Molt is a critical life-history stage for birds. Feathers wear out, and they need to be replaced so that the functions of plumage are not compromised. Because feathers account for a considerable proportion of total body protein (Newton 1966, Murphy and King 1986, Lindström et al. 1993), and molt is normally separated temporally from other life-history...
stages, feather replacement during molt presumably presents a significant physiological and energetic burden. Indeed, metabolic rate is increased during molt (Lindström et al. 1993, Schieltz and Murphy 1995). There is also a constraint on the rate at which new feather mass can be accumulated. Late-breeding birds start molting late, but then molt more rapidly. Rapid molt results in feathers that are less massive and of poorer quality (Dawson et al. 2000). Although Murphy and King (1991) found that a moderately poor diet did not affect duration of molt or length of feathers, they did not assess mass and quality of those feathers. However, severe malnutrition did impair molt.

In European Starlings (Sturnus vulgaris), total mass of new primary feathers increases at a constant rate throughout most of the duration of molt (Dawson 2003). The first aim of the present study was to find whether that holds true for other species; the second aim was to make use of the constant rate of increase in new feather mass to develop an improved method for scoring molt. The most widely used method was proposed by Newton (1966). In that method, each primary feather on one wing is given a score depending on its stage of growth: from 0 for an old feather to 5 for a fully regrown feather. Scores for all individual feathers are added to produce a molt score. For species with nine primary feathers, molt score therefore increases to 45 when molt is complete.

The standard scoring method is convenient for assessing the stage of molt, because primary-feather molt spans the duration of molt for all feather tracts. However, it has the weakness that equal weight is given to each primary feather even though the actual length and mass of primary feathers differ. In starlings, the outer primary has 2.4 times the mass of the inner primary. The rate of increase in total mass is constant because the number of feathers being grown concurrently decreases as molt progresses toward the more massive outer primaries (Dawson 2003). By assigning equal scores to all feathers, the standard method exaggerates rate of molt in the early stages and underestimates it later. Thus, molt score does not accurately reflect the increase in mass, and in most species it does not increase linearly with time.

That nonlinearity presents problems when molt-score data are used to estimate timing and duration of molt. Analyses of molt-score data using regression methods are clearly inappropriate (Ginn 1975, Pimm 1976, Summers et al. 1983). Underhill and Zucchini (1988) and Underhill et al. (1990) produced a model that avoids problems associated with regression analyses. Nevertheless, when molt-score data are used (Underhill-Zucchini types 2 and 3) nonlinearity in rate of increase of molt-score data will create biases (see Newton and Rothery 2000, Rothery et al. 2001, Rothery and Newton 2002).

We performed a comparative study of five passerine species: European Starlings and European Greenfinches (Carduelis chloris), both of which have pointed wings, in which the outer primaries have the greatest mass; magpies (Pica pica) and Carrion Crows (Corvus corone), which have more-rounded wings, in which the middle primaries are the most massive; and Eurasian Bullfinches (Pyrrhula pyrrhula), which are intermediate in wing shape and primary-feather mass.

The rate at which new feather mass is accrued is a physiologically and energetically important factor. A molt scoring system designed to take feather mass into account would therefore provide information with greater physiological and energetic relevance. Such a method would yield a linear increase in score, which would enable less complicated and potentially more accurate estimations of molt start dates and molt durations.

**METHODS**

**Testing Linear Increase in New Feather Mass**

A previous study had shown that total mass of new primary feathers increased linearly with time in starlings (Dawson 2003). Here, that finding was tested in four other species.

