Fuel deposition and speed of early autumn migration of juvenile Bluethroats *Luscinia s. svecica* leaving their natal area in Swedish Lapland

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——————————————————————————— **Abstract** ———————————————————————————

The period between independence and the early phase of autumn migration is a difficult period for juvenile birds and a relatively poorly known part of the annual cycle. We present data on post-juvenile moult, fuel deposition and speed of early autumn migration of "red-spotted" Bluethroats *Luscinia s. svecica*, studied during 14 years (1984–1997) in Ammarnäs, Swedish Lapland. The juvenile Bluethroats leave their natal site from early August onwards, while still being in active post-juvenile moult. They do not put on any noticeable fuel stores, probably because foraging conditions are generally poor. This is reflected in a very slow initial speed of migration (11–21 km/d) between the natal area and stopover sites in eastern Sweden.

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Introduction

For many migrants it may be important to start the autumn migration as early as possible. There are several reasons for this. Some birds, especially those breeding at high latitudes, must depart before conditions at the summer quarters become too harsh. Migrants may also need to hurry to be able to make use of superabundant food sources along the route (Bibby & Green 1981), or to arrive relatively early at the wintering grounds (Price 1981, Alerstam & Lindström 1990).

However, migratory departure can not take place without preparations. Before they leave, juvenile birds must moult the rather poor body plumage they grew in the nest (Jenni & Winkler 1994). The juveniles also need to put on some fuel for the first migratory flight. Especially at high latitudes and altitudes, moult and fuel deposition must take place when energy expenditure rates are further elevated by low ambient temperatures making thermoregulatory costs high. Thus, the time between independence and migratory departure is a risky and costly period for inexperienced juveniles (Perrins & Geer

1980, Weathers & Sullivan 1989, Lindström et al. 1990, Hansson 1997).

There is large variation in the pattern of fuel deposition prior to leaving the natal site. Juveniles of some species seem to commence migration without, or with very small fuel stores, as found previously in a pilot study on Bluethroats *Luscinia s. svecica* (Lindström et al. 1985, and see Rhyzanovsky 1988b). The same pattern holds for Willow Warblers *Phylloscopus trochilus*, as shown in a Swedish nation-wide study (Lindström et al. 1996). In contrast, juveniles of some species put on substantial amounts of fuel before leaving their natal sites, such as Sedge Warblers *Acrocephalus schoenobaenus* and Reed Warblers *A. scirpaceus* (Gladwin 1963, Bibby & Green 1981, Hall 1996).

Here we present data from a 14-year study of post-juvenile moult and fuel deposition of juvenile Bluethroats in their natal area in Swedish Lapland. We show that juvenile Bluethroats leave well before post-juvenile moult is finished and that they do this without putting on any sizeable fuel stores. We discuss the causes and consequences of this behaviour.

The study species

The nominate race of the Bluethroat *L. s. svecica* ('Red-spotted') breeds in Scandinavia and throughout northern Asia, eastward to Alaska (Cramp 1988, Franz 1998). In Scandinavia, Bluethroats breed primarily in sub-alpine birch forest (Arheimer 1982) along the Fennoscandian mountain ridge, from southern Norway to northernmost Scandinavia and migrate east-southeast in autumn to yet unknown wintering grounds in southern Asia (Ellegren & Staav 1990a). In July and August, juveniles make a partial post-juvenile moult (including body feathers and the lesser and middle wing coverts). The adults make a complete post-breeding moult (Svensson 1984). Most of the moult takes place on the breeding grounds, although a large proportion of the juveniles trapped at early migration stopover sites 200 km away from the nearest breeding grounds have been found to still be in post-juvenile moult (Lindström et al. 1985, Lindström & Hasselquist 1989).

Whereas much attention has been paid to the early stages of Bluethroat autumn migration (e.g., Stolt & Mascher 1962, Lindström et al. 1985, 1990, Ryzhanovsky 1988a,b, Lindström & Alerstam 1992, Ellegren 1990a,b, 1991, Ellegren & Staav 1990a,b), comparatively little is known about the details of post-juvenile moult and early migratory fuelling at departure from the breeding areas (Lindström et al. 1985, Ryzhanovsky 1988a,b).

Methods

Daily trapping of birds was carried out each summer 1984–1997 in sub-alpine birch forest near Lake Tjulträsk, Ammarnäs, in Swedish Lapland (65°58'N, 16°07'E), as a part of the LUVRE project (Enemar et al. 1984). Trapping seasons started on average 16 July (range 15–18 July) and ended on average 19 August (range 13–21 August, once 31 August), with an average length of the trapping season of 34 days (range 27–37 days, but 45 days in 1988). Catching was totally cancelled on average on 3 days per year (range 0–8 days). Twenty-two mist-nets were erected between 0700 and 1300 local time, in the same positions throughout the study. On some days each year, trapping was carried out in the afternoon, normally because rain had prevented trapping in the morning.

After ringing the bird, wing length was measured to the nearest full mm according to Method 3 of Svensson (1984) and body mass was measured to the nearest 0.1 g using a 50-g Pesola spring balance. Visible fat was scored according to the scale of Pettersson & Hasselquist (1985). A bird with fat score 0 has no visible fat, and in fat score 6 the belly and inter-clavicular region (but not the chest) is completely covered with fat. From frequent calibrations between the ringers of our study it is clear that stages 0 and 1 are very difficult to separate, whereas there is a large agreement concerning fat scores 2 and higher. The stage of post-juvenile moult was also recorded (see below). All individuals recaptured one or more days after ringing were examined again.

