The conflict between moult and migratory fat deposition: a photoperiodic experiment with bluethroats

ÅKE LINDSTRÖM*†, SERGE DAAN* & G. HENK VISSER*‡

*Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

‡Centre for Isotope Research, University of Groningen, Nijenborgh 4, 9747 AG Groningen, The Netherlands

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Abstract. The post-breeding moult and fat deposition of adult male bluethroats, *Luscinia svecica*, were studied in captivity. One group (Control group) was held under light conditions simulating the natural light regime of their moulting grounds at 66°N latitude. The light regime of another group (Shifted group) was similar to the Control group, but shifted 1 month forward, simulating light conditions further into autumn. All birds had food ad libitum. In addition, comparisons were made with free-living bluethroats. There were no differences in moult performance (start and speed) between the Control group and the Shifted group, and moult was similar to that of free-living birds. The start of moult may be endogenously controlled and set earlier in the season so the change in light regime for the Shifted group may have come too late to influence moult performance. The rate of moult may also be inflexible, in spite of the imposed time stress. In addition, bluethroats may moult so fast that further acceleration would hamper flight manoeuvrability and feeding efficiency. Whereas the Control group birds first started to deposit fat when moult was finished, as free-living birds do, the Shifted group birds started fat deposition in mid-moult. Also, the fat deposition rate following completion of moult was higher in the Shifted group. Thus, adult bluethroats can adjust the timing and speed of fat deposition in relation to moult and time of season. Such flexibility should be advantageous for migratory birds moulting at high latitudes where time available between breeding and migration is short.

Many bird species in temperate regions breed, moult and put on fat for autumn migration in the course of the summer. The energetic and behavioural demands on each of these activities are high. There is usually no or little overlap between reproduction and moult (Payne 1972; Murton & Westwood 1977). Should moult and breeding nevertheless overlap, as for instance in doves and pigeons, moult is normally carried out at a reduced rate (e.g. Murton & Westwood 1977; Boddy 1983; Morton & Morton 1990). The time interval needed for successful breeding is probably hard to change and it is reasonable to assume that short-lived passerines, for example, will give priority to breeding. Therefore, in a period of time stress, we would expect small passerines to adjust primarily, if possible, moult, fat deposition or both. (As far as moult is concerned we consider

here species that moult all body feathers and flight feathers after breeding.)

Should the time available after breeding be limited, or should the cost of not having finished moult and fat deposition increase steeply at the end of summer, birds have three principal options of how to deal with the time stress imposed on moult and fat deposition. First, they could skip or postpone one or both of these activities. Second, they could speed up or restrict the extent of moult and fat deposition. Third, they could let the activities overlap in time, that is, they could put on fat during moult.

(1) Considering the importance of both moult and fat deposition, especially for birds aiming for a long migration, omitting or postponing these activities may have severe effects on survival. Some species, though, are known to have a 'moult migration' where the whole moult, or parts of it, is carried out at stopover sites along the migration route (e.g. Ellegren & Staav 1990a; Jehl 1990).

†Present address: Department of Ecology, Animal Ecology, Ecology Building, S-22362 Lund, Sweden.

(2) Laboratory studies have shown that birds may adjust both the start and speed of post-breeding moult in relation to daylength (Blackmore 1969; Dolnik & Gavrilov 1980; Moore et al. 1982). Also, late starting individuals moult faster, especially in species with relatively slow moult (references in Dolnik & Gavrilov 1980; see also Morton & Morton 1990; Meijer 1991). Thus, many birds have the option to accelerate moult if time runs short. In some species, however, moult speed is unaffected by changes in light regimes (Gwinner 1973; Chilgren 1978; Dolnik & Gavrilov 1980). In many passerine species, moult is so fast that flightlessness may occur during the most intense part of moult (Haukioja 1971). For these species, many of them breeding at high latitudes, the options of changing the moult performance may be limited. The energy cost of feather production may also be high, especially for small birds (Lindström et al. 1993), and in cold environments thermoregulatory costs and low food abundance may make the energy budget during moult tight (Murton & Westwood 1977). Thus, energetic limitations may also preclude a faster moult.

