

The influence of weather and food supply on condition and behaviour of juvenile Bluethroats *Luscinia svecica* in northern Sweden

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Abstract

In this study, performed in a subalpine birch forest in northern Sweden, I examined the weight and fat status of juvenile Bluethroats *Luscinia svecica* in relation to the weather (measured as minimum temperature, precipitation and wind-force) and food supply (measured as number of insects). The results showed that the birds suffered weight losses during days with high wind-forces, probably caused by increased energy expenditure and decreased foraging activity during these days. Moreover, the number of insects, and hence the food supply, decreased after periods with rainfall and with progress of the season.

These factors were, at least partly, the reason why the birds showed overall low fat scores and were unable to accumulate extra fat at the locality. However, individuals that left the area early in the season were relatively old and carried relatively large fat reserves. These birds probably performed a short-distance migration, and presumably had the advantage of reaching more favourable sites in terms of foraging conditions.

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Introduction

Birds is the group of endotherm vertebrates with the highest body temperature, *i.e.* 40–42° C (Whittow 1986). To keep the body temperature the birds need to have an effective insulation and a high rate of metabolic combustion, which corresponds to approximately 40–60% of the total energy demand of a free living bird (Walsberg 1983). The energy expenditure due to thermoregulation affects the possibility of an individual to allocate resources to other demands, such as moulting, breeding and fat deposition (Walsberg 1983). Individuals of species living in the temperate zone have to moult as fast as possible after the breeding season in order to store extra fat to be used as fuel during the migration (Alerstam 1982). This is the case both for adult and juvenile birds. The species that generally are most time-stressed are the insectivorous long-distance migrants (Berthold 1993).

How abiotic factors, such as low temperature, heavy precipitation and high wind-force, physiologically affect birds due to an increase in energy expenditure has been investigated both empirically and theoretically (*e.g.* Kendeigh *et al.* 1977, Walsberg 1983, Elkins 1988) whereas the influence by these

factors on the behaviour of passerines is poorly examined (Elkins 1988).

The Bluethroat *Luscinia svecica* is a long-distance migrant. The subspecies *L. s. svecica* migrates to southern Asia, probably to Pakistan and India, and the breeding areas are located in northern Scandinavia and parts of Russia (Cramp 1988). In the northern parts of Sweden the weather conditions can be harsh and night frost occurs already in August. These conditions made it possible to study how birds under natural conditions are affected by different weather conditions.

In this study I examine and discuss how temperature, precipitation, wind-force and available amount of insects affect the body condition and behaviour of juvenile Bluethroats during the post-hatching period.

Material and methods

I trapped and ringed juvenile Bluethroats at a locality approximately 5 km west of the village of Ammarnäs, Swedish Lapland (65°58'N, 16°07'E), from 25 July to 17 August 1994. This locality, called A, is located close to the outlet of Lake Tjulträsk

into the river Tjulån and is surrounded by water in the south. The vegetation in the area is characterized as meadow birch forest with birch *Betula betularis*, *Salix* spp., different herbs (such as *Cicerbita alpina* and *Aconitum lycoctonum*) together with grasses and mosses as dominating species. Birds were caught daily between 07.00 and 14.00 using 22 mist-nets. At each netting occasion the weight (to the nearest 0.1 g using a 50 g pesola spring-balance) and wing-length (to the nearest mm using a stop-ruler) of the bird were measured. Fat deposits were estimated according to a 7-grade scale for visual fat classification (Pettersson & Hasselquist 1985) and post-juvenile moult (as an indicator of age) according to a 6-grade moult scale (Lindström *et al.* 1985). The moult stage and fat class of individuals recaptured at least one day after ringing were reexamined.

I caught insects within the netting area, using a sweep net (25 cm diameter) and constant beat frequency (approximately 5 beats/m). I did this during 18 of the 24 days at noon each day, along three lines of 10 m each within representative habitats of locality A. No insects were collected during rain or when the ground was wet. The insects were classified to order and the total amount of individuals were summed for each day.

At another locality (B), situated 1 km from the netting area, I experimentally increased food abundance during the later part of the season. In total I put one kilogram of mealworms in a bowl to which the Bluethroats had free access. The mealworm supply was evenly distributed during the last two weeks. At some occasions birds using the food resource at locality B were netted and the same data as at locality A were obtained.

