ORNIS SVECICA 4:1–24, 1994 https://doi.org/10.34080/os.v4.23028

Moult in relation to migration in birds – a review

NILS KJELLÉN

Abstract

This study reviews different ways of combining the moult with other essential activities like breeding and migration. Most species tend to avoid moult during the breeding. A majority of short-distance migrants change their feathers in summer before autumn migration, while most long-distance migrants perform a winter moult in the tropics after autumn migration. A complete moult both in summer and winter has only been recorded in a few passerines. Birds like albatrosses and larger eagles have a serial moult, changing only a number of their primaries every year. Another strategy common among long-distance migrants is to change some feathers on the breeding grounds, suspend moult, and complete it in the winter quarters. A special adaptation allowing faster moult is the simultaneous shedding of all wing quills. During this time birds are flightless and many species perform spectacular moult migrations to congregate in areas rich in food and free of predators. The moult strategy may vary between closely related species and a comparative study of three different groups (raptors, waders and warblers) is presented. The most clear differences in strategy seem to be related to migration distance.

Nils Kjellén, Department of Ecology, Animal Ecology, University of Lund, Ecology Building S-223 62 Lund, Sweden.

Received 19 July 1993, Accepted 20 September 1993, Edited by S. Svensson

Introduction

The chief characteristic that separates birds from other animals are their feathers. These occur in many different shapes and sizes, with various functions such as thermal isolation and flight. Due to wear and bleaching the feathers have to be renewed at regular intervals. This process, known as moulting, is essential to the birds' basic activities such as breeding and migration. This paper examines the relationship between moult and migration and ways of combining the two during the yearly cycle within various genera, species and populations. The scheduling of moult in relation to the breeding cycle will also be reviewed where relevant. I will concentrate on adult birds and the moult of remiges (the primary and secondary wing feathers), simply because this has been studied in a large number of species.

Costs of moult

In most species, primarily in the temperate regions, moult, migration and breeding do not overlap significantly, indicating that each process often is too costly to allow combination. In Pied Flycatchers *Ficedula hypoleuca* the onset of moult depended on the brood size and was retarded if a large brood was reared (Slagsvold & Lifjeld 1989). The total mass of plumage that has to be renewed corresponds to almost a fourth of the lean body mass (King 1980, Murphy & King 1991). Moult also intensifies amino acid metabolism (Newton 1968a), modifies water balance (Chilgren 1975), increases body temperature (Payne 1972), blood volume (Chilgren & deGraw 1977) and oxygen consumption (King 1980). The extra energy required for moult may be supplied by (1) increasing the nutrient intake, (2) reducing some other component of the energy budget (e. g. locomotor activity) or (3) utilizing body reserves of energy and protein (King 1980). King considers only the last alternative to create ”stress” in the physiological sense. Normally the fat reserves do not become reduced during moult but instead sometimes increase, especially in birds with a protracted moult period (Payne 1972).

An increase of between 5 and 30 % in metabolic rate during moult has been recorded, and some authors report even higher figures (Payne 1972). The feathers consist mainly of proteins and some birds consume food in excess of caloric require-

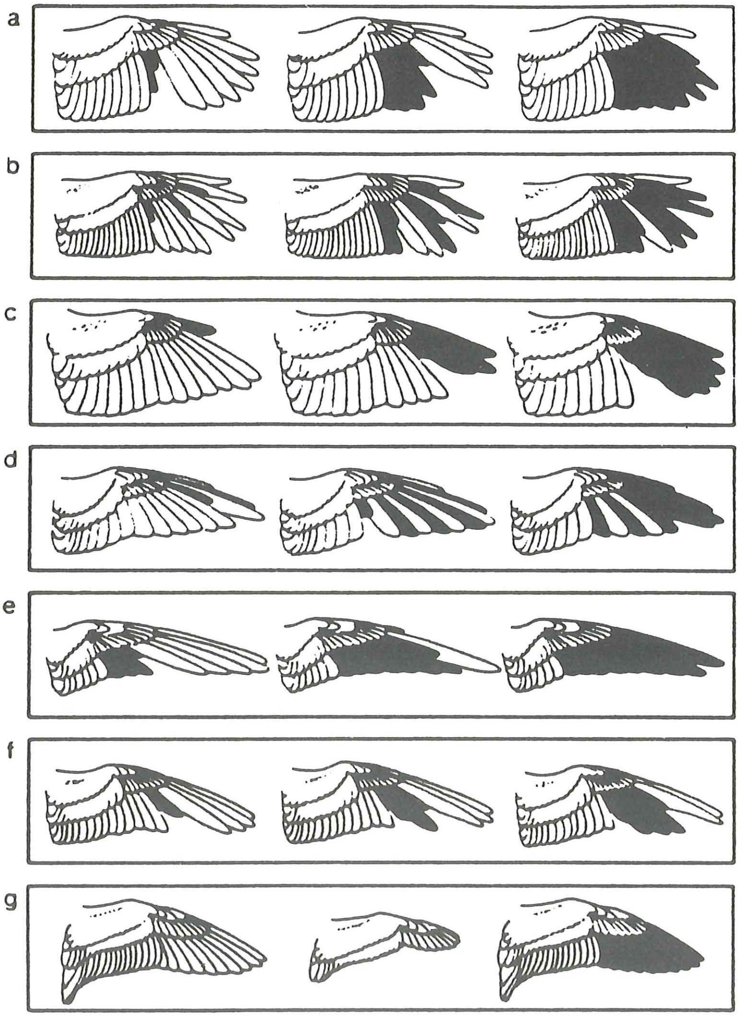


Figure 1. Patterns of primary moult in flying bird species. Of each pattern, three stages are shown (newly grown feathers black, old white). From Noordhuis 1989.
(a) Descendant (b) Serial (c) Ascendant (d) Alternating ascendant (e) Convergent (f) Divergent (g) Simultaneous.

Olika ruggningsföljder hos fåglar. För varje variant visas tre olika stadier (nyruggade fjädrar svarta, äldre fjädrar vita). Från Noordhuis 1989.

ments in order to extract essential amino acids for feather production (King 1980). Certain pigmentary colours, like carotenoids, cannot be synthesised by birds and must be obtained from the food (Ginn & Melville 1983). Ginn & Melville give three reasons why moulting birds need extra energy:

1. Energy is required to produce replacement plumage.
2. Extra energy is required to regulate body temperature when feather insulation is reduced.
3. Extra energy is required when gaps in the wing caused by dropped/growing feathers result in less efficient flight.

Deteriorated gliding performance in a wing-moulting Harris's Hawk *Parabuteo unicinctus* has been demonstrated by Tucker (1991). Although some workers have been able to correlate metabolisable energy with moult intensity, others have failed to do so (King 1980). Nowadays most authors seem to agree that moult is costly to the bird. One important factor is the speed of moult. Resident birds normally have a more prolonged moult than migrants and thus use less energy per time unit (Newton 1968a, Snow 1969).

Another type of cost connected to moult is a higher risk of predation due to lower mobility. Increased mortality during moult has been recorded in Reed Bunting *Emberiza schoeniclus* and in late-moulting Bullfinches *Pyrrhula pyrrhula* (Haukioja 1969, Newton 1966).

Sequence of moult

The moult of the remiges (primaries and secondaries) and rectrices (tail feathers) starts at certain centres, loci, and proceeds according to a regular pattern (Stresemann & Stresemann 1966, with historical references). Odd feathers lost accidentally can sometimes be replaced directly but are later shed in the normal pattern. Different sequences of primary moult are shown in Fig. 1, taken from Noordhuis (1989). Most of these were originally described by Stresemann & Stresemann (1966). Patterns of moult are now believed to be highly adaptive. Flight-feathers will be replaced in a sequence that gives the growing feathers maximal protection and affects the power of flight as little as possible (Noordhuis 1989). The most widespread pattern is primaries being replaced in a descendant way, starting with the innermost one (Fig. 1:a), while the secondaries are shed ascendantly, from the carpal joint towards the body. The rectrices are moulted from the centre outwards, i. e. centrifugally. This type of moult is believed to represent the original one since it occurs in a number of orders which are distantly related and differ in habitat requirements as well as in manner of flight (Stresemann 1967). Stresemann believed that this deep-rooted pattern has later been modified in various ways. The rate of moult may be accelerated to a wholly synchronous loss of flight-feathers (Fig. 1:g) or slowed down to such a degree that it takes the distal juvenile primaries several years to be replaced by the next feather generation. In the latter case, another descending moult cycle will start (with the innermost primary), while the preceding one is still on the move in the outer primaries (Fig. 1:b). Ascendant moult of the primaries (Fig. 1:c) is rare and probably of rather recent origin (Stresemann 1967). Descendant replacement is most likely the easiest way to prevent a growing primary from being bent upward by lift forces during flight (Noordhuis 1989). In strictly ascendantly moulting species a shed primary will leave the still growing fresh primary underneath unprotected. This problem can be solved by moulting odd and even primaries in separate series as occurs in the partly alternating ascendant moult of cuckoos and parrots (Fig. 1:d). Secondaries are believed to be less affected by aerodynamic forces, due to their smaller size and denser spacing (Noordhuis 1989).

Moult strategies

After a varying number of moults from juvenile plumage a bird attains a full adult plumage. This often coincides with sexual maturity which varies from an age of half a year in many passerines up to 5–6 years in some albatrosses and eagles. From then on the changing of plumages normally follows a fixed annual cycle. Shorter cycles are however found in certain tropical and oceanic species. In the tropics moult is usually more constant within a population, while the breeding varies more e. g. due to differences in the amount of rain. Birds of different species display a great variety of patterns in their annual moult cycle, both in timing and sequence in which the feathers are replaced (Stresemann & Stresemann 1966, Palmer 1972, Ginn & Melville 1983).