In some species, especially long-distance migrants, individuals are often found that have arrested their moult prematurely. These birds have normally left several secondaries unmoulted, which is often interpreted as a response to being late in the season (Hyytiä & Vikberg 1973; Norman 1991).

(3) In migratory passerine birds, fat deposition starts either after post-breeding moult is completed (King et al. 1965; Dolnik & Blyumental 1967; Evans 1969; Newton 1969) or in the last phases of moult (Dolnik & Blyumental 1967; Morton & Welton 1973; Morton et al. 1973). The energy demands of both activities are high. Since there is a limited amount of energy an animal can metabolize from its food per day (Kirkwood 1983), and food availability as such may be low, the energy budget may not allow simultaneous moult and fat deposition. Also, the metabolic pathways for the two processes may be antagonistic and overlap will retard both processes (Dolnik & Blyumental 1967). Further, additional mass in the form of fat will hamper the flight performance of a bird (Hedenström 1992). In a moulting bird this would add to an already reduced manoeuvrability stemming from feather replacement (Haukioja 1971). Overlapping moult and fat

deposition may be disadvantageous because of an increased risk of predation and reduced feeding efficiency.

Bluethroats of the subspecies *Luscinia s. svecica* breed in subalpine birch forest in northern Scandinavia (Arheimer 1982). By the end of August the adults commence the migration back to wintering grounds in southwestern Asia (Ellegren & Staav 1990b; Ellegren 1991). During the short summer they breed, undergo a complete moult (Haukioja 1971), and must then prepare themselves for the autumn migration by putting on fat. Earlier studies have shown that feeding conditions may be poor for both adult and juvenile bluethroats at the end of the summer (Lindström et al. 1990). Many adults leave the breeding grounds with a few flight and body feathers still growing (Lindström & Hasselquist 1989). A minority of adults even leave directly after breeding to moult at stopover sites further southeast (Ellegren & Staav 1990a). Thus, adult bluethroats seem to be under both temporal and energy stress in the post-breeding moulting period.

To investigate how adult bluethroats may adjust moult and fattening to time of season, we conducted an indoor experiment on adult bluethroats in which the autumn light regime of shortening days was shifted forward in time. A control group was kept under light conditions similar to those bluethroats normally experience in the wild.

METHODS

We caught bluethroats near Ammarnäs in Swedish Lapland (65°58'N, 16°07'E) between 26 May and 5 June 1991, under licence from the National Swedish Environmental Protection Board and the Malmö/Lund Ethical Committee for Animal Experiments. The birds were brought by car to Lund in south Sweden and then by aeroplane to Groningen in The Netherlands on 10 June. The work in The Netherlands was performed under licence from the Ministry of Agriculture and the University of Groningen (Project BG10191).

The birds (all males) were randomly divided into two groups. Thirteen birds were given a light regime (civil twilight) of 66°N latitude, which meant continuous light until 1 August and from

Figure 1. The night lengths given to the birds of the two experimental groups. The Control group was kept under simulated natural daylengths of 66°N latitude. The Shifted group was shifted 1 month forward in relation to the Control group, simulating light conditions further into autumn.

then on nights of increasing length (Fig. 1). This group is referred to as Controls. The light regime of the other six birds (Shifted group) was similar to the Control group, but shifted 1 month forward, simulating light conditions further into autumn. Thus, they received their first night on 1 July (Fig. 1), that is, 20 days after arrival at the laboratory. The birds were given fresh food *ad libitum* (a mixture of boiled eggs, dry bread, commercial insect food, ground calf hearts, minerals and vitamins containing 23.6 kJ and 29% crude protein per g dry mass), as well as 10–15 mealworms and water daily. They were kept individually in cages (40 × 40 × 40 cm) at +15°C. The unequal number of birds in the two groups was due to the test protocol of a parallel study on the energy costs of moult. For further details on maintenance, see Lindström et al. (1993).

The birds were weighed at 1200–1700 hours every fifth day, and their flight feather moult recorded according to Ginn & Melville (1983). The birds of the different groups were weighed on separate days, and there was no trend over the season for birds to be weighed earlier or later in the day. During the early and late stages of the study, the cages were checked every day for shed feathers to record accurately the start and completion of moult. Moult always started with the shedding of the innermost primary. We used the stage of primary moult (primary score from 0 to 45) as a general measure of moult progress, since primary moult covers most of the moult period.

