



Moult and plumage

IAN NEWTON*

Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB

Moult is one of the three main energy-demanding events in the yearly cycles of birds, and in most species occurs at a different time from breeding and migration. The sequence in which these events occur varies according to the ecological circumstances in which particular populations live, and in general moult is more variable in timing than other events. Some migratory birds moult in their breeding areas after nesting is over; others moult at a staging area on migration; while others moult in winter quarters. Yet others show a split moult, replacing part of their plumage in one place and part in another, moult being arrested during the intervening migration. Different variants in these patterns occur in different populations of the same species. Some types of birds overlap breeding and moult, and some also overlap moult and migration, especially body moult which can occur without reducing flight efficiency. Most of our knowledge of moult is based on museum skins and, now that appropriate statistical models are available to analyse it, moult is increasingly being studied in free-living birds, the main parameters of ecological interest being its timing and duration. Recent models for analysing moult data, and some of the pitfalls, are discussed briefly in this paper. More field study of moult is needed, particularly because of its relevance to annual cycle and population processes, and hence to its potential application in conservation-based research. Ringers are the only people at present able to fill this gap in knowledge.

My aim in this paper is to describe how moult (the period of plumage renewal) fits within the annual calendar of different bird species, how it can be studied during ringing operations, and analysed using appropriate statistical methodology to estimate its timing and duration. Although moult is one of the three major events in the annual cycles of birds, it has been much less studied than breeding and migration (for reviews see Stresemann & Stresemann 1966, Jenni & Winkler 1994, Kjellén 1994, Newton 2008). This is partly because of a general lack of appreciation of its relevance to the annual cycle and population processes, and its potential role in conservation-driven research.

Feathers are special lightweight structures consisting of a tough, inert protein called keratin. They form one of the defining features of birds, whether the soft insulating feathers that cover the body surface or the stiffer flight and tail feathers that provide the aerofoils which permit flight. Once they are formed, feathers become attached dead structures in which damaged parts cannot be repaired. They deteriorate mainly through the action of physical wear, sunlight and feather mites, and must therefore be renewed periodically. During a moult, feathers are generally replaced sequentially, in predetermined order, so that body insulation and (in most birds) flight are maintained throughout. Each feather is shed as a new one begins to grow below, and each has a characteristic growth curve,

taking its own set period to reach full length. Within species, equivalent feathers in different individuals take about the same time to grow, so that individual variation in moult duration is due much more to variations in the intervals between the shedding of successive feathers than to variation in the growth rates of their replacements (eg Newton 1967, 1969, Serra 2000). Many birds moult only once a year, others two or more times. Moults may be complete, involving body, wing and tail feathers, or partial, involving body feathers alone (and sometimes a few flight feathers).

MOULT AS A COMPONENT OF THE ANNUAL CYCLE

The processes of breeding, moult and migration all require extra food above the needs of daily maintenance and in many birds occur mainly at different seasons. Moult cannot, therefore, be considered in isolation from other events in the annual cycle, and to a large extent the three main events should be viewed as an integrated whole. In addition, many birds show a quiescent period in winter, during which they are not breeding, moulting or migrating. Outwardly, they seem to be doing little except eating and surviving, but inwardly they may be undergoing some physiological change, such as growing gonads in preparation for breeding at a later date. Not all species show this quiescent stage,