During the period information about temperature and precipitation every third hour were available from the village of Ammarnäs (Swedish Meteorological and Hydrological Institute). The highest and the lowest temperature, and the total amount of precipitation during the 24 hours before 06.00 (GMT+1) were obtained for each day. At locality B I collected comparable measurements of maximum and minimum temperature and amount of precipitation during the day. Because the minimum temperature and the amount of precipitation measured by me at locality B significantly correlated with corresponding data from SMHI, I use their data concerning minimum temperature and precipitation ($r = 0.93$, $n = 28$, $P < 0.001$ and $r = 0.92$, $n = 29$, $P < 0.001$). At locality A or B the wind-force was estimated every third hour according to the Beaufort system (Boseaus & Melin 1988).

The weather 1994

During May and June the weather was cold and rainy. In June the average temperature was 2.4° less than normal and the precipitation was 128 % of the normal values. From the middle of July and for three weeks ahead a heat-wave with temperatures up to 26° C occurred. The amount of precipitation from 25 July to 17 August was very low and only approximately 20 mm rain fell, mainly during 27–28 July and 5 August and to some extent also during 12–13 August. The wind-force varied between 0 and 5 Beaufort (5 Beaufort = 10 m/s). The first night with frost was 17 August (wind-force own obs., other data from SMHI).

Analyses

A: Condition and developmental age of recaptured and not recaptured Bluethroats

The condition and moult stage at ringing of juvenile Bluethroats that were not recaptured were compared with those of birds recaptured later in the season. As a measurement of condition I used the calculated residual of the weight on wing-length, using linear regression. These residuals are measurements of weight where the size of the individuals (here measured as wing-length) is compensated for. The value zero indicates the size-independent average weight.

To form a picture of seasonal effects on condition and moult stage, I compared the birds captured within the two different three days periods with the highest number of netted individuals: 30 July–1 August and 11–13 August.

B: Change in weight and fat-score of individuals which were captured both at locality A and B

Those individuals first captured at locality A and later recaptured at locality B were analysed with respect to change in weight and fat-score between the two occasions. If an individual was netted more than once at either of the localities, an average of the measured values was used.

C: Number of Bluethroats and insects caught over the season

The number of netted (*i.e.* both ringed and recaptured) birds showed a first peak on 1 August (Figure 1), and from this date I consider the majority of juvenile Bluethroats in the area as fledged. By choosing the period 1–17 August the result would there-

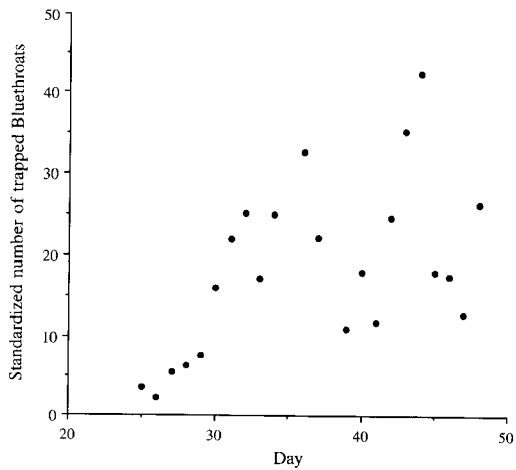


Figure 1. Standardized number of captured Bluethroats during the season 1994. Day 1 = 1 July.

Standardiserat antal fångade blåhakar under säsongen 1994. Dag 1 = 1 juli.

fore not be affected by a change in abundance due to newly fledged individuals. In the calculations, differences in netting time between days are taken into account.

In the correlations, for birds and insects, I used (1) the minimum temperature the night before capture, (2) the amount of precipitation until 07.00, and (3) the average wind-force from 09.00 and 12.00 the considered day.

D: Change of weight in Bluethroats captured on two consecutive days

Change of weight (%) between day(n) and day(n+1) was calculated for those individuals that were netted at an interval of one day. I used individuals in moult stage 2–4 to obtain a homogenous group of birds which certainly was independent of their parents. The difference in time between the netting occasions (maximally 24 ± 4 hours) was compensated for by using linear regression. The resulting residual is a measurement of the change of weight (%) where the difference in time at ringing compared to recapture is compensated for, and this measurement I use in this analysis.