*Crows and magpies.—Two Carrion Crows (a male and a female) and three magpies (two males and one female) were trapped in the wild by local gamekeepers as part of their pest-control programs. They were kept in outdoor aviaries and fed ad libitum with dog food and day-old chickens (Gallus gallus). From the start of molt in late May (Table 1) until end of molt (late October for Magpies and late November for crows), in situ length of each growing primary feather on the right wing was recorded at intervals of four to five days. Each primary was held alongside a rule, and length recorded to the nearest millimeter. At the end of molt, the primary feathers were plucked post mortem. Total length and mass of each were recorded. Each feather was then cut into 10 segments of equal length. Mass of the most distal segment was recorded, then the most distal segment plus the next-most-
distal, and so on, until the mass of the whole feather was reconstituted—a cumulative increase in mass, from tip to base, equivalent to the increase in mass during growth of the feather. The difference between total feather length and final \textit{in situ} length was equivalent to the length of feather rachis embedded within the skin. That difference was added to all the \textit{in situ} measurements to estimate total length of each feather during its growth. Those lengths were then converted to mass, using the information on increase in feather mass from tip to base for each particular feather. Finally, total new feather mass at each interval during molt was assessed by summing the calculated masses of each growing or recently grown primary feather. A more detailed description of the methodology is given in Dawson (2003).

Greenfinches and bullfinches.—Daily changes in the \textit{in situ} lengths of primary feathers of captive European Greenfinches and Eurasian Bullfinches were recorded during 1965 (Newton 1967). Raw data for two greenfinches from that study were used here, together with data on one bullfinch that were expressed graphically in figure 1 of the Newton (1967) paper (see Table 1). Those \textit{in situ} lengths were converted to mass in the same way as described above, using data on total feather length and mass, and the distribution of mass along the length of each feather, obtained from dead greenfinches and bullfinches.

**Testing the Mass-corrected Scoring System**

Molt was recorded in eight female starlings held captive in an outdoor aviary. Molt started at the beginning of June and ended in early September. At weekly intervals during that period, each of the nine primary feathers on the right wing was assigned a score: 0 = dropped feather; 1 = approximately one-quarter grown (i.e. from eruption from the follicle to one-third fully grown); 2 = approximately half grown (i.e. one-third to two-thirds fully grown); 3 = approximately three-quarters grown; and 4 = fully grown. The score (0–4) for each primary was divided by 4 (because a score of 1 = one-quarter total feather length) and multiplied by the proportion that the final mass of that particular primary contributes to total mass of all nine primaries (see Table 2). Summing the scores for individual feathers gave a total molt score ranging from 0.0 before molt to 1.0 in a fully molted bird. The recording system is shown in the Appendix.

To compare this scoring system with the widely used “standard” system based on Newton (1966), scores for individual feathers were increased by 1; thus, 1 = dropped feather; 2 = approximately one-quarter grown; 3 = approximately half grown; 4 = approximately three-quarters grown; and 5 = fully grown. Summing scores from individual feathers gave a molt score that increased from 0 to 45 (in the case of a starling with nine primary feathers).

**Results**

**Testing Linear Increase in New Feather Mass**

Rate of increase in estimated mass of new primary feathers was fairly constant throughout molt for all individuals in all four species—crow, magpie, bullfinch, and greenfinch. To correct for differences in molt start dates and molt duration between individuals and species, data on new feather mass were interpolated at 20 equally spaced intervals throughout the molt of each individual. Those data (Fig. 1) showed that increase in mass was fairly constant throughout molt, as it had been in starlings. Rate of increase was slightly less at the beginning and end of molt, corresponding to the time that only the first and last primaries, respectively, were being grown. Increase in mass in real time is shown for one individual of each species in Figure 2.