In late summer, juvenile Bluethroats can be easily separated from adults on their spotted juvenile plumage. Also, the adults almost always have some growing flight feathers. When post-juvenile moult is completed in late August/early September juveniles can still be separated on the buff fringes or dots of the unmoulted greater coverts (Svensson 1984). Body moult of juveniles was scored according to a seven-grade scale (Lindström *et al.* 1985), where a bird in stage 0 (MS0) has not yet started body moult (and outer primaries are not yet fully grown). A bird in MS5 has dropped all the spotted nestling feathers, but some feathers are still growing on the flanks. In MS6 no more feathers are growing. In MS3 most males can be recognised on the emerging blue and orange feathers on their throat and chest. Females can not be safely recognised until they are in MS4.

Statistics were carried out using SYSTAT 6.0.1 (SPSS Inc.) and the Analysis Tools package of Microsoft Excel 7.0a. Parametric tests were used throughout, except when testing fat score data.

Results

A total of 2549 juvenile Bluethroats were trapped and ringed (average 182 birds/year, range 88–395). Of these individuals, 1103 (43 %) were re-trapped at least once the same season, resulting in a total of 2489 controls. N-values differ between analyses due to missing measurements for some individuals.

Post-juvenile moult

Most birds, 90 %, were trapped in MS1-MS4 (Table 1). Partly because few Bluethroats were caught after 10 August, only 6.1 % of the birds were in MS5. Just a single bird in MS6 (moult completed) was recorded (20 August 1986).

Fuel deposition

Average body mass differed significantly between birds in different moult stages (one-way ANOVA,

Table 1. The number of juvenile Bluethroats in different moult stages when ringed in Ammarnäs, Swedish Lapland, in 1984–1997.
Antalet unga blåhakar i olika juvenila ruggningsstadier vid ringmärkningstillfället i Ammarnäs åren 1984–1997.

| Year *År* | Moult stage *Ruggningsstadium* | | | | | | | Total |
	0	1	2	3	4	5	6	
1984	9	110	38	44	103	33	0	337
1985	4	49	34	29	28	6	0	150
1986	2	78	141	68	56	48	1	394
1987	5	72	67	34	16	5	0	199
1988	19	99	44	29	22	18	0	231
1989	31	114	50	35	15	3	0	248
1990	6	24	37	25	22	2	0	116
1991	4	26	22	22	15	8	0	97
1992	6	38	40	22	35	6	0	147
1993	6	24	36	14	7	1	0	88
1994	2	34	73	32	37	3	0	181
1995	3	17	29	31	20	6	0	106
1996	6	39	21	16	18	4	0	104
1997	1	34	25	25	47	13	0	145
Total	104	758	657	426	441	156	1	2543

$F_{[6, 2509]} = 13.64$, $p < 0.001$), but absolute differences were small (Figure 1). Body mass was on average highest at the intermediate moult stages. Also fat score varied significantly between moult stages (Kruskal-Wallis test, [n = 2526]: H = 143.62, p < 0.001, df = 6), but as for body mass, the absolute variation was small (Figure 1).

Among the sexed birds trapped in MS4-5, where departure is likely to be imminent, there was a significant yearly variation in both fat score (Kruskal-Wallis test, males [n = 313]: H = 91.03, p < 0.001, df = 13; females [n = 246]: H = 74.61, p < 0.001, df = 13) and body mass (one-way ANOVA, males: $F_{[13, 297]} = 1.88$, p = 0.032; females: $F_{[13, 231]} = 2.13$, p = 0.013). However, the absolute variation in both fat scores and body mass was small (Table 2). Yearly median fat scores were always either 0 or 1 in both sexes, and yearly averages of body mass varied between 17.0 and 18.1 g in males, and between 16.2 and 17.3 g in females.

There was no significant correlation between the yearly averages of body mass in the two sexes (r = 0.03, p = 0.91), whereas the average fat scores correlated to a high degree (r = 0.83, p < 0.001). Given the small absolute variation in fat scores, and the problems of accurately separating fat scores 0 and 1, it is likely that the correlation in fat scores is the result of different ringers being active in different

years. Clearly, juvenile Bluethroats do not put on any significant amounts of fat at any stage between independence and departure from their natal area.

Ringing recoveries

The ringing in Ammarnäs has resulted in six recoveries and one control that give information about the early phase of autumn migration in the Bluethroats (Figure 2). Clearly, the birds are heading mainly southeast. Four recoveries are from late August/early September along the east coast. Three of these were trapped by ringers at known stopover sites. The fourth bird (12 Sep) was found dead, probably killed by cat. Two inland recoveries (4 and 28 Aug, both killed by cat) give indications of what the birds may do after leaving the Ammarnäs area (see further below).

Departure from the natal area

The actual departure of individual Bluethroats from our study site is never seen, but departure is apparent from the gradual decrease in numbers present in August (Figure 3). Trapping numbers peak in the last days of July and some birds may start to depart already then. Support for such early movements come from a bird ringed by us on 20 July when in
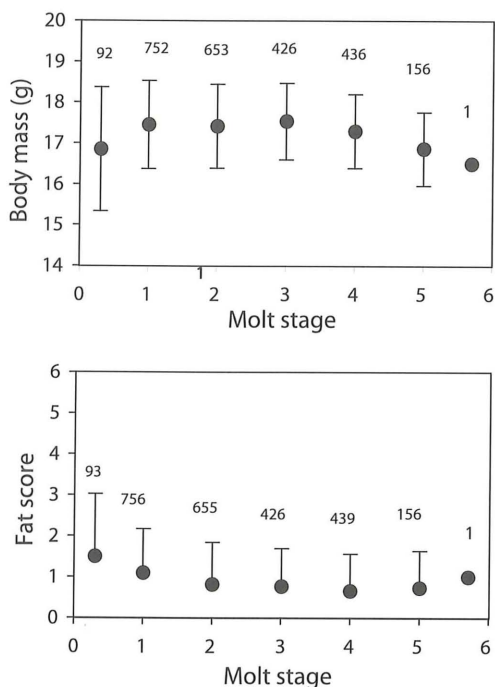
Figure 1. Average body mass and fat score (± standard deviation) of juvenile Bluethroats in relation to moult stage. Data for both sexes and all years have been pooled. The symbols for moult stage 0 and 6 have been moved slightly sideways for sake of clarity. Figures above symbols are n-values.
Genomsnittlig vikt och fettklass (± standardavvikelse) hos unga blåhakar i olika ruggningsstadier. Data för båda könen och alla år är inkluderade. Symbolerna för ruggningsstadium 0 och 6 har flyttats något i sidled för öka figurens läsbarhet. Antalet fåglar i varje ruggningsstadium anges också.

