 2003; Dawson, 2005, 2008), and food availability (Barta *et al.*, 2008). The physiological basis underlying facultative changes in the extent of moult (e.g. split-moult *versus* complete moult, see Section III.2) remains unknown but is likely to involve cellular processes, changes in feather and lipid tissues, as well as whole-organism endocrinological and behavioural alterations (see also Berthold & Querner, 1982a).

Another important aspect of moult physiology relates to the metabolic costs of moult, including feather synthesis (Murphy & King, 1992; Lindström *et al.*, 1993b). Whenever it takes place, moult metabolism likely has consequences on the ability of migrants to deposit the required energy and nutrients for the journey. There is empirical evidence

for a higher resting metabolism during moult (Dolnik & Gavrilov, 1979; Klaassen, 1995; Cyr *et al.*, 2008; but see Jenni-Eiermann & Jenni, 1996). In addition to the actual synthesis of feathers, associated processes such as protein transport are upregulated during active moult (Murphy & King, 1992). A clearer understanding of the amount of energy required for moulting, how it varies among individuals, populations and species, and implications of moult metabolism on pre-migration fattening would improve our understanding of moult in general and specifically how it relates to the metabolic demands of a subsequent migration.

(4) Consistency and variability in moult patterns

As described above, there is a high diversity of moult strategies among long-distance migratory Western-Palearctic passerines (Figs 2, 4 and 5). This diversity likely arose from the effects of factors such as breeding latitude, time limitations during the post-breeding period and temporal variation in food abundance (Barta *et al.*, 2008; Kiat & Sapir, 2017). It is, however, notable that the identity of feathers moulted during a partial moult is highly consistent among different species that undergo a similar extent of partial moult. For example, specific flight feathers in the mid-wing are not replaced during an extensive partial moult in many passerine species, including species in the families Locustellidae, Sylviidae, Passeridae, Fringillidae and Laniidae (Fig. 7). We suggest that this consistent pattern in the identity of moulted and non-moulted feathers is functionally determined, with moulted feathers having a more important role than those that are not replaced. For example, the secondaries are always retained during the main moult period of split-moulters while the primaries are replaced (Fig. 2E, F). Furthermore, in species that perform a complete moult (e.g. Lesser Grey Shrike, Garden Warbler *Sylvia borin* and Rosy Starling *Pastor roseus*), these same feathers are retained by some first-year individuals when they do not complete their moult, while the primaries are always replaced.

This largely overlooked consistency in the identity of moulted feathers may shed light on the selective forces that underlie different moult strategies. Fig. 7 illustrates three patterns of moult extent and the bird families in which each pattern can be found. Interestingly, different bird families show consistent patterns of moulted *versus* retained feathers. The moult sequence is fixed among passerines, which may possibly reflect the bio-mechanical implications of moulting specific feathers. We presume that the sequence is maintained such that the most functionally important feather within each feather tract is replaced first, followed by the replacement of additional, less important feathers. We presume that if the moult is paused (e.g. due to food shortage or time constraints) this hierarchy ensures that negative bio-mechanical implications of an incomplete moult are minimized (see also Gargallo, 2013).