A number of moult terminologies have been published (e. g. Dwight 1900, Humphrey & Parkes 1959). Here I will follow that of Cramp & Simmons (1977). They separate post-juvenile (the first more or less complete moult from juvenile plumage), post-breeding (partial or complete) and pre-breeding (partial or complete) moults. Moults fall into two broad categories: complete moult in which all the plumage is replaced, and partial moult. Although species like Ptarmigan *Lagopus mutus* and Willow Grouse *L. lagopus* may have four partial feather changes annually (Salomonsen 1939, Palmer 1972) it is normally sufficient to separate two annual moults in adult birds. The remiges are usually exchanged once a year but some passerines shed them twice annually.

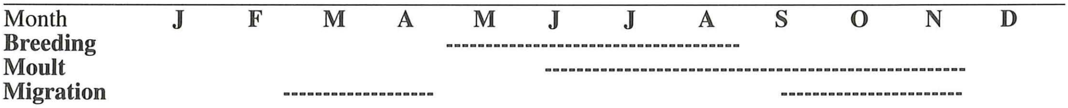
Stresemann & Stresemann (1966) listed six different moult strategies for long-distance migrants:

(1) Moult during breeding.
(2) Moult before autumn migration (summer moult).
(3) Moult after autumn migration (winter moult).
(4) Moult both before and after autumn migration.
(5) Serial moult (periodic stepwise moult).
(6) Suspended moult.

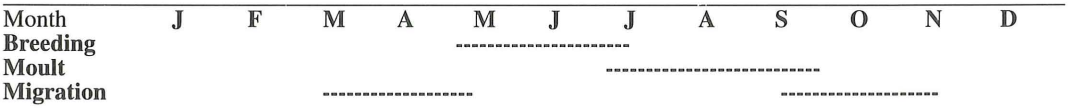
These will be discussed below together with the split moult strategy first described by Hasselquist et al. (1988). Fig. 2 shows examples of the timing of moult during the annual cycle in relation to breeding and migration for the seven moult strategies. The figure presents average duration of the three different activities in populations from Western Europe, and the overlap between these activities is normally smaller in individual birds.

Moult during breeding

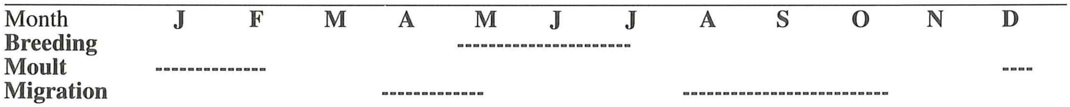
In temperate regions moult and breeding normally do not overlap significantly (Ginn & Melville 1983).



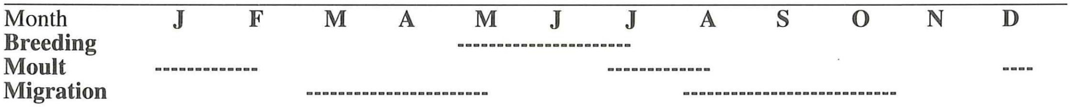
I. Moult during the breeding cycle: Crag Martin *Ptyonoprogne rupestris*
Ruggning under häckningen: klippsvala



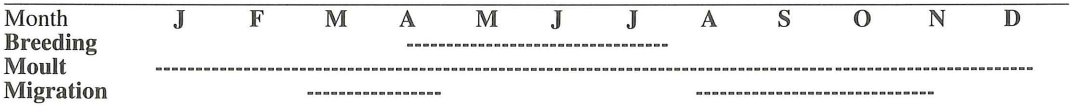
II. Moult before autumn migration: Chiffchaff *Phylloscopus collybita*
Ruggning före höstflyttningen: gransångare



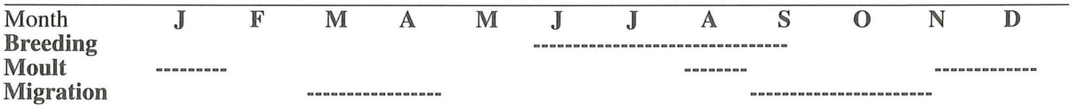
III. Moult after autumn migration: Wood Warbler *P. sibilatrix*
Ruggning efter höstflyttningen: grönsångare



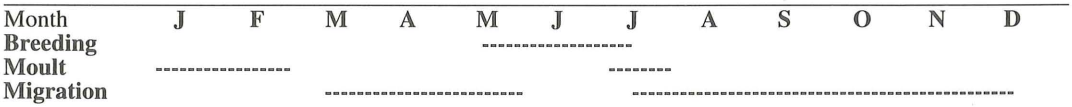
IV. Moult both before and after autumn migration: Willow Warbler *P. trochilus*
Ruggning både före och efter höstflyttningen: lövsångare



V. Serial moult: Osprey *Pandion haliaetus*
Stegvis ruggning: fiskgjuse



VI. Suspended moult: Turtle Dove *Streptopelia turtur*
Uppskjuten ruggning: turturduva



VII. Split moult: Barred Warbler *Sylvia nisoria*
Delad ruggning: höksångare

Figure 2. The timing of breeding, moult and migration within the annual cycle in seven species with different moult strategies. The overlap between the different activities may be smaller in individual birds (data primarily from Cramp & Simmons 1980, Cramp 1985, 1988, 1992).

Den årsmässiga utsträckningen av häckning, ruggning och flyttning hos sju arter med olika ruggningsstrategier. Överlappningen av de olika aktiviteterna är oftast mindre hos en enskild individ (efter Cramp & Simmons 1980, Cramp 1985, 1988, 1992).

It is however not uncommon for immature non-breeders to start moult when their conspecifics have just begun to breed. Some Holarctic large-sized passerines like Nutcrackers *Nucifraga* and Raven *Corvus corax* start moulting the primaries during egg-laying or incubation and replace the greater part of the plumage before their young become independent. Such an early start of moult in passerines seems to be connected with large body size and long primaries (Stresemann 1967). If these species had to delay the change of feathers until the end of the breeding period, food shortage would be likely to occur during the moult. It is also noteworthy that these species normally are residents.

It seems to be rare for migrating passerines to start moult during breeding. One notable exception is the Crag Martin *Ptyonoprogne rupestris* which begins to replace the wing quills while rearing the young (Elkins & Etheridge 1974, 1977). This species often finishes moult on the breeding grounds. It migrates south later than other swallows and winters further to the north, around the Mediterranean (Cramp 1985). Here the food conditions may not be adequate for a winter moult. Another aerial species, the Alpine Swift *Apus melba*, breeds in the same habitats as the Crag Martin but winters south of the Sahara. It generally changes a number of primaries on the breeding grounds before the relatively late autumn migration and completes moult during winter in Africa (Elkins & Etheridge 1977, Cramp 1985).

In general, breeding and moult tend to overlap more with increasing latitude (Dolnik & Blyumental 1967, Lundberg & Eriksson 1984). A number of passerines commence moult during the later stages of breeding. An early start in resident Willow Tits *Parus montanus* in northern Finland was explained by a need of time later in autumn to hoard enough food for the winter (Orell & Ojanen 1980). Both male and female Yellow Warblers *Dendroica petechia* in Ontario, Canada started remigial moult while still caring for their fledged young (Rimmer 1988). Depletion of insect food and deteriorating weather are believed to have selected for a rapid intensive moult of 35–45 days in southern Canada (Rimmer 1988). In White-crowned Sparrows *Zonotrichia leucophrys* breeding in the mountains of California, cessation of reproduction was followed more closely by onset of moult as the season progressed. In those birds that nested latest moult sometimes began when they still had eggs (Morton & Morton 1990). In Willow Warblers *Phylloscopus trochilus* there is an increased constraint on the timing of breeding and of post-breeding moult events at higher latitudes, leading to overlap between them in the northernmost part of the European range (Underhill et al. 1992). Male Willow Warblers participate much less than females in the raising of the young and start moulting approximately 14 days before the females (Tiainen 1981). Furthermore, in northern Sweden, female Willow Warblers with small broods began their moult earlier than females with large broods (Bensch et al. 1985). Especially late-breeding individuals of some migratory passerines may change one or a few primaries before a second breeding attempt (Harper 1984). Since this appears to be irregular it probably represents behavioural plasticity.

An overlap of moult with breeding is more common in non-passerines that often require longer time to exchange the remiges. Because of the short summer, all non-migratory petrels of the Antarctic region are forced to renew their entire plumage during breeding (Stresemann 1967). Even more extreme are the Penguins *Spenisciformes* moulting completely while incubating (Croxall 1982). In the Arctic, the Glaucous Gull *Larus hyperboreus* breeding in Iceland and Alaska starts moulting during the incubation period, while the Ivory Gull *Pagophila eburnea* begins moulting in March or April and has renewed many, if not all, of its primaries before the onset of breeding towards the end of June or the beginning of July (Stresemann 1963). Wood Pigeons *Columba palumbus* in Great Britain normally have only one primary growing at the time. The moult takes 8–9 months and covers most of the breeding (Boddy 1981).

A special adaptation in order to complete moult while tending the young is the simultaneous shedding of the flight feathers in swans and geese, rendering them flightless for a period. This has also been demonstrated in a number of other species (see below).

Most of the raptors breeding in northern Europe start to moult the primaries in connection with the breeding (Cramp & Simmons 1980, Forsman 1984). Usually the female sheds a few primaries during incubation when the male brings food to the nest. The male normally starts to moult a few weeks later. In larger species with serial moult, like the Osprey *Pandion haliaetus*, 2–4 moult waves may occur simultaneously in the primaries. Although most feathers are shed on the wintering grounds, moulting to a lesser extent also occurs during breeding (Prevost 1983).