MS1, which was recovered 4 August the same year, 59 km away from the ringing site in a southerly direction (Figure 2). This bird moved a considerable distance despite being in the early post-juvenile moult. There is probably a continuous departure of birds from early August onwards. At 18 August, the average number of birds trapped was only half of that in late July (Figure 3). Further information of what the birds may do after leaving Ammarnäs come from a second recovery. A young bird ringed 8 August in MS2 was recovered 28 August outside Arvidsjaur, 140 km eastsoutheast of Ammarnäs, but still more than 100 km from the coast. Thus, there are two recoveries showing that after leaving Ammarnäs some birds stop at sites between their natal area and known stopover sites near the coast.

Discussion

Moult and migration

Most birds probably leave Ammarnäs when in moult stages MS3–MS5. As shown by one recovery, some may leave even earlier. The fact that birds in MS5 are recorded frequently on stopover along the Swedish east coast in late August (Lindström & Hasselquist 1989) shows that Bluethroats indeed migrate while in post-juvenile moult. Although a moult-migration overlap put high energetic demands on the birds (both fuel deposition and moult cost energy), the phenomenon has been reported for several passerine species (Lindström et al. 1985, 1996, Ryzhanovsky 1988a, Norman 1990, Jenni & Winkler 1994, Merilä 1997).

Fuel deposition and departure

Juvenile Bluethroats were heaviest in mid-moult, although the fat scores were the lowest. This seems contra-intuitive, since fat scores normally are highly correlated with body mass (e.g. Pettersson & Hasselquist 1985, Ellegren 1989). The explanation is most likely that during moult the birds have an increased amount of water (blood) in their bodies (Chilgren 1977). Thus, significant changes in body mass during moult may have little to do with changes in fat stores (Lindström et al. 1994, 1996).

As far as fuel deposition for migration is concerned, juvenile Bluethroats do not put on fuel stores of any significance before departure from their natal area. Almost all birds had fat scores 0–2 and the average body mass was around 17–18 g in males and 16–17 g in females in the last stages of moult (close to departure). Possibly, Bluethroats do not put on any significant fuel stores until reaching stopover sites along the Swedish east coast, 200–300 outside the breeding range (Lindström et al. 1985, Ekholm 1988, Ellegren 1991). There, average body masses of arriving birds are around 17 g in males and 16 g in females, but close to departure many birds reach 19–20 g and some birds are found weighing 20–24 g (Stolt & Mascher 1962, Lindström et al. 1985, Ekholm 1988, Ellegren 1991, Kvist et al. 1993). Even higher values have been found: up to 26 g in birds during supplemental feeding in the field, and 33 g in captive Bluethroats (reviewed by Kvist et al. 1993). Clearly, Bluethroats start out on migration more or less without fuel stores. Lindström *et al.* (1996) found that also in juvenile Willow Warblers, the first part of autumn migration is carried out with small fuel stores.

Table 2. Average fat score and body mass (mean, standard deviation and n-values) of male and female juvenile Bluethroats in moult stages 4 and 5. At these late moult stages the birds are likely to be very close to departure. For fat score also the median (md) is given.
Genomsnittlig fettklass och vikt (medelvärde, standardavvikelse och antal) hos hanar och honor av unga blåhakar i ruggningsstadium 4 och 5. För fåglar i denna sena fas av ruggningen är troligen bortflyttningen nära förestående. För fettklass presenteras även medianvärden (md).

| | Males *Hanar* | | | | Females *Honor* | | | |
| | Fat score *Fettklass* | | Body mass *Vikt* (g) | | Fat score *Fettklass* | | Body mass *Vikt* (g) | |
Year *År*	Mean *Medel* (s.d., n)	Range (md)	Mean *Medel* (s.d., n)	Range	Mean *Medel* (s.d., n)	Range (md.)	Mean *Medel* (s.d., n)	Range
1984	0.88 (0.52, 76)	0–2 (1)	17.7 (0.8, 75)	15.4–20.0	1.03 (0.55, 60)	0–3 (1)	17.1 (0.9, 60)	15.0–19.0
1985	0.06 (0.25, 16)	0–1 (0)	17.7 (0.6, 16)	16.2–18.5	0.53 (0.64, 15)	0–2 (0)	17.1 (0.7, 15)	16.0–18.3
1986	0.82 (0.69, 56)	0–2 (1)	17.3 (0.9, 56)	14.5–19.1	0.96 (0.70, 46)	0–3 (1)	16.5 (0.8, 45)	15.0–18.0
1987	1.29 (1.07, 14)	0–4 (1)	17.7 (1.2, 14)	15.5-19.9	0.86 (0.69, 7)	0–2 (1)	17.2 (0.9, 7)	15.9–18.5
1988	0.70 (0.63, 23)	0–2 (1)	17.0 (1.1, 23)	15.1–19.2	1.00 (0.89, 16)	0–3 (1)	16.7 (0.5, 16)	15.9–17.9
1989	1.25 (0.46, 8)	1–2 (1)	17.9 (0.6, 8)	17.3–18.8	1.00 (0.94, 10)	0–3 (1)	16.7 (1.1, 10)	15.6–18.7
1990	0.93 (0.70, 15)	0–2 (1)	17.5 (1.0, 15)	15.5–19.1	1.00 (0.00, 6)	1 (1)	16.2 (0.7, 6)	15.2–17.3
1991	0.75 (0.45, 12)	0–1 (1)	17.6 (0.7, 12)	16.0–18.6	0.70 (0.48, 10)	0–1 (1)	16.7 (0.9, 10)	15.4–18.7
1992	0.59 (0.50, 22)	0–1 (1)	17.2 (0.8, 22)	15.6–19.3	0.82 (0.60, 11)	0–2 (1)	17.3 (0.8, 11)	15.6–18.3
1993	0.80 (0.44, 5)	0–1 (1)	17.1 (1.3, 5)	15.8–18.8	1.00 (0.00, 2)	1 (1)	16.8 (0.8, 2)	16.2–17.4
1994	0.38 (0.62, 16)	0–2 (0)	17.5 (0.9, 16)	15.5–18.9	0.48 (0.60, 21)	0–2 (0)	16.6 (0.5, 21)	15.4–17.3
1995	0.20 (0.45, 5)	0–1 (0)	18.1 (0.9, 5)	16.9–19.5	0.12 (0.33, 17)	0–1 (0)	16.7 (0.9, 17)	15.0–18.6
1996	0.15 (0.38, 13)	0–1 (0)	17.8 (0.8, 13)	16.4–19.2	0.29 (0.49, 7)	0–1 (0)	16.9 (0.6, 7)	16.1–17.9
1997	0.09 (0.30, 32)	0–1 (0)	17.5 (0.7, 31)	16.2–18.9	0.00 (0.00, 18)	0 (0)	16.6 (0.7, 18)	15.6–18.0
Total	0.67 (0.66, 313)	0–4 (1)	17.5 (0.9, 311)	14.5–20.0	0.75 (0.68, 246)	0–3 (1)	16.8 (0.8, 245)	15.0–19.0