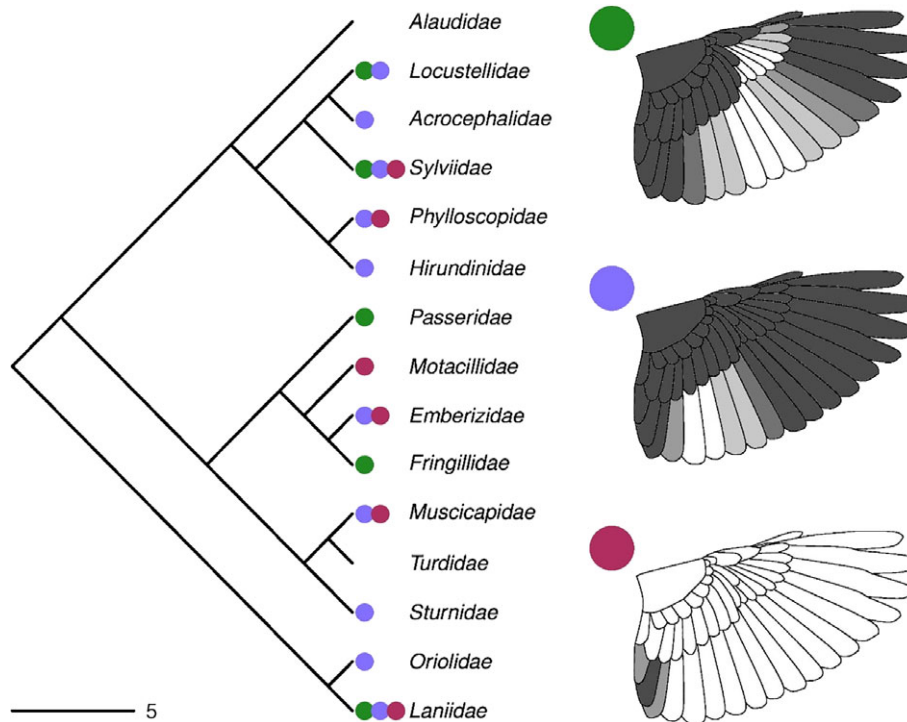


Fig. 7. Moulting patterns among different passerine families, in relation to the identity of the feathers that are replaced during a partial moult. Wing illustrations show three patterns of partial feather moult based on field data and museum collections (Y. Kiat, unpublished data). Darker feathers represent a higher likelihood of moult of specific feathers. The three patterns shown are: (1) moult of most of the wing feathers but retention of the central flight feathers (innermost primaries and outermost secondaries) and primary coverts (green); (2) moult of most of the wing feathers but retention of all or part of the secondaries (blue); and (3) limited partial moult that includes the replacement of the tertials and retention of all other wing feathers (purple). The phylogenetic tree of 15 Western-Palearctic families follows the phylogeny of Jetz *et al.* (2012) using BirdTree.org (Rubolini *et al.*, 2015). The consensus tree was built using BEAST version 1.8.4. The scale (lower left corner) represents a timescale of 5 million years.

(5) Effects of climate change on the moult of long-distance migrants

The mean global surface temperature has increased by an average of 0.6 °C over the past century (Metz, 2001; Trenberth & Fasullo, 2013). This change in climate has altered the phenology and distribution of many species, mainly by changing the abundance of food in different periods and regions during the yearly cycle (Forchhammer, Post & Stenseth, 1998; Crick & Sparks, 1999; Dunn & Winkler, 1999; Roy & Sparks, 2000; Sæther *et al.*, 2000; Fitter & Fitter, 2002; Evans & Gustafsson, 2017). Climate change may pose particular challenges for Western-Palearctic long-distance migrants because they may be affected by environmental changes along their migration route, in their Afro-tropical and Indo-Malayan wintering areas, and in their Western-Palearctic breeding areas (Cotton, 2003; Ahola *et al.*, 2004). Environmental changes taking place in the breeding areas will not impact migratory species until they return to breed, and thus their ability to respond to these changes could be substantially limited (Both & Visser, 2001). In a seasonal environment, the timing of peak food abundance, which may depend on environmental factors that are sensitive to climate change, is one of the most

crucial factors to which birds must entrain the timing of their breeding, specifically in the context of food provisioning to nestlings (Marra, Hobson & Holmes, 1998; Both & Visser, 2001). Because moult is likely time constrained, climate change and particularly global warming may affect properties of the moult process in both Western-Palearctic breeding and Afro-tropical or Indo-Malayan wintering areas through changes in food abundance and availability, and also by changing migration and breeding phenology. For example, changes in the timing of migration arrival and departure will impact the time available for moulting (Gordo, 2007).

Findings from several studies suggest that climate change may already affect the scheduling of feather moult. For example, during 1999–2009 the timing of winter moult by Barn Swallows was delayed and as a result the spring migration did not advance in this period (Møller *et al.*, 2011). The speed of flight feather moult in this species is slightly higher in years with higher rainfall and greater abundance of insects in its African over-wintering grounds (van den Brink, Bijlsma & Van der Have, 2000). This may indicate indirect but nevertheless substantial climate-change-related effects on the moult cycle. In European Starlings, experimental increases in temperature can advance the timing of testicular regression after breeding, resulting in earlier onset of the

post-breeding moult (Dawson, 2005). Such effects may have other consequences when feathers are used in sexual display, as in the Barn Swallow, and consequently feather moult timing may have multiple consequences on bird fitness. Saino *et al.* (2004) found that tail-streamer length in male Barn Swallows from northern Italy was longer after food-rich winters in Africa. Because male sexual attractiveness depends on tail ornaments (Møller, 1988), ecological conditions in the wintering region could impact individual fitness through sexual selection during the following breeding season. This carry-over effect may involve factors such as moult scheduling, migration connectivity and rain distribution that combine to determine individual breeding performance and eventually the viability of migratory passerine populations throughout the Western Palearctic.