**Table 1. Timing of molt of birds in the present study.**

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Start</th>
<th>End</th>
<th>Duration*</th>
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<tr>
<td>Crow</td>
<td>1</td>
<td>14-Jun-02</td>
<td>25-Nov-02</td>
<td>164</td>
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<tr>
<td>Crow</td>
<td>2</td>
<td>20-May-02</td>
<td>29-Nov-02</td>
<td>193</td>
</tr>
<tr>
<td>Magpie</td>
<td>1</td>
<td>24-Jun-02</td>
<td>1-Nov-02</td>
<td>130</td>
</tr>
<tr>
<td>Magpie</td>
<td>2</td>
<td>10-Jun-02</td>
<td>27-Oct-02</td>
<td>139</td>
</tr>
<tr>
<td>Magpie</td>
<td>3</td>
<td>5-Jun-02</td>
<td>18-Oct-02</td>
<td>135</td>
</tr>
<tr>
<td>Bullfinch</td>
<td>2*</td>
<td>8-Aug-65</td>
<td>5-Nov-65</td>
<td>89</td>
</tr>
<tr>
<td>Greenfinch</td>
<td>1*</td>
<td>14-Jul-65</td>
<td>8-Nov-65</td>
<td>117</td>
</tr>
<tr>
<td>Greenfinch</td>
<td>2*</td>
<td>19-Jul-65</td>
<td>10-Nov-65</td>
<td>114</td>
</tr>
</tbody>
</table>

*In days. Numbers used in Newton (1967).

**Table 2. Relative contribution of each primary feather to total primary-feather mass.**

<table>
<thead>
<tr>
<th>Primary number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starling</td>
<td>0.073</td>
<td>0.081</td>
<td>0.088</td>
<td>0.095</td>
<td>0.103</td>
<td>0.114</td>
<td>0.129</td>
<td>0.147</td>
<td>0.170</td>
<td>1.000</td>
</tr>
<tr>
<td>Crow</td>
<td>0.068</td>
<td>0.074</td>
<td>0.081</td>
<td>0.095</td>
<td>0.124</td>
<td>0.139</td>
<td>0.140</td>
<td>0.133</td>
<td>0.103</td>
<td>0.043</td>
</tr>
<tr>
<td>Magpie</td>
<td>0.087</td>
<td>0.094</td>
<td>0.104</td>
<td>0.119</td>
<td>0.130</td>
<td>0.131</td>
<td>0.128</td>
<td>0.114</td>
<td>0.076</td>
<td>0.017</td>
</tr>
<tr>
<td>Greenfinch</td>
<td>0.072</td>
<td>0.078</td>
<td>0.084</td>
<td>0.090</td>
<td>0.104</td>
<td>0.129</td>
<td>0.143</td>
<td>0.146</td>
<td>0.154</td>
<td>1.000</td>
</tr>
<tr>
<td>Bullfinch</td>
<td>0.084</td>
<td>0.088</td>
<td>0.090</td>
<td>0.100</td>
<td>0.119</td>
<td>0.131</td>
<td>0.131</td>
<td>0.130</td>
<td>0.127</td>
<td>1.000</td>
</tr>
</tbody>
</table>

To compare this scoring system with the widely used “standard” system based on Newton (1966), scores for individual feathers were increased by 1; thus, 1 = dropped feather; 2 = approximately one-quarter grown; 3 = approximately half grown; 4 = approximately three-quarters grown; and 5 = fully grown. Summing scores from individual feathers gave a molt score that increased from 0 to 45 (in the case of a starling with nine primary feathers).
Testing the Mass-corrected Scoring System

Individual feather scores were recorded for eight starlings and converted into a mass-corrected molt score using the calculation shown in the Appendix. To correct for differences in start date and molt duration between individuals, the increase in that mass-corrected molt score was interpolated at 10 equally spaced intervals throughout the molt of each individual. The resulting increase in mass-corrected score departs only slightly from linearity (Fig. 3). However, the increase in mass-corrected score is more linear than the standard method of simply summing individual feather scores—that method exaggerates molt rate during the early part of molt when (in the case of starlings) shorter and less-massive primaries are being grown. The slight nonlinearity in the mass-corrected method results, in part, from the fact that equal weight is apportioned to each quarter of each feather (i.e. an increase in score of 1). In reality, the base of the feather—the last quarter to be grown—is more massive than the distal quarter (feather tip), and that difference becomes greater for the outer primaries (Dawson 2003). Thus, molt score during the early part of molt, when feather tips of inner feathers are being grown, is exaggerated; at the end of molt, when the bases of the outer primaries are being grown, it is underestimated. That was demonstrated in a “refined” version of the mass-corrected method, in which, instead of assuming an equal distribution of mass along the feather, an extra term was inserted to accurately account for distribution of mass along the length of each feather. This refined method decreased the slight nonlinearity of the mass-corrected molt score (Fig. 3).