The moult of body feathers was also recorded (Lindström et al. 1993). Primary moult was considered to be completed when the outermost large primary no longer had waxy sheaths. The complete moult was over when neither body nor flight feathers had waxy sheaths.

Subcutaneous fat loads were scored (0–8) using an extended version of the scale of Pettersson & Hasselquist (1985). In bluethroats studied at a stopover site in east Sweden, body mass was strongly positively correlated with the fat scores recorded with this scale (Ellegren 1989).

The moult, fat levels and body mass of free-living adult bluethroats have been studied in the wild at Ammarnäs within a standardized ringing scheme in 1983–1992 (Lindström 1987). When trapped, these birds were examined for moult, body mass and fat score as described for the captive birds above. In addition, body mass and fat levels were recorded in a few moulting free-living adult bluethroats that had access to food *ad libitum* in the field in 1987–1988. We refer to this largely unpublished data set when appropriate.

RESULTS

Timing and Speed of Moults

In general, the sequence in which feathers were shed, and the growth rate of single feathers, indicate that moult performed by our captive bluethroats was representative of what happens in the wild (Haukioja 1971). Contrary to normal, however, two birds in the control group lost several newly grown primaries and secondaries during the last part of moult. These birds were excluded from the analysis of moult duration and fat deposition.

Neither the start nor the duration of primary moult, nor the duration or the extent of the complete moult, was affected by the difference in light regime (Table I). The Control group started to moult at dates (on average 21 July; Table I) close to those of their conspecifics in the wild (on average 19 July, $N=17$). The duration of primary moult (54 days; Table I) was longer than the 42–45 days reported by Haukioja (1971). Unfortunately, too few wild birds at Ammarnäs have been caught in the final stage of moult to calculate a reliable estimate of primary moult duration. The difference in moult duration between our birds and Haukioja's (1971) may stem from the different calculation methods used.

Table 1. Average start of primary moult, and duration (days) of both primary moult and complete moult (median and range), in bluethroats kept under different light regimes

	Control group ($N=11$)	Shifted group ($N=6$)	<i>U</i> -test <i>P</i>
Start of primary moult	21 July (14 July–8 August)	19 July (17–24 July)	0.451
Duration of primary moult	54 (47–68)	52.5 (48–64)	1.000
Duration of complete moult	61 (52–77)	59.5 (55–71)	0.920

The Control group was held under conditions simulating those of their breeding grounds. The Shifted group was shifted 1 month forward in relation to the Control group.

Timing and Speed of Fat Deposition

The birds of the Control group increased both in body mass and fat score when moult started

(Fig. 2). During the latter part of moult, body mass decreased, but fat levels were stable. In some species the water content of the body is higher

Figure 2. Average body mass and fat score ($\pm$ SD) of male bluethroats before, during and after post-breeding primary moult. Birds were kept under two different light regimes (Fig. 1). The Control group ($N=11$) was kept under simulated natural daylengths of 66°N latitude. The Shifted group ($N=6$) was shifted 1 month forward in relation to the Control group, simulating light conditions further into autumn. For the period of primary moult (hatched), which spans almost the complete period of moult, average values are given for periods spanning a primary score of five. Because there were individual differences in the length of the moult period, the scale during moult is not completely proportional to time. Before and after primary moult, values are given for every 5 days.

Table II. Average changes in body mass and fat scores (median and range) after the completion of primary moult in bluethroats kept under different light regimes

	Control group (N=9)	Shifted group (N=6)	U-test P
Rate of body mass increase (g/day)	0.05 (0.02–0.15)	0.20 (0.06–0.29)	0.013
Rate of fat score increase (score/day)	0.06 (0.00–0.09)	0.09 (0.06–0.20)	0.021
Body mass at end of experiment (g)	19.6 (18.0–21.2)	24.1 (21.0–27.5)	0.003
Fat score at end of experiment	6 (6–7)	8 (7–8)	0.002
Length of post-moult period (days)	18 (10–23)	15 (10–23)	0.547