In the tropics, temperatures are high and the daylength more uniform throughout the year, causing less limitations for moulting. There is however often a marked difference in available food between dry and wet seasons. Normally moult occurs outside the breeding season but partial overlap between breeding and moult is more common than in temperate regions (Ward 1969, Stiles 1980). Since most tropical species do not spend a long period on migration every year, there is more time available for the feather change, and moult is generally more prolonged in the tropics. Also due to a prolonged period of parental care in the post-fledging period of some species adults may start wing moult whilst still feeding young. While the timing of moult remains fairly constant, that of breeding may vary with rainfall. This causes a rather high degree of overlap between breeding and moult in certain years (Payne 1972). The Mousebirds *Colliidae* are peculiar in having a continuous moult with no break either for breeding or during the dry season (Payne 1972). In a lowland rain forest in Costa Rica the two most common understorey frugivores moulted when fruit was most abundant and bred when fruit was relatively scarce (Levey 1988). Levey suggests that insect abundance may be more important than fruit abundance in determining breeding cycles in these birds. In the tropical oceans conditions are unusually stable and some seabirds have an annual cycle of less than one year. For instance, Sooty Terns *Sterna fuscata* on Ascension Island breed at intervals of 41 to 51 weeks (Ginn & Melville 1983). The moult normally occupies the non-breeding part of the year but, for instance, the Black Noddy *Anous tenuirostris* may start breeding well before the end of the moult (Ashmole 1962).

Moult before autumn migration

It is always an advantage to migrate with new flight feathers. However, large birds do not have time to complete wing moult before autumn migration. This is especially true in tropical migrants leaving early. Large raptors may shed a number of primaries on the breeding grounds, suspend the moult and then complete it in the winter quarters (Cramp & Simmons 1980, Forsman 1984). Short-distance migrants that leave later in autumn have more time available for moult and for instance the Sparrow Hawk *Accipiter nisus* completes moult before migration (Newton & Marquiss 1982, Newton 1986). The American Woodcock *Philohela minor* completes moult in June–October and is not assumed to be physiologically ready for migration until the middle of October (Owen & Krohn 1973).

Passerines moult faster than most larger birds and thus often complete moult before autumn migration. The different moult strategies appear to depend on the distance between the breeding and wintering areas (Ginn & Melville 1983). Most short-distance migrants moult before and most long-distance migrants after autumn migration. However, a complete summer moult is also found in some tropical migrants, e. g. Yellow Wagtail *Motacilla flava*, Nightingales *Luscinia sp.* and Redstart *Phoenicurus phoenicurus* (Svensson 1992). Most European *Sylvia* warblers wintering in the Mediterranean region, moult on the breeding grounds, and most *Locustella, Acrocephalus* and *Hippolais* warblers, wintering south of the Sahara, delay moult until reaching the winter quarters (Ginn & Melville 1983). The Chiffchaff *Phylloscopus collybita,* a short-distance migrant, has one moult on the breeding grounds, whereas the closely related Willow Warbler has two complete moults, one after breeding and one in tropical Africa. Since the Willow Warbler generally migrates much further its plumage may not be sufficiently durable to last for two full migrations. However, other long-distance migrants within the genus, the Arctic Warbler *P. borealis* and Greenish Warbler *P. trochiloides*, have only one complete moult in the winter quarters (Cramp 1992). The further north a species breeds, the shorter time is available for moult before autumn migration.

Though less well studied, migrants within the tropics usually seem to moult in the breeding area. An exception is the Violet-backed Starling *Cinnyricinclus leucogaster* migrating within Africa. Different populations have separate moult strategies in relation to migration. Some do not migrate until after a complete moult, while others only change the remiges and rectrices before migration and others still migrate with only half the number of primaries new (Traylor 1971,1973).

Moult after autumn migration

This strategy is adopted by a large number of long-distance migrants, passerines as well as non-passerines. It has not been documented in short-distance migrants. Pearson (1973) suggested that birds gain two advantages from delaying wing moult until arrival in the tropics. Firstly, the feathers will be fresh for the spring migration, which tends to be more rapid and demanding than the autumn journey. Secondly, more time is available in the winter quarters than the few weeks between end of breeding and start of migration. Furthermore moult in a tropical climate may fascilitate heat dissipation (Moreau 1972). Many species leave their northerly breeding grounds long before the food resources are depleted. It may be of importance to leave early and migrate fast in order to secure a good winter territory, allowing plenty of time for moult and formation of fat reserves before spring migration and breeding. Alerstam & Högstedt (1982) suggested that moult may be delayed in species which defend territories in the winter quarters. As an example, Greenish Warblers defend a territory in winter and delay their complete moult until before the northward migration in spring (Price 1981).

Generally, moult is more prolonged in tropical than in temperate regions. This is normally explained by a longer period of suitable temperature and food conditions. However, Bensch et al. (1991) found that seven species of warblers wintering in Ghana, West Africa moulted unexpectedly fast compared to warblers moulting in Europe. This was explained by a need to complete the moult before an assumed decline of invertebrates through the dry season, starting in November.

There are also species migrating from the Southern to the Northern Hemisphere to moult. Great and Sooty Shearwaters *Puffinus gravis* and *P. griseus* breed in the South Atlantic Ocean during the southern summer. They leave their fat young in the nests and migrate across the equator to winter and moult in the northern Atlantic. In the Pacific the same strategy is adopted by Short-tailed Shearwater *P. tenuirostris*, while Manx Shearwater *P. puffinus* breeds in the northern and moults in the southern Atlantic. Similar long-distance migrations are carried out by a number of other seabirds, such as skuas, gulls and terns moulting mainly within their winter ranges (Alerstam 1990).

Some species stop to moult, wholly or partly, in an area of plentiful food between summer and winter quarters. This strategy is adopted by a number of shorebirds like Dunlin *Calidris alpina* (Hardy & Minton 1980), Green Sandpiper *Tringa ochropus* (Kittle 1975), Grey Plover *Pluvialis squatarola* (Branson & Minton 1976) and Common Snipe *Gallinago gallinago* (Muenster 1975). It is also found in the North American passerine Lazuli Bunting *Passerina cyanea.* This species interrupts the migration in the southwestern United States where most of the post-breeding moult is completed before the birds continue to the wintering grounds in Mexico (Young 1991). The first part of the flight in these cases is functionally a moult migration (see below).

Moult both before and after autumn migration

Many species may change a few body feathers on the breeding grounds even though the main moult occurs in the winter quarters. It is however quite rare to accomplish two complete moults, including all the primaries, each year, one before and one after the autumn migration (Prys-Jones 1991). This requires a rather rapid moult and is only known from a few passerines.

The Ashy Minivet *Pericrocotus divaricatus* breeds in Japan and southeasternmost Russia and winters in the Philippine Islands and Indonesia, being the most migratory member of its family. It has a complete moult after breeding from July till the middle of September, and another complete moult on the winter grounds between the middle of December and March (Stresemann & Stresemann 1972). The summer moult is faster than the one in winter. Both autumn and spring migration take place soon after the moult is completed. A similar moult system has also been demonstrated in the Willow Warbler (Ticehurst 1938, Underhill et al. 1992, detailes given below) and in two Asiatic long-distance migrants: Brown Shrike *Lanius cristatus* and Tiger Shrike *L. tigrinus* (Stresemann & Stresemann 1971).

In North America, the only long-distance migrant for which two complete moults have been demonstrated is the Bobolink *Dolichonyx oryzivorus* (Pyle et al. 1987). However, it seems that a short-distance migrant, the Marsh Wren *Cistothorus palustris* may sometimes have the same moult system (Kale 1966, Pyle et al. 1987). In South America the widespread Rufous-collared Sparrow *Zonotrichia capensis* shows two complete annual moults only in resident equatorial populations, while a number of other populations only have the post-breeding moult complete (King 1976).

The seven species mentioned above represent six separate families, long-distance migrants as well as residents, insectivores and omnivores, and both one and two breeding cycles per year. All the Asiatic species are, however, long-distance migrants with fairly similar summer and winter plumages. It is difficult to understand why the pattern has evolved in these species and not in a number of closely related ones. For example, the Brown Shrike was earlier considered conspecific with Red-backed Shrike *Lanius collurio* and Isabelline Shrike *L. isabellinus.* Despite this both the latter only change the primaries once a year (Prys-Jones 1991). According to Neufeldt (1981), however, there is some variation in the autumn moult between different subspecies of

Brown Shrike so that it is not always completed before migration.

Further research will undoubtedly reveal more species with two annual complete moult cycles, but this strategy will still remain very unusual. Several species may change some remiges more than once annually. The River Warbler *Locustella fluviatilis* has a complete moult in Southeast Africa in January–March. In addition a majority also change the outer 1–5 primaries in stop-over areas in Northeast Africa during September–November (Pearson & Backhurst 1983), i. e. only a few months before the complete moult.

Serial (periodic stepwise) moult

In general, large birds have larger wing load and thus must replace their flight feathers more slowly in order to retain flight ability. This has resulted in a serial moult of the remiges in some species. In the first post-juvenile moult a wave starting from the innermost primary stops before it has reached the outermost. The following summer a new moult wave starts from the innermost primary but at the same time the old wave resumes from the point of interruption. The bird then has two separate but simultaneous moult waves in the outer part of the wing. This is the basis of the serial moult (Stresemann & Stresemann 1966, Edelstam 1969). The strategy is found in a number of non-passerines like albatrosses, cormorants, most large raptors and large owls. In Buzzards of the genus *Buteo* 1–3 moult waves can be found at the same time, but asymmetry between the wings may occur (Forsman 1984). Larger raptors usually only change a few primaries each year. For example, in the first post-juvenile moult the four innermost primaries may be changed, in the next year primaries 5–7 and in the third year primaries 8–9. In this third moult a new wave may also start from the innermost primary. The serial moult allows an adult eagle to change a larger number of primaries at a time, with little impairment of flight performance. If the primaries instead were changed at one place in the hand the bird wouldn't have time to change enough feathers during the moult period.

The secondaries are changed from three or four different loci and single feathers may last for one, two or three moult periods. Adult Golden Eagles *Aquila chrysaetos* normally change all their remiges in a two-year period (Forsman 1984). An extreme case of stepwise moult is found in the Osprey, being in active moult for most of the year (Prevost 1982, 1983). As in other species moult is however usually suspended during migration.