* Email: ine@ceh.ac.uk

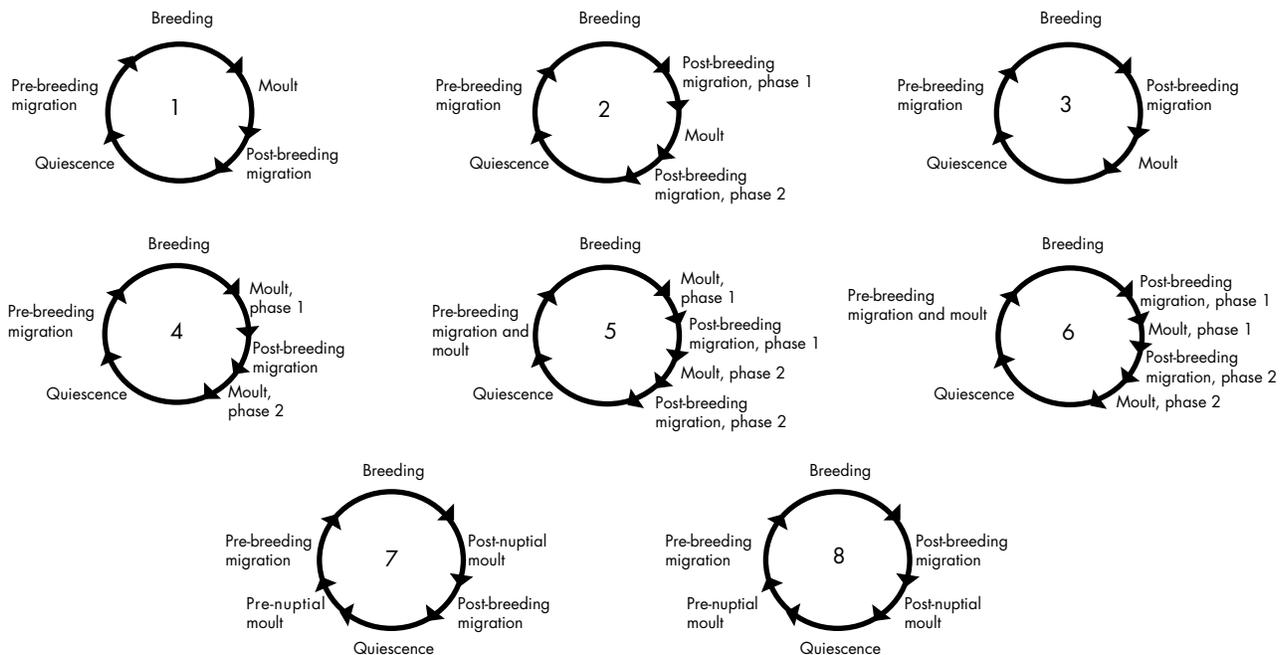


Figure 1. Eight common sequences of annual cycle events described among European migratory birds. The term 'quiescence' denotes a period when the bird is not breeding, moulting or migrating.

1. Pre-breeding migration – breeding – moult – post-breeding migration. Examples: Chaffinch *Fringilla coelebs*, Common Redpoll *Carduelis flammea*, Thrush Nightingale *Luscinia luscinia*, Fieldfare *Turdus pilaris*, Jack Snipe *Lymnocyptes minimus*.
2. Pre-breeding migration – breeding – post-breeding migration part 1 – moult – post-breeding migration part 2. Examples: Great Reed Warbler *Acrocephalus arundinaceus*, River Warbler *Locustella fluviatilis*, Northern Lapwing *Vanellus vanellus*, some populations of Green Sandpiper *Tringa ochropus*.
3. Pre-breeding migration – breeding – post-breeding migration – moult. Examples: Common Rosefinch *Carpodacus erythrinus*, Barn Swallow *Hirundo rustica*, Common Swift *Apus apus*, Whimbrel *Numenius phaeopus*, Harlequin Duck *Histrionicus histrionicus*, together with some shearwaters, terns and skuas that breed and winter in opposite hemispheres. In some of these species, the moult is prolonged and the quiescent period short or non-existent (as in Barn Swallows wintering in South Africa).
4. Pre-breeding migration – breeding – moult part 1 – post-breeding migration – moult part 2. Examples: Barred Warbler *Sylvia nisoria*, Alpine Swift *Apus melba*, Scops Owl *Otus scops*,

5. Pre-breeding migration – breeding – moult part 1 – post-breeding migration part 1 – moult part 2 – post-breeding migration part 2. Examples: Kentish Plover *Charadrius alexandrinus*, Spotted Redshank *Tringa erythropus*, some individuals of Curlew Sandpiper *Calidris ferruginea*.
6. Pre-breeding migration – breeding – post-breeding migration part 1 – moult part 1 – post-breeding migration part 2 – moult part 2. Examples: Wilson's Phalarope *Phalaropus tricolor*, Spotted Sandpiper *Actitis macularia*, and other populations of shorebirds.
7. Pre-breeding migration – breeding – first (post-nuptial) moult – post-breeding migration – second (pre-nuptial) moult. Example with two complete moults per year: Willow Warbler *Phylloscopus trochilus*; examples with one complete and one partial moult per year: Melodious Warbler *Hippolais polyglotta* and many shorebirds.
8. Pre-breeding migration – breeding – post-breeding migration – post-nuptial moult – pre-nuptial moult. Examples: Lanceolated Warbler *Locustella lanceolata* and some other *Locustella* warblers, Curlew Sandpiper *Calidris ferruginea*.

however, as some pass without obvious break from one major process to another (Newton 2008).

