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A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylviidae)

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Adult birds replace their flight feathers (moult) at least once per year, either in summer after termination of breeding or (in the case of some long-distance migratory species) in the winter quarters. We reconstructed the evolutionary pathways leading to summer and winter moult using recently published molecular phylogenetic information on the relationships of the Western Palearctic warblers (Aves: Sylviidae). Our phylogenetic analysis indicates that summer moult is the ancestral pattern and that winter moult has evolved 7–10 times in this clade. As taxa increased their migratory distance and colonized northern breeding areas, summer moult disappeared and winter moult evolved. Our data also allows us to trace the historical origins of unusual moult patterns such as the split-moult and biannual moult strategies: the most parsimonious explanations for their origins is that they evolved from ancestral states of summer moult. We briefly discuss our results in the light of recent criticisms against phylogenetic comparative methods and the utility of historical versus functional definitions of adapation.

ADDITIONAL KEY WORDS:—adaptation – biannual moult – birds – breeding – character maintenance – comparative study – migration – split-moult.

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INTRODUCTION

Birds have evolved the ability to renew their flight and body feathers at regular intervals (Stresemann & Stresemann, 1966). This process is termed 'moult' and it is necessary to ensure future survival since old feathers are constantly abraded and worn due to behavioral activities, exposure to sunshine and many other environmental stresses (Jenni & Winkler, 1994). The functional and evolutionary significance of different moult strategies among extant bird groups has been the subject of much interest since Stresemann and Stresemann's pioneering study, but our understanding about the ecological factors influencing the patterns is still very limited (see Jenni & Winkler, 1994 for a recent review and discussion). The moulting process is costly, both in terms of energy and nutrients (Lindström *et al.*, 1993; Klaassen, 1995; Murphy, 1996) and time (Langston & Rohwer 1996) and it may therefore be in conflict with reproductive activities. Such a conflict between adult somatic maintenance and repair functions (feather renewal) and breeding activities could be viewed as a life-history trade-off between current and future reproduction (cf. Williams, 1966; Calow, 1979; Svensson & Nilsson, 1997). In spite of this, ecological and evolutionary studies of avian moult strategies are still few (but see Holmgren & Hedenström, 1995; Nilsson & Svensson, 1996; Siikamäki *et al.*, 1994; Svensson & Nilsson, 1997).

Small passerine birds moult all their flight feathers at least once a year (Jenni & Winkler, 1994). The most common pattern is that moulting occurs immediately after termination of breeding, which is employed by adult breeders of all sedentary species in temperate and arctic regions as well as most migratory species. Some, but not all, long-distance migratory species do, however, skip moult directly after breeding, moulting instead in their tropical winter quarters (Price, 1981; Jenni & Winkler, 1994). Despite much speculation (Alerstam & Högstedt, 1982; Jenni & Winkler, 1994; Holmgren & Hedenström, 1995) the adaptive significance of these different strategies remains largely unknown.

The Old World warblers (Aves: Sylviidae) is a group of birds which has been much studied with respect to phylogenetic relationships, community structure and foraging ecology (Richman & Price, 1992; Richman, 1996; Marchetti *et al.*, 1995; Blondel *et al.*, 1996, Leisler *et al.*, 1997), plumage patterns, communication and sexual selection (Marchetti, 1993; Price & Pavelka, 1996) and biogeography (Price *et al.*, 1997). Most warbler species are migratory and among them we find some of the most astonishing long-distance migrants that breed in Eastern Siberia and migrate to their winter quarters in Africa and Asia (Williamson, 1962; Moreau, 1972). In this group we also find a wide diversity of moult strategies compared to other avian groups. The majority of species follow the regular pattern and moult at their summer quarters immediately after breeding (Williamson, 1962; Norman, 1997), while other species moult after they have arrived at their winter quarters

(Williamson, 1962; Price, 1981; Norman, 1997). A few species have evolved a split-moult strategy, whereby they replace some flight feathers at their breeding quarters in summer and the rest of the feathers at their winter quarters in tropical Africa (Hasselquist *et al.*, 1988; Lindström *et al.*, 1993; Norman, 1997). One species, the willow warbler *Phylloscopus trochilus*, even has a biannual moult, that is, it replaces its flight feathers twice a year, both after termination of breeding and in its winter quarters (Salomonsen, 1945; Underhill, *et al.* 1992; Hedenström, *et al.* 1995). This diversity of moult strategies among the warblers makes them an interesting group for analysis of ecological factors and selective pressures moulding different moult patterns.