Serial moult is also found in the albatrosses, where some species only breed every second year. It takes a young Black-browed Albatross *Diomedea melanophris* four years to replace all the remiges the first time. Adults of both this species and the Grey-headed Albatross *D. chrysostoma* moult primaries biennially (Prince et al. 1993). Successful Grey-headed Albatrosses, which breed again 16 months later, moult their three innermost primaries after breeding in the remainder of the current year and, after a period when moult is interrupted, renew the remaining primaries the following year. The moult rate in albatrosses seems not to be linked to the length of the interval between breeding attempts. Differences between species are better explained by breeding latitude, with tropical albatrosses moulting twice as fast as sub-Antarctic species, possibly reflecting food availability outside the breeding season (Prince et al. 1993).

Suspended moult

If conditions do not allow a complete moult on the breeding grounds a bird may change part of the flight-feathers there, interrupt the moult and later finish it in the wintering area. This means that growing feathers continue to grow to full length but no more feathers are shed. It is generally thought that birds suspend moult for the following reasons: (1) when there is strong selection to migrate quickly from the area and therefore insufficient time to undergo wing moult (Mead & Whatmough 1976) or (2) when food supply is insufficient to provide enough protein to complete the moult in a single sequence (King 1972, Mewaldt & King 1977).

Norman (1991) stresses the importance of separating arrested (restoration at the point of origin) from suspended (re-start from the point of suspension) moult. However, it is generally difficult to clearly distinguish these two patterns. The most common strategy seems to be to resume moult at the point of suspension and I will use the expression suspended moult onwards.

Although suspension most often occurs in connection with migration it may also be associated with breeding in resident birds. For example Galapagos Finches *Geospiza sp.* stop moulting if the unpredictable autumn rainfall is heavy enough to allow them to start breeding (Snow 1966). Several tropical species with prolonged moult periods routinely suspend their moult while breeding (Snow & Snow

1964). Birds seem to be able to control the suspension of moult at least to some degree. Kasparek (1979) recorded a male Tree Sparrow *Passer montanus* suspending his moult while making a late breeding attempt. A male Robin *Erithacus rubecula* having lost his first mate started primary moult. It then suspended moult after changing three primaries when making a breeding attempt with a new female, only to resume it when the breeding failed (Harper 1984). Fan-tailed Warblers *Cisticola juncidis* may suspend the post-juvenile moult to make a breeding attempt in their first autumn (Gauci & Sultana 1981). However, suspended wing moult in non-migratory birds of the temperate zone seems to be rare. Many female raptors start to moult during incubation and later suspend it when feeding large young (Newton 1979).

Among migrants suspension is most common in species migrating long distances. In raptors the majority of tropical migrants breeding in the Northern Hemisphere shed only a few primaries before autumn migration, while most of the wing moult takes place in the tropics (Cramp & Simmons 1980, Palmer 1988). Species belonging to this category include Honey Buzzard *Pernis apivorus*, Montagu's Harrier *Circus pygargus* and Osprey. Other non-passerines regularly suspending moult before the migration to Africa are Turtle Dove *Streptopelia turtur*, Scop's Owl *Otus scops*, Red-necked Nightjar *Caprimulgus ruficollis* and Bee-eater *Merops apiaster* (Mead & Watmough 1976, Swann & Baillie 1979). Also several species of waders may interrupt moult on their long autumn migration. The considerable variation in the length of the arctic summer may lead to yearly variation in the proportion undergoing suspended moult in some species. Interrupted moult may also allow the full utilization of suitable feeding areas between breeding and wintering grounds (Pienkowski et al. 1976).

Suspended moult has also been found in a number of European passerines such as Savi's Warbler *Locustella luscinoides* (Thomas 1977), Whitethroat *Sylvia communis* (Pimm 1973), Woodchat Shrike *Lanius senator* (Ullrich 1974) and Spotted Flycatcher *Muscicapa striata* (Hansen 1985). In Sudan it was found in migrant Pale Rock Sparrows *Petronia brachydactyla* from Asia (Nikolaus & Pearson 1991) and in North America it has been demonstrated in Rose-breasted Grosbeak *Pheucticus ludovicianus* (Cannell et al. 1983). In many of these species only a certain fraction of the population seems to suspend moult.

Adult Orphean Warblers *Sylvia hortensis* caught during breeding and kept in captivity, all suspended their moult in the first autumn. In the second experimental year when these birds were prevented from breeding they moulted several weeks earlier and completed their moult before the migratory period (Berthold & Querner 1983). This demonstrates that the process can be adapted on a facultative basis to various experienced conditions.

Split moult

A distinct variety of suspension is when the primaries are moulted on the breeding grounds in summer, while the secondaries are shed in the tropics during winter. This was first demonstrated in the Barred Warbler *Sylvia nisoria* (Hasselquist et al. 1988). In this species the juveniles moult their secondaries in Africa initiating a seasonally divided flight feather moult already in the first winter. This is interpreted by the authors as a preparation for an early departure from the breeding grounds the following summer. After breeding, Barred Warblers normally change all their primaries and tertials but a very limited number of other secondaries. They migrate south comparatively early and spend a large part of the autumn in Northeast Africa. In late autumn they continue migration to south of the equator in Kenya where the secondaries are changed almost six months later than the primaries (Pearson et al. 1988). Ringing in Sudan has demonstrated a similar strategy in four other tropical migrants (Nikolaus & Pearson 1991), viz. Ortolan Bunting *Emberiza hortulana*, Orphean Warbler, Masked Shrike *Lanius nubicus* and Woodchat Shrike, all of which winter in the northern tropics.

Norman (1991) questioned the split moult strategy of African migrants, arguing that suspended secondary moult is normally induced by time stress rather than being an endogenously controlled strategy. The stress explanation however applies only to species normally undergoing a complete post-breeding moult where occasional individuals suspend secondary moult (Hedenström et al. 1992).

Duration of the moult

While large birds may take several years to renew the whole plumage, small passerines may complete moult in not much more than a month (Ginn & Melville 1983). Generally resident birds use longer time than migrants (Berthold 1984). A new feather is usually not full-grown before the next in sequence is dropped so that there are feathers of various lengths in a "growth wave". The number of feathers growing at any time depends on the rate of growth of the individual feathers, the length of the feathers and the length of interval between the start of growth of adjacent feathers. Large birds need longer time because they have longer feathers but also because the feathers tend to be replaced in a less rapid sequence. Feather growth rate in Barnacle Geese *Branta leucopsis* was similar in all birds irrespective of age and sex (Owen & Ogilvie 1979). Pienkowki et al. (1976) studying shorebirds in Morocco found that differences between species in the rate of moulting were related to differences in the rate of feather growth. Differences between individuals of the same species depended mainly on the number of feathers growing simultaneously, but feather growth rate also varied between different populations within the same species. In finches individual feather growth rate may vary between different species but is relatively constant within a species. Thus, differences in the overall rate of moult within a species depends primarily on the number of feathers growing at the same time (Evans 1966, Newton 1968b). In captive Bullfinches, Newton (1967) found that the outer primaries grew slower than the rest. In White-crowned Sparrows, females starting to moult with young in the nest grew fewer primaries simultaneously than other females during the second week of moult. When the fledglings had become independent growth rates of the primaries was accelerated (Morton & Morton 1990).

The duration of moult is clearly affected by latitude. Several widespread species show a clinal variation in this respect. Willow Warblers of the nominate subspecies spend an average 36.5 days in post-breeding moult while the more northerly *P. t. acredula* in general use 38.3 days (Underhill et al. 1992). The moult in the nominate subspecies starts about 3.5 days later for each degree of latitude northwards and *acredula* is about 10 days later than the most northerly *trochilus* studied. Southward migration commences as soon as the post-breeding moult is complete. Thus there is an increasing constraint on the timing of breeding and moult at higher latitudes leading to an overlap between them. The duration of the pre-breeding moult is longer than that of post-breeding moult and it is completed shortly prior to the northward migration (Underhill et al. 1992).

In the White-crowned Sparrow, the duration of moult decreases northwards by an average of 2.6 days per degree of latitude within the breeding range (Mewaldt & King 1978).The overlap of breeding and moult in individuals increases with latitude and elevation (King 1979). A similar decrease in the duration of moult along a latitudinal gradient has been demonstrated in the Chaffinch *Fringilla coelebs* (Dolnik & Blyumental 1967). Dunlins used 70 days for the primary moult in northern compared to 97 days in western Alaska (Holmes 1971). One of the fastest primary moults recorded in any species, only 28 days, occurs in Snow Buntings *Plectrophenax nivalis* in Greenland (Ginn & Melville 1983). Gwinner & Schwabl-Brenzinger (1982) have shown that endogenous circannual rhythms are involved in the organisation of the annual cycles among related species.

Generally, resident populations use longer time for moult compared to migratory ones. Resident Starlings *Sturnus vulgaris* at Andöya, Norway used about 55 days for post-juvenile moult while migrants at Umeå, Sweden finished in about 40 days (Lundberg & Eriksson 1984). Galbraith (1977) found only small differences in moult duration between migratory Pied Wagtails *Motacilla alba yarrellii* from central Scotland and a resident population in southern England. Also King (1974) found no geographical trends in the post-breeding moult duration of Rufous-collared Sparrows within Argentina. In European Swallows *Hirundo rustica*, Kasparek (1976) discovered a negative correlation between latitude of breeding range and moult. A certain proportion of Swallows breeding in the Mediterranean countries started to moult before autumn migration while hardly any birds breeding in northern Europe did so (Ginn & Melville 1983).