At least eight different sequences of events occur commonly among different European bird populations and others less commonly, depending on the particular ecological circumstances in which each population lives (Fig 1). In general, residents and short-distance migrants moult in summer after breeding (residents more slowly: Fig 1, sequence 1). Long-distance migrants moult either in late summer in the breeding area (as in sequence 1), in autumn

at a migratory staging area (sequence 2) or in winter quarters (sequence 3) (Bensch *et al* 1991, Jenni & Winkler 1994, Newton 2008). Moulting in wintering areas is widespread among northern-hemisphere species which spend their non-breeding period in the southern hemisphere, where the seasons are reversed (the southern summer coinciding with the northern winter). Less constrained by time, they also spread the moult over a longer period.

In many other migratory species, the moult occurs partly in one area and partly in another, separated by migration.

The moult can be split between the breeding area and wintering area (sequence 4), between the breeding area and a staging area (sequence 5), or between a staging and wintering area (sequence 6). The moult normally stops during migration, so that the bird can fly with a full set of flight feathers, some new and others old. The bird resumes the second part of moult wherever it left off in the first part (with few exceptions). In the last two of these patterns (sequences 5 and 6), a split moult is associated with a split migration. In other (mostly large) species, split moults are associated with breeding (as moult stops temporarily during chick feeding), or with periods of winter food shortage. Comparing these various patterns among species, moult is much more variable in timing than is breeding or migration, probably because moult scheduling is less crucial.

The story does not end here, for while some migratory species have a single split moult, replacing their feathers once but in two bouts, other species have two separate moults, replacing the same feathers twice in one year. One moult occurs either before or after autumn migration (the post-nuptial moult), and the other before and during spring migration (the pre-nuptial moult) (sequences 7 and 8). In most twice-yearly moulting species, the autumn moult is complete and the spring moult is partial, involving body feathers only (and sometimes a few tertial, secondary or tail feathers). However, in a small proportion of species that moult twice each year, such as the Willow Warbler *Phylloscopus trochilus*, both moults are complete, involving the replacement of both body and wing feathers. In some species with two moults per year, both plumages look the same (as in Willow Warbler), but in other species pre-nuptial moult gives rise to a special breeding plumage, more brightly coloured than the drab winter garb. Some species, such as the Linnet *Carduelis cannabina* and Brambling *Fringilla montifringilla*, acquire their breeding plumage, not by a pre-nuptial moult, but by abrasion, in which dull feather tips wear off to expose colour below. Pre-nuptial moults of the body feathers occur in many species of waders, and usually overlap with spring migration. In diving and dabbling ducks, the pre-nuptial moult (mainly body feathers) follows a few weeks after the post-nuptial moult (complete). In consequence, drakes are in dull 'eclipse' plumage (equivalent to winter plumage) for only a few weeks each year and in bright breeding plumage for most of the year (Cramp & Simmons 1977, Bluhm 1988). In association with this, many species of ducks form pairs while in winter quarters, whereas most other birds pair up in breeding areas.

These various generalisations apply mainly to small or medium-sized birds, in which moult occurs as a distinct event in the annual cycle, typically lasting two to three

months (Fig 1). In many species, moult, breeding and migration each occupy short enough periods that they can all be fitted within a year without overlap, and often with a quiescent period as well. In some large birds, however, such as vultures and albatrosses, breeding cycles and moult take so long that they cannot both be fitted within a calendar year without overlapping, and in some such species moult may also overlap with migration, especially body moult which does not reduce flight efficiency (Stresemann & Stresemann 1966).

In most raptors, moult begins during incubation (earlier in females than males) and overlaps with most of the breeding cycle, although it may be arrested during chick rearing (as in the Sparrowhawk *Accipiter nisus*, Newton & Marquiss 1982). Smaller raptor species can normally finish their moult before the post-breeding migration, but larger ones, which take longer to grow their feathers, arrest moult during migration, and continue after reaching winter quarters (as in the Osprey *Pandion haliaetus* and Honey Buzzard *Pernis apivorus*). In some of the largest flying birds, such as vultures, condors, storks and albatrosses, each moult cycle lasts more than a year, but again may be interrupted during difficult periods, such as chick-rearing. Otherwise such birds appear to moult more or less continuously, and may have two or more moult waves in the primary and secondary flight feathers at once (so-called serial moult). In addition, some large aquatic birds, such as waterfowl and grebes, circumvent the problem of slow feather growth in a different way, by moulting all their flight feathers simultaneously (becoming temporarily flightless). The whole feather series is then replaced within the time taken to grow the longest primary (about four weeks in ducks, six weeks in geese).