But why do they not put on any fuel? We can exclude that there are basic physiological mechanisms making fuel deposition and moult incompatible, since juvenile Bluethroats during moult do put on substantial fuel stores when offered food *ad libitum* in the field (Lindström et al. 1990). The question is then whether juveniles 1) choose not to become fatter (to avoid potential costs of being heavy, such as increased predation risk and higher cost of locomotion, Witter & Cuthill 1993), or 2) whether generally poor conditions in combination of poor feeding capacity (Weathers & Sullivan 1989) simply preclude more substantial fuel deposition, especially since the birds also must spend energy on moult and thermoregulation.

We believe that juvenile Bluethroats have small fuel stores because they do have a difficult time in the post-juvenile moult period. Night temperatures in

Figure 2. Recoveries (circles) of juvenile Bluethroats ringed in Ammarnäs (star) and recovered during their first autumn migration (recovery date is shown for each recovery). The bird recovered in Finland was ringed as a juvenile, but recovered as an adult two years later. One bird was ringed as a juvenile near the coast (30 Aug) and recovered in Ammarnäs as a breeding bird the following year.

Återfynd (cirklar) av unga blåhakar ringmärkta i Ammarnäs (stjärnan) och återfunna samma höst (återfyndsdatum visas för respektive fynd). Fågeln i Finland återfanns dock som adult, två år efter märkningen som ungfågel, och en fågel (30 Aug) ringmärktes som ungfågel vid kusten och återfanns som häckande fågel i Ammarnäs påföljande år.

Ammarnäs in mid August are normally below +5°C and regularly below 0°C (Hansson 1997, pers. obs.). In a one-year study in Ammarnäs, Hansson (1997) found that poor weather, specifically strong winds and heavy rain, had considerable negative effects on the (already small) fuel stores of juvenile Bluethroats. In addition, a series of feeding experiments in Ammarnäs have all resulted in birds putting on considerable fuel stores when presented with large amounts of food (Lindström *et al.* 1990, Hansson 1997). It is therefore reasonable to believe that the energetic conditions for juvenile Bluethroats at their natal sites are normally very poor, precluding substantial fuel deposition before departure.

If the energetic conditions in general are poor at their natal site, juvenile Bluethroats probably do best in leaving as soon as possible. The departure at even early stages of moult may be the result of such a selection pressure. Hansson (1997), who also studied Bluethroats in Ammarnäs, found that at a given date, birds that had come further in moult were less likely to be re-trapped the same season. This indicates that the Bluethroats may still rather depart at a certain moult stage than at a certain date. It is
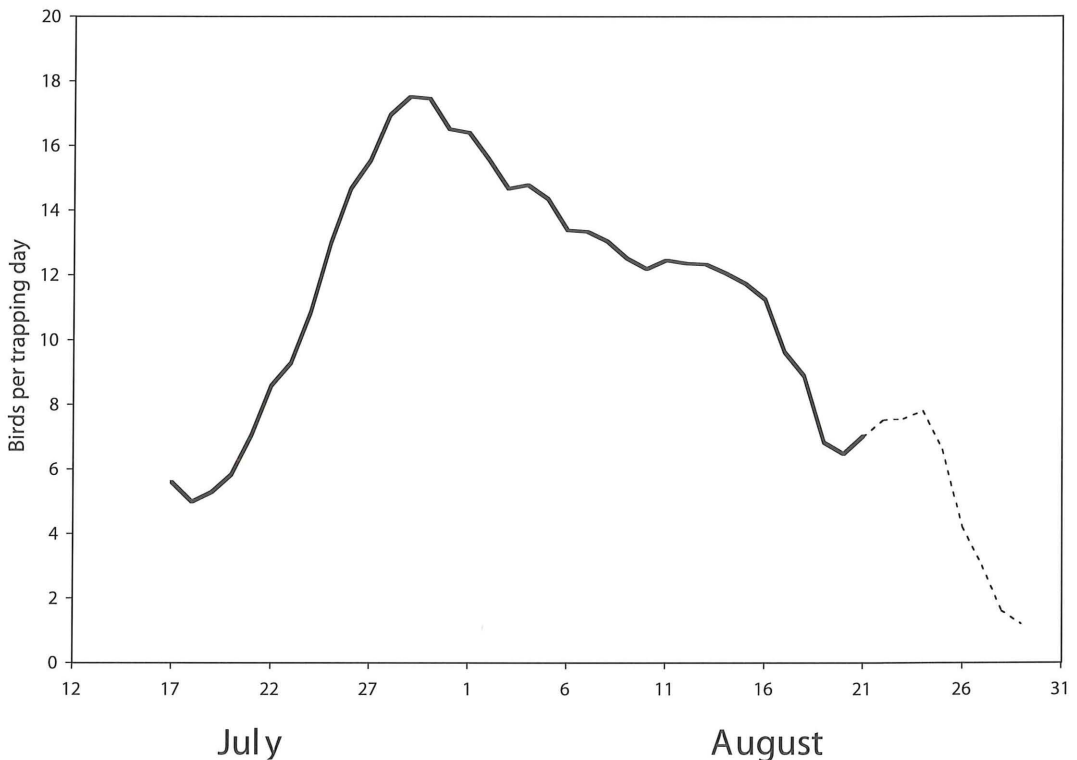
Figure 3. Average daily number of juvenile Bluethroats trapped (ringed birds as well as all retraps) during standardised trapping in Ammarnäs during July and August in 1984–1997. The line shows running five-day averages. The data has been corrected for the number of years trapping was carried out any given day and hence indicate the average number of birds trapped in the study area at any given date. Between 17 July and 17 August, data is based on 10–14 years of trapping for each day. The period 18–21 August is based on 4–6 years of trapping. From 22 August onwards data is based on only one year (as indicated by the stippled line).