Correlations with five different parameters were made. These parameters were defined as follows: minimum temperature (the night between day(n) and day(n+1)), precipitation (during 24 hours to 07.00 day(n+1)), wind-force (average wind-force

from 09.00 and 12.00 day(n+1)), number of insects (day(n+1)) and date (day(n+1)). When the correlations regarding minimum temperature, precipitation and date were made, only birds netted between 07.00 and 11.00 were considered. For analyses of wind-force and number of insects I only used birds netted between 09.00 and 13.00.

Statistical analyses

Statistical methods and probability tests were made according to Sokal & Rohlf (1995). Correlations, regressions and *t*-tests were performed with SYSTAT (Wilkinson 1987). Two tailed tests were used in all analyses. Data are given as mean \pm SD unless otherwise stated.

Results

A: Condition and developmental age of recaptured and not recaptured Bluethroats

When comparing the size-independent weights of juvenile Bluethroats at the ringing occasion, captured during 30 July –1 August, the birds that were not recaptured later in the season were significantly heavier than those that were recaptured later. Birds ringed during 11–13 August showed no difference in weight between these two groups. During both periods, the birds in the non-recaptured category showed a tendency of more progressed moult than those belonging to the group of recaptured birds (Table 1).

B: Change in weight and fat score of individuals which were captured both at locality A and B

Individuals, that were trapped both at locality A and B, showed a tremendous increase in weight and fat score after using the artificial food supply at locality B. At locality A and B the average weights were 17.1 ± 0.8 and 20.0 ± 0.7 (paired *t*-test, $P < 0.001$, $n = 5$). The average fat-scores were 0.9 ± 0.6 at A and 4.0 ± 0.5 at B (Mann-Whitney *U*-test, $P = 0.009$, $n = 5$). Three of these five individuals retrapped at locality A before they were controlled at locality B, showed only a slight change in weight (0.2 g; paired *t*-test, $P = 0.78$, $n = 3$) between ringing and recapture at locality A.

C: Number of Bluethroats and insects caught over the season

Minimum temperature and number of insects but not precipitation, wind-force and standardized number

Table 1. Weight (wing-length independent) and moult stage, at ringing, of Bluethroats that were recaptured and not recaptured later in the season, during two different three days periods.

Vikt (vinglängdsberoende) och ruggningsklass, vid ringmärkningstillfället, hos blåhakar som återfångades och inte återfångades senare under säsongen, under två olika tredagersperioder.

	Ringling period	Weight (g) mean±SD	n	P ¹	Moult stage mean±SD	n	P ²
	Ringmärknings- period	Vikt (g) medel±SD			Ruggningsklass medel±SD		
Recaptured Återfångad	30/7–1/8	-0.22±0.81	26	0.035	1.70±0.61	27	0.058
Not recaptured Inte återfångad	30/7–1/8	0.39±1.06	19		2.11±0.57	19	
Recaptured	11–13/8	-0.10±0.76	12	0.778	2.83±1.03	12	0.078
Not recaptured	11–13/8	-0.16±0.69	31		3.48±0.81	31	

¹ *t*-test

² Mann-Whitney *U*-test

Table 2. The correlation between time of season (1–17 August) and minimum temperature, precipitation, wind-force, number of insects and standardized number of netted Bluethroats. Correlation coefficient (*r*), number of days (*n*) and probability value (*P*) are shown.

Sambandet mellan tid på säsong (1–17 augusti) och minimitemperatur, nederbörd, vindstyrka, antal fångade insekter och standardiserat antal fångade blåhakar. Korrelationskoefficient (*r*), antal dagar (*n*) och sannolikhetsvärde (*P*) visas.

	Temperature (°C)			Precipitation (mm)			Wind-force (Beaufort)			Insects (number)			Bluethroats (number)		
	<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>
Date (1–17/8) Datum (1–17/8)	-0.06	17	**	-0.04	17	ns	-0.05	16	ns	-0.71	13	***	-0.01	15	ns

ns: $P > 0.05$, **: $P < 0.01$, ***: $P < 0.001$

of trapped Bluethroats showed a negative correlation with date between 1–17 August (Table 2).

