The timing and duration of moult in adult Starlings 
*Sturnus vulgaris* in east-central England

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The timing and duration of primary moult were estimated for wild adult Starlings *Sturnus vulgaris* near Monks Wood in 1977-78, and for captive birds in 1999. The model of Underhill and Zucchini (1988) was modified to allow for a non-linear increase in the moult score, based on scores of captive birds. For wild birds, estimates of moult duration in 1977 and 1978 were 100 days and 98 days, with mean and standard deviation in start dates of 6 June and 7.3 days in 1977, and 2 June and 9.7 days in 1978. For captive birds, moult duration was 85 days, with mean and standard deviation of 31 May and 4.1 days. Differences between these estimates and those reported for other wild and captive Starling populations are discussed.

We apply models of avian moult to estimate the timing and duration of moult in adult Starlings *Sturnus vulgaris* from samples of birds obtained near Monks Wood (1977-78), eastern England, where British breeding Starlings are resident all year-round, and from studies on captive birds in 1999. Although several previous studies have been made of Starling moult, all were in regions different from our own, and for various reasons none is directly comparable with ours. The most thorough previous study refers to South Africa where the Starling was introduced more than a century ago (Cooper & Underhill 1991), and where the different latitude affects both the timing and duration of moult. Ginn and Melville (1983) gave estimates of moult timing and duration in free-living birds in Britain on the basis of moult cards. General details of moult in different parts of the natural range can be found in Dement'ev and Gladkov (1954) and Cramp & Perrins (1994). Studies on captive birds in Scandinavia (Lundberg & Eriksson 1984) and Britain (Dawson 1987, 1994) were not comparable because birds were held under artificial daylength, which affects both timing and duration of moult.

**METHODS**

**Captive birds**

Ten captive adults, obtained as juveniles during the previous summer near Monks Wood, were kept on natural daylengths in outdoor aviaries and fed with turkey starter crumbs (under Home Office licence PPL 80/1211). Wing moult score was recorded repeatedly at approximately weekly intervals. Starlings have nine primary feathers in each wing, which are shed in sequence from inner to outer (descendently). Each wing usually has 2-4 primaries in growth at once, but at different stages, with the two wings in phase with one another. In these birds, each primary feather was given a score of 0-5, depending on the stage they had reached, and fully moulted birds scored 45. For purpose of analysis, all scores were converted to a scale of 0-1 (unmoulted-moulted).

In each of these captive birds the moult score showed a similar non-linear increase, with a lower rate of increase in the later stages (Fig. 1). Changes in the moult score through time were described by the model:

\[
S = \frac{at^b}{1+(a-1)t^b}
\]

where \(S\) denotes the moult score standardized to lie in the range (0-1) and \(t\) is the elapsed time into moult as a proportion of the moult duration, i.e. \(t = (\text{Date - Start date})/(\text{End date - Start date})\). This gives \(S(0) = 0\) and \(S(1) = 1\). For \(b > 1\), the curve is sigmoidal with maximum rate of increase at \(S = a(b-1)/2(a-1)b\). For
in these birds were initially obtained by applying the model of avian moult proposed by Underhill and Zucchini (1988). The basic assumptions of this model are that: (a) moult score in each individual increases linearly with time; (b) the dates of onset of moult in the population follow a Normal distribution; (c) the birds caught on each day are a random sample of those available. The approach distinguishes three different data types corresponding to different categories of moult score: Type 1, in which each bird is classified as ‘moult not started’, ‘in moult’ or ‘moult completed’; Type 2, in which each bird is classified as in Type 1, except that moultng birds are given a moult score to reflect the stage of moult; and Type 3, in which each bird in moult is given a score, but non-moultng birds are ignored.