Discussion

A previous study on starlings (Dawson 2003) had shown that new primary feather mass increased at a constant rate for most of the duration of molt. The present study has shown that this is also true for four other passerine species. In starlings, the wing is pointed and the outer primaries are the most massive. The four species in the present study had wings that differed widely in shape. Greenfinches are similar to starlings; at the other extreme, magpies have particularly rounded wings and the sixth primary (of 10) is the most massive. That all five species show a constant rate of increase in new feather mass for most of the duration of molt suggests that this is probably true for passerines in general. Seel (1976) found a constant rate of increase in primary-feather mass in captive Eurasian Jackdaws (Corvus monedula). This may also be true for other bird orders, but clearly that hypothesis needs to be tested.

The most accurate estimation of molt progress involves an exact assessment of new feather mass. That requires accurate measurement of the length of each feather and conversion of that length into mass, allowing for the distribution of mass along the length of the feather (Redfern 1998). A more useful estimate of molt involves
a trade-off between accuracy and convenience of use. The method proposed here has the conveniences of (1) using a simple scoring system (0–4 as an estimate of feather length) rather than accurate measurement of feather length; and (2) assuming uniform distribution of mass along the length of the feather, rather than accurately allowing for the real distribution of mass.

Inaccuracies introduced by those convenient approximations are investigated here. Inaccuracy resulting from assumption of a linear distribution of mass along the length of a feather is shown in Figure 3. Clearly, there is a difference between the mass-corrected score and the refined mass-corrected score. In the former, molt score is exaggerated during the early part of molt, when the tips of inner feathers are being grown, and underestimated at the end of molt, when the bases of the outer primaries are being grown. However, the difference between the two results is slight, and the extra deviation from linearity resulting from the assumption is considerably less than in the standard system.

Inaccuracy resulting from assigning a score to feather length rather than using exact measurement is shown in Figure 2. Exact increases in feather mass for all four species, calculated from exact measurements of feather length, are shown by solid lines. Exact feather lengths were retrospectively converted into scores for each feather, and total score calculated by the method described, weighting individual scores by proportion of total mass contributed by that feather. The resulting total molt score is shown by the line connecting open circles. Clearly, that line closely tracks the accurate estimation of real feather mass. Simple summation of individual feather scores as in the standard method is shown by the solid circles and results in a line that deviates considerably from mass and from linearity. In the case of greenfinches and bullfinches, which, like starlings, have relatively massive outer primaries, molt rate is exaggerated (steeper slope) during the early part of molt and underestimated later. In the case of magpies and crows, where middle primaries
are the more massive, molt rate is exaggerated early in molt, underestimated midway through molt, and exaggerated again later.

Estimations of timing and duration of molt from molt-score data assume that molt score increases linearly with time—deviations from linearity introduce biases (see Newton and Rothery 2000). The standard method clearly results in molt scores that do not increase linearly with time. The nature of the deviation from linearity depends on the distribution of mass between primaries, and the size of the deviation depends on how skewed that distribution is. Molt score in waders shows a considerable deviation from linearity because mass of the outer primary is approximately 3 to 5× greater than that of the innermost primary (Summers et al. 1983, Underhill and Zucchini 1988). Summers et al. (1983) converted molt scores of free-living Common Redshanks (Tringa totanus) to account for mass in a method similar to the one described here. Using data from birds caught twice during molt, they showed that the rate of increase in mass was only slightly less toward end of molt than during the early part of molt.

In contrast, there was a large difference in rate of increase in the standard molt score.