The standardized number of Bluethroats showed a significant negative correlation with wind-force but not with any of the other parameters (Table 3). The number of insects did not correlate with any weather parameter (Table 3) but when the rain fell in the afternoon (day(*n*)), after a period of mainly dry weather, more insects were collected at day(*n*) than at day(*n*+1) (paired *t*-test, $P = 0.017$, $n = 3$; Figure 2). Late in the season (from 5 August) the insect population did not reestablish its former numbers (Figure 2).

D: Change of weight in Bluethroats captured on two consecutive days

Birds that were captured and examined on two consecutive days showed a significant relative decrease in weight considering wind-force (Table 4; Figure 3), whereas, there was a tendency of an increase in relative weight in relation to the amount of insects day(*n*+1) (Table 4; Figure 4). Other factors, such as minimum temperature, amount of precipitation and day of season, did not affect the weight of the birds (Table 4).

It is most likely that heavy birds run the risk of losing weight whereas the opposite is expected in

Table 3. The effect of minimum temperature, precipitation, wind-force and number of insects on standardized number of captured Bluethroats and collected insects, during 1–17 August. Correlation coefficient (r), number of days (n) and probability value (P) are shown.

Effekten av minimitemperatur, nederbörd, vindstyrka och antal insekter på standardiserat antal fångade blåhakar och insekter mellan 1–17 augusti. Korrelationskoefficient (r), antal dagar (n) och sannolikhetsvärde (P) visas.

	Number of Bluethroats <i>Antal blåhakar</i>			Number of insects <i>Antal insekter</i>		
	r	n	P	r	n	P
Temperature (°C) <i>Temperatur (°C)</i>	0.11	15	ns	0.16	13	ns
Precipitation (mm) <i>Nederbörd (mm)</i>	0.10	15	ns	-0.27	13	ns
Wind-force (Beaufort) <i>Vindstyrka (Beaufort)</i>	-0.61	15	*	-0.19	13	ns
Number of insects <i>Antal insekter</i>	-0.02	13	ns			

ns: $P > 0.05$, *: $P < 0.05$

Table 4. Individual change of weight (%) of Bluethroats captured on two consecutive days correlated with the minimum temperature, amount of precipitation, wind-force and number of insects and date (day($n+1$)). Number of individuals (n), linear regression coefficient (r), intercept (a), slope (b ; change of weight in % per unit) and probability (P) are shown.

Individuell viktskillnad (%) hos blåhakar kontrollerade vid två efter varandra följande dagar korrelerat till minimitemperatur, nederbörds mängd, vindstyrka, antal insekter och datum (dag($n+1$)). Antal individer (n), regressionskoefficient (r), intercept (a), lutning (b ; vikt förändring i % per enhet) och sannolikhetsvärde (P) visas.

	n	r	a	b	P^1
Minimum temperature (°C) <i>Minimitemperatur (°C)</i>	18	0.14	1.01	-0.15	0.57
Amount of precipitation (mm) <i>Nederbörds mängd (mm)</i>	18	0.22	0.45	-0.37	0.39
Wind-force (Beaufort) <i>Vindstyrka (Beaufort)</i>	27	0.63	5.04	-2.18	0.001
Number of insects <i>Antal insekter</i>	24	0.36	-1.80	0.02	0.09
Date <i>Datum</i>	18	0.06	-1.69	0.04	0.82

¹ Linear regression

light individuals. Therefore, I included the birds' weight on day(n) in the regressions (*i.e.* multiple regression analyses), but only minor changes of the above correlations were found. As expected, there was a positive (but not significant) correlation between the birds' weight on day(n) and their weight loss to the next day in all five multiple analyses.

Because the precipitation often differ in intensity I made a detailed analysis of the only period with steady downpour, the night between 27 and 28 July. The average weight (wing-length independent) for ringed Bluethroats was 5.3 ± 0.6 g ($n = 2$) the day before and -3.6 ± 8.2 g ($n = 3$) the day after the rainfall (t -test, $P = 0.24$).