In this paper, we discuss the evolutionary history and adaptive significance of present-day moult strategies among Western Palearctic warbler species. We adopt a historical perspective, based on recent phylogenetic information from molecular genetic studies (Richman & Price 1992; Price *et al.*, 1997; Blondel *et al.*, 1996; Leisler *et al.*, 1997) and discuss the ecological factors selecting for winter, summer, split-moult and biannual moult strategies. In particular, we address the question that long-distance migratory species have evolved winter moult as an adaptation resulting from time constraints for breeding and migration (cf. Jenni & Winkler, 1994). Finally, we discuss the historical pathways between summer and winter moult and the origin and adaptive significance of the biannual moult present in *P. trochilus*.

METHODS

Data set and literature

We based our phylogenetic analyses on moult strategies and migratory distances from published information for warbler taxa breeding in the Western Palearctic provided by Cramp (1992) and Norman (1997). We restricted our analysis to taxa breeding in the Western Palearctic, since ecological information for taxa breeding outside this biogeographic region is scarce or unavailable for most species. A notable exception of this general pattern are the leaf warblers (genus *Phylloscopus*): where ecological information is also available for some of the Asian taxa. Since this genus is also unusually well-studied with respect to molecular phylogenetic relationships (see Price *et al.*, 1997), we performed an additional and separate analysis on this group using data provided by Ali and Ripley (1983), Cramp (1992) and Williamson (1962). Migratory distances were not available for the Asian *Phylloscopus* species in Norman's (1997) review, and so we calculated it as the orthodrome distance (great circle) between the summer and winter distribution midpoint values of longitudes and latitudes, using the formula provided by Imboden and Imboden (1972). The taxonomic status of several species and subspecies in the *Phylloscopus*-genus are still not yet resolved (see Price *et al.*, 1997), and we therefore tried to obtain data down to the subspecies level whenever possible. We classified taxa as short-distance migrants if their migratory distance was 1000 km or less between the breeding and winter quarters, whereas taxa whose migration distance were at least 2000 km were considered to be long-distance migrants (using data in appendix 1 of Norman, 1997). Although migration distance is strictly not a discrete character, there were no ambiguous cases using this criterion of migratory status, since no taxon had a migratory distance in the interval between 1000 and 2000 km. Given the difficulties of calculating exact migratory distances for most species with wide distributions, we feel confident that our classification correctly identifies migratory habits, especially in the light of the fact that migratory distances are non-normally distributed and the distribution of distances may actually be bimodal (see Norman, 1997).

With the exception of our special analysis of the *Phylloscopus* warblers, our criteria for including a taxon in our study were as follows: (i) that the species or subspecies breeds in the Western Palearctic and hence was included in Norman's (1997) review and (ii) that molecular phylogenetic information had been published for that taxon. Following Helbig *et al.* (1995) we consider the eastern and western populations of Bonelli's warbler (*Phylloscopus b. bonelli* and *Phylloscopus b. orientalis*) to be two separate species. The booted warbler *Hippolais caligata* and the olivaceous warbler *Hippolais pallida* were considered to belong to the *Acrocephalus* group, in accordance with the recent molecular phylogenetic results by Leisler *et al.* (1997). We considered the western and eastern populations of the whitethroat (*Sylvia c. communis* and *Sylvia c. icterops*, respectively), as separate taxa in our analyses, since these populations are geographically separated from each other and differ markedly in migratory habits and winter distributions (Cramp, 1992). In this paper we only consider the flight feather moult (primaries and secondaries) among adult birds; we do not discuss moult of body feathers or the moult among juvenile birds. Taxa were classified as having 'summer moult', 'winter moult', 'split-moult' (half of the flight feathers moulted in summer and half in winter) or 'biannual moult' (two complete annual moults, one in summer and one in winter).