Birds clearly show great variation between species in the sequence of events through the year, their duration and extent of overlap. Moreover, unlike a successful breeding attempt, moult and migration can be stopped while the bird does something else. This facility adds yet more variation to the range of annual schedules found among birds, fitting the various patterns in food availability and risk to which different migratory populations are exposed during the year. This variation in annual schedules is shown mostly in comparisons between species, but also to some extent between different geographical populations of the same species. For example, with increasing latitude, the migrations of many species lengthen, and take up more of the year, while the periods devoted to breeding and moult decline in association with the decreasing length of the favourable season. In some species, populations at lower latitudes moult in breeding areas, whereas those from higher latitudes postpone their moult for winter quarters. Thus, Barn Swallows *Hirundo rustica* in the southernmost

breeding areas, which are resident or short-distance migrants, moult during June–August after breeding; whereas those in the most northerly breeding areas begin moulting in September–October, after they have reached their distant wintering areas. At intermediate latitudes (including Britain and Ireland), varying proportions of individuals show a split moult, starting in breeding areas, arresting during migration, and resuming in winter quarters (Cramp 1988). Likewise, most European populations of Ringed Plovers *Charadrius hiaticula* moult rapidly in their breeding areas in August–September, before migrating short distances within Europe, whereas arctic-nesting birds leave their nesting areas after breeding, and postpone their moult until November–March after reaching their wintering areas in southern Africa (Stresemann & Stresemann 1966). Other geographical variants in the timing and duration of moult occur in many other wader species, mainly in association with the latitudes at which they breed and winter (see Cramp & Simmons 1983, Serra 1998, Underhill 2003). Some species also show sex differences in the timing of moult and migration, according to their different parental roles (Newton 2008). Otherwise, individual variations in the start dates of moult in the same population relate chiefly to variations in the dates they finish their preceding activities. Among populations which moult in their breeding areas, adults that continue breeding later in the year than others start their moult later, and young raised late in the year start moulting later than earlier-hatched young (eg Newton 1966, 1999, Newton & Rothery 2005, Flinks *et al* 2008). It is also common for late-nesting adults to start moulting while they still have young in the nest, and to replace their feathers more rapidly or less completely than earlier-moulting individuals. Similarly, late-fledged juveniles start moulting at an earlier age than early-hatched ones, thereby lessening the delay in their migration (Jenni & Winkler 1994, Newton 2008).

THE RECORDING OF MOULT

Most of our knowledge of moult timing, of the kind mentioned above, is based on generalisations made from museum skins. Until the 1960s we had no method of systematically recording the state and progress of moult in a way that would enable its timing and duration in a population to be estimated accurately. However, it was clear that, in many birds, moult of the primary flight feathers spanned the whole (or almost the whole) moult period; they were shed in sequence through the series, so that, for most of the moult, several primaries were in growth at once, at different stages. A recording system was therefore devised in which each primary in one wing was given a score, according to its stage of growth: old feathers were scored as

0, new ones as 5, and growing ones as 1–4. Adding together the scores of the different primaries produced a single score reflecting the stage of moult in the individual concerned (Ashmole 1962, Evans 1966, Newton 1966). Species with nine large primaries in each wing scored a maximum of 45 per wing, and species with ten large primaries scored 50. On this system, the intensity of moult could also be assessed from the number of flight feathers growing simultaneously (or from the ‘residual raggedness score’: Bensch & Grahn 1993). Because wings normally moult in step with one another, it is not necessary to record both. This was the method used in the British Trust for Ornithology’s moult recording scheme started in the 1960s.

Regression methods

Plotting the scores of different birds against date enabled the mean start date and mean rate (or duration) to be estimated. Regression methods were used in early studies (Evans 1966, Newton 1966, Ginn & Melville 1983), but were unsatisfactory because the regression line tends to run diagonally across the long axis of the parallelogram enclosing the scatter of points. It effectively gave the start and end dates for the population as a whole, rather than for the average bird, thus underestimating the mean start date and overestimating the mean duration (Pimm 1976, Summers *et al* 1983). More realistic estimates of start dates and duration were obtained by calculating the regression of date on score. Such estimates tend to give the closest fit to estimates of moult rate obtained from examining individual birds more than once during moult, but this approach does not meet some of the assumptions of standard regression analysis (Underhill & Zucchini 1988). It tends to underestimate mean start date and overestimate mean duration, especially in populations in which individuals show wide variation in start dates. Moreover, regression methods were based only on birds in active moult, ignoring birds which had not started or had finished, and thus discarded some potentially useful information.