However, where the increase in moult score is non-linear, application of the Underhill & Zucchini model to Type 2, and especially Type 3, data can produce underestimates of moult duration and hence additional errors in mean start and end dates (Newton & Rothery 2000). For the Starling data, the basic model was therefore modified to allow for non-linearity by using a sigmoidal curve of the same general form as found in captive Starlings (see above and Appendix). The model was then fitted to Type 2 data to provide estimates of the parameters of the curve, together with the timing and duration of moult. The effect of a non-linear increase in moult score was further examined by applying the Underhill–Zucchini model to Type 3 data with linearized moult scores derived from the fitted non-linear model. For each model and data type, parameters were estimated by the method of maximum likelihood using the Newton–Raphson numerical technique implemented in the statistical package Genstat 5 (Genstat 5 Committee, 1993).

RESULTS

Captive birds

Table 1 shows estimated parameters $a$ and $b$ of the fitted curve, together with the start and end dates of moult and the duration for each bird. The model provided a close fit for each bird, with all values of $R^2$ exceeding 98% (Fig. 2). Mean values are as follows: $a = 3.44$ (se = ±0.21, sd = ±0.67), $b = 1.48$ (se = ±0.05, sd = ±0.16), Start date = 31 May (se = ±1.3, sd = ±4), End date = 24 August (se = ±1.7, sd = ±5), Duration = 85 days (se = ±2.0, sd = ±6).

Mean values of $a$ and $b$ are both significantly greater than unity, reflecting the non-linear increase. The esti-

Figure 1. Moult scores in ten captive adult Starlings.

**Wild birds**

Details of moult were recorded from adult Starlings shot under licence near Monks Wood, Cambridgeshire (52°20′ N, 0°20′ W), by the late Peter Ward for a study of body composition. Birds were obtained from late May to early October in 1977 ($n = 291$) and 1978 ($n = 109$). On examination, each primary feather was given a score from 0 (old) to 4 (new) depending on its stage of moult (1, new feather up to one-quarter grown; 2, new feather one-quarter to half grown; 3, new feather half to three-quarters grown; 4, new feather three-quarters to full grown), and the sum of the scores of one wing gave the ‘moult score’. Thus birds that had not yet started moult scored 0, those in moult scored 1–35 depending on the stage they had reached, and fully moulted birds scored 36. This was a different scoring system to that used on captive birds (see above), but for analysis these scores were also converted to a 0–1 scale (unmoulted–moulted). No details were recorded from juveniles obtained at the same time as the adults, but fully-moulted juveniles were distinguished from fully-moulted adults by degree of skull ossification. Migrant birds started to arrive in late September by which time the major flight feather moult was complete in both migrants and residents so that problems of population mixing did not arise.

Estimates of the mean timing and duration of moult

Table 1. Estimated moult parameters for ten captive adult Starlings.

<table>
<thead>
<tr>
<th>Bird</th>
<th>b</th>
<th>a</th>
<th>Start</th>
<th>End</th>
<th>Duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.63</td>
<td>3.91</td>
<td>29 May</td>
<td>3 Sep</td>
<td>96.3</td>
</tr>
<tr>
<td>2</td>
<td>1.60</td>
<td>2.90</td>
<td>22 May</td>
<td>16 Aug</td>
<td>86.4</td>
</tr>
<tr>
<td>3</td>
<td>1.20</td>
<td>2.52</td>
<td>5 Jun</td>
<td>16 Aug</td>
<td>72.6</td>
</tr>
<tr>
<td>4</td>
<td>1.53</td>
<td>3.75</td>
<td>3 Jun</td>
<td>24 Aug</td>
<td>82.1</td>
</tr>
<tr>
<td>5</td>
<td>1.31</td>
<td>2.93</td>
<td>4 Jun</td>
<td>23 Aug</td>
<td>80.7</td>
</tr>
<tr>
<td>6</td>
<td>1.57</td>
<td>3.61</td>
<td>29 May</td>
<td>23 Aug</td>
<td>86.9</td>
</tr>
<tr>
<td>7</td>
<td>1.65</td>
<td>3.41</td>
<td>30 May</td>
<td>27 Aug</td>
<td>88.8</td>
</tr>
<tr>
<td>8</td>
<td>1.51</td>
<td>4.90</td>
<td>30 May</td>
<td>25 Aug</td>
<td>87.0</td>
</tr>
<tr>
<td>9</td>
<td>1.49</td>
<td>3.44</td>
<td>2 Jun</td>
<td>23 Aug</td>
<td>82.3</td>
</tr>
<tr>
<td>10</td>
<td>1.27</td>
<td>3.05</td>
<td>4 Jun</td>
<td>29 Aug</td>
<td>85.9</td>
</tr>
<tr>
<td>Mean</td>
<td>1.48</td>
<td>3.44</td>
<td>31 May</td>
<td>24 Aug</td>
<td>84.9</td>
</tr>
<tr>
<td>se</td>
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<td>0.21</td>
<td>1.3</td>
<td>1.7</td>
<td>2.0</td>
</tr>
<tr>
<td>sd</td>
<td>0.16</td>
<td>0.67</td>
<td>4.1</td>
<td>5.3</td>
<td>6.2</td>
</tr>
</tbody>
</table>