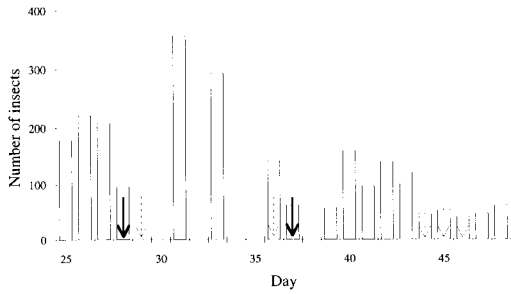


Figure 2. Number of collected insects and amount of precipitation during the season 1994. Day 1 = 1 July. Missing values are due to no collection of insects these days (6 of 24). Arrows indicate the amount of precipitation during 24 hours until 07.00 (bold arrow: 6-7 mm rain; ordinary: 1-2 mm; dotted: <1 mm).

Antal fångade insekter och nederbördsmängd under säsongen 1994. Dag 1 = 1 juli. Vissa dagar då fångst ej genomfördes saknas värden (6 av 24). Pilar indikerar regnmängd under 24 timmar till kl. 07.00 (fetstilt pil: 6-7 mm regn; normal: 1-2 mm; streckad: <1 mm).

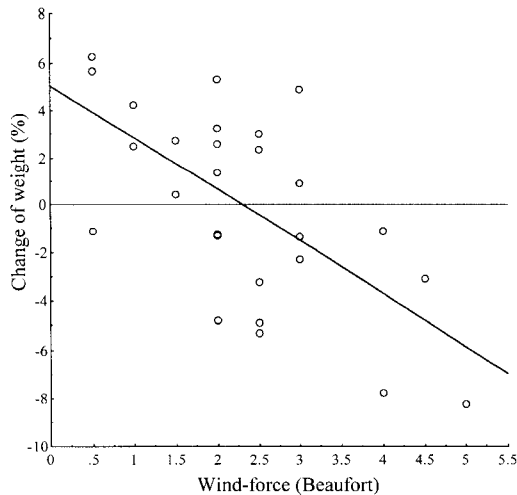


Figure 3. Change of weight (%) of Bluethroats captured on two consecutive days correlated with wind-force day(n+1). The change of weight showed a significant decrease with increasing wind-force (Linear regression, $P = 0.001$, $n = 28$).

Viktförändring (%) hos blåhakar kontrollerade vid två efter varandra följande dagar korrelerat till vindstyrkan dag(n+1). Viktskillnaden visade en signifikant minskning med ökad vindstyrka (Linjär regression, $P = 0.001$, $n = 28$).

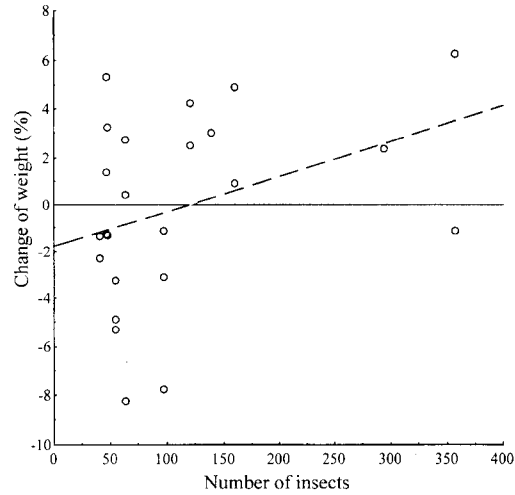


Figure 4. Change of weight (%) in Bluethroats captured on two consecutive days correlated with the number of insects day(n+1). The change of weight showed a tendency to increase with increasing number of insects (Linear regression, $P = 0.09$, $n = 24$).

Viktförändring (%) hos blåhakar kontrollerade vid två efter varandra följande dagar som en funktion av insektsmängden dag(n+1). Viktskillnaden visade en tendens åt ökning med ökad skillnad i insektsmängd mellan dygnet (Linjär regression, $P = 0.09$, $n = 24$).

Discussion

In this study of juvenile Bluethroats at the moulting area, recaptured individuals were significantly lighter and tended to be relatively younger at the ringing occasion than individuals which were not recaptured. Late in the season these groups did not differ in weight but the tendency of a difference in developmental age remained (Table 1). During the study period the birds were in the middle of their partial postjuvenile moult, and in August the first individuals completed the moult (unpublished data). Lindström *et al.* (1993) have shown that the moult is a highly energy demanding process and that an adult Bluethroat demands approximately twice the basal metabolic rate during its most intensive part of the moult. The amount of fat a passerine needs to accumulate to be able to perform the migration in one long step (Alerstam 1982) is much higher than the fat score values estimated for the Bluethroats in this study. This indicates that the birds only migrate a short distance from the moulting areas, which has previously been discussed by Lindström *et al.* (1985). This is also true for the birds in relatively good condition, which left the area early in the season.