Flightlessness during moult

One way to reduce the duration of moult is to shed a large number of feathers at the same time. In the most extreme case, simultaneous dropping of all flight feathers renders the bird flightless for a period. Avian taxa having simultaneous moult of the remiges are listed in Table 1, based primarily on information from Stresemann & Stresemann (1966). This strategy is adopted by the majority of wildfowl. Breeding swans and geese have a complete moult while tending the young and individual birds are flightless for a period of 4–6 weeks (Ginn & Melville 1983). It is thus essential to breed in an area were the family can escape to safe areas to avoid predation. Both parents share the guarding of the young and being large birds they can scare away many potential predators. In geese, both sexes normally moult at the same time while females start ahead of males among swans. In the Mute swan *Cygnus olor*, the female

Table 1. Avian taxa having simultaneous moult of the remiges. After Jehl (1990).
Fågeltaxa med simultan ruggning av vingpennorna. Efter Jehl (1990).

Taxon	Comments
Divers *Gaviidae*	All species
Grebes *Podicipedidae*	All species except the flightless *Rollandia microptera*
Diving-Petrels *Pelecanoididae*	Probably all species
Anhingas *Anhingidae*	All species
Flamingos *Phoenicopteridae*	All as a rule
Wildfowl *Anseriformes*	All except *Anseranas*
Cranes *Gruidae*	All exept *Balearica* and *Anthropoides virgo*
Rails *Rallidae*	Most species
Heliornithidae	Sungrebe *Heliornis* only
Jacanas *Jacanidae*	All except *Jacana* and *Microparra*
Auks *Alcidae*	All exept *Aethia pusilla* and *Ae. pygmaea*
Hornbills *Bucerotidae*	Females only in all species

drops her remiges two to three weeks after the cygnets hatch but the male does not do so until the female has regained the power of flight some weeks later (Cramp & Simmons 1977). In moulting flocks of non-breeders, on the other hand, males moult before females (Mathiasson 1973).

The Common Crane *Grus grus* nests on extensive bogs and marshlands and leads a very secluded life when breeding. Adults drop all flight-feathers within two days when the young are small and are then flightless for about 5 weeks. However, the remiges may be moulted only every second year. All cranes of the genus *Grus* seem to have a simultaneous wing moult while the Demoiselle Crane *Anthropoides virgo* sheds its flight feathers irregularly over a longer period (Cramp & Simmons 1980). The difference may be caused by a higher risk of predation in this species nesting in dryer and more open habitats.

Also in the family *Rallidae* most species seem to shed their flight feathers simultaneously, as has been demonstrated in for example Common Gallinule *Gallinula chloropus* (Karhu 1973) and Water Rail *Rallus aquaticus* (De Kroon 1986). Most species complete this moult on the breeding grounds but delay it until the young are independent. In species with several clutches, like the Common Gallinule, moult may overlap with breeding (Ginn & Melville 1983). In the order Charadriiformes, simultaneous moult of remiges seems to occur only in the family Jacanidae. However Marks et al. (1990) found that 45 % of Bristle-thighed Curlews *Numenius tahitiensis* moulting on Laysan Island, Hawaii lost the ability to fly during approximately two weeks. This is a result of their wintering on islands free of predators.

Most bird species depend on flight for feeding and thus must retain enough remiges to secure their flight ability during moult. This is true in most passerines, and the only species normally being flightless during moult seems to be the Dipper *Cinclus cinclus*, dropping the five inner primaries simultaneously after breeding (Ginn & Melville 1983). However, Haukioja (1971) found that a small proportion of Bluethroats *Luscinia svecica*, Willow Warblers and Whitethroats caught during post-breeding moult in Finland were unable and/or unwilling to fly. Flightlessness depended not only on the fact that many wing feathers were lost simultaneously but also on the loss of most of the tail feathers at the same time. These species have a fairly short moult period, lasting between 35 and 50 days, probably because of the short summer season at northern latitudes (see also Snow Bunting in the previous section). The reduced manoeuvrability, rendering the bird more vulnerable to predation, leads to a more skulking behaviour. Since the ability to fly affects the probability of being caught, flightlessness is probably more common in passerines, especially in northerly regions, than can be deduced from moult card data.

Moult migration

During late spring or shortly after the breeding season large numbers of ducks and geese in the temperate zone migrate to traditional assembly areas were they congregate in large numbers and undergo a simultaneous wing moult rendering them flightless for several weeks. This phenomenon known as moult migration was first documented comprehensively by Salomonsen (1968). He defined it as "Birds moving from the breeding grounds to a special moulting area where they can rapidly replace their flight feathers at a low risk of predation before resuming their migration to the winter quarters". It differs from ordinary autumn migration because the direction is usually different and all age and sex classes may not participate. The distance to the moult area may range from a few to many hundred kilometres within the same species (Ogilvie 1978).

The numbers involved may be huge, with for example up to 200 000 Shelducks *Tadorna tadorna* gathering at the German Wadden Sea. This site may be occupied for up to four months, first by non-breeders in late spring followed by adult breeders in late summer (Salomonsen 1968, Jehl 1990). Another impressive concentration is the King Eiders *Somateria spectabilis* gathering in Disko Bay, southwest Greenland where at least 200 000 may be present in August (Alerstam 1990). As in most ducks, only males and non-breeders participate in the moult migration while the females tend the young. Females may follow when the young are independent or moult on the breeding grounds. Among geese and swans both parents remain with the young when moulting but non-breeders and birds that have failed to nest undertake moult migration in many species (Ogilvie 1978). There is large regional variation so that certain species or populations don't participate. Most of the dabbling ducks breeding in northwestern Europe show no large-scale moult migration, while more easterly populations may travel thousands of kilometres to gather in enormous numbers at moulting grounds like the Volga Delta (Alerstam 1990).

Moult migration is not restricted to Anseriformes, and Jehl (1990) has compiled data from other taxa. A very impressive gathering of Black-necked Grebes *Podiceps nigricollis*, including hundreds of thousands of individuals occurs at Mono Lake, California. Here the birds exploit a superabundant food source, Brine Shrimp *Artemia monica.* Compared with moult migration of anatids this migration is unusual because both sexes and all age groups are involved (Storer & Jehl 1985, Winkler & Cooper 1986). Also other species of grebes, like the Great Crested Grebe *P. cristatus*, have been found to set out on moult migrations but the phenomenon seems to be irregular involving mainly non-breeders (Cramp & Simmons 1977, Piersma 1988). In alcids a northward moult migration has been demonstrated in non-breeding Little Auks *Alle alle*, where the moulting localities vary between years according to ice conditions (Bradstreet 1982).

Waders do not have a synchronous wing moult but at least four species engage in post-breeding movements that combine elements of moult migration and fat accumulation at a single locality (Jehl 1990). The best example occurs in Wilson's Phalarope *Phalaropus tricolor* where several hundreds of thousands of birds gather at saline lakes in western USA. Here they replace the entire body plumage, the rectrices and several primaries before continuing to winter quarters in South America, where the moult is completed. Females precede males by two weeks (Jehl 1987, 1988). Another well studied species with similar moult concentrations is the Lapwing *Vanellus vanellus* (Imboden 1974).

The main factors characterising a moult area seem to be plentiful food and low predation risk. Sometimes different species may compete for food. Madsen & Mortensen (1987) found that moulting Barnacle Geese in eastern Greenland had to shift to less nutritious food and increase their foraging time when together with Pink-footed Geese *Anser brachyrhynchus.* The moult of Grey-lag Geese *A. anser* at Oostvaardersplassen, Netherlands coincides with a period of fast growth in the main food, Reed *Phragmites australis.* During the moult quality as well as quantity of food decreases. As a consequence, late arriving geese chose not to moult here but returned to Scandinavia (Loonen et al. 1991). Although the snow-free period in high arctic areas is too short to permit breeding in most species of geese, the food resources can be utilised by moulting non-breeders. Thus a number of goose species have a northbound moult migration in summer (Salomonsen 1968). These birds also avoid food competition on the breeding grounds. Ebbinge & Ebbinge-Dallmeijer (1977) suggested that, by moulting in the constant light of the far north, the geese are able to detect predators in time to escape by swimming out to sea. The need to avoid potentially dangerous dark periods may thus be another factor causing northward moult migration in geese.

A comparative study of moult in three different groups

Raptors

While small and medium sized raptors normally change the whole plumage annually, some of the large eagles and vultures may shed their wing quills only every second to fourth year (Cramp & Simmons 1980, Forsman 1984). There is however large individual variation, which may depend on for instance varying food conditions. Thus Forsman (1984) found that Common *Buteo buteo* and Rough-legged *B. lagopus* Buzzards changed fewer remiges in years of food scarcity.

In most raptors moult starts when the birds are still breeding. Very few species seem normally to postpone it until after the young are fledged. Due to different parental roles the sexes normally show different timing of the moult. The female, responsible for incubation and guarding the small young, stays close to the nest and starts to moult during this time. The male starts later since he needs to retain flight ability to feed the female and the small young. In *Accipiter* hawks, the female may be almost flightless during incubation due to intense moult of primaries, while the male changes his flight feathers at a slower and more uniform rate (Newton & Marquiss 1982). Sylvén (1982) suggested that the earlier moult of female Common Buzzards, as compared with males, enables them to accumulate more fat before the winter. This might contribute to the higher survival rate of females in this species. In the Honey Buzzard where both sexes share incubation there is no difference in the timing of moult (Forsman 1984). Most species slow down the pace of or suspend moult during the most intensive phase of breeding, that with large young in the nest.

Among migrating European raptors there are basically three moult strategies (Newton 1979, Forsman 1984). Short-distance migrants like Buzzards *Buteo* and Hawks *Accipiter* normally complete the moult on the breeding grounds before the comparatively late migration towards the south. Most of these birds normally spend the winter well north of the Mediterranean. Medium-distance migrants, wintering in southern Europe or northern Africa, change most of the remiges before migration but moult the rest on the winter grounds. They include Marsh Harrier *Circus aeruginosus*, Red Kite *Milvus milvus* and Merlin *Falco columbarius,* often migrating with large visible gaps in the wings (pers. observ.). Long-distance migrants, leaving early and wintering in the tropics, normally only have time to change a few primaries before autumn departure. They suspend moult during migration and most of the moult takes place in tropical Africa. Representatives of this group include Honey Buzzard and Hobby *Falco subbuteo,* which feed primarily on invertebrates. Table 2 classifies European raptors according to migration/moult strategy. A similar pattern is also found in the New World with long-distance migrants breeding in North America and wintering in South America, feeding primarily on insects. Representatives include Mississippi Kite

Table 2. Moult strategies of European raptors (after Cramp & Simmons 1980, Forsman 1984).