*Calculated on the model: $S = at^b/[1 + (a-1)t^b]$ where $S$ denotes the standardized moult score and $t$ denotes the proportion of the total time in moult, i.e. $(Date - Start date)/Duration$. See Figures 1 and 2.

The estimated mean curve is sigmoidal with maximum rate of increase at a score of about 0.23 (corresponding to primary moult extending up to feathers 2–3). Figure 3 illustrates the goodness-of-fit of the model by showing standardized scores of individual birds plotted against the proportion of time into moult (calculated from the individual estimates of Start date and End date), together with the mean curve.

Estimates of the Start and End dates may be biased because they are obtained by extrapolating the fitted curve to scores of zero and unity at the beginning and end of moult, where the detailed fit of the model cannot be assessed from the data. As a check on the magnitude of the bias, estimates of Start and End dates were compared with their lower and upper limits obtained from the last recorded date of a zero score and the first recorded date of a unit score in each bird.

The time of the latest zero score on each bird was less than its estimated start of moult by a mean of 4.2 days (range 1.2–7.5 days). The dates of first recorded unit scores (obtained for only two birds) both exceed their estimated end dates of moult by 3.9 days and 4.0 days. This indicates that the estimated mean moult duration in captive birds of 85 days could be underestimated by as much as about 8 days.

Wild birds

Using Type 1 data, estimates of moult duration for 1977 and 1978 were 100 days (se = ±2) and 98 days (se = ±7) respectively (Table 2). Corresponding estimates of the mean and standard deviation of start of moult were 6 June (se = ±6.3) and 7.3 days (se = ±0.8) in 1977, and 2 June (se = ±3.4) and 9.7 (se = ±2.0) in 1978. None of the moult parameters showed statistically significant differences between years, but the standard errors of estimation are relatively large.

Estimates of moult duration using Type 2 and 3 data were markedly reduced (Table 2), as expected from the non-linear increase in the moult score. Allowing for non-linearity, Type 2 data gave estimates of moult duration for 1977 and 1978 respectively as 101 days (se = ±2) and 95 days (se = ±5.4). These values and associated estimates of mean and standard deviation of onset of moult were very similar to those estimated from Type 1 data. The parameters $a$ and $b$ in the fitted curve were estimated as follows: for 1977, $a = 5.5$ (se = ±0.84), $b = 2.1$ (se = ±0.18); for 1978, $a = 5.0$ (se = ±1.9), $b = 2.2$ (se = ±0.33). Differences between years were not statistically significant. Figure 4 illustrates the goodness-of-fit of the model for describing the pattern of moult score data from the two years.

Using linearized scores from the fitted curve produced estimates close to those for Type 1 data and for Type 2 data using the modified model, effectively removing the bias in estimates arising from non-linearity.