There is at least two explanations for the overall low fat loads recorded in this study. Either the natural amount of food is too low for both the moulting and the fat accumulating process to occur at the same time, or the birds themselves chose not to add any extra fat. One reason not to add any extra fat is that large fat scores negatively affect the manoeuvrability of the bird (Hedenström 1992). However, those individuals that were using the food provided at locality B were increasing their weight and fat load (cf. Lindström *et al.* 1990). Therefore, the energy intake rate and/or the amount of food seem to be the limiting factors on the rate of fat accumulation at this locality.

Factors controlling the energy intake rate of the Bluethroats in their native area could either be the absolute number of insects, the birds' foraging success or a combination of these factors. Which external factors affect the energy intake rate and in what way?

Temperature

Temperatures below the lower limit of thermoneutrality (T_{lc} ; approximately 20°C) imply an increased energy requirement compared to temperatures within thermoneutrality (Kendeigh *et al.* 1977). In the House Sparrow *Passer domesticus* the metabolic rate at thermoneutrality is approximately 8 kcal/day while the rate at temperatures 10 degrees below T_{lc} is approximately 13 kcal/day (Kendeigh *et al.* 1977), *i.e.* an increase of approximately 50% in the energy demand by a decrease in temperature of 10 degrees. Values similar to these have been determined in the Knot *Calidris canutus* (Wiersma & Piersma 1994), and are probably valid also for Bluethroats.

The minimum temperature of the nights at Amarnäs was, during the whole study period, below T_{lc} and varied between -0.6 and 13.8°C. Consequently, the energy consumption of the Bluethroats should be about 75% higher during especially cold nights compared to warm nights. Nevertheless, the results reported in this study show that the birds did not lose more weight during cold compared to warm nights (Table 4). The likely explanation is that the birds compensate the increasing energy expenses after a cold night and a cold morning with an increase in food intake rate. Hutto (1981) has shown that the feeding activity of some species of Wood Warblers is negatively correlated with the activity of insects which, in turn, varies with the day. The pattern is: low insect activity in the morning and evening and a marked peak at noon (Hutto 1981). If

this pattern could be explained by a temperature dependent insect activity, a corresponding difference in activity should be true both between days as well as within days. The higher energy requirement of the Bluethroats after a cold night could then be compensated for by an increase of energy intake early in the morning. This can be facilitated due to a low insect activity and more easily caught preys in the morning. The reasoning above may suggest that the Bluethroats were foraging early in the morning, and were able to compensate for their increased energy expenditure before I measured their weight and fat-status later in the morning. Therefore, their foraging success was not deteriorated due to motionless prey which might have been hard to locate. Both the high number of netted birds also early in the morning (unpublished data) and observations of foraging individuals early in the morning (own obs.) indicate that the birds actually started their foraging activity before I examined them. This could explain why there was no correlation between body condition of the birds and temperature in this study, even if there were differences in temperature between nights.

Precipitation

From a general point of view, the influence of precipitation on the energy expenditure of the birds is relatively weak and varies between species due to differences in their morphology and physiology (Elkins 1988). Most species are able to resist shorter periods of precipitation and present normal activity in gentle rain (Kennedy in Elkins 1988). However, if the plumage gets wet after heavy or prolonged rainfall, the heat loss from the body will increase (Kendeigh *et al.* 1977).

The reason for not finding any correlation between weight and amount of precipitation in this study could have been due to the character of the precipitation; *i.e.* either gentle rain or short showers. The only occasion with prolonged rainfall, during the night and morning between 27 and 28 July, indicates that the Bluethroats indeed suffered in terms of weight loss at least due to some kind of precipitation. However, the sample size was too small to statistically secure this pattern.

Wind-force

The plumage of a bird enclose air. When the body heats the enclosed air it rises and is replaced by cold air from the surrounding; a convection loss is taking

place. This loss is accelerating as the movements of the surrounding air is increasing (Kendeigh *et al.* 1977). In the White-crowned Sparrow *Zonotrichia leucophrys