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Evolutionary perspective

Phylogenetic analyses of the diversity of moult strategies in Sylviidae in relation to migration

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Abstract. Moult in birds is highly variable both within and among bird genera. The aim of the present study was to make an extended phylogenetic analysis of the diversity of moult strategies within Sylviidae in light of the recent phylogenies based on molecular data, and with the methodology of matched-pairs analysis. In the present study we analysed 141 sylviid taxa and, to improve character reconstruction, 22 outgroup taxa. The study could corroborate the earlier results that post-breeding moult is the ancestral state in Sylviidae. Migratory habits were found to be ancestral within Sylviidae but resident habits have evolved several times with a few reverse transitions back to migratory habits. Transitions in main moult strategy were significantly related to both migratory vs. resident habits and to migratory distance, giving support to the hypothesis that moult in the non-breeding season is related to migration as such and long-distance migration, respectively. Both resident and migratory taxa used minor alternative moult strategies besides the main moult strategy and such within-taxon flexibility might be a basal trait in Sylviidae. We investigated three variables that included minor strategies and found no relationship between these and migratory habits. However, two of these variables (the potential to interrupt moult and the occurrence of moult in both the post- and non-breeding seasons) were significantly related to migration distance. We conclude that migration patterns has some influence on the choice of moult strategy, and that flexibility in timing of moult is widespread within Sylviidae and might be a basal trait. We argue that such flexibility might be a prerequisite for changes in migratory strategies.

Key words: babblers, Cisticolidae, migration, molt, moult, passerines, Prinia, Sylviidae, Timaliidae, warblers

Introduction

Moult in birds is highly variable within and between bird genera as well as within taxa but the understanding of the factors underlying the variation is scarce (cf. Jenni and Winkler, 1994). Moult performance on an individual level depends both on genetic and environmental factors (cf. Gwinner, 1996; Helm

and Gwinner, 1999, 2001) and may differ between years (cf. Berthold and Querner, 1982; Hall and Fransson, 2001) but the factors determining the variation in moult strategies used among taxa is less well understood. Norman (1997) suggested that long migration distance might explain the occurrence of moult in the non-breeding season as compared to the most common strategy of moult in the post-breeding season. Holmgren and Hedenström (1995) modelled the timing of moult in relation to several life history traits and found a relation between feather abrasion and timing of moult. They predicted that the timing of moult should be as close as possible to the time period most crucial to a high fitness and concluded that the scheduling of moult is the optimal compromise between maximising breeding success and maximising survival to the next breeding season (Holmgren and Hedenström, 1995). In 1999 Svensson and Hedenström made a phylogenetic analysis of moult strategies including 61 taxa of Western Palearctic Sylviidae warblers and one outgroup (*Regulus*) with a special focus on *Phylloscopus*. The study indicated that moult strategy is linked to migration strategy, and gave an indication that moult in the post-breeding season is the ancestral state among Western Palearctic warbler taxa. Since the study of Svensson and Hedenström (1999) several new phylogenies covering Sylviidae based on molecular data have been published. These have mainly been concerned with inter-generic relationships (Cibois *et al*., 1999, 2001; Barker *et al*., 2002) and thereby facilitated a strengthened analysis in a broader inter-generic perspective. Additionally, the *Sylvia* genus has been re-analysed and does now include five African resident taxa of the former genus *Parisoma* (Shirihai *et al*., 2001).

In a Western Palearctic perspective most Sylviidae warblers are migrants and the theory and understanding of moult strategies have been dependent on this perspective. However, there are several mainly resident genera in Sylviidae and these have to be included in the analysis for a deeper understanding of the evolutionary history of moult strategies. The aim of the present study was to make an extended analysis of the diversity of moult strategies in as large a part of Sylviidae as possible from data available in the literature. Further, we wanted to include several outgroups in order to improve character reconstruction. A final aim was to use a methodology where independent changes in migration strategy were considered as a basis for independent changes in moult strategy, i.e. matched-pairs analysis. We were especially interested in investigating whether main moult strategy as well as the existence of moult in the non-breeding season were correlated to migration and migration distance, if minor alternative moult strategies were common, and whether flexibility in timing of moult was ancestral or not. Specifically, we tested the hypothesis that non-breeding moult is related to migratory habits/long-distance migration and that post-breeding moult is related to resident habits/short-distance migration.

Methods

Information on character states was available in Cramp (1988, 1992), Cramp and Perrins (1993), Baker (1997), Pyle (1997), Shirihai *et al.* (2001) and Herremans (in press) and supplemented by data on partially biannual moult in *Cisticola juncidis* (Gauci and Sultana, 1981) and *Sylvia borin* (Jenni and Winkler, 1994).

In total 141 sylviid taxa (following Sibley and Monroe, 1990) and 22 outgroup taxa were investigated with respect to moult. Due to lack of information for some taxa only 137 sylviid and 21 outgroup taxa were investigated with regard to migratory habits (migratory distance was possible to estimate only for 16 outgroup taxa).

Moult

This study focussed on the moult of primary and secondary wing feathers of adult passerines within Sylviidae with *Regulus*, Hirundinidae and *Pycnonotus* as outgroups (following Barker *et al.*, 2002). Juvenile birds moulting some remiges during their first non-breeding season were not considered.

The terminology of moult strategies often includes the timing of moult, for example the common terms summer moult vs. winter moult (cf. Svensson, 1992). This terminology is fully appropriate from a northern hemisphere perspective, but creates confusion when taxa from the southern and northern hemisphere are investigated together. In this study several taxa with at least part of the population in the southern hemisphere were included and we have thus chosen to use the terminology 'moult in the post-breeding season' and 'moult in the non-breeding season'. This emphasises the important relation between moult and the termination of breeding and makes it unnecessary to keep in mind the breeding season of different taxa. For resident taxa moult was considered to occur in the non-breeding season if it did not directly follow upon termination of breeding. We have used the term 'interrupted moult' for any moult that starts, without being finished in the breeding season (or the reverse). The moult is 'suspended' (cf. Mead and Watmough, 1976; Aidley and Wilkinson, 1987; Norman, 1991) when it is interrupted in the main moult season to be resumed later and 'arrested' (Norman, 1991) if it is known not to be resumed, but the knowledge of whether the moult will actually be resumed or not is scarce for most taxa. Moult is considered a 'split-moult' (Hasselquist *et al.*; 1988; Lindström *et al.*, 1993) if it starts with some remiges being moulted by juveniles in the season prior to the first adult moult, i.e. it is kind of a 'planned' interrupted moult. Thus, all these three categories were included in the term 'interrupted moult'. Three *Sylvia* taxa were recorded to sometimes moult some remiges in the non-breeding season although moult was complete

in the post-breeding season (Appendix 1). This is to be interpreted either as the occurrence of interrupted moult or as a partially biannual moult. Due to the uncertainty of interpretation these taxa were not included in the analysis of neither interrupted nor partially biannual moult.