Comparison of captive and wild birds

The estimated moult duration in captive birds was 85 days (se = ±2.0) compared to 100 days (se = ±2.0) and 98 days (se = ±6.9) for wild birds in 1977 (difference = 15 days, $z = 3.47, P < 0.001$) and 1978 (difference =
13 days, $z = 1.81, P = 0.07$). However, as noted above, some of this difference may be due to bias in the estimated moult duration in captive birds, which could have been underestimated by as much as 8 days. Even allowing for this, it seems that the captive birds moulted faster than the wild ones. They also started slightly earlier, but not significantly so.

**DISCUSSION**

One major finding of our analysis, confirming an earlier study on the Bullfinch *Pyrrhula pyrrhula*, is that different estimates of moult timing and duration are obtained depending on the types of data used (Newton & Rothery 2000). Estimates based solely on moult scores give faster moult rates and later start dates than estimates that include non-moulting birds, and faster and later estimates still than those based solely on three categories of birds: not started, in moult and finished. By using data from birds retrapped at different stages of moult, the latter emerged as the most accurate. This is an important finding because most previous studies of avian moult are based on moult scores alone, so may be liable to error. The error arises mainly from the non-linear increase in the moult score. We show in this paper that, after allowing for non-lin-
**Moult in adult Starlings**

It may be largely because of the problem of non-linearity that Ginn and Melville (1983) obtained, using scores alone, an estimate of moult duration of about 80 days from Starlings in southern England, a shorter period than recorded in our study. Juvenile Starlings from two localities in Scandinavia, and studied under constant daylength in captivity, took on average 55 days and 42 days respectively to moult (Lundberg & Eriksson 1984). Dawson (1994) estimated moult duration as 90 days for captive adult birds obtained near Monks Wood and kept at constant daylength. Although in the individuals in these different studies moult duration was recorded accurately, differences in area of origin, daylength regime, migratory habit and age-class between studies mean that the results are not comparable with ours.

A notable feature of our wild Starlings was the narrowness of the period in which birds started to moult. This was in turn due partly to the fact that laying was highly synchronized in this population, and normally only one brood was raised (unpubl. data). Most young fledged in late May, after which the adults started moult. The slightly earlier start to moult in captive birds may be because they did not breed. There was no evidence in our birds for arrested moult, as described for some individuals by Evans (1986). We have no explanation of the difference in moult duration between our wild and captive birds, although the captives may have had a more consistently good protein-rich food-supply than the wild birds. At the start of moult in the wild, the main invertebrate foods decrease in availability and consumption of plant-based foods increases (Feare 1984). Plant-based foods appear inferior for body mass maintenance (Feare &

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**Figure 3.** Individual standardized moult scores plotted against estimated proportion of time into moult, together with the average curve for ten captive Starlings. For clarity, scores on the same bird have not been joined.

Table 2. Estimated moult parameters for wild Starlings using three different data types and models (see text).