Ruggningsstrategier hos europeiska rovfåglar (efter Cramp & Simmons 1980, Forsman 1984).

Short-distance migrants –
Most of moult on the breeding grounds
Kortflyttare –
Det mesta av ruggningen i häckningsområdet

- White-tailed Eagle *Haliaeetus albicilla*
- Goshawk *Accipiter gentilis*
- Sparrowhawk *A. nisus*
- Common Buzzard *Buteo buteo buteo*
- Rough-legged Buzzard *B. lagopus*
- Golden Eagle *Aquila chrysaetos*

Medium-distance migrants –
Moult both in summer and winter quarters
Mellandistansflyttare –
Ruggar både i sommar- och vinterkvarteren

- Red Kite *Milvus milvus*
- Marsh Harrier *Circus aeruginosus*
- Hen Harrier *C. cyaneus*
- Long-legged Buzzard *Buteo rufinus*
- Spotted Eagle *Aquila clanga*
- Kestrel *Falco tinnunculus*
- Merlin *F. columbarius*
- Saker *F. cherrug*
- Peregrine *F. peregrinus*

Long-distance migrants –
Most of moult in winter quarters
Långdistansflyttare –
Det mesta av ruggningen i vinterkvarteren

- Osprey *Pandion haliaetus*
- Honey Buzzard *Pernis apivorus*
- Black Kite *Milvus migrans*
- Egyptian Vulture *Neophron percnopterus*
- Short-toed Eagle *Circaetus gallicus*
- Montagu's Harrier *Circus pygargus*
- Levant Sparrowhawk *Accipiter brevipes*
- Common Buzzard *Buteo buteo vulpinus*
- Lesser Spotted Eagle *Aquila pomarina*
- Booted Eagle *Hieraaetus pennatus*
- Lesser Kestrel *Falco naumanni*
- Red-footed Falcon *F. vespertinus*
- Hobby *F. subbuteo*
- Eleonora's Falcon *F. eleonorae*

Ictinia mississippiensis, Broad-winged Hawk *Buteo platypterus* and Swainson's Hawk *B. swainsoni,* (Newton 1979).

Even within species different populations may have separate moult strategies. Many raptors are leap-frog migrants, where birds breeding furthest to the north have the longest migration, wintering south of other populations. A good example is the Common Buzzard. The nominate race, breeding in western Europe, is a resident or short-distance migrant moulting before migration. The more easterly subspecies *B. b. vulpinus,* being a long-distance migrant, only has time to change a few primaries before migration to southern Africa where the moult is not completed until late winter (Forsman 1984). In the Peregrine Falcon *Falco peregrinus* southerly populations finish the moult in October–November while arctic populations suspend and complete moult in the tropics (Stresemann & Stresemann 1966).

Thus in raptors migration distance seems to affect the "choice" of moult strategy in a similar way as among passerines (Ginn & Melville 1983).

Waders

Generally, migrant wader populations have a more rapid moult than resident ones. Normally, waders spread their moult over as long a period as possible, compatible with other energy-demanding activities such as breeding and migration. In the Northern Hemisphere moult starts as early as possible in summer or autumn to be completed while food availability is likely to be high, daylight period long and temperatures high (Pienkowski et al. 1976). Non-breeding birds which remain in the winter quarters moult earlier and more slowly during the summer. Adult birds spending the northern winter in the Southern Hemisphere also have a long and slow moult in the favourable summer conditions there. Interspecific variation in moult duration is due largely to differences in the growth rate of wing quills (Pienkowski et al. 1976).

Few long-distance migrants among the waders of the Northern Hemisphere have time to complete the wing moult on the breeding grounds. Among Palearctic species wintering in Kenya only the Marsh Sandpiper *Tringa stagnatilis*, with a comparatively southerly breeding range, normally has completed moult before arrival in the tropical winter destinations (Pearson 1981). In the Ruff *Philomachus pugnax*, males start to moult while females incubate and often have time to change all flight feathers, as observed in Germany (Glutz von Blotzheim et al. 1975, Muenster 1991). Also in the Netherlands some Ruffs complete moult of the primaries and they are believed to winter there (Koopman 1986). Most Ruffs, however, only commence moult in Europe and complete it in the African winter quarters after suspension. The primary moult is faster in Europe than in East Africa (Pearson 1981, Table 3). Zdarek (1987) reports that some Green Sandpipers complete their moult of the remiges at ponds in Czechoslovakia, but the majority only change a few flight feathers before they reach the winter quarters (Cramp & Simmons 1983). Some shorebirds shed a few remiges already on the breeding grounds, while several species start to moult at stop-over sites along the migration route and later complete it in the winter quarters. Others delay the whole moult until after autumn migration (Ginn & Melville 1983, Cramp & Simmons 1983).

Generally, the duration of moult and the variation between individual birds increase with decreasing latitude. In Table 3 I have compiled data on primary moult of some widespread wader species, divided into three groups depending on the timing of moult in relation to breeding and migration. These estimates may not be comparable in every case since various methods may have been used by different workers but they clearly demonstrate the general trends. The fastest recorded moult is achieved by Purple Sandpipers *Calidris maritima* in Iceland and Sanderlings *C. alba* in the Dutch Wadden Sea, both completing primary moult in 50 days (Morrison 1976, Boere 1976). These birds have a large number of primaries growing simultaneously, rendering them almost flightless. The Purple Sandpipers in Iceland are residents but populations wintering in the Netherlands, believed to originate in arctic Canada, arrive after completion of the primary moult (Boere et al. 1984). On the other extreme, many species wintering in the tropical region spread the wing moult over a period of 3–4 months (Table 3). This is probably the best strategy as long as food conditions are relatively stable over the winter.

There may be a considerable variation in moult strategy within single species. In the Turnstone *Arenaria interpres*, the Canadian-Greenland population wintering in western Europe has approximately 45 days shorter duration of the primary moult compared to the Siberian population wintering in South Africa (Summers et al. 1989, Table 3).

The Dunlin breeds in most of the northern Holarctic. At least six subspecies have been described and the variation in primary moult is considerable. In *C. a. sakhalina* of northern Alaska the moult is com-

Table 3. Estimates of primary moult duration in Holarctic waders.
Uppskattningar av handpenneruggningens längd hos holarktiska vadare.

Species	Moult locality	Duration (days)	Source
Art	*Ruggningsplats*	*Längd*	*Källa*
Moult on or near the breeding grounds *Ruggning i eller nära häckningsområdet*			
Purple Sandpiper	Iceland	50	Morrison 1976
Dunlin	NE Siberia+Alaska	60–70	Cramp & Simmons 1983
Dunlin	Northern Alaska	70	Holmes 1971
Dunlin	Western Alaska	97	Holmes 1971
Ruff	Netherlands	72	Koopman 1986
Ruff	Germany	75	Muenster 1991
Turnstone	Iceland	70	Ginn & Melville 1983
Moult in temperate winter quarters after migration *Ruggning i tempererade övervintringsområden*			
Golden Plover	Netherlands	125	Jukema 1982
Grey Plover	England	90	Branson & Minton 1976
Knot	Netherlands	90–100	Ginn & Melville 1983
Sanderling	Netherlands	50	Boere 1976
Dunlin	England	59–89	Ginn & Melville 1983
Dunlin	Netherlands	87–94	Ginn & Melville 1983
Dunlin	Morocko	60–80	Pienkowski et al 1976
Curlew Sandpiper	Morocko	40+	Pienkowski et al 1976
Little Stint	Morocko	50–60	Pienkowski et al 1976
Redshank *T. t. robusta*	Western Europe	125	Cramp & Simmons 1983
Redshank *T. t. totanus*	North Africa	135	Cramp & Simmons 1983
Turnstone	Netherlands	70–75	Boere 1976
Turnstone	England	80	Branson et al 1979
Moult in tropical winter quarters after migration *Ruggning i tropiska övervintringsområden*			
Sanderling	South Africa	100	Cramp & Simmons 1983
Curlew Sandpiper	Mauretania	60	Wilson et al 1980
Curlew Sandpiper	South Africa	140	Elliott et al 1976
Curlew Sandpiper	Tasmania	125–130	Thomas & Dartnall 1971
Little Stint	Kenya	100–150	Pearson 1981
Little Stint	South Africa	100–115	Ginn & Melville 1983
Red-necked Stint	Tasmania	110–115	Thomas & Dartnall 1971
Ruff	Kenya	110–130	Pearson 1981
Turnstone	South Africa	110–120	Summers et al 1989

pleted in only 70 days, overlapping in part with breeding. Only 10°latitude further south, *C. a. pacifica* in western Alaska needs 97 days to change the primaries, moving to the coast when the young fledge. This difference is interpreted as an adaptation to the shorter summer at higher latitudes, governed primarily by the availability of food (Holmes 1971). It may however also be affected by the length and time of the migratory journey. The nominate race of the Dunlin, breeding in northern Scandinavia and Russia eastwards at least to the Jenisey River, normally does not moult on the breeding grounds. This is especially true in populations breeding west of the Ural Mountains, while more easterly populations may commence moult during the breeding season (Greenwood 1983). Most of the Dunlins reaching western Europe after their autumn migration perform a complete moult in the Wadden Sea or Great Britain (Boere et al. 1973, Hale 1980). However, Gromadzka (1986) found that 56 % of the Dunlins migrating through Poland had already started their wing moult. Studies of migrating birds in southern Sweden in the autumns of 1985–88 showed that between 27 and 61 % of the adult Dunlins had initiated the primary moult (Holmgren et al. 1993). The proportion was higher in second year birds compared to older birds and a greater fraction was found moulting in years when the passage occurred relatively late in the season. No large gaps in the wings, typical of birds moulting at the Wash in England, were found in Sweden. Hence birds probably adjust their moult speed to maintain the wing area as large as possible when moulting during migration (Holmgren et al. 1993). However, Dunlins moulting in Morocco and migrating shorter distances, often had large gaps in the wing (Pienkowski & Dick 1975). Dunlins of the subspecies *C. a. schinzii* breeding around the Baltic never start the moult on the breeding grounds and leave the nesting site already in June–early July to winter and moult in southwestern Europe and North Africa (Jönsson 1986). Dunlins of the races *schinzii* and *arctica* from Iceland and Greenland also pass through the British Isles early without moulting on their way to the wintering grounds (Hardy & Minton 1980).