Phylogeny and comparative analyses

We base our comparative analyses on published molecular phylogenetic information on the relationships within and among the following genera: *Sylvia* (Blondel *et al.*, 1996), *Acrocephalus, Hippolais, Locustella, Cisticola* (Leisler *et al.*, 1997) and *Phylloscopus* (Price *et al.*, 1997). Although different molecular methods were used in these separate studies (DNA-DNA hybridizations vs. analyses of mtDNA-sequence), the topology of this phylogenetic tree corresponds well to the traditionally recognized relationships among the warblers based on morphological classifications (cf. Williamson, 1962; Cramp, 1992). Hence, this phylogeny is likely to be robust and our statistical tests do not require any information about branch lengths, which are assumed to be equal in the concentrated-change test (see below).

We mapped the character states of moult strategies onto the phylogenetic tree using McClade 3.0 (Maddison & Maddison, 1992), and assumed an unordered parsimony with summer moult as the ancestral state. We used the goldcrest *Regulus regulus* as an outgroup in our analyses, since this species is closely related to the warbler family (Richman & Price, 1992; Cramp, 1992), however in our analysis of the *Phylloscopus* warblers we instead used the blackcap *Sylvia atricapilla* in accordance with previous phylogenetic analyses of this genus (Richman & Price, 1992; Price *et al.*, 1997). When investigating patterns of correlated evolution, we used the simulation version of the concentrated-change correlation test (Maddison, 1990; Maddison & Maddison, 1992). This tests if certain evolutionary changes in traits occur randomly on the phylogenetic tree (the null hypothesis), or if they are more likely to occur following the arisal of a new selective regime (e.g. changed migratory habits, see

Harvey & Pagel, 1991). We employed the Equivocal Cycling Algorithm when several equally parsimonious reconstructions of character evolution were available (Maddison & Maddison, 1992). We did this to evaluate alternative evolutionary scenarios and investigate how sensitive our statistical results were to violations of assumptions about the number of gains and losses of winter moult. We performed the tests using both actual changes as well as reconstructed changes, using the MAXSTAT and MINSTAT options in MacClade (with two or three steps compensation; see Maddison & Maddison, 1992). Counting only actual changes may bias the P values in a conservative way in parsimony-based analyses (Maddison, 1990), hence the tests using reconstructed changes may be more powerful.

Recently, Schluter *et al.* (1997) pointed out that parsimony-based comparative studies are sensitive to uncertainities in the inferences regarding underlying ancestral state reconstructions. They recommended the use of maximum-likelihood (ML) analysis instead of parsimony to overcome these difficulties. Our study, as well as other studies using the parsimony approach, is susceptible to the problem of uncertain ancestral character states. However, it is worth pointing out that for slowly evolving characters, the results from ML and parsimony analysis tend to give the same answer (Schluter *et al.*, 1997). Furthermore, ML-methods also have questionable assumptions, the most obvious one being that characters are assumed to evolve at a constant rate across the entire phylogenetic tree (Cunningham *et al.*, 1998). We agree with Martins and Hansen (1996), that the use of explicit assumptions should be regarded as a strength, rather than a weakness of different phylogenetic comparative methods.

RESULTS

Origins of winter moult, split-moult and biannual moult

We were able to extract data on moult strategies and migratory habits for 49 warbler taxa breeding in the Western Palearctic and for which molecular phylogenetic relationships were also known (Figs 1, 2). The data indicate that summer moult and short-distance migration are ancestral states among the warblers (cf. Cox, 1985), and that winter moult has independently evolved at least seven and possibly ten times in this clade.

Our data allow us to trace the historical origin of the split-moult and biannual moult strategies in Figure 1. The most parsimonious explanation for the origin of the split-moult strategy in the barred warbler *Sylvia nisoria* and the orphean warbler *Sylvia hortensis* is that they evolved from an ancestral state of summer moult. These species moult half their flight feathers (the primaries) at their breeding quarters in summer before migration, and the rest of the flight feathers (the secondaries) at their winter quarters in Africa (Hasselquist *et al.*, 1988; Lindström *et al.*, 1993; Norman, 1997). Similarly, the biannual moult found in the willow warbler *Phylloscopus trochilus* probably evolved from an ancestral state of summer moult only, and one extra moult in winter was added to this ancestral pattern (Fig. 1).