<table>
<thead>
<tr>
<th>Year</th>
<th>Type</th>
<th>Start (se)</th>
<th>SD (se)</th>
<th>Duration (se)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>1</td>
<td>6 June (6.3)</td>
<td>6.3 (0.81)</td>
<td>100 (2.0)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>9 June (1.2)</td>
<td>9.2 (0.53)</td>
<td>92 (1.8)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>18 June (2.1)</td>
<td>7.8 (0.47)</td>
<td>66 (4.1)</td>
</tr>
<tr>
<td></td>
<td>2NL</td>
<td>6 June (1.7)</td>
<td>7.7 (0.47)</td>
<td>101 (2.0)</td>
</tr>
<tr>
<td></td>
<td>2L</td>
<td>6 June (1.0)</td>
<td>7.7 (0.45)</td>
<td>102 (1.6)</td>
</tr>
<tr>
<td></td>
<td>3L</td>
<td>5 June (1.5)</td>
<td>8.0 (0.56)</td>
<td>103 (3.0)</td>
</tr>
<tr>
<td>1978</td>
<td>1</td>
<td>2 June (3.4)</td>
<td>9.7 (2.0)</td>
<td>98 (6.9)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>6 June (2.2)</td>
<td>8.9 (1.0)</td>
<td>82 (4.0)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>14 June (3.1)</td>
<td>7.4 (0.77)</td>
<td>65 (6.0)</td>
</tr>
<tr>
<td></td>
<td>2NL</td>
<td>2 June (2.8)</td>
<td>8.4 (0.88)</td>
<td>95 (5.4)</td>
</tr>
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<td></td>
<td>2L</td>
<td>2 June (2.2)</td>
<td>8.4 (0.86)</td>
<td>95 (4.2)</td>
</tr>
<tr>
<td></td>
<td>3L</td>
<td>3 June (3.0)</td>
<td>7.9 (0.88)</td>
<td>92 (5.5)</td>
</tr>
</tbody>
</table>

2NL: application of the model modified to allow for non-linear increase to Type 2 data. Estimates of model parameters a and b for the fitted curve as follows. 1977: a = 5.5 (se = ±0.84), b = 2.7 (se = ±0.18); 1978: a = 5.0 (se = ±1.9), b = 3.3 (se = ±0.33). 2L, 3L: application of the model using Type 2 and Type 3 data respectively with linearized scores from fitted model in 2NL.
McGinnity 1986) and may also be inferior for the energy and protein requirements of moult.

The only other study of moult in wild Starlings known to us, and using the same analytical methodology as ours, was that by Cooper and Underhill (1991) in South Africa. Based on percentage feather mass growth (PFMG), adult birds started moult on 8 November (se = ±1.7), equivalent to 8 May in the northern hemisphere, with a standard deviation of 15.4 days (se = ±0.7) and duration of 108 days (se = ±2.7). The larger spread in date of onset could be due to multiple broods or a reduced synchrony, both of which could result from the smaller amplitude in the annual cycle of daylength at the lower latitude. The greater duration fits the general trend towards longer moult at lower latitudes (shown also by the birds in Sweden mentioned above).

We are grateful to Les Underhill, Tim Sparks and to two referees for helpful comments on the manuscript.

REFERENCES


APPENDIX

Modification of model of avian moult to allow for non-linear increase in moult score

In the model of Underhill and Zucchini (1988), the moult score of a bird captured at time \( t \) and which started moult at time \( t' \) is given by:

\[ s = \frac{(t' - t)}{T}, \quad t < t' < t + T \]

where \( T \) denotes the duration of moult.

If \( f(t) \) denotes the probability density function (pdf) of
the time of onset of moult, then the pdf of the moult score of a bird in moult at time $t_i$ is given by:

$$q(s_i) = T f (t_i - T s_i), \quad 0 < s_i < 1$$

For non-linear increase the score at time $t_i$ can be written as:

$$s_i = g \{ (t_i - t) / T \}, \quad t < t_i < t + T$$

where $g(.)$ is a non-linear function. The pdf of the moult score is then given by:

$$h(s_i) = 1 / |\partial g / \partial t| f (t_i - T g^{-1}(s_i)), \quad 0 < s_i < 1$$

where $g^{-1}$ denotes the inverse of the function $g$ and $|\partial g / \partial t|$ denotes the absolute value of the partial derivative of $g$ with respect to $t$.

The likelihood for type 2 data is then given by:

$$L = \prod_{i=1}^{J} \prod_{j=1}^{I} p_j \prod_{k=1}^{K} h(s_j) \prod_{k=1}^{K} R_k$$

where the three product terms refer to birds in the categories 'not started moult', 'in moult' and 'completed moult', $P_i$ denotes the probability that a bird has not started moult at time $t_i$ and $R_k$ denotes the probability that a bird has completed moult at time $t_k$. 

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