Underhill–Zucchini models for avian moult

In response to these problems, Underhill & Zucchini (1988) proposed a model for avian moult data which made use of non-moulting as well as moulting birds, fitting the model using the method of maximum likelihood. They considered three data types: Type 1, each bird placed in one of three categories – moult not started, in moult and moult finished; Type 2, each bird classified as in Type 1, except that moulting birds were given a moult score to reflect the stage of moult; and Type 3, in which each bird in moult was given a score, but non-moulting birds were ignored (as in the early regression methods). The underlying assumptions were that: (a) birds caught on each day were

a random sample from the relevant population, (b) the times of onset of moult followed a specified distribution, such as the Normal Distribution, and (c) for Type 2 and Type 3 data the moult score increased linearly with time, and consistently between individuals.

In an analysis of Bullfinch *Pyrrhula pyrrhula* moult, the effects on estimated moult parameters of deviations from these assumptions were explored using simulated data (Newton & Rothery 2000). It emerged that only slight deviation from linearity in Type 3 data had substantial effects on estimates. The most reliable estimates for this species were obtained by using Type 1 data, ignoring scores. Among birds in general, the rate of increase in moult score is seldom expected to be linear throughout moult, partly because near the start and end the bird has only one primary per wing in growth, whereas for the rest of moult it has up to several at once. The progress of moult would therefore be expected to follow an S-shaped curve, slower at the start and end than in the middle (as confirmed in studies of moult based on captive birds: Newton 1967, Dawson & Newton 2004).

The problem of non-linearity is accentuated in some birds, such as waders, in which different primary feathers vary greatly in length, with long outer ones taking more than twice as long to grow as short inner ones (Summers *et al* 1983). One method devised to correct for this variation is to weigh each of the primary feathers (obtained from dead birds), and then correct the scores of living birds to an appropriate weight of new feather material produced (Summers *et al* 1983, Underhill & Joubert 1995). The total score of a bird obtained visually can then be converted to a feather mass score, reflecting the percentage weight of new feather material produced. Such 'feather mass scores' (FMS), or 'percentage feather mass grown' (PFMG: Summers *et al* 1983) generally give a more linear relationship with date than do the original scores based on feather lengths (as also confirmed in five species of passerines: Dawson & Newton 2004). They make a bigger difference to estimates of moult start dates and durations for waders, whose feathers vary more in length than those of most passerines. Some researchers have additionally allowed for the fact that feathers vary in structure along their length, calculating a separate weight for each part of each feather (Redfern 1998). Other potential approaches to allowing for the non-linearity in the moult score or PFMG are (a) to transform the data in some way, and (b) to extend the Underhill-Zucchini model to allow for non-linear increase in moult scores.

Testing the validity of different methods depends critically on estimates of the rate of increase in moult score obtained from individuals caught more than once during moult. These individual figures give direct measures of moult rate which are immune to the biases that affect

overall estimates of moult rate obtained from scattergrams of moult score against date. However, in most studies such data are limited because few individuals are retrapped. Comparing Type 1, 2 and 3 values against individual values for three species (Starling *Sturnus vulgaris*, Bullfinch and Sanderling *Calidris alba*) showed that estimates of start and end dates (and hence durations) based on Type 1 data were either better or as good as those obtained using Types 2 and 3 data (Rothery & Newton 2002). Type 1 data are the easiest to collect because they do not need the allocation of a moult score or its conversion to mass. The Type 1 method could also be used for partial moults (including post-juvenile moult) in which flight feathers are not replaced. It is easy to implement using the standard binary regression models that are available in most statistical packages (such as Minitab Release 12).