The effects of climate change on moult extent, duration and timing are largely unknown. Surprisingly, most studies that investigate the effects of climate change on avian life-history traits do not mention moult (Stenseth & Mysterud, 2002; Winkler, Dunn & McCulloch, 2002; Crick, 2004; Both & Visser, 2005; but see Hedenström *et al.*, 2007; Tomotani *et al.*, 2018*b*), despite its importance for understanding bird ecology and evolution, particularly with regard to life-history transitions under current and expected global climate changes.

V. CONCLUSIONS

(1) The evolution of moult strategies among Western-Palearctic long-distance migrants is poorly understood even though about a third of Western-Palearctic passerines perform long-distance migration. Our understanding of the evolutionary dynamics of moult strategies has been hampered by a lack of basic data on moult from the wintering areas of those species, particularly from the Afro-tropical region.

(2) Long-distance migrants cope with time constraints on their moult during the post-breeding period by using several non-exclusive adaptations, including increased speed of moult, overlap between moult and breeding or migration, replacement of only part of the plumage, and delaying part or all of the moult process to the winter. These adaptations demonstrate the high variation that characterizes the properties of moult, especially its timing, as opposed to breeding and migration, the two other major energy-demanding processes in the annual routine of Western-Palearctic passerines.

(3) The environmental conditions during winter for long-distance migrant passerines that winter in the Afro-tropical and Indo-Malayan regions are very different from those encountered by resident or short-distance migrant passerines that spend the winter in the Western-Palearctic region. More clement environmental conditions in their wintering grounds enabled the use of a variety of moult strategies such as extensive winter moult, splitting of moult into two partial moults and the suspension of moult to

complete it in winter. For juveniles, these conditions may also allow an extensive moult during their first year of life, which, due to time constraints, is unusual for resident or short-distance migrant species that over-winter in the Western-Palearctic region. This may carry advantages in terms of their survival and reproductive success, especially during their first breeding season.

(4) We offer an alternative hypothesis regarding the evolution of Western-Palearctic passerine moult strategies, specifically for long-distance migrants. This hypothesis considers the moult of both adults and juveniles during their first year of life. We suggest that the ancestral moult strategy was a complete moult during the post-breeding period in the tropics for resident species, before migration developed. This hypothesis is contrary to the commonly accepted theory suggesting that the ancestral moult strategy is a complete post-breeding summer moult in the breeding areas of the Western-Palearctic region and the winter moult is an adaptation that developed later among long-distance migrants.

(5) We assume that climate plays a more central role in the ecology and evolution of feather moult than has been appreciated to date. The complex combined effects of different environmental factors, such as rainfall distribution, on the evolution of feather moult, implies that climate change may potentially have multiple direct and indirect effects on moult strategies by changing food abundance dynamics and time constraints during the annual cycle.

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VII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. The duration of complete moult (number of days), moult season (S, summer; W, winter) and migration category (N, resident; S, short-distance migrant; L, long-distance migrant) of 90 passerine species. Data are from published literature (Pearson, 1973; Ginn & Melville, 1983; Aidley & Wilkinson, 1987; Svensson, 1992; Shirihai *et al.*, 2001; Kennerley & Pearson, 2010; Kiat & Sapir, 2017).

Table S2. The extent of wing and tail moult (proportion of feathers moulted) of summer and winter moults (mean \pm S.E.; $N = 74$ long-distance migrant species) in relation to wintering latitude in their Afro-tropical wintering areas (22°N to 32°S). Data are from our own data (Y. Kiat, unpublished data) as well as published literature (Pearson, 1973; Cramp, 1977; Ginn & Melville, 1983; Aidley & Wilkinson, 1987; Svensson, 1992; Shirihai *et al.*, 2001; Kennerley & Pearson, 2010).

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