Two advantages of mass-corrected molt score are that it is more physiologically and energetically relevant, because it tracks changes in new feather mass, and that it increases more linearly. Because it increases more linearly, two measurements from the same individual at any time during molt will give a fairly accurate estimation of start date, end date, and hence of duration and rate of molt, for that individual. Even a single molt score recording will indicate how far, in terms of time, an individual is through its molt, and the proportion of new feather mass the bird has already synthesized. Also, a single molt score recording may give an indication of molt rate. In general, birds do not start to molt until they have finished breeding. If, as a result of breeding late, they start to molt late, they then molt more rapidly. Mass-corrected molt score still increases linearly in late-molting birds (A. Dawson and I. Newton unpubl. results), but increases more rapidly. Thus, a lower molt score at the same time of year may indicate that a bird is molting more rapidly and is therefore under greater physiological stress.

There can be considerable variation in molt rate among individuals, resulting from differences in timing of the start of molt, which in turn is related to timing of the end of breeding. Timing can be affected by weather (e.g. Morton and Morton 1990) or by habitat quality (e.g. Hinsley et al. 2003). Molt rate can affect plumage quality (Dawson et al. 2000) and hence overwinter survival (Nilsson and Svensson 1996). A methodology that provides a simple but fairly accurate assessment of molt rate in individuals can therefore be useful in ecological studies. Variation in molt rate among individuals is exemplified by the birds studied here. They had particularly long molt durations (Table 1), at the extremes of the ranges reported for wild birds (Cramp and Perrins 1994). That is presumably because the start of molt in these individuals was not delayed by breeding activity.

Use of the Mass-corrected Method

The method proposed here requires that molt scores of individual primaries—rather than just the sum-total molt score—be recorded, so that data can be used to calculate mass-corrected score. Individual feather scores are often routinely
recorded already, and the British Trust for Ornithology produces molt score cards for that purpose (Ginn and Melville 1983, Redfern and Clark 2001). The method also requires data on primary-feather mass of the species being studied, so that the relative contribution of each primary to total primary-feather mass can be assessed, as in Table 2. A single dead individual or a set of plucked feathers is sufficient to supply that information. Although there are differences in absolute mass between individual birds, relative contribution of each primary to total primary mass was very consistent in each of 120 European species examined (A. Dawson unpubl. data; see also Underhill and Joubert 1995). Data on the contribution of each primary are used in a simple algorithm in a spreadsheet (see Appendix).

Individual feather growth is scored in a way similar to the standard method, except that a dropped feather scores 0 rather than 1. That may seem trivial, but it does have an important consequence. If the increase in length (or mass) of an individual feather is extrapolated back to 0 (i.e. the apparent time that new feather growth starts), this occurs some time after the old feather has dropped (at least in starlings). Although an old feather is dropped when it is forced out by growth of the new feather (Watson 1963), growth of the new feather at that early stage is slow (Heinroth 1906), followed by a phase during which feather elongation is rapid and fairly constant. Allocating a finite score to a dropped feather can therefore impart a degree of sigmoidality to the increase in score for each feather and for total molt score.

In conclusion, total mass of new primary feathers increases almost linearly with time in five passerine species with a range of wing shapes. A new method for scoring molt, in which individual feather scores are weighted by feather mass, creates a cumulative score that follows the increase in total mass and is therefore largely linear. This mass-corrected method is only marginally less convenient to use than the standard method, but has the advantages that it is physiologically relevant and, being linear, can be used to estimate the date that molt started and the duration of molt.

Acknowledgments

We would like to thank H. Turk for recording molt scores of starlings, and P. Rothery and S. Hinsley for helpful discussions.

Literature Cited


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Appendix. Spreadsheet for the calculation of molt score for European Starlings. Column B is the contribution made by each primary to total primary-feather mass. Individual feather score is entered in column C.

<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Primary</td>
<td>Score (0–4)</td>
<td>=C2/4*B2</td>
</tr>
<tr>
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<td>1</td>
<td>0.073</td>
<td>=C2/4*B2</td>
</tr>
<tr>
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</tr>
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<td>0.170</td>
<td>=C10/4*B10</td>
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<tr>
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