Genomsnittligt antal unga blåhakar fångade i den standardiserade nätfångsten i Ammarnäs i juli och augusti 1984–1997. Linjen visar rullande femdagarsmedelvärde. I analysen har tagits hänsyn till attt fångsten en given dag ställts in under vissa år (på grund av regn). Perioden 17 juli–17 augusti baseras kurvan på 10–14 års fångst för varje datum. Perioden 18–21 augusti har fångst bedrivits endast under ett år (indikeras av den streckade kurvan).

noteworthy, however, that of the birds that were supplementary fed in Ammarnäs and became very fat (Lindström et al. 1990, unpubl. data, Hansson 1997), many were still present at the feeding sites when most other birds had left Ammarnäs. This indicates that both physiological (moult) and environmental variables (food availability) influence when Bluethroats depart from their natal area.

Speed of migration

Speed of migration is the speed at which a bird moves between two sites, including the time spent on fuel deposition before and between migratory flights (Alerstam & Lindström 1990). The speed of

migration is to a large degree dependent on the rate of fuel deposition (Lindström 1991). In juvenile Bluethroats, the speed of migration the first part of the trip is very slow. The birds start departing from Ammarnäs already in late July and most likely the main departure is 10–20 August. However, the first Bluethroats do not start to appear at the nearby stopover sites (200–300 km away) until 20 August, with median trapping dates at most sites around 1 September (Douhan 1986, Ellegren 1990b, 1991). If we assume a median departure from Ammarnäs on either 10 or 20 August, and an average migration distance of 250 km, the average speed of migration to the stopover sites is only 11–21 km/d. This is considerably slower than the migration speed of

Bluethroats further away along the migration route. Based on ringing recoveries, Ellegren (1990b) estimated the speed of migration of juvenile Bluethroats to be 30–40 km/d between stopover sites in eastern Sweden, 40–65 km/d from Sweden to Finland, and around 100 km/d during migration in Asia.

The reason for the initially very slow speed of migration seems clear. Poor feeding conditions in combination with foraging inexperience (cf. Weathers & Sullivan 1989), and the cost of moult and thermoregulation in addition, preclude fast fuel deposition and result in very slow migration. It is not clear whether the gradual increase in migration speed of Bluethroats along the route depends on improving foraging skills, or richer resources, or a combination of these factors (Ellegren 1990b, Lindström & Alerstam 1992).

What do the Bluethroats do after leaving Ammarnäs?

There are on average about 10–20 days between departure from Ammarnäs and the appearance at stopover sites along the Swedish east coast. What do the Bluethroats do then? It is not easy to determine whether the birds leaving Ammarnäs are involved in some kind of exploratory post-natal dispersal or whether they actually commence migration. Apart from the single short-distance (<100 km) recovery described, we do not know in which direction birds move *if* they first make short-distance movements. Southeasterly directions are the most likely, however, since in westerly directions the birds mainly meet large areas of seemingly unsuitable alpine terrain. However, in southeasterly directions, the birds mainly meet spruce forest and bogs, both probably being poor habitats for migrating Bluethroats.

The most plausible scenario is that the Bluethroats cross the inland of northern Sweden in short flights. First, the fuel stores they have when leaving Ammarnäs simply do not allow any longer flights. A young male Bluethroat with fat score 1 weighs on average 17.5 g (Table 2). Assuming a wing span of 22 cm and an aspect ratio of 4.5 (A. Hedenström, pers. comm.), a fuel store of 0.4 g (Ellegren 1989) and that 70% of this is fat (the rest is protein, Klaassen et al. 2000), the bird would only be able to fly about 90 km, if it exhausted all its fuel (Pennycuick 1989). Hence, it simply would not make it to the coast in one flight. In addition, it is not likely that the bird would like to use all its fuel, leaving no spare energy to be used at arrival to stopover sites of unknown quality. Second, there are at least two recoveries showing that some Bluethroats land at sites between Amma-

rnäs and the coast. The likelihood of recovering birds from the inland of northern Sweden must be considered small given the low number of people living there and the lack of trapping activities of birds on passage. Therefore, short-distance hopping through the forested inland may be the common strategy, but there is a strong need for studies from the inland of northern Sweden to confirm, or reject, this hypothesis.