The Control group was held under conditions simulating those of their breeding grounds. The Shifted group was shifted 1 month forward in relation to the Control group. Only individuals with data for 10 days or more are included.

during than both before and after moult (e.g. Newton 1968; Chilgren 1977; Dolnik & Gavrilov 1979). It is likely that this is why body mass decreased while fat loads were stable in the bluethroats. The completion of primary moult was followed again by increases in both body mass and fat scores. Data were available for all individuals only up to 10 days after primary moult ended (since we wanted to release the birds back to nature as soon as possible). However, for the birds that completed moult early, body mass and fat were recorded for a longer period after moult. In these birds, both body mass and fat scores continued to increase at a slow but steady rate after moult completion (Table II).

The development of body mass and fat levels in the Shifted group during the first half of moult was similar to the corresponding period in the Control group. However, from mid-moult onwards there were significant differences between the two groups. First, both body mass and fat scores increased in the Shifted group from about mid-moult onwards (Fig. 2). Whereas five out of six Shifted birds increased in body mass and fat score from primary score 22 to end of moult, only one and three, respectively, out of 11 Control birds did so (Fisher exact test; $P=0.005$ for mass and $P=0.050$ for fat score). In the Shifted group the median change in body mass and fat score during the second half of moult was +1.7 g (range 0.0–5.0) and +2.25 (0–3), respectively. The corresponding values for the Control group were –1.5 g (–2.7 to 0.1) and 0 (–1 to 1). The differences between the groups were highly

significant (U-test: $U=1.5$, $P=0.002$ and $U=6.5$, $P=0.005$ for mass and fat score, respectively). Second, when primary moult was finished the increase in body mass was about four times faster in the Shifted group than in the Control group, leading to much higher body masses at the end of the study (Table II).

The pattern of body mass changes found in the Control group was qualitatively similar to that of free-living males at Ammarnäs (Fig. 3), although fat levels in the field are generally much lower. It should be noted, however, that only few wild birds were caught in the latter part of moult, and any comparison in that period must be tenuous. Three free-living males that had access to supplementary food all had substantially higher body masses and fat scores than the non-fed free-living birds (Fig. 3).

DISCUSSION

We expected the time-stressed birds (the Shifted group) to respond in at least one of three different ways: (1) skip moult or fat deposition, or both, at least partly, (2) speed up or limit the extent of moult or fat deposition, or both, or (3) start fat deposition before moult was finished.

(1) All bluethroats from both groups moulted in a natural sequence, and they all increased their fat depots after or at the end of moult. Thus, there were no indications that option 1 was favoured.

(2) There were no indications that either timing, speed or extension of moult was affected by the

Figure 3. Average (a) body mass and (b) fat score ($\pm$ SD) of free-living male bluethroats before, during and after post-breeding moult. The birds were caught near Ammarnäs in Swedish Lapland (66°N latitude) 1983–1992. For the period of primary moult (hatched), which spans almost the complete period of moult, average values are given for periods spanning primary scores of five (the last period and the two first periods, respectively) or 10 (the three intermediate periods). All birds caught before moult had started (approximately within 10 days) were lumped into one group. Sample sizes for each period are presented in (a). ○: Free-living bluethroats that had access to food ad libitum. Lines connect individual birds.

shortened daylengths. The Shifted group had their first nights on 1 July, that is, 20 days before they started moult. Thus, they had the possibility (at least theoretically) to use the light cycle as a cue for accelerating onset and speed of moult, should they have experienced themselves as being late in the season. Why then was there no response in moult performance to shortened daylengths?

The birds may not have been susceptible to short daylengths as far as moult performance was concerned. The post-breeding moult in bluethroats may be governed by an endogenous

rhythm (Gwinner 1986), where moult simply follows gonadal regression. Thus, the start of breeding, and thus moult, may be set much earlier in the season and, accordingly, the change in light regime for the Shifted group came too late. The advantage of a relatively fixed date for the start of moult would be to make sure that moult is successfully completed before environmental conditions deteriorate in late summer (Morton & Morton 1990).