Migration distance and moult strategy

Winter moult only occurs among the long-distance migrants, although not all of these species moult in their winter quarters (Figs 1, 2). Of the 34 species that are

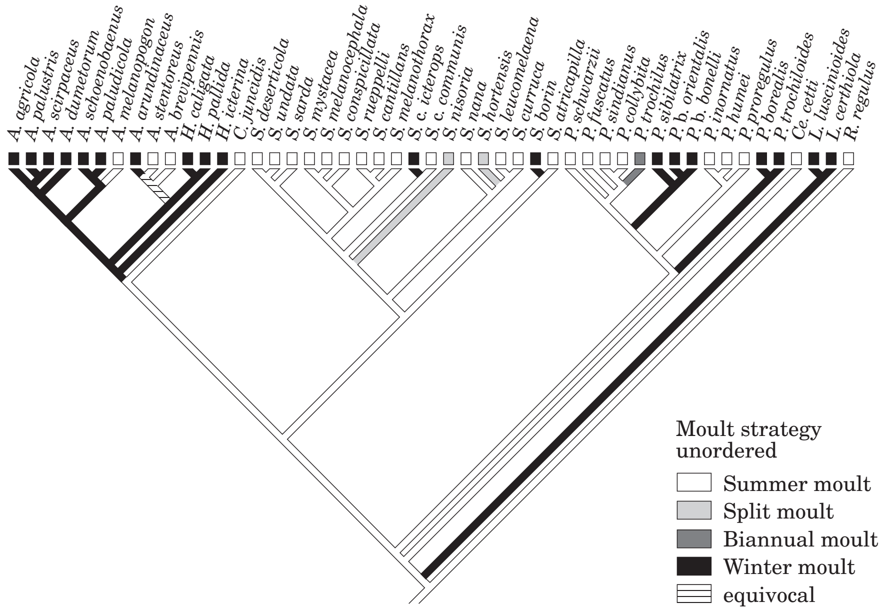

Figure 1. Phylogenetic distribution of moult strategies in Western Palearctic warbler genera using the goldcrest *Regulus regulus* as an outgroup. For details about tree reconstruction and migratory classifications, see Methods. Abbreviations of genera: *A* = *Acrocephalus*; *H* = *Hippolais*; *Ci* = *Cisticola*; *S* = *Sylvia*; P = *Phylloscopus*; *Ce* = [*Cettia*]; *L* = *Locustella*; *R* = *regulus*.