The closely related Curlew Sandpiper *Calidris ferruginea* breeds in fairly limited regions of northern Siberia but winters over a vast area in the tropics from western Africa to Australia (Hayman et al. 1986). After breeding it performs a long and fast migration to the moulting and wintering grounds with males preceding females. In populations moulting in Morocco and Mauritania both sexes have a comparatively fast moult of 40–60 days (Table 3). The moult seems to be faster in Morocco and most of these birds later move on to winter further south (Wilson et al. 1980). On the other hand, birds wintering in South Africa and Tasmania moult there and during a much longer period (Table 3).

Most waders have a partial moult of body feathers in spring when they attain summer plumage. At Banc d'Arguin, Mauritania, adults in nearly half of the wintering species were in complete summer plumage at the end of April, but there were large differences between species in timing. This pre-breeding moult was most intensive about four weeks before the average date of spring departure. It may ultimately depend on the start of breeding and there was a positive association between late pre-breeding moult and high latitude of the midpoint of the breeding area (Zwarts et al. 1990). Curlew Sandpipers leaving South Africa or Australia in early April start the pre-breeding moult a month before their conspecifics departing from Mauritania (Elliott et al. 1976). Many waders, however, apparently suspend the body moult during migration and Bar-tailed Godwits *Limosa lapponica* were not moulting when they arrived at the Wadden Sea in spring (Zwarts et al. 1990). On this Dutch staging area moulting individuals had a more complete breeding plumage than non-moulting birds and were always heavier. Piersma & Jukema (1993) argued that due to tight time/energy schedules faced by godwits on long-distance migration, only individuals with sufficient energy reserves can afford to fully upgrade their body plumage in the spring staging areas.

To summarize, few waders moult on the breeding grounds. They either renew their feathers on stopover sites en route or on the wintering grounds. The duration of moult generally increases with falling latitudes, most likely reflecting the amount and stability of the food resources.

Warblers

Passerines moulting faster than large birds have a greater potential for variation in moult strategy. A good example is provided by the Palearctic warblers of the family *Sylviidae* . They exhibit great variation within genera and sometimes even within species. Table 4 (compiled from Ginn & Melville 1983, Cramp 1992, Svensson 1992) summarises moult strategies of migrating members in six genera.

The six members of the genus *Locustella* are all long-distance migrants which normally have a complete moult in the winter quarters in Africa or southern Asia. There may be great individual variation though, and at least Grasshopper Warbler *L. naevia*, Lanceolated Warbler *L. lanceolata* and Savi's Warbler sometimes change a few flight feathers in the breeding area. Especially the latter species often shows centrifugal moult of the primaries. Thomas (1977) suggested that this may enable Savi's Warblers to replace the important outermost primaries more quickly before autumn migration. That these outer primaries are especially important is also indicated by the fact that most adult River Warblers change the outermost one to five pairs in Northeast Africa in September–November. After this they continue to Southeast Africa where a complete renewal of the primaries in the normal sequence is performed during January–March (Pearson & Backhurst 1983). The three eastern species in the genus are less well studied. Stresemann & Stresemann (1976) reported two complete annual moults in Pallas's Grasshopper Warbler *L. certhiola*, but this was questioned by Svensson (1992).

The genus *Acrocephalus* is generally associated with wetlands both in summer and winter. Most species are long-distance migrants and a total of nine have a complete winter moult (Table 4). The only European member with a summer moult is the Moustached Warbler *A. melanopogon*, the species with the shortest migration. This is also the only *Acrocephalus* with a complete post-juvenile moult in the birth year. Juveniles in the Neusiedler See moult locally in August–October, while other populations moult further south in late autumn (Leisler 1972).

While Great Reed Warbler *A. arundinaceus* has a winter moult, the closely related Eastern Great Reed Warbler *A. orientalis*, often regarded as conspecific, normally completes moult on the breeding grounds or on stop-over sites slightly to the south (Nisbet & Medway 1972). These authors interpret the differences between the two species as adaptations to different climatic factors experienced during migration and in the breeding area. The Great Reed Warbler winters over a large area south of the Sahara. The timing of moult however varies considerably, most likely as an effect of food availability in relation to the rainy and dry seasons. Birds passing Sudan in late autumn all had old flight feathers (Nikolaus & Pearson 1991). In equatorial Africa two groups could be identified. One group arrived in November–January with fresh plumage, after a presumed moult in Northeast Africa. The other group arrived in November–December in worn plumage and started to moult. The relative abundance of the latter group was higher at winter sites further to the south in Africa (Pearson 1975). A fast moult, completed before mid–November, in Great Reed Warblers and Sedge Warblers *A. schoenobaenus* in Ghana, coincides with a brief period of favourable food conditions after the rainy season (Bensch et al. 1991). Birds using more stable areas spread the moult over a considerably longer time (Pearson 1975). In northern Ghana, Great Reed Warblers disappeared after a rapid moult, while birds in the southern part of the country arrived later in fresh plumage, established territories and presumably wintered in that area (Hedenström et al. 1993). In India migration between a moulting and a final wintering area occur in Blyth's Reed Warblers *A. dumetorum* which spent 8–9 weeks in autumn moulting in the New Delhi area but did not winter there (Gaston 1976). Marsh Warblers *A. palustris* passing Ngulia in Kenya in late autumn had not started moulting and were presumed to moult in Southeast Africa (Pearson & Backhurst 1976).

The genus *Hippolais* consists of six closely related species breeding from western Europe east to Central Asia. All can be labelled long-distance migrants and all share the strategy of a complete winter moult. The pattern seems to vary less than in other genera although the moult may be performed early in the winter as in Melodious Warbler *H. polyglotta* wintering in western Africa, or prior to spring migration as in Icterine Warbler *H. icterina* wintering in East Africa (Svensson 1992).

Most *Sylvia* species have a complete summer moult. This is true in residents breeding around the Mediterranean, a number of short-distance migrants as well as in some long-distance migrants, like Lesser Whitethroats *S. curruca* travelling from northern Siberia to Northeast Africa (Table 4). There are, however, some species that have adopted other strategies. The only species always moulting completely in the winter quarters is the Garden Warbler *S. borin*. It has a rather northern breeding range and winters from tropical Africa southwards to South Africa. In the Whitethroat, a species with a similar summer range but generally wintering closer to the Sahara, the variation is much greater. Most Whitethroats breeding in Europe have a complete summer moult before migration. Boddy (1992) found that some adults in Lincolnshire commenced moult whilst others were beginning a further breeding attempt, but he could not document any pre-migratory moult suspension. Some individuals, primarily late breeders, suspended moult at various stages in the wing and completed it in Africa (Pimm 1973, Da Prato & Da Prato 1983). In the eastern subspecies *S. c.*

Table 4. Moult strategies of six genera of Palearctic warblers in the family *Sylviidae* (data from Ginn & Melville 1983, Cramp 1992 and Svensson 1992).

Ruggningsstrategier hos sex olika släkten palearktiska sångare inom familjen Sylviidae (efter Ginn & Melville 1983, Cramp 1992 och Svensson 1992). Split=delad ruggning, Suspended=uppskjuten ruggning

	Summer	Split	Suspended	Winter	Summer+Winter
Pallas's Grashopper Warbler *Locustella certhiola*				X	
Lanceolated Warbler *L. lanceolata*			X	X	
Grashopper Warbler *L. naevia*			X	X	
River Warbler *L. fluviatilis*				X	
Savi's Warbler *L. luscinioides*	X		X	X	
Gray's Grashopper Warbler *L. fasciolata*				X	
Moustached Warbler *Acrocephalus melanopogon*	X		X	X	
Aquatic Warbler *A. paludicola*				X	
Sedge Warbler *A. schoenobaenus*				X	
Paddyfield Warbler *A. agricola*				X	
Blyth's Reed Warbler *A. dumetorum*				X	
Marsh Warbler *A. palustris*				X	
Reed Warbler *A. scirpaceus*				X	
Great Reed Warbler *A. arundinaceus*				X	
Eastern Great Reed Warbler *A. orientalis*	X				
Clamorous Reed Warbler *A. stentoreus*	X				
Thick-billed Warbler *A. aedon*				X	
Olivaceous Warbler *Hippolais pallida*				X	
Booted Warbler *H. caligata*				X	
Upcher's Warbler *H. languida*				X	
Olive-three Warbler *H. olivetorum*				X	
Icterine Warbler *H. icterina*				X	
Melodious Warbler *H. polyglotta*				X	
Marmora's Warbler *Sylvia sarda*	X				
Dartford Warbler *S. undata*	X				
Spectacled Warbler *S. conspicillata*	X				
Subalpine Warbler *S. cantillans*	X				
Ménétries's Warbler *S. mystacea*	X				
Sardinian Warbler *S. melanocephala*	X				
Cyprus Warbler *S. melanothorax*	X				
Rüppell's Warbler *S. rueppelli*	X				
Desert Warbler *S. nana*	X				
Barred Warbler *S. nisoria*		X			
Orphean Warbler *S. hortensis*	X	X	X		
Lesser Whitethroat *S. curruca*	X				
Whitethroat *S. communis*	X		X	X	
Garden Warbler *S. borin*				X	
Blackcap *S. atricapilla*	X				
Greenish Warbler *Phylloscopus trochiloides*				X	
Arctic Warbler *P. borealis*				X	
Pallas's Warbler *P. proregulus*	X				
Yellow-browed Warbler *P. inornatus*	X				
Radde's Warbler *P. schwarzi*	X				
Dusky Warbler *P. fuscatus*	X				
Bonelli's Warbler *P. bonelli*				X	
Wood Warbler *P. sibilatrix*				X	
Chiffchaff *P. collybita*	X				
Willow Warbler *P. trochilus*					X
Goldcrest *Regulus regulus*	X				
Firecrest *R. ignicapillus*	X				