Methods that depend on recording non-mouling as well as moulting birds work well for species that are resident year-round in the same area, for samples can then be drawn from the entire population throughout. But sometimes birds start moulting soon after they have moved into an area, and stay on later, in which case non-mouling birds are under-represented in the initial period before all have arrived. One way round this problem is to restrict analysis to moulting and post-moult birds, omitting any pre-moult birds (the Type 4 method of Underhill *et al* 1990). In other situations, birds leave on migration after completing moult, so non-mouling birds are under-represented in the later period, once the first birds start to leave. In this case

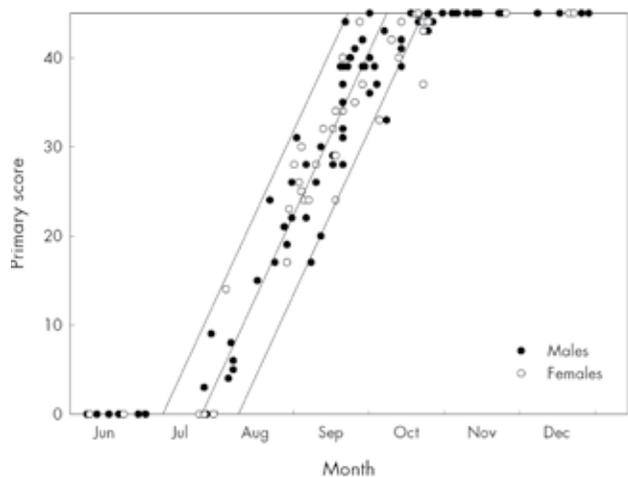


Figure 2. Numerical primary scores of Goldfinches plotted in relation to date, with the line fitted using the Underhill-Zucchini procedure, Type 5, which excluded birds that had finished moult (● - males; ○ - females). Mean start date was estimated as 25 July, with 95% of the birds starting within the 31-day period, 9 July – 9 August, and finishing within the period 22 September – 24 October. The mean duration was 76 days ($se = \pm 4$ days). No significant sex differences emerged. From Newton & Rothery 2009.

analysis is best restricted to pre-moulting and moulting birds (the Type 5 method of Underhill *et al* 1990). This last procedure was used to estimate moult parameters in Stonechats *Saxicola torquatus* and Goldfinches *Carduelis carduelis*, because it was suspected that many birds left the study area on completing their moult (Fig 2; Flinks *et al* 2008, Newton & Rothery 2009).

The Underhill–Zucchini procedure has provided a means to obtain reliable estimates of moult timing and rate (and their standard deviations) from only two or three categories of birds (pre-moult, in moult, post-moult). It has been used in at least 30 studies so far. In some species in which it was tested, the Type 1 method gave estimates at least as reliable as any measures which included the use of moult scores. However, further testing is required on a wider range of species, and including separate analyses for juveniles undergoing body moult alone. Almost certainly, different models will prove the most appropriate for different species. This is mainly because species vary in the extent to which they deviate from each of the assumptions underlying the models, and different models vary in their sensitivity to each assumption.

CONCLUDING REMARKS

For most European birds we still lack detailed studies of moult in which the data are adequate for statistical analysis. Yet moult is one of the easiest things for ringers to record, especially if they ignore moult scores, and instead place each bird in one of three categories: pre-moult, in moult, and post-moult. Providing the population can be sampled appropriately throughout the moult period, such data should be sufficient to provide reliable estimates of moult start dates and durations for the population (with separate estimates for juveniles changing only their body feathers). Only with sustained study over the years will we reach a position in which annual variation and time trends in these parameters can be examined as a matter of routine.

We now have detailed information on the annual breeding of many bird species in Britain and Ireland, but almost nothing on the equivalent annual variation in moult. What are we missing? How much does the spread of moult within a population, its timing and duration vary between years, habitats or regions? And how does this variation relate to breeding and other events in the annual cycle, or to environmental variables, including climate? If we are to venture into this enticing field of avian ecology, it is bird ringers who must take the lead, for only they are handling sufficient numbers of live birds year after year in the same places. Moreover, because of its close interconnection with breeding and migration, moult can be used to throw light on aspects of bird ecology

otherwise hard to study. For example, in some multi-brooded passerine species, the amount of late breeding can vary greatly from year to year. In species which moult immediately after breeding (like most British passerines), this annual variation can be assessed much more easily by obtaining estimates of moult start dates in different years than by the more laborious procedure of late-season nest-searching. Among Bullfinches studied over five years near Oxford, the proportion of adults which started moult after 20 August (implying successful breeding from eggs laid after mid July) varied between 7% and 68% in different years. End-of-season young-to-adult ratios varied twofold between years, according to the amount of late nesting (Newton 1999). This story would not have emerged without a detailed and fascinating, but undemanding, study of moult.

ACKNOWLEDGEMENTS

I am grateful to Lukas Jenni, Chris Redfern and Peter Rothery, and an anonymous referee for helpful comments on the manuscript.

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