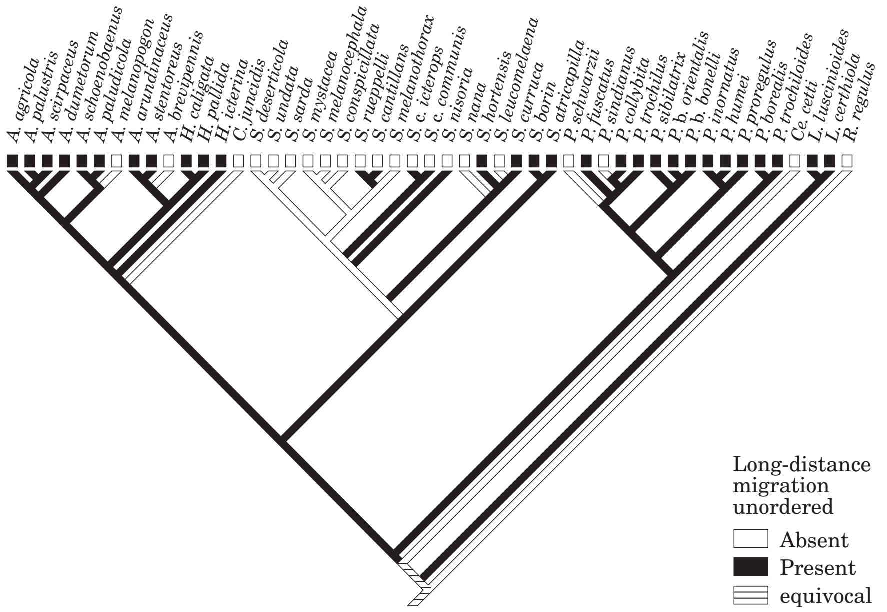

Figure 2. Phylogenetic distribution of migratory habits among Western Palearctic warbler genera using the goldcrest *Regulus regulus* as an outgroup. For details about tree reconstruction and migratory classifications, see Methods. Abbreviations as per Fig. 1.

Table 1. Summary of statistical results testing the relationship between the presence of long-distance migration and the occurrence of winter moult using the simulated version of the concentrated change test. For details about migratory classifications and test procedures see Methods. Since several equally parsimonious scenarios were available, *P* values from tests using different assumptions about the number of gains and losses in summer moult are shown. Tests were performed counting both actual and reconstructed changes (MAXSTAT and MINSTAT-options in MacClade). Summer moult was assumed to be the ancestral state and 1000 replicates were used in the simulations. Note that we also performed the tests classifying the split-moulters (*Sylvia nisoria and Sylvia hortensis*) as either winter-moulters (upper part of table) or summer moulters (lower part of table)

Number of winter moulters	Procedure	Gains	Losses	*P*
22 (including *S. nisoria* and *S. hortensis*)	Actual	10	2	0.017
	MAXSTAT	10	2	0.003
	Actual	9	3	0.018
	MINSTAT	9	3	0.013
20 (excluding *S. nisoria* and *S. hortensis*)	Actual	8	2	0.032
	MAXSTAT	8	2	0.042
	Actual	7	3	0.072
	MINSTAT	7	3	0.033

long-distance migrants, 22 moult at least some of their flight feathers in winter, whereas more than one third of the long-distance migrants (12) have retained their summer moult and still replace all their flight feathers at their breeding quarters prior to autumn migration (Figs 1, 2). However, in spite of the fact that the relationship between migration distance and moult strategy is far from clearcut, winter moult is nevertheless significantly associated with the presence of long-distance migration (Table 1). The relationship is significant under several different evolutionary scenarios and assumptions about the number of gains (7–10) and losses (2–3) in winter moult (Fig. 1). Note that we performed these analyses counting the ambiguous split-moulters (*S. nisoria* and *S. hortensis*) as either summer or winter moulters, and the relationship is significant in both cases, although it is weaker when these taxa are classified as summer moulters (Table 1).

The Phylloscopus *warblers*

We performed a separate and additional analysis of the evolution of moult strategies in the leaf warblers (genus *Phylloscopus*), incorporating both the Western Palearctic taxa in the previous analyses augmented with additional data from some of the Asian species (see Methods). We were able to extract data for 26 taxa in this genus for which molecular phylogenetic relationships were known (Fig. 3). Our phylogenetic reconstruction of character state evolution indicates that winter moult has evolved at least three and possibly five times in the *Phylloscopus* clade, namely in the *trochilus* group (1 gain), the *bonelli–sibilatrix* group (1 gain), the *magnirostris–borealis* group (0–2 gains) and the *trochiloides* group (1 gain, see Fig. 3). Winter moult may have been lost one or two times: in the East Asian species *Phylloscopus tenellipes* and possibly in the *reguloides–occipitalis* group (Fig. 3). Although winter moult only occurs among long-distance migrants in *Phylloscopus* as well, the relationship between winter moult and migratory strategy is far from significant (data not shown, but all *P* values >0.15, using the same criteria and tests as in the previous analyses). We stress,