References

Alerstam, T. & Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. Pp. 331–351 in *Bird Migration: The Physiology and ecophysiology*. Gwinner, E. (ed) Springer-Verlag, Berlin.

Arheimer, O. 1982. Blåhakens (*Luscinia svecica*) häckningsbiologi i fjällbjörkskog vid Ammarnäs. *Vår Fågelvärld* 41:249–260.

Bibby, C. J. & Green, R. E. 1981. Autumn migration strategies of reed and sedge warblers. *Ornis Scand*. 12:1–12.

Chilgren, J. D. 1977. Body composition of captive White-crowned Sparrows during post-nuptial molt. *Auk* 94:677–688.

Cramp, S. (ed.) 1988. *Handbook of the birds of Europe, the Middle East and North Africa*. Vol. V. Oxford University Press, Oxford.

Douhan, B. 1986. Ringmärkning av blåhake i Roslagen. *Roskarlen* 8:19–29. (In Swedish)

Ekholm, A. 1988. Viktutveckling hos rastande blåhakar. *Fåglar i X-län* 19:14–26. (In Swedish)

Ellegren, H. 1989. Weight and wing length as indicator parameters for accumulated fat levels in migrating birds – a methodological study of autumn migrating Bluethroats. *Vår Fågelvärld* 48:75–85. (In Swedish with English summary)

Ellegren, H. 1990a. Timing of autumn migration in Bluethroats *Luscinia s. svecica* depends of timing of breeding. *Ornis Fennica* 67:1–5.

Ellegren, H. 1990b. Autumn migration speed in Scandinavian Bluethroats *Luscinia s. svecica*. *Ring. & Migr*. 11:121–131.

Ellegren, H. 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. *Ornis Scand*. 22:340–348.

Ellegren, H. & Staav, R. 1990a. The migration of the Bluethroat, *Luscinia s. svecica* – a recovery analysis based on birds ringed in Finland and Sweden. *Vår Fågelvärld* 49:323–336. (In Swedish with English summary)

Ellegren, H. & Staav, R. 1990b. Moult migration in the Bluethroat. *Vår Fågelvärld* 49:279–292. (In Swedish with English summary)

Enemar, A., Nilsson, L. & Sjöstrand, B. 1984. The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. *Ann. Zool. Fennici* 21:321–338.

Franz, D. 1998. *Das Blaukehlchen: von der Rarität zum Allerweltsvogel?* AULA, Wiesbaden.

Gladwin, T. W. 1963. Increases in weight of Acrocephali. *Bird Migration* 2:319–324.

Hall, S. 1996. The timing of post-juvenile moult and fuel deposition in relation to the onset of autumn migration in Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus*. *Ornis Svecica* 6:89–96.

Hansson, B. 1997. The influence of weather and food supply on condition and behaviour of juvenile Bluethroats *Luscinia svecica* in northern Sweden. *Ornis Svecica* 7:11–20.

Jenni, L. & Winkler, R. 1994. *Moult and ageing of European passerines*. Academic Press, London.

Klaassen, M., Kvist, A. & Lindström, Å. 2000. Flight costs and fuel composition of a bird migrating in a wind tunnel. *Condor* 102:445-452.

Kvist, A., Lindström, Å. & Tulp, I. 1993. Excessive migratory fattening in a captive Bluethroat *Luscinia s. svecica*. *Ornis Svecica* 3:161–164.

Lindström, Å. 1991. Maximum fat deposition rates in migrating birds. *Ornis Scand.* 22:12–19.

Lindström, Å. & Alerstam, T. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *Am. Nat.* 140:477–491.

Lindström, Å., Bensch, S. & Hasselquist, D. 1985. Autumn migration strategy of young Bluethroats, *Luscinia svecica*. *Vår Fågelvärld* 44:197–206. (In Swedish with English summary)

Lindström, Å., Daan, S. & Visser, G. H. 1994. The conflict between moult and migratory fat deposition: a photoperiodic experiment with bluethroats. *Anim. Behav.* 48:1173–1181.

Lindström, Å. & Hasselquist, D. 1989. Varför mata blåhakar med mjölmask? *Roskarlen* 11:8–16. (In Swedish)

Lindström, Å., Hasselquist, D., Bensch, S. & Grahn, M. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. *Anim. Behav.* 40:453–461.

Lindström, Å., Hedenström, A. & Pettersson, J. 1996. The autumn migration of Willow Warblers *Phylloscopus trochilus* in Sweden: results from a nation-wide co-operative project. *Ornis Svecica* 6:145–172.

Merilä, J. 1997. Fat reserves and moult-migration overlap in goldcrests, *Regulus regulus* – A trade-off? *Ann. Zool. Fennici* 34:229–234.

Norman, S. C. 1990. A comparative study of post-juvenile moult in four species of Sylvia warblers. *Ring. & Migr.* 11:11–22.

Pennycuick, C. J. 1989. *Bird Flight Performance*. Oxford University Press, Oxford.

Perrins, C. M. & Geer, T. A. 1980. The effect of sparrowhawks on tit populations. *Ardea* 68:133–142.

Pettersson, J. & Hasselquist, D. 1985. Fat deposition and migration capacity of Robins *Erithacus rubecula* and Goldcrests *Regulus regulus* at Ottenby, Sweden. *Ring. & Migr.* 6:66–76.

Price, T. 1981. The ecology of the Greenish Warbler *Phylloscopus trochiloides* in its winter quarters. *Ibis* 123:131–144.

Ryzhanovsky, V. N. 1988a. Postnesting period in life of *Luscinia svecica*. 1. Disintegration of broods and postjuvenile molting. *Zool. Zhurnal* 67:68–78.

Ryzhanovsky, V. N. 1988b. Postnesting period in life of *Luscinia svecica*. 2. Postnesting migrations, development of migration state and autumn migration. *Zool. Zhurnal* 67:417–425.