In contrast to our results, it has been shown both for chaffinches, *Fringilla coelebs* (Dolnik & Gavrilov 1980) and white-crowned sparrows, *Zonotrichia leucophrys gambelli* (Moore et al. 1982) that post-breeding moult can be changed in relation to daylength when the light regime is changed close to onset of moult. Birds transferred to short daylengths had speeded up moult 30 and 14 days after the shift, respectively. Similar effects on onset and duration of moult have also been found for first autumn birds of several warbler species (Berthold et al. 1970; Gwinner et al. 1971).

The bluethroats of the Shifted group did respond to the shorter days (as indicated by the different body mass patterns, see below), but without changing moult performance. Moult in this species may already be so fast that flightlessness would occur if moult was faster (cf. Haukioja 1971). Losing the ability to fly may be detrimental, as far as both safety and feeding efficiency are concerned. This factor may have set evolutionary constraints to moult speed in birds. It is less clear whether nutritional constraints should confine the speed at which moult can be performed (Murphy & King 1982). The energy cost of feather production in bluethroats is high, though: about two times the basal metabolic rate during peak intensity (Lindström et al. 1993). However, given the favourable ad libitum food situation for our captive birds, and the limited possibility for the birds to expend energy on flying, it seems unlikely that moult speed was limited by a tight energy budget.

Whereas the moults of the Shifted and Control groups were unaffected by the experiment, there were significant differences in the pattern of fat deposition. Following the completion of primary moult, the Shifted group birds deposited fat at a much faster rate. For a bird that is late in relation to its seasonal cycle, a fast fat deposition makes sense, especially in a species that may favour a rapid migration (Alerstam & Lindström 1990; Lindström & Alerstam 1992). The question

remains why the Control group did not put on fat at a similarly high rate to gain the same advantages. An unexplored possibility is that there are costs connected with putting on fat at a high rate.

(3) A major difference between the two groups was that the Shifted group birds started to increase their fat loads when they were half way through primary moult, creating a clear overlap between moult and migratory fat deposition. The controls started their fat deposition when primary moult was over. Thus, bluethroats are able to adjust the timing of autumnal fat deposition within a few weeks of its onset, by using the light:dark cycle as a zeitgeber (in contrast to what was suggested for white-crowned sparrows; King et al. 1963).

A bird moulting as fast as a bluethroat may become almost incapable of flying (Haukioja 1971). Adding fat will further hamper its flight ability (Hedenström 1992), and a fat bird in mid-moult may be more vulnerable to predator attacks, although the risks of fatness remain to be experimentally shown (Witter & Cuthill 1993). Also, feeding efficiency may be reduced for a fat bird. Therefore, if time permits, it may be most advantageous to separate moult and fat deposition. However, late moulting birds, here represented by the Shifted group, may have to accept the costs of overlap of the two activities, to be able to migrate before environmental conditions become detrimental.

An alternative explanation to why the Shifted group started fat deposition relatively earlier is that they adjusted their fat loads to meet the energy demands of longer nights. However, given the long migration distances the bluethroats have to cover in a few autumn months at a very high speed (>100 km per day; Ellegren 1990), there are good reasons to believe that fat deposition for oncoming flights have highest priority. Experiencing longer nights in the course of autumn, which may hamper high fat deposition rates, is something they simply have to live with. In addition, the fat reserves our birds had, even before the late-moult (or post-moult) increase in fat loads started, were more than enough for surviving several nights and days without food (own observations on other captive bluethroats). Thus, we do not believe that fattening for surviving longer nights had any significant influence on the fat loads in our study birds.

Although patterns of body mass and fat loads in the Control group were qualitatively similar to those under natural conditions, the fat levels were higher in captivity than in the wild. Three free-living adult males, supplementary fed with mealworms in Ammarnäs also increased their fat loads substantially during moult (Fig. 3; see also Lindström et al. 1990). Thus, if possible, adult bluethroats both in captivity and in the wild do put on moderate fat loads if feeding conditions permit. The size of fat loads may be seen as a trade-off between risks in terms of increased susceptibility for predator attacks, and benefits in the form of increased probability of surviving periods of food shortage (Lima 1986).

The present study demonstrates that bluethroats are able to adjust the timing of fat deposition to time of season, independently of moult. Such flexibility should be advantageous for migratory birds moulting at high latitudes where the time available between breeding and migration may be short.

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