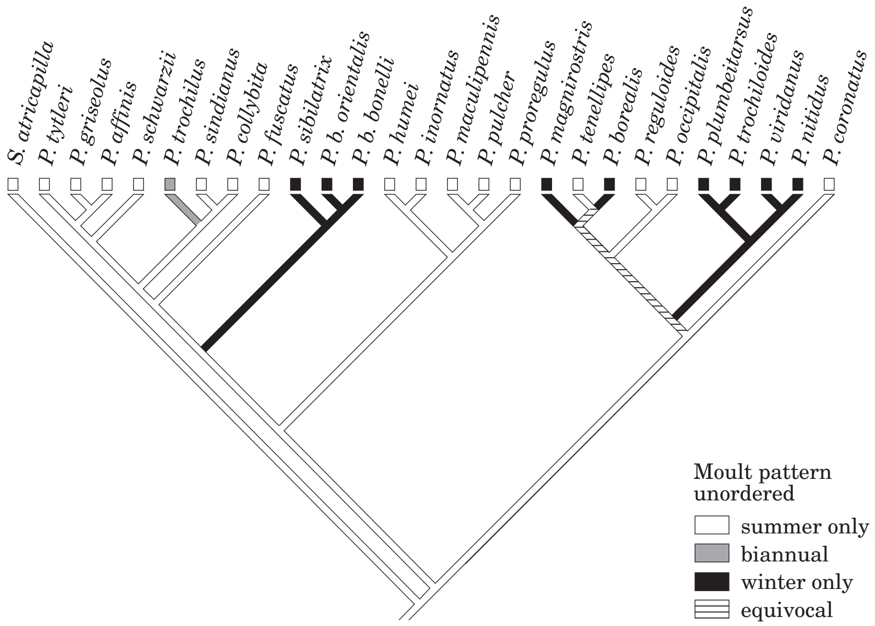

Figure 3. Phylogenetic distribution of moult strategies among Eurasian leaf warblers (genus *Phylloscopus*) using the blackcap *Sylvia atricapilla* as an outgroup. Abbreviations as per Fig. 1.

however, that the statistical power in this analysis is low due to the few times (3–5) that winter moult has evolved in this clade.

DISCUSSION

Multiple independent evolutionary origins of winter moult

To our knowledge, this is the first study investigating the adaptive significance of avian moult strategies from a phylogenetic perspective. Previous analyses addressing these questions (e.g. Jenni & Winkler, 1994) have used data from individual species, which may cause problems if species share a common phylogenetic history and cannot be considered as statistically independent units (Felsenstein, 1985; but see Price, 1997). Our data indicate that winter moult independently evolved between 7 and 10 times among the Western Palearctic warblers. Such multiple and independent evolutionary changes in characters provide strong inference for a role of selection causing these evolutionary transitions and are usually taken as evidence that the changes were adaptive, rather than caused by drift or by other non-adaptive forces (see Losos *et al.*, 1998), for another recent example).

Our phylogenetic analysis indicates that as taxa increased their migratory distances summer moult was likely to disappear and winter moult was likely to evolve. Since Gould and Vrba (1982) outlined their historical definition of adaptation, many workers have advocated the use of cladistic tests and argued that traits should only be considered as adaptations provided that it can be demonstrated that they arose during evolutionary history in response to a selection pressure that has a direct connection to their current function (e.g. Larson & Losos, 1996; see Björklund, 1991, for a particularly strict and extreme view). According to these criteria, the presence of winter moult could be regarded as an adaptation that has repeatedly evolved in response to changes in a selective regime, in this case the evolutionary transition to long-distance migration.

Although our data provide phylogenetic evidence for the adaptive significance of winter moult, we note a few caveats of phylogenetic comparative methods which are not limited to our study but are relevant to comparative studies in general. The vague notion of a 'selective regime' in comparative analyses has been criticized (Leroi *et al.*, 1994) and often relevant data on important ecological or physiological factors are not available in the literature (Lauder, 1996). Alerstam and Högstedt (1982) suggested that one advantage of moulting during winter as opposed to during summer would be that in species defending winter territories (cf. Price, 1981) there would be a strong selective pressure to migrate rapidly from the breeding areas to arrive early in the winter quarters. Unfortunately, we are not able to test this hypothesis since data on winter ecology are virtually absent in the literature and when they exist they are difficult to interpret and quantify. Finally, we note that although winter moult is significantly associated with long-distance migration, a considerable fraction of the species migrating long distances have retained their summer moult (Figs 1, 2). Thus, the presence of long-distance migratory habits seem to be a necessary, but far from sufficient, condition for winter moult to evolve. We will therefore briefly discuss the maintenance of summer moult among long-distance migrants.