Stolt, B.-O. & Mascher, J. W. 1962. Untersuchungen an rastenden Blaukelchen (*Luscinia s. svecica*) in Uppland, Mittelschweden, unter besonderer Berücksichtigung der Körpermasse und Gewichtsvariationen. *Vogelwarte* 21:319–326.

Svensson, L. 1984. *Identification Guide to European Passerines*. 3rd edition, Stockholm.

Weathers, W. W. & Sullivan, K. A. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monogr.* 59:223–246.

Witter, M. S. & Cuthill, I. C. 1993. The ecological cost of avian fat storage. *Phil. Trans. R. Soc. Lond.* B. 340:73–92.

Sammanfattning

Fettupplagring och inledande höstflyttningshastighet hos juvenila blåhakar Luscinia s. svecica *i Lappland*

Att starta flyttningen mot övervintringskvarteren så tidigt som möjligt kan vara viktigt av flera anledningar. Förhållandena i häckningsområdet försämras snabbt ju närmare hösten kommer, fåglarna vill kunna utnyttja goda rastplatser på vägen (Bibby & Green 1981) och det kan vara viktigt att snabbt nå övervintringsområdet (Alerstam & Lindström 1990). Men att flytta iväg kräver förberedelser. Ungfåglarna hos många småfåglar byter ut sin första fjäderdräkt innan flyttningen och de behöver ackumulera energi i form av fett att använda som bränsle under flyttningen. Det är känt att tidsperioden mellan att ungfåglarna blir oberoende av sina föräldrar och att flyttningen påbörjas är en riskfylld och kostsam tid.

Variationen är stor i hur ungfåglar löser detta problem. Hos vissa arter, såsom lövsångare, lämnar ungfåglarna födelseplatsen med mycket små fettreserver (Lindström et al. 1996), medan hos till exempel sävsångare och rörsångare lämnar ungfåglarna sina födelseplatser med relativt stora fettreserver (Bibby & Green 1981, Hall 1996). Här presenteras en långtidsstudie av unga blåhakars ruggning och fettupplagring inför den första höstflyttningen bort från Lappland.

Blåhaken

Nominatrasen av blåhake, *Luscinia s. svecica* häckar i norra Skandinavien, österut genom Asien ända till Alaska (Cramp 1988). Blåhakar i Skandinavien häckar uteslutande i fjällbjörkskog (Arheimer 1982) och flyttar på hösten till, ännu okända, övervintringsområden i södra Asien (Ellegren & Staav 1990a). Unga blåhakar ruggar sina kroppsfjädrar och en del vingtäckare under juli och augusti, framför allt i häckningsområdet. Blåhakens höstflyttning genom östra Sverige är relativt välkänd men tiden för bortflyttningen från uppväxtplatsen vet vi avsevärt mindre om.

Metoder

Ringmärkning utfördes dagligen varje sommar mellan 1984–1997 i fjällbjörkskog nära Tjulträsk, Ammarnäs, Lappland, som en del av LUVRE-projektet (Enemar et al. 1984). Fångstperioden startade i medel den 16 juli och pågick i genomsnitt till den 19 augusti. Vi använde 22 slöjnät dagligen mellan 0700 och 1300 och näten stod på samma plats varje år. Vid märkningen noterades vinglängd (metod 3, Svensson 1984), kroppsvikt och synligt fett enligt skalan från Pettersson & Hasselquist (1985). Ungfågelruggningen noterades efter en sju-gradig skala (Lindström et al. 1985). En fågel i stadie 0 har ännu inte påbörjat ruggningen, i stadie 5 har alla juvenila prickiga fjädrar bytts ut men en del fjädrar växer fortfarande på flankerna och i stadie 6 är ruggningen klar. Hanar kan kännas igen redan i stadie 3, men honor kan inte säkert könsbestämmas förrän i stadie 4.

Resultat

Totalt fångades och ringmärktes 2549 juvenila blåhakar och 1103 (43%) av dessa återfångades minst en gång samma säsong. Nästan alla (90%) av de fångade fåglarna befann sig i ruggningsstadierna 1–4 (Tabell 1), men några hade kommit längre i ruggningen (6,1% i stadie 5, men endast en individ i stadie 6). Unga blåhakars vikt skiljde sig signifikant mellan olika ruggningsstadier, med de högsta vikterna i mitten av ruggningen (Figur 1). De absoluta skillnaderna var däremot små. Även synligt fett skiljde sig signifikant mellan olika stadier av ruggningen, men även här var de absoluta skillnaderna mycket små. Årliga medelvärden i kroppsvikt (g) vid det förmodade bortflyttningstillfället varierade mellan 16,2 och 17,3 hos honor och mellan 17,0 och 18,1 hos hanar (Tabell 2). Den genomsnittliga fettklassen var antingen 0 eller 1 hos båda könen alla

år. Det är alltså tydligt att juvenila blåhakar inte lägger på sig någon fettreserv i tidsperioden mellan separationen från föräldrarna och bortflyttningen.

När lämnar då blåhakarna den plats där de föds upp av sina föräldrar? Det är näst intill omöjligt att se enskilda fåglars bortflyttning, men fångstantalet är tydligt högst de sista dagarna av juli och det är möjligt att en del individer börjar lämna platsen redan strax därefter. Detta antagande styrks också av ett återfynd från en blåhake som ringmärktes den 20 juli, i ruggningsstadie 1, och återfångades 59 km söderut från Tjulträsk den 4 augusti samma år (Figur 2). Denna fågel rörde sig alltså över ett avsevärt avstånd redan i tidig ruggning. Förmodligen försvinner det blåhakar kontinuerligt under augusti. Antalet fångade blåhakar per dag var bara hälften så stort den 18 augusti som i slutet av juli (Figur 3).