icterops suspension is more common, and a large proportion of the birds have a complete winter moult (Pearson & Backhurst 1976, Cramp 1992). In southern Africa birds arrive in heavily worn plumage in December or early January and sometimes fail to finish moult completely before spring migration (Clancey 1976). The late arrival of birds in southern Africa indicates that these birds spend the autumn at stop-over sites in Northeast Africa without moulting. In Switzerland, locally breeding Garden Warblers and Whitethroats migrated south ahead of passing migrants from further north. The short-distance migrant Blackcap *S. atricapilla* showed the opposite pattern with migrants passing through before local breeders left (Turrian & Jenni 1989). These local Blackcaps most likely have time for a prolonged moult while the other category is in a greater rush to migrate south as soon as breeding and moult allow.

Another long-distance migrant, the Barred Warbler, has evolved a special split moult strategy, as already mentioned. It changes the primaries in summer and most of the secondaries in the African winter quarters (Hasselquist et al. 1988, Pearson et al. 1988). Easterly populations of the closely related Orphean Warbler apparently also have a similar split moult strategy (Nikolaus & Pearson 1991). The split moult may be regarded as a compromise between the complete summer and winter moult strategies. It indicates an urge to leave the breeding grounds early perhaps in order to make use of favourable stop-over conditions in Northeast Africa before moving on to the winter quarters further south in East Africa.

The large genus *Phylloscopus* with a majority of species in Asia also shows great variability in moult strategies (Table 4). In Europe the Chiffchaff is a resident or short-distance migrant with a complete summer moult. Two long-distance migrants wintering south of the Sahara, Bonelli's Warbler *P. bonelli* and Wood Warbler *P. sibilatrix,* moult in the winter quarters as do also the two long-distance migrants wintering in Southeast Asia, the Arctic and Greenish Warblers. The Willow Warbler is also a long-distance migrant wintering in Africa but this species has time to perform two complete moults annually as described above. In northern Asia four other long-distance migrants (Pallas's *P. proregulus,* Yellow-browed *P. inornatus,* Radde's *P. schwarzii* and Dusky *P. fuscatus* Warbler) moult completely in summer. This is also true of Asian populations of the Chiffchaff which may also be regarded as long-distance migrants. The moult of several other *Phylloscopus* species breeding further south in Asia is less well studied but most of them are residents or short-distance migrants, most likely having a summer moult.

No intraspecific differences in moult strategies have been recorded within the genus *Phylloscopus* although some species have a vast breeding range. In English Willow Warblers the majority of males commenced moult in June, regardless of whether replacement or second broods were reared in July, while females synchronised the onset of moult with the independence of their young (Norman 1990). Some Willow Warblers, most likely females, may not have time to change all remiges in the summer and they arrest moult until all feathers are again renewed in the next winter moult. Underhill et al. (1992) questioned if birds of the subspecies *P. t. yakutensis,* breeding far to the northeast in Siberia but still wintering in Africa, really have time to complete two moults annually. Another interesting question is whether the feather quality of the Willow Warbler is poorer compared to species like the Arctic Warbler performing an equally long migration but only changing the flight feathers once a year.

This compilation of moulting strategies among *Sylviidae* gives no single answer to what determines the strategy in different species. The most clear trend is an increased tendency of winter moult in species with a longer migration (Ginn & Melville 1983). Long-distance migrants often hold winter territories as has been demonstrated in Marsh Warbler, Great Reed Warbler and Greenish Warbler (Kelsey 1989, Hedenström et al. 1993, Price 1981). If it is important to be early on the winter grounds to establish a territory, the birds may not have time for a summer moult.

Acknowledgements

This review was originally written as an introductory paper at the Department of Ecology, Lund University with Thomas Alerstam as supervisor. Staffan Bensch and Carl Edelstam gave many valuable comments on the manuscript.

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Sammanfattning

Ruggningsstrategier i förhållande till flyttningen

Fåglarnas årliga fjäderbyte (ruggning) är nödvändigt för att kunna fullfölja häckning och flyttning. I tempererade områden överlappar dessa aktiviteter sällan vilket indikerar att ruggningen innebär kostnader för fågeln. En sådan kostnad kan vara högre predationsrisk.

De flesta arter byter handpennorna inifrån och ut (descendant), men sex andra ruggningsföljder illustreras i Fig. 1. Med ruggningsstrategi avses när under året fjädrarna byts i förhållande till häckning och flyttning. Sju olika strategier har beskrivits och dessa illustreras i Fig. 2. Flertalet arter undviker att rugga under häckningstiden. På grund av en kortare säsong ökar överlappningen mellan de båda aktiviteterna generellt med latitud på norra halvklotet. Större fåglar, främst icke-tättingar, behöver längre tid för att fullborda fjäderbytet och måste därför ibland även utnyttja en del av häckningstiden. Mest extrema är pingvinerna där ruggningen helt sammanfaller med häckningen.

En majoritet av våra kortflyttande småfåglar byter fjäderdräkten efter häckningen, innan de sträcker söderut på hösten (sommarruggning). Bland rovfåglar och vadare är det emellertid endast en del sena sträckare som hinner fullborda ruggningen i häckningsområdet. Flertalet tropikflyttare ruggar inte förrän efter höststräcket i vinterkvarteren (vinterruggning). En del av dessa försvarar ett vinterrevir och kan därför sprida fjäderbytet över en längre tidsperiod. Det finns emellertid ett antal tättingar bland långflyttarna, t. ex. gulärla och rödstjärt, som ruggar i häckningsområdet. Endast ett fåtal småfåglar hinner med att förnya fjäderdräkten två gånger årligen, både i sommar- och vinterkvarteren.

Då det tar längre tid att byta större fjädrar hinner en del större fåglar inte byta alla fjädrar varje år.

Exempelvis albatrosser och örnar ruggar i stället stegvis ett antal vingpennor varje år. Ruggningsvågen rör sig utåt vingen samtidigt som en ny våg startar från utgångspunkten. Detta medger en bättre manövreringförmåga jämfört med om alla pennorna byttes på ett ställe. Ett sätt att hinna med ruggningen är att dela upp den så att en del fjädrar byts i häckningsområdet och återstoden i vinterkvarteren. Denna strategi (uppskjuten ruggning) är vanligast bland långflyttande icke-tättingar.

Höksångaren, som ruggar handpennorna på sommaren men byter armpennorna i Afrika sex månader senare, utgör ett specialfall (delad ruggning).

Mindre fåglar ruggar snabbare därför att deras kortare fjädrar växer fortare men också genom att fler vingpennor är växande samtidigt. Skillnader i ruggningshastighet mellan likstora arter är huvudsakligen betingade av fjädrarnas tillväxthastighet. Ett radikalt sätt att påskynda ruggningen är att byta alla vingpennor samtidigt. Förutom hos de mer välkända andfåglarna förekommer detta inom ett antal familjer bland icke-tättingarna (Tab. 1). Många fåglar företar årligen speciella ruggningsflyttningar och arter som gravand och praktejder kan samlas i 100 000-tal på gynsamma ruggningsplatser. Desssa flyttningar går ofta i en annan riktning än det senare höststräcket.

Ruggningsstrategierna kan variera en hel del mellan närbesläktade arter och i vissa fall även inom en art. Jag har gjort en jämförelse inom tre olika familjer; rovfåglar, vadare och sångare. Rovfåglarna kan delas in i tre distinkta grupper (Tab. 2). Flertalet kortflyttare fullbordar ruggningen i häckningsområdet före höstflyttningen och en del populationer är mer eller mindre stannfåglar. Arter som flyttar medellångt, ungefär till Medelhavsområdet, påbörjar ofta ruggningen i norra Europa. De avbryter sedan fjäderbytet under höststräcket och fullbordar det i vinterkvarteren. Majoriteten av långflyttarna som övervintrar söder om Sahara hinner endast byta enstaka pennor i häckningsområdet, medan huvuddelen av ruggningen genomförs i Afrika.

Större delen av vadarna häckar i de nordliga delarna av norra halvklotet och endast ett fåtal ruggar i häckningsområdet. Stora skillnader inom olika populationer förekommer hos globalt välspridda arter som kärrsnäppa. Generellt tar ruggningen längre tid ju längre från häckplatsen (söderut) den äger rum (Tab. 3). Detta avgörs möjligen av hur stabila näringsförhållandena är i olika områden.

Tabell 4 visar ruggningsstrategier hos sex olika släkten inom sångarfamiljen *Sylviidae.* Den mest tydliga trenden är ökande antal vinterruggare bland långflyttande arter jämfört med kortflyttarna. Inom släktet *Phylloscopus* förekommer intressanta skillnader mellan närbesläktade arter. Medan gransångaren ruggar i häckningsområdet en gång per år, hinner lövsångaren med två kompletta fjäderbyten årligen, ett på sommaren och ett i Afrika. Andra långflyttare som nordsångare och lundsångare ruggar däremot enbart i vinterkvarteren i Sydostasien.