Maintenance of summer moult among long-distance migrants

We find it surprising that winter moult is not more common and that so many long-distance migratory species have retained the summer moult strategy. In spite of the fact that the majority of the *Phylloscopus* warblers migrate over long distances, only 10 out of the 26 species moult during winter (Fig. 3). For example, consider *P. inornatus, P. proregulus* and *P. fuscatus*, which all breed in northern Siberia, migrate to southern Asia, and have retained the summer moult (Fig. 3). There seems to be a strong phylogenetic component in explaining which species moult during winter, since 7 of the 10 taxa having winter moult cluster in two groups: the *bonelli–sibilatrix* group and the *throchiloides* group (Fig. 3). Similarly, in the *Sylvia* warblers, only 4 out of 9 long-distance migrants moult some of their flight feathers in winter (Figs 1, 2). These results may indicate that the evolution of winter moult is influenced by some phylogenetic inertia, perhaps acting through some common ecological factors shared by the taxa within a group (e.g. length of breeding season, habitat selection) or through some internal developmental constraints (e.g. hormonal factors) that may prevent winter moult from evolving. As more molecular phylogenies are becoming available for avian taxa where ecology and moult patterns are known, this issue should be investigated further.

Comparisons with other avian groups that have a similar ecology to that of the Old World warblers may also shed some light on these questions. In the ecologically equivalent, but phylogenetically distant, North American warblers (genus *Dendroica*), there are no known species moulting in their tropical winter quarters in Central and South America, but all moult at their breeding quarters after termination of breeding (Curson *et al.*, 1994). Interestingly, recent molecular phylogenetic analyses indicate that the *Dendroica* warblers is an evolutionary much younger group than the Old World warblers (Price *et al.*, 1998). If the occurrence of winter moult for some reason is affected by evolutionary inertia, the younger age of the *Dendroica* warblers may partly explain why winter moult has not yet appeared in this clade.

A slightly different explanation for the maintenance of summer moult among the long-distance migrants is that the summer moult is still beneficial due to, for example, the advantages of having fresh flight feathers available for autumn migration (Holmgren & Hedenström 1995). Recent criticisms against the strict historical definition of adaptation and its use in phylogenetic comparative methods emphasize that these methods mainly focus on the origin of adaptations, whereas the equally important issue of character maintenance through long-term stabilizing selection is neglected (Reeve & Sherman 1993; Price, 1997; Hansen, 1997). These critics point out that a large number of traits subject to functional and optimality analyses are clearly adaptive in the sense that they are maintained by selection ('aptions', see Hansen, 1997 for a discussion) and the fact that a character is ancestral should not be taken as evidence against its adaptive significance (*contra* Björklund, 1991). That the summer moult in many long-distance migrants has been maintained indicates that it may currently have some important function that outweighs its costs. There is clearly a need for detailed field studies to elucidate this question. In addition to further phylogenetic studies dealing with the evolution of moult strategies, we would therefore also need to know much more about the ecological and physiological factors selecting for winter and summer moult. Experimental studies on single species (Nilsson & Svensson, 1996; Svensson & Nilsson, 1997; Hemborg & Lundberg, 1998) as well as general optimization models (Holmgren & Hedenström, 1995) should thus be necessary complements to comparative studies in this regard.