Diskussion

Ruggning och flyttning

Juvenila blåhakar lämnar häckningsplatserna mitt under pågående ruggning, förmodligen främst när de är i ruggningsstadierna 3–5. Några individer kan lämna ännu tidigare, vilket ett av återfynden visar. Att blåhakarna ruggar under flyttningen stämmer väl med observationer vid rastplatser längs den svenska ostkusten, då juvenila fåglar vid dessa platser ofta ses i ruggningsstadie 5 i slutet av augusti (Lindström & Hasselquist 1989). Att överlapp finns mellan ruggning och flyttning har tidigare setts hos flera arter.

Energireserver och flyttning

Trots att blåhakarna hade högst kroppsvikt i mitten av ruggningen hade de under samma period lägst fettreserv. Detta verkar märkligt eftersom högre kroppsvikter generellt är förknippade med större fettreserver. Men då de absoluta skillnaderna var små, förklaras detta troligast av att fåglarna under ruggningen har en ökad vattenhalt i kroppen eftersom fjädertillväxten kräver en ökad blodtillförsel (Chilgren 1977). Denna kroppsviktsvariation har förmodligen väldigt lite att göra med fettreserver.

Vad gäller fettupplagring inför flyttningen, lämnar de juvenila blåhakarna fjällen utan några substantiella fettreserver. Nästan alla fåglar hade fettreserv kring 0–2 enligt fettskalan och kroppsvikterna låg mellan 17–18 g hos hannar och 16–17 hos honor. Det verkar alltså som att blåhakar inte lägger på sig nämnvärda fettreserver förrän de når rastplat-

ser vid den svenska ostkusten 200–300 km från häckningsområdena. Kroppsvikter hos fåglar som anländer vid dessa rastplatser är i medel 17 g hos hannar och 16 g hos honor, men i takt med att fettreserver ackumuleras når en del fåglar 20–24 g innan de lämnar dessa rastplatser (Stolt & Macher 1962, Lindström et al. 1985, Ekholm 1988, Ellegren 1991, Kvist et al. 1993).

Blåhakarna startar alltså flyttningen med mycket små reserver. Frågan är huruvida blåhakarna *väljer* att inte lägga på sig stora fettreserver, eller om svåra förhållanden gör att de *inte kan* lägga på sig en stor fettreserv. Höga fettreserver är förknippade med höga kostnader (Witter & Cuthill 1993), och blåhakarna kanske undviker att lägga på sig fett för att undvika ökade flygkostnader, ökade energetiska kostnader och ökad predationsrisk. Alternativt så gör kombinationen av dålig födotillgång och höga energikostnader förknippade med ruggning och kallt väder att knappt någon energi blir över till fettupplagring. Vi vet att de rent fysiskt kan lägga på fett och rugga samtidigt, eftersom blåhakar som givits extra mat (i samband med mjölmaskmatning under andra studier av blåhakar i Ammarnäs) lägger på sig rejäla fettlager (Lindström m.fl. 1990). Den troligaste anledning är faktiskt att fåglarna inte klarar att lägga på sig en fettreserv samtidigt som de ruggar. Att fåglarna påverkas av omvärldsbetingelserna visade Hansson (1997), som i Ammarnäs fann att dåligt väder ledde till en minskning i de juvenila blåhakarnas redan små fettreserver.

Flyttningshastighet

Flyttningshastigheten är den hastighet med vilken en fågel flyttar mellan två lokaler och inkluderar den tid som läggs på den nödvändiga bränslepålagringen innan flygningen kan påbörjas. Flyttningshastigheten hos juvenila blåhakar är till en början mycket långsam. Vissa blåhakar lämnar troligen Ammarnäs redan i slutet av juli, men majoriteten av blåhakarna flyttar förmodligen från fjällen mellan den 10 och 20 augusti. Men de första blåhakarna kommer inte till rastplatserna vid ostkusten förrän omkring den 20

augusti och i genomsnitt först runt 1 september (Douhan 1986, Ellegren 1990b, 1991). Om man antar att mediandatum för blåhakar som lämnar Ammarnäs ligger mellan den 10 till 20 augusti och att medelavståndet till dessa rastplatser vid kusten är omkring 250 km, blir medelflytthastigheten bara 11–21 km per dag. Detta är avsevärt långsammare än för blåhakar senare under flyttningen. Med hjälp av ringmärkningsåterfynd uppskattade Ellegren (1990b) blåhakarnas flyttningshastighet till 30–40 km per dag mellan rastplatser i östra Sverige, 40–65 km per dag från Sverige till Finland och cirka 100 km per dag under flyttningen genom Asien.

Förklaringen till ökningen i flyttningshastighet under höstflyttningen kan vi bara spekulera kring. Juvenila blåhakar kanske blir effektivare på att lägga upp reserver under flyttningen, de kanske kommer till rastplatser med rikare resurser, eller så beror det på en kombination av dessa och kanske andra faktorer.

Vad gör blåhakarna efter att de lämnat Ammarnäs?

Det är i genomsnitt troligen 10–20 dagar mellan det att blåhakarna lämnar Ammarnäs och att de når rastplatserna vid Norrlandskusten. Vad gör dom under den tiden? Det troligaste är att många (de flesta?) förflyttar sig små sträckor åt gången ner genom Norrlands inland för att först vid kusten förbereda sig för längre flygetapper. Det finns i alla fall två stöd för denna hypotes. Först och främst så räcker de mycket små bränslereserver som fåglarna bär strax innan avfärd i genomsnitt bara till c. 90 km flygning (enligt flygteoretiska beräkningar, Pennycuick 1989), och det är 200–300 km till kusten. Dessutom visar två återfynd (Figur 2) att unga blåhakar påträffas i området emellan häckningsområdena och kusten. Sannolikheten att överhuvudtaget återfinna en ringmärkt fågel i Norrlands inland är rimligen jämförelsevis liten, varför det inte är omöjligt att den ovan föreslagna strategin faktiskt är den vanligaste. Fångst och ringmärkning på potentiella rastplatser i Norrlands inland är av största vikt för att ge stöd åt, eller förkasta, denna hypotes.