In many taxa it is common that at least some individuals deviate from the main moult strategy and we have therefore considered both the main moult strategy and the occurrence of minor alternative strategies. Migratory birds might moult during extensive stop-over periods in the non-breeding season, before reaching the final non-breeding quarter. We have noted this in Appendix 1 but moult during stop-over was otherwise included in 'moult in the non-breeding season'. Moult is known to be flexible on an individual level (cf. Hall and Fransson, 2001) but in this study we concentrate on the flexibility in timing of moult on a taxon level.

Moult was analysed in a hierarchical mode from the broad view of main moult strategies to more detailed analysis. In the analysis of the potential to moult in the non-breeding season all taxa with moult in the non-breeding season, interrupted moult or biannual moult as main or alternative strategies were considered to have this potential. In the analysis of the occurrence of moult in both the post-breeding and non-breeding seasons all taxa with moult in both seasons, including interrupted moult but not biannual moult, were considered. In the analysis of the potential to interrupt moult only taxa with interrupted moult as main or alternative strategy were considered.

Migration

The migratory strategy of each taxon was estimated from distribution maps in Baker (1997), Cramp (1988, 1992) and Cramp and Perrins (1993). A taxon was considered fully migratory if breeding and non-breeding areas did not overlap. If breeding and non-breeding areas overlapped to some extent the taxon was considered partially migratory. Partially migratory taxa were included among migrants when migration distance was considered. Taxa with no separate area for breeding or non-breeding distribution were treated as residents. This means that taxa migrating within their breeding area, for example altitudinal migrants, have been included among residents. Migration distances were estimated from distribution maps (Cramp, 1988; 1992; Cramp and Perrins, 1993; Baker, 1997) with the help of Peters Atlas of the World (Peters, 1989). The distances (in km) were calculated by the computer program 'disttest' based on a formula presented by Imboden and Imboden (1972). This program uses the longitudes and latitudes to calculate the great circle distance between two places, in this case the distance between the mid point of the breeding area and the mid point of the non-breeding area. In taxa with a broad distribution and with populations using different breeding or non-breeding areas migration

distances were estimated to the most likely breeding or non-breeding area of each population. In partially migratory taxa the distances were estimated from pure breeding area to pure non-breeding area for the migrating population. When only one of these, the breeding or the non-breeding area, differed from the resident distribution the migration distances were estimated from this area to the border of the resident population.

The estimation of migration distance is sensitive to the location of the mid points of the breeding and non-breeding areas and the broader the distribution the more uncertain the estimation of migration distances. Also, in some cases the distribution followed country borders which is highly unlikely but may indicate that the distribution is poorly known across the border. For these reasons the migration distances are to be seen as crude estimates that give only an idea of whether the taxa migrates shorter or longer distances. If it had been possible the appropriate migration distances should preferably have been estimated from recovery data of ringed birds.

There is, to our knowledge, no consensus concerning the distinction between a long, medium and a short-distance migration. Scandinavian birds migrating to Western Europe are generally considered short-distance migrants, birds migrating to southern Europe and North Africa are considered medium distance migrants and those crossing the Saharan Desert are considered long-distance migrants. For example, if estimated from the middle of Sweden the distances would be around 1300 km for short-distance, 2500–3600 km for medium distance and 5000 km for long-distance migrations. Estimated from Ottenby Bird Observatory, in SE Sweden, the distances would be around 900 km for short, 1500–2600 km for medium and 3900 km for long-distance migrations. Based on this we have chosen the intervals 1–1000 km for short-distance migration, 1100–2900 km for medium distance migration, and ≥3000 km for long-distance migrations.

Phylogeny

The phylogeny (see Appendix 1) was constructed from available phylogenies based on molecular data as far as possible but Shirihai *et al.* (2001) used a combination of molecular, morphological and DNA–DNA hybridisation data. Intra-generic relationships follow Leisler *et al.* (1997, *Acrocephalus, Hippolais, Locustella*), Price *et al.* (1997, *Phylloscopus*), Shirihai *et al.* (2001, *Sylvia*) and Helbig and Seibold (1999, *Hippolais*). The inter-generic relationships follow Cibois *et al.* (1999, 2001), Leisler *et al.* (1997), Helbig and Siebold (1999), Barker *et al.* (2002) and Sheldon *et al.* (1999, Hirundinidae). *Cisticola* and *Prinia* were considered a separate family, Cisticolidae, by Sibley and Monroe (1990) but Cibois *et al.* (2001) placed these taxa within the Sylviidae (sensu Sibley and Monroe, 1990). We have followed Cibois *et al.* (2001)

in this case. The monophyly of Sylviidae has been challenged by new phylogenetic data and it is possible that both *Sylvia* and *Turdoides* belong to Timaliidae rather than Sylviidae (Cibois, 2003). We leave this for future studies to solve and follow Cibois *et al*. (2001, 2002) for the position of *Turdoides* in relation to the other genera and Helbig and Seibold (1999) for the position of *Sylvia*.

In order to improve the character reconstruction for Sylviidae we have included several outgroup taxa (*Regulus*, Hirundinidae, *Pycnonotus*). Only taxa with some data on their inter-generic relationship to some other taxon in the study were included. All genera were considered monophyletic except *Hippolais* which was split into two groups and included in *Acrocephalus* by both Leisler *et al*. (1997) and Helbig and Siebold (1999). Species were separated into subspecies or populations if they differed significantly in moult or migration strategy, according to our migration distance criteria, and were geographically distinct. *Phylloscopus bonelli orientalis* and *P. b. bonelli* were treated as subspecies by Sibley and Monroe (1990), but in the phylogeny by Price *et al*. (1997) these subspecies makes up a paraphyletic group with *Phylloscopus sibilatrix* in between. For this reason the two subspecies have been treated as different taxa, although they do not differ neither in moult strategy nor migration distance. For the same reasons *Phylloscopus trochiloides nitidus* and *P. t. plumbietarsus* were also treated as separate taxa. *Acrocephalus stentoreus brunnescens* have a northern migratory population with moult in the non-breeding season as the main strategy and a southern resident population with moult in the post-breeding season as main strategy. To separate these taxa we denoted them the 'Northern' and the 'Southern' *A. s. brunnescens*. Taxon names follow Sibley and Monroe (1990) when other sources were not congruent. Only taxa with data on adult wing moult available were included.

Analyses

The characters were reconstructed using parsimony in the program MacClade 4.0 (Maddison and Maddison, 2000). Both moult and migration characters were reconstructed as unordered. The relation between moult strategy and migratory habits was investigated in two steps (1) between resident taxa and migratory taxa and (2) among migrants between short or medium distance migrants and long-distance migrants. We identified phylogenetically independent pairs of taxa where the two member clades differ in migration strategy. The number of transitions in moult strategy was then compared between the two migration strategies within each pair. Pairs without any transitions in moult strategy were disregarded, and a sign test was performed on the remaining pairs (all significance tests were two-tailed). We tested the hypotheses that moult in the non-breeding season should be more common in

migratory and long-distance migratory taxa, respectively, and, correspondingly, that moult in the post-breeding season should be more common in residents and short-distance migrants, respectively. If the same type of transition in moult strategy occurred in each member of a matched pair or if different types of transitions occurred in one of the members of the matched pair the number of transitions were divided by the number of branches where such transitions can potentially take place before comparison (see Tullberg and Hunter, 1996).

In parts of the tree there were equivocal resolutions with regard to moult strategy. We dealt with this by considering two extreme resolutions, namely either maximising transitions to moult in the post-breeding season (and branches with moult in the non-breeding season), or maximising transitions to moult in the non-breeding season (and branches with moult in the post-breeding season). Such uncertainties could give rise to a range in the number of matched-pairs with transitions in the predicted direction according to our hypothesis.

Results

Moult

A single complete moult a year was the dominant (93%) and the ancestral main moult strategy within Sylviidae (Appendix 1). Ten taxa moulted biannually (*Phylloscopus trochilus* and *Prinia* spp.) and additionally eight taxa moulted some remiges twice a year, i.e. a partially biannual moult (*Locustella certhiola, L. fasciolata, L. fluviatilis*, *Sylvia hortensis hortensis, S. h. jerdoni, S. h. crassirostris, S. borin* and *Prinia socialis*). Biannual moult was inferred to have evolved at least twice and partially biannual moult five times and there were no reverse transitions. Partially biannual moult occurred both in taxa with moult in the post-breeding season (*Sylvia hortensis hortensis, S. h. jerdoni, Prinia socialis*), interrupted moult (*Sylvia hortensis crassirostris*) and moult in the non-breeding season (*Locustella pleskei, Sylvia borin*) as the main moult strategy.

Moult in the post-breeding season as a main strategy was inferred to be the ancestral and, consequently, moult in the non-breeding season the derived state in Sylviidae. There were 8–11 transitions from moult in the post-breeding season to moult in the non-breeding season, two transitions to interrupted moult (*Sylvia nisoria* and *Sylvia hortensis crassirostris*) and two transitions to biannual moult (see above). The ancestral strategy was also the dominant main moult strategy (64% of the sylviid taxa). There were 4–7 reverse transitions from moult in the non-breeding season to moult in the post-breeding season,

but there were no transitions from interrupted or biannual moult strategy to any other strategy.

In 52% of the sylviid taxa moult in the non-breeding season occurred either as main moult strategy or as a minor alternative strategy used by some individuals ($n = 141$). If the biannually moulting taxa were excluded moult in the non-breeding season occurred among 48% of the sylviid taxa ($n = 131$). The potential to moult in the non-breeding season was inferred to be either ancestral or evolving at the base of Sylviidae.

Interrupted moult was the main strategy in only two sylviid taxa but as a minor alternative strategy it was quite common (38 taxa). In total 28% of the sylviid taxa investigated were recorded to interrupt moult sometimes. It was not possible to conclude whether the potential to interrupt moult was ancestral or not in Sylviidae. If a moult with potential for interruptions was ancestral there were 10–14 transitions to this state. If the ancestral state was a moult without interruptions there were 19–23 transitions to a moult with potential for interruptions.

Moult in both the post-breeding and the non-breeding seasons occurred within 38% of the sylviid taxa investigated ($n = 141$) or, with biannually and partially biannually moulting taxa excluded, in 33% of taxa ($n = 130$). The potential to moult in both seasons was inferred to be either ancestral or evolving at the base of Sylviidae.

Migration

Migratory habits were ancestral in Sylviidae and 69% of the sylviid taxa investigated were migratory or partially migratory (Appendix 1). Residency was inferred to have evolved from migratory habits 8–9 times but there were only 2–3 transitions from residency to migratory habits. There were 12 transitions to partially migratory habits, 9–10 times from fully migratory habits and 2–3 times from resident habits.

Long-distance migration was ancestral within Sylviidae although the closest outgroup *Pycnonotus* was resident. A medium migratory distance was generally an intermediate state between long and short-distance migration. There were 21 transitions between close migratory distance categories but only 1–2 transitions between the long- and the short-distance migration categories.

Moult in relation to migration

Moult in the non-breeding season as the main moult strategy was significantly correlated to migratory habits and moult in the post-breeding season to resident habits (Table 1). Among migratory taxa moult in the non-breeding season as the main moult strategy was, likewise, significantly correlated to long-dis-

Table 1. Transitions in main moult strategy in matched pairs of migratory (M) and resident (R) taxa of Sylviidae

Matched pair	Transitions to moult in the non-breeding season	Transitions to moult in the post-breeding season
1. +		
M: *Sylvia nisoria, S. c. curruca, S. nana deserti – S. undata*	1	0
R: *S. boehmi – S. subcaeruleum*	0	0
2. +		
M: *Phylloscopus armandii – P. subviridis, P. inornatus humei – P. chloronotus, P. b. bonelli – P. tenellipes*	2–4	0–2
R: *P. umbrovirens – P. trivirgatus*	0	0
3. +		
M: Northern *Acrocephalus stentoreus brunnescens*	1	0
R: Southern *Acrocephalus stentoreus brunnescens*	0	0
4. +		
M: *Acrocephalus a. arundinaceus/zarudnyi*	a. 1	b. 1/3
R: *Acrocephalus brevipennis*	a. 0	b. 1
5. +		
M: *Hippolais languida – Acrocephalus griseldis*	1	2/42
R: *Turdoides fulvus – T. altirostris*	0	0
6. +		
M: *Sylvia borin*	1/3	0
R: *Orthotomus atrogularis – Cisticola juncidis*	1/26	0

The hypothesis to be tested is that transitions to moult in the non-breeding vs. in the post-breeding season is more likely in migrants and/or that transitions to moult in the post-breeding vs. in the non-breeding season is more likely in residents. If both kinds of transitions occur in the same group or matched pair, the number of transitions are divided by the number of branches in which such transitions could potentially take place (i.e. branches with the opposite moult strategy). Uncertainties in the character reconstruction are denoted by a range in the number of transitions or as alternative solutions (a, b). Pairs with transitions in the expected direction according to the hypothesis are denoted by +. All six of the matched pairs had transitions in the expected direction (Sign test, $P = 0.026$).

tance migration and moult in the post-breeding season to short or medium distance migration (Table 2).

The within taxon potential to moult in the non-breeding season (i.e. including moult in the non-breeding season both as a main strategy and a minor alternative strategy) was not significantly correlated to migratory habits, i.e. whether a taxon was migratory or resident (6–7 out of 9 matched-pairs, n.s.) and it was neither significantly correlated to migration distance among migratory taxa (6 out of 10 matched-pairs, n.s., or 8 out of 11 matched-pairs, n.s.).

The occurrence of moult in both the post-breeding and the non-breeding seasons (biannual moult excluded) was not correlated to migratory habits (5

Table 2. Transitions in main moult strategy in matched pairs of long-distance (L) and short/medium (S, M) distance taxa of Sylviidae

Matched pair	Transitions to moult in the non-breeding season	Transitions to moult in the post-breeding season
1. +		
L: *Locustella certhiola – L. luscinoides*	0	0
S, M: *L. pleskei*	0	1
2. +		
L: *Sylvia c. communis/volgensis – S. c. icterops/rubicola*	1	0
S, M: *S. conspicillata – S. rueppeli, S. melanocephala – S. undata*	0	0
3. +		
L: *Phylloscopus b. bonelli – P. fuscatus, P. trochilus*	1	0
S, M: *P. p. proregulus – P. pulcher*	0	0
4. −		
L: *Phylloscopus borealis – P. tenellipes*	a. 1/3	b. 1
S, M: *P. magnirostris*	a. 1/1	b. 0
5. +		
L: *Phylloscopus trochiloides viridanus – P. t. nitidus*	a. 1	b. 0
S, M: *P. reguloides – P. magnirostris*	a. 0	b. 1
6. +		
L: *Acrocephalus bistrigiceps*	0	0
S, M: *A. m. melanopogon – A. melanopogon mimica*	0	1
7. +		
L: *Hippolais pallida elaeica/opaca*	0	0
S, M: *H. p. pallida/laeneni/reiseri*	0	1
8. +		
L: *Acrocephalus a. aedon – A. a. stegmanni, A. dumetorum, A. paludicola – A. schoenobaenus, A griseldis, A. a. arundinaceus/zarudnyi, A. orientalis,* Northern *A. stentoreus brunnescens*	a. 2/5 b. 1/2	a. 1/16 b. 1/19
S, M: *A. sorghophilus*	0	0
9. +		
L: *Hippolais languida – H. polyglotta*	1	0
S, M: *Cisticola juncidis*	0	0
10. +		
L: *Sylvia borin – S. atricapilla dammholzi*	1	0
S, M: *Cettia cetti – C. diphone, C. pallidipes*	0	0

The hypothesis to be tested is that transitions to moult in the non-breeding season are relatively more common in long-distance migrants and/or that transitions to moult in the post-breeding season are relatively more common in short/medium distance migrants. If both kinds of transitions occur in the same group or matched pair, the number of transitions are divided by the number of branches in which such transitions could potentially take place (i.e. branches with the opposite moult strategy). Uncertainties in the character reconstruction are denoted by alternative solutions (a, b). Pairs with transitions in the expected direction according to the hypothesis are denoted by + and pairs with transitions in the unexpected direction are denoted by −. Nine of the 10 matched pairs had transitions in the expected direction (Sign test, $P = 0.026$).

Table 3. Transitions to moult in both the post- and non-breeding seasons in matched pairs of long-distance (L) and short/medium (S, M) distance taxa of Sylviidae

Matched pair	Transitions to flexibility in timing of moult
1. +	
L: *Sylvia c. communis/volgensis – S. c. icterops/rubicola*	1/1
S, M: *S. conspicillata – S. rueppeli, S. melanocephala – S. undata*	1/14
2. +	
L: *Sylvia nisoria*	1/1
S, M: *S h. hortensis – S. h. crassirostris, S. nana deserti – S. n. nana*	1/4
3. −	
L: *Phylloscopus i. inornatus*	0
S, M: *P. inornatus humei*	1
4. −	
L: *Phylloscopus schwarzi*	0
S, M: *P. tytleri – P. griseolus*	1
5. 0	
L: *Phylloscopus trochiloides viridanus – P. t. nitidus*	1/3
S, M: *P. reguloides – P. magnirostris*	1/3
6. +	
L: *Phylloscopus b. bonelli – P. fuscatus, P. trochilus*	2
S, M: *P. p. proregulus – P. pulcher*	0
7. +	
L: *Acrocephalus scirpaceus – A. palustris*	1
S, M: *A c. concinens – A. agricola*	0
8. +	
L: *Acrocephalus bistrigiceps*	1
S, M: *A. m. melanopogon – A. melanopogon mimica*	0
9. +	
L: *Hippolais pallida elaeica/opaca*	0
S, M: *H. p. pallida/laeneni/reiseri*	1 reverse transition
10. +	
L: *Acrocephalus a. aedon – A. a. stegmanni, A. dumetorum, A. paludicola – A. schoenobaenus, A griseldis, A. a. arundinaceus/ zarudnyi, A. orientalis,* Northern *A. stentoreus brunnescens*	3
S, M: *A. sorghophilus*	0
11. +	
L: *Hippolais languida – H. polyglotta*	1
S, M: *Cisticola juncidis*	0
12. +	
L. *Phylloscopus coronatus*	1
S, M: *P. armandii – P. subviridis*	0
13. +	
L: *Sylvia borin – S. atricapilla dammholzi*	1/2
S, M: *Cettia cetti – C. diphone, C. pallidipes*	1/5

Table 3. (Continued)

The analysis is based on a character resolution that maximises the number of transitions to moult in both seasons. The hypothesis to be tested is that transitions to moult in both seasons are relatively more common in long-distance migrants or that reverse transitions to moult in one season are relatively more common in short/medium distance migrants. If transitions occur in the same pair, the number of transitions are divided by the number of branches in which such transitions could potentially take place (i.e. branches without moult in both seasons). Pairs with transitions in the expected direction according to the hypothesis are denoted by +, pairs with no difference between the groups by 0, and pairs with transitions in the unexpected direction are denoted by −. There was one matched pair with no difference between the groups. Ten of the 12 remaining matched pairs had transitions in the expected direction (Sign test, $P = 0.04$).

out of 8 matched-pairs, n.s.) but among migratory taxa there was a correlation to migratory distance (Table 3).

The potential to interrupt moult (i.e. including interrupted moult both as main moult strategy and as minor alternative strategy) was not correlated with migratory habits (5 out of 8 matched-pairs, n.s.) but it did correlate with migration distance among migratory taxa (Table 4).

Discussion

As expected, a single complete moult a year was the dominant and ancestral main strategy within Sylviidae. Biannual moult is rare among passerines (cf. Prys-Jones, 1991) and it is common only in the resident genus *Prinia* (Herremans, in press). Both biannual and partially biannual moult strategies occur within *Prinia* but due to the lack of an intra-generic phylogeny of this genus we could not conclude anything about the relationship between the two strategies. Biannual moult is supposed to be the best option if cost of moult is extremely low (Holmgren and Hedenström, 1995) or ecto-parasite load unusually high (Jenni and Winkler, 1994) but, unfortunately, none of these factors have, to our knowledge, yet been investigated.

The present study corroborates the earlier findings (Norman, 1997; Svensson and Hedenström, 1999) that the main moult strategy is related to migration distance but showed also that moult strategy is correlated with migratory habits as such. It seems, thus, as if migration can explain a part of the differences in main moult strategies between taxa, but another possibility is that the correlation seen is an artefact of the rainfall patterns in Africa. The timing of the rain season varies with latitude and longitude and the resulting rainfall pattern may explain both migration patterns and timing of moult in migrants (Jones, 1995). Moult duration in the non-breeding season is normally much longer than in the post-breeding season in migrants (cf. Pearson, 1973). A

Table 4. Transitions to interrupted moult in matched pairs of long-distance (L) and short/medium (S, M) distance taxa of Sylviidae

Matched pair	Transitions to interrupted moult
1. +	
L: *Sylvia c. curruca*	1
S, M: *S. c. minula*	0
2. +	
L: *Sylvia c. communis/volgensis – S. c. icterops/rubicola*	1/1
S, M: *S. conspicillata – S. rueppeli, S. melanocephala – S. undata*	1/12
3. +	
L: *Sylvia nisoria*	1/1
S, M: *S. h. hortensis – S. h. crassirostris, S. nana deserti – S. n. nana*	1/6
4. –	
L: *Phylloscopus i. inornatus*	0
S, M: *P. inornatus humei*	1
5. +	
L: *Phylloscopus b. bonelli – P. fuscatus, P. trochilus*	2
S, M: *P. p. proregulus – P. pulcher*	0
6. +	
L: *Acrocephalus scirpaceus – A. palustris*	1
S, M: *A c. concinens – A. agricola*	0
7. +	
L: *Acrocephalus bistrigiceps*	1
S, M: *A. m. melanopogon – A. melanopogon mimica*	0
8. +	
L: *Hippolais pallida elaeica/opaca*	1
S, M: *H. p. pallida/laeneni/reiseri*	0
9. +	
L: *Acrocephalus a. aedon – A. a. stegmanni, A. dumetorum, A. paludicola – A. schoenobaenus, A griseldis, A. a. arundinaceus/ zarudnyi, A. orientalis,* Northern *A. stentoreus brunnescens*	2
S, M: *A. sorghophilus*	0
10. +	
L: *Hippolais languida – H. polyglotta*	1
S, M: C*isticola juncidis*	0
11. +	
L: *Sylvia borin – S. atricapilla dammholzi*	1/1
S, M: *Cettia cetti – C. diphone, C. pallidipes*	1/3

The analysis is based on a character resolution that maximises the number of transitions to interrupted moult. The hypothesis to be tested is that transitions to interrupted moult are relatively more common in long-distance migrants than in short/medium distance migrants. If transitions occur in the same pair, the number of transitions are divided by the number of branches in which such transitions could potentially take place (i.e. branches without interrupted moult). Pairs with transitions in the expected direction according to the hypothesis are denoted by + and pairs with transitions in the other direction are denoted by –. Ten of the 11 matched pairs had transitions in the expected direction (Sign test, $P = 0.016$).

slower moult might be favourable for the quality of the feathers (Dawson *et al.*, 2000) but Holmgren and Hedenström (1995) predicted that moult duration was unlikely to affect the timing of moult.

Table 5. The occurrence of statistically significant correlation between moult strategy and migration as well as migration distance among migrants

	Correlation to migratory/resident habits	Correlation to migration distance
Main moult strategy	Yes	Yes
Potential to moult in the non-breading season	No	No
Moult in both seasons	No	Yes
Potential to interrupt moult	No	Yes

Besides the main moult strategy this study investigated the occurrence of three characters related to flexibility in timing of moult. The characters were dependent in a hierarchical way so that one was a smaller subsection of the other with 'potential to moult in the non-breeding season' the most inclusive and 'potential to interrupt moult' the least inclusive character (cf. Table 5). The present study showed that although moult in the post-breeding season as the main strategy was ancestral the potential to moult in the non-breeding season was too, or this potential evolved at the base of Sylviidae. Moult in the non-breeding season is thought to have evolved as an adaptation due to time constraints for breeding and migration (cf. Holmgren and Hedenström, 1995; Norman, 1997; Svensson and Hedenström, 1999) but the theory might be valid for resident taxa too if migration is substituted by, for example, an oncoming dry season. Likewise, the idea that the securing of non-breeding season territories (Norman, 1997) is a reason to delay moult could apply to resident taxa if, for example, environmental fluctuations necessitates intra-breeding-range movements.

Twenty-eight percent of the Sylviidae taxa investigated interrupted moult on occasions. If we assume that moult interruption is a way to handle for example a time constraint during moult, then the potential to interrupt moult is probably more widespread than the present data suggests. The time constraint experienced by different taxa during a year varies and many taxa might only on rare occasions experience a time constraint during moult. Although the potential to interrupt moult was not correlated to migratory habits it was correlated to migration distance which might indicate that the time constraint hypothesis is correct.

A special case of interrupted moult, the split-moult (Hasselquist *et al*., 1988; Lindström *et al*., 1993), starts in juvenile birds with a moult of some remiges in the non-breeding season prior to their first reverse migration to breeding grounds. Although only one taxon, *Sylvia nisoria*, has been categorised as having split-moult Shirihai *et al*. (2001) reported that moult of secondaries or both primaries and secondaries in the non-breeding season occurred among juveniles of 12 *Sylvia* species. A closer study of these might reveal that split-

moult is not as uncommon as previously thought or that it is only an extreme form of a gradual variation in moult flexibility.

None of the three characters related to flexibility were correlated to migratory habits and neither did they exclusively occur among migrants (Table 5). These characters are all measurements of flexibility in timing of moult and, taken together, they strengthen the idea that moult is a flexible process that can be adjusted to environmental circumstances. Only birds living in stable, predictable environments, never experiencing time constraints are supposed to show no flexibility in timing of moult but such stable circumstances are probably rare (see for example Fogden, 1972). The literature data on moult strategies was limited for many taxa and we believe that the knowledge of flexibility in timing of moult will increase the more moult is studied. If within taxon flexibility in timing of moult is important it is probably a latent quality only not shown under stable circumstances. Therefore the flexibility in timing of moult shown in the present study is to be considered a minimum.

The potential for flexibility in timing of moult is widespread in Sylviidae and both resident and migrant taxa use alternative moult strategies occasionally. There is a strong genetic component influencing the timing of moult (cf. Gwinner, 1996; Helm and Gwinner, 1999, 2001) but it is unclear to which extent there is a within taxon genetic variation (multiple genes or alleles) as a base for the flexibility in timing (but see Helm and Gwinner, 1999, 2001), and, consequently the relative influence of genetic and environmental factors determining which moult strategy to use is unknown. Reasonably, though, the flexibility in timing of moult seen is the result of both a genetic variation and an individual flexibility in moult performance. The flexibility in timing of moult may be a basal trait and, as such, it is not to be forgotten when evaluating moult patterns and life history traits in sylviid warblers.

A flexible timing of moult might be favourable in a variable environment. There are strong indications that the oscine passerines (i.e. including Sylviidae) radiated in Australia and spread through Asia to Europe, Africa and the New World (Ericson *et al*., 2002). For such mobile animals as birds the colonisation of new areas might be relatively fast and a potential for flexible timing of moult as well as flexibility in moult performance might then be advantageous when encountering new habitats. Migratory habits are ancestral within Sylviidae and resident habits have evolved from this state, but reverse transitions from residency back to migratory habits have occurred as well. Thus, migratory habits have changed several times. If migratory habits change the entire life history of the bird will be affected. Besides migration, breeding and moult are the most time and energy demanding phases in a bird's yearly life cycle and these phases are, more or less, mutually exclusive. In terms of flexibility the timing of the breeding period is probably more rigid than timing of moult. For example, a

successful breeding depend on, among other things, high availability of food whilst moult can be performed in a slower rate if the environmental conditions are less favourable. Although migratory habits could not explain very much of the variation in moult strategies found (but migratory distance could) it is possible that the flexibility in timing of moult might be a prerequisite for changes in migratory habits.

Zink (2002) suggested that migration evolved early in avian history and that the genetic programs for migration are more likely to be suppressed than eliminated in sedentary birds. This might be valid also for flexibility in moult.

The present study focussed on Sylvidae sensu Sibley and Monroe (1990). Recently, two of the genera included, *Sylvia* and *Turdoides*, have been suggested to belong to Timaliidae or, as an alternative, that Timaliidae and Sylviidae should be joined together into one family (Cibois, 2003). The resolution of relationships among taxa in these two families must await further study (Cibois, 2003) and the conclusions from the present study should be checked against eventual new phylogenies in the future.

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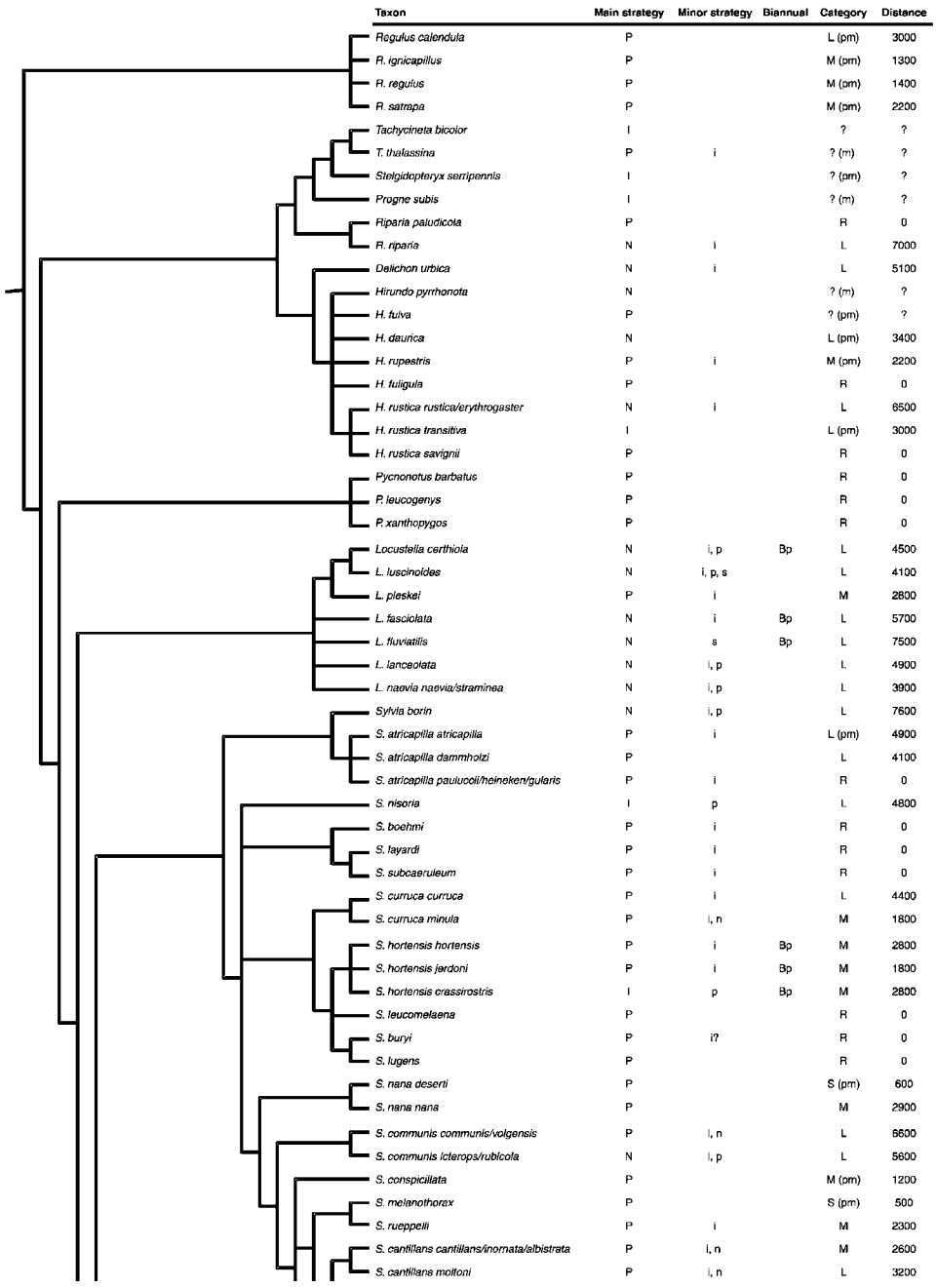
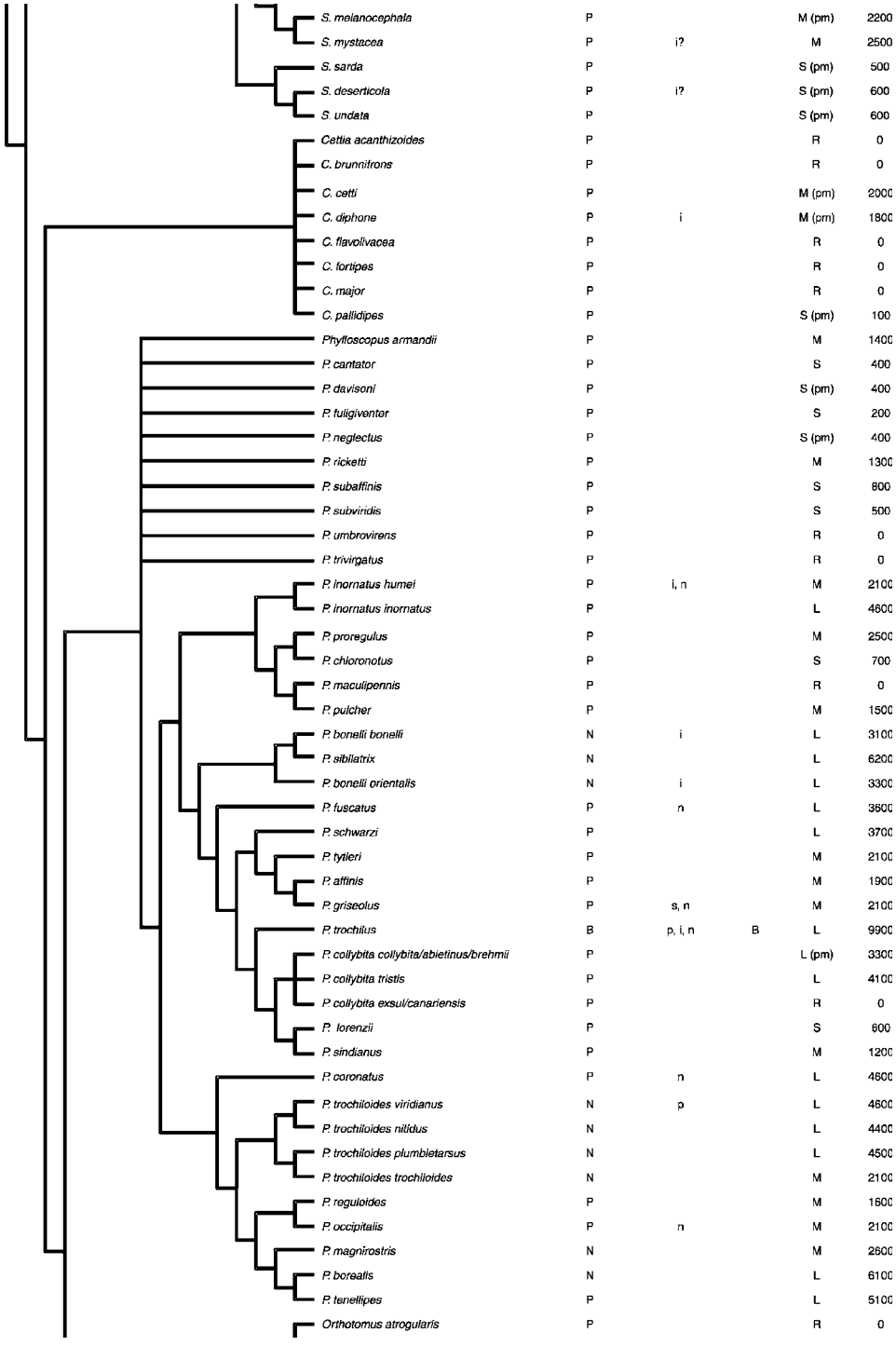
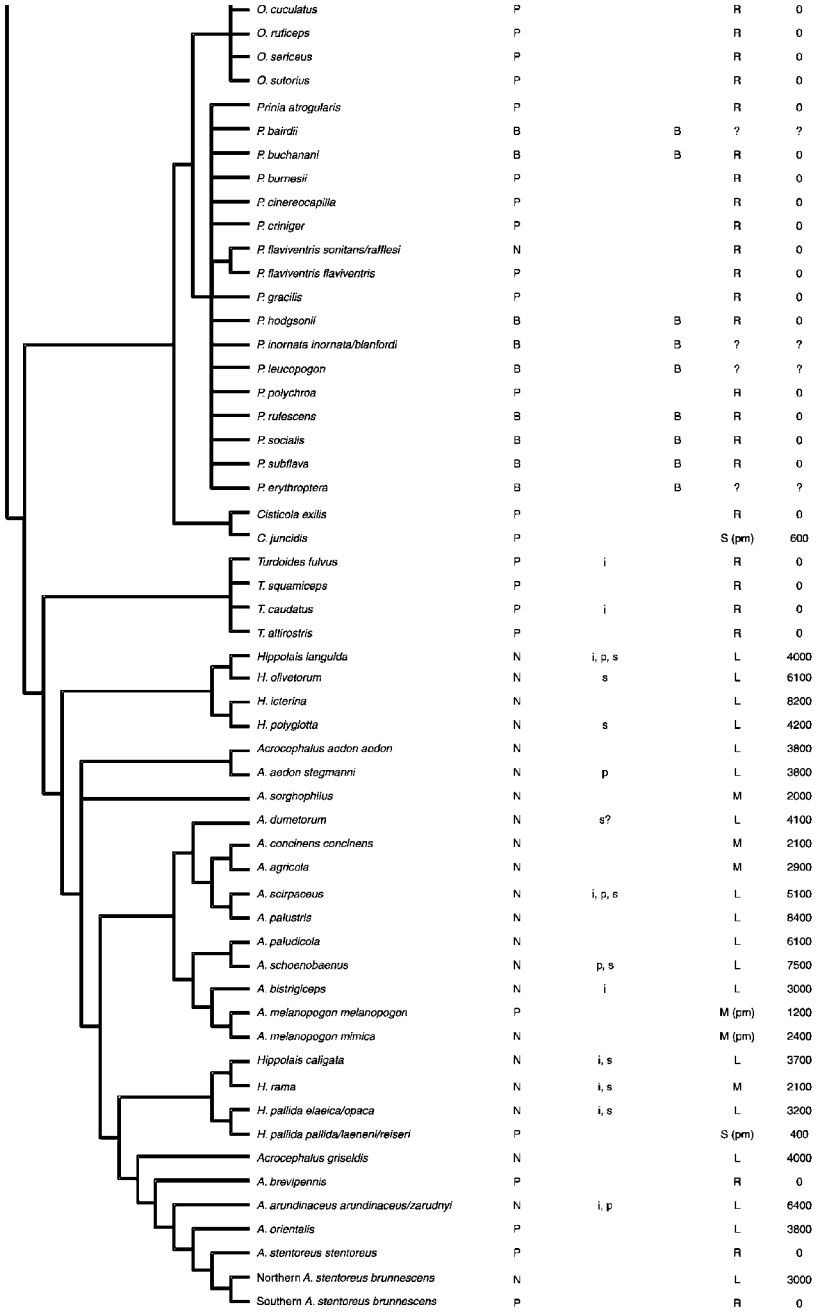
Appendix 1

Taxa investigated following Sibley and Monroe (1990), *Regulus* to *Pycnonotus* are outgroup taxa (for details on phylogeny construction, see Methods). Main moult strategy (P = moult in the postbreeding season, N = moult in the non-breeding season, I = interrupted moult), minor alternative moult strategies (p, n and i as above, s = moult at stop-over site, s? = moult at stop-over site might occur, i? = moult of remiges in the non-breeding season reported but unclear if this means interrupted moult as a minor alternative strategy or partially biannual moult of some individuals), existence of biannual or partially biannual moult (B = biannual moult, Bp = partially biannual moult), migration category (R = resident, S = short-distance migration, M = medium distance migration, L = long distance migration, (pm) = partially migratory taxon, (m) = migratory taxon) and average migratory distance (km).



Taxon	Main strategy	Minor strategy	Biannual	Category	Distance
Regulus calendula	P			L (pm)	3000
R. ignicapillus	P			M (pm)	1300
R. regulus	P			M (pm)	1400
R. satrapa	P			M (pm)	2200
Tachycineta bicolor	I			?	?
T. thalassina	P	i		? (m)	?
Stelgidopteryx serripennis	I			? (pm)	?
Progne subis	I			? (m)	?
Riparia paludicola	P			R	0
R. riparia	N	i		L	7000
Delichon urbica	N	i		L	5100
Hirundo pyrrhonota	N			? (m)	?
H. fulva	P			? (pm)	?
H. daurica	N			L (pm)	3400
H. rupestris	P	i		M (pm)	2200
H. fuligula	P			R	0
H. rustica rustica/erythrogaster	N	i		L	6500
H. rustica transitiva	I			L (pm)	3000
H. rustica savignii	P			R	0
Pycnonotus barbatus	P			R	0
P. leucogenys	P			R	0
P. xanthopygos	P			R	0
Locustella certhiola	N	i, p	Bp	L	4500
L. luscinioides	N	i, p, s		L	4100
L. pleskei	P	i		M	2800
L. fasciolata	N	i	Bp	L	5700
L. fluviatilis	N	s	Bp	L	7500
L. lanceolata	N	i, p		L	4900
L. naevia naevia/straminea	N	i, p		L	3900
Sylvia borin	N	i, p		L	7600
S. atricapilla atricapilla	P	i		L (pm)	4900
S. atricapilla dammholzi	P			L	4100
S. atricapilla pauluccii/heineken/gularis	P	i		R	0
S. nisoria	I	p		L	4800
S. boehmi	P	i		R	0
S. layardi	P	i		R	0
S. subcaeruleum	P	i		R	0
S. curruca curruca	P	i		L	4400
S. curruca minula	P	i, n		M	1800
S. hortensis hortensis	P	i	Bp	M	2800
S. hortensis jerdoni	P	i	Bp	M	1800
S. hortensis crassirostris	I	p	Bp	M	2800
S. leucomelaena	P			R	0
S. buryi	P	i?		R	0
S. lugens	P			R	0
S. nana deserti	P			S (pm)	600
S. nana nana	P			M	2900
S. communis communis/volgensis	P	i, n		L	6600
S. communis icterops/rubicola	N	i, p		L	5600
S. conspicillata	P			M (pm)	1200
S. melanothorax	P			S (pm)	500
S. rueppelli	P	i		M	2300
S. cantillans cantillans/inornata/albistrata	P	i, n		M	2600
S. cantillans moltoni	P	i, n		L	3200


S. melanocephala P M (pm) 2200
S. mystacea P i? M 2500
S. sarda P S (pm) 500
S. deserticola P i? S (pm) 600
S. undata P S (pm) 600
Cettia acanthizoides P R 0
C. brunnifrons P R 0
C. cetti P M (pm) 2000
C. diphone P i M (pm) 1800
C. flavolivacea P R 0
C. fortipes P R 0
C. major P R 0
C. pallidipes P S (pm) 100
Phylloscopus armandii P M 1400
P. cantator P S 400
P. davisoni P S (pm) 400
P. fuligiventer P S 200
P. neglectus P S (pm) 400
P. ricketti P M 1300
P. subaffinis P S 800
P. subviridis P S 500
P. umbrovirens P R 0
P. trivirgatus P R 0
P. inornatus humei P i, n M 2100
P. inornatus inornatus P L 4600
P. proregulus P M 2500
P. chloronotus P S 700
P. maculipennis P R 0
P. pulcher P M 1500
P. bonelli bonelli N i L 3100
P. sibilatrix N L 6200
P. bonelli orientalis N i L 3300
P. fuscatus P n L 3600
P. schwarzi P L 3700
P. tytleri P M 2100
P. affinis P M 1900
P. griseolus P s, n M 2100
P. trochilus B p, i, n B L 9900
P. collybita collybita/abietinus/brehmii P L (pm) 3300
P. collybita tristis P L 4100
P. collybita exsul/canariensis P R 0
P. lorenzii P S 600
P. sindianus P M 1200
P. coronatus P n L 4600
P. trochiloides viridianus N p L 4600
P. trochiloides nitidus N L 4400
P. trochiloides plumbietarsus N L 4500
P. trochiloides trochiloides N M 2100
P. reguloides P M 1600
P. occipitalis P n M 2100
P. magnirostris N M 2600
P. borealis N L 6100
P. tenellipes P L 5100
Orthotomus atrogularis P R 0


O. cuculatus P R 0
O. ruticeps P R 0
O. sericeus P R 0
O. sutorius P R 0
Prinia atrogularis P R 0
P. bairdii B B ? ?
P. buchanani B B R 0
P. burnesii P R 0
P. cinereocapilla P R 0
P. criniger P R 0
P. flaviventris sonitans/rafflesi N R 0
P. flaviventris flaviventris P R 0
P. gracilis P R 0
P. hodgsonii B B R 0
P. inornata inornata/blanfordi B B ? ?
P. leucopogon B B ? ?
P. polychroa P R 0
P. rufescens B B R 0
P. socialis B B R 0
P. subflava B B R 0
P. erythroptera B B ? ?
Cisticola exilis P R 0
C. juncidis P S (pm) 600
Turdoides fulvus P i R 0
T. squamiceps P R 0
T. caudatus P i R 0
T. altirostris P R 0
Hippolais langulda N i, p, s L 4000
H. olivetorum N s L 6100
H. icterina N L 8200
H. polyglotta N s L 4200
Acrocephalus aedon aedon N L 3800
A. aedon stegmanni N p L 3800
A. sorghophilus N M 2000
A. dumetorum N s? L 4100
A. concinens concinens N M 2100
A. agricola N M 2900
A. scirpaceus N i, p, s L 5100
A. palustris N L 8400
A. paludicola N L 6100
A. schoenobaenus N p, s L 7500
A. bistrigiceps N i L 3000
A. melanopogon melanopogon P M (pm) 1200
A. melanopogon mimica N M (pm) 2400
Hippolais caligata N i, s L 3700
H. rama N i, s M 2100
H. pallida elaeica/opaca N i, s L 3200
H. pallida pallida/laenenl/reiseri P S (pm) 400
Acrocephalus griseldis N L 4000
A. brevipennis P R 0
A. arundinaceus arundinaceus/zarudnyi N i, p L 6400
A. orientalis P L 3800
A. stentoreus stentoreus P R 0
Northern A. stentoreus brunnescens N L 3000
Southern A. stentoreus brunnescens P R 0

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