Evolutionary transitions between summer and winter moult

The evolutionary transition between summer and winter moult has been suggested to be facilitated by the occurrence of a split-moult strategy, whereby flight feather moult is partially suspended in the breeding quarters and a progressively increasing number of flight feathers are moulted in the winter quarters (Hasselquist *et al.*, 1988; Lindström *et al.*, 1993). The split-moult strategy may thus be an intermediate step between summer and winter moult, and we believe that this is the most likely evolutionary pathway that has resulted in winter moult among the warblers. Although there is no phylogenetic evidence for this hypothesis, we think that the split-moult strategy is a more likely intermediate step than the biannual moult strategy (see discussion below) because it allows breeding birds to gradually reduce their extent of summer moult and avoid a costly moult-breeding overlap that may interfere with parental care (Svensson & Nilsson, 1997). The fact that the split-moult strategy is so rare overall, however, suggests that this intermediate step is unlikely to persist for a long evolutionary time, presumably due to strong directional or disruptive selection, favouring either winter or summer moult, but rarely both (Fig. 1). Finally, we would like to emphasize that there is also substantial variation in timing among winter moulters; some species moult in early autumn before reaching their final winter quarters whereas others postpone moult until early spring before migrating to their breeding quarters (Price, 1981; Jenni & Winkler, 1994).

Our data indicate that the willow warbler *Phylloscopus trochilus* has not followed the usual pathway from summer moult to winter moult via the intermediate split-moult strategy, but has instead added an extra moult in its winter quarters while still maintaining its ancestral summer moult. This biannual moult pattern is very rare both among passerine bird species (Prys-Jones, 1991) and among avian taxa in general and the functional significance of this strategy has been much discussed (see Jenni & Winkler, 1994). Holmgren and Hedenström (1995) speculated that the metabolic costs of moult in this species may be low compared to its relatives. *P. trochilus* may also have a life style that leads to an extensive amount of feather wear, making it necessary to moult twice a year. While we do not question these purely adaptive explanations for the existence of biannual moult in *P. trochilus*, our historical perspective allows us to reformulate and refine the questions. First, why has this species evolved a winter moult? Second, why has it maintained its summer moult?

The reason why winter moult has evolved in *P. trochilus* could be due to the advantages of having fresh flight feathers available for a rapid and demanding spring migration from Africa to its breeding quarters in Eurasia (Pearson, 1973; Holmgren & Hedenström, 1995). The hypothesis by Alerstam and Högstedt (1982) that winter moult is adaptive because of the possibility it affords of being able to leave the breeding quarters early is unlikely to apply in this species since the time-consuming summer moult still prevails. The winter moult in *P. trochilus* is thus likely to be an adaptation in the historical sense as well as in the other leaf warblers (cf. Gould & Vrba, 1982; see discussion above).

The significance of the maintenance of summer moult in this species is a more difficult question. There is empirical evidence, both from *P. trochilus* and other passerine birds, that the moulting process may be in conflict with breeding activities and that moult-breeding overlap leads to fitness costs (Bensch *et al.*, 1985; Siikamäki *et al.*, 1994; Svensson & Nilsson, 1997). Given these costs and given that winter moult has evolved in *P. trochilus*, we would expect that the summer moult should gradually dissapear unless some selective pressure(s) maintained it. There is evidence that a considerable proportion of the individuals from northern populations of *P. trochilus* leave their breeding grounds and commence fall migration with one or several unmoulted inner flight feathers (secondaries), presumably due to time constraints for breeding and moulting at high latitudes (Hedenström *et al.*, 1995). This might indicate that northern populations of this species may currently be in the stage of losing their summer moult, although the process may be retarded by gene flow from southern populations where the summer moult still prevails.

Nevertheless, the fact that summer moult is maintained in southern populations of this species strongly indicates that it is adaptive in the sense that it has an important function (see discussion above), although we do not know if it is now selectively maintained because of its original function or if it is now beneficial because of other advantages arising from the general benefits of having two moults per year. In the latter case it may perhaps be classified as an ‘exaptation’ according to the terminology of Gould and Vrba (1982). Interestingly, *P. trochilus* is one of the most successful species of leaf warblers judged by its exceptionally large breeding and winter ranges (Cramp, 1992). Perhaps the fact that this species moults twice a year and hence has two possibilities to renew worn feathers has made it possible for it to broaden its habitat selection and invade new ecological niches. Individuals of this species forage in very open, sun-exposed habitats in their African winter quarters, compared to their congeneric relatives that spend the winter at similar latitudes (Cramp, 1992). Ultra-violet (UV) rays from exposure to sunshine are known to cause damage to avian feathers (Bergman, 1982), and hence the utilization of such exposed habitats may select for the maintenance of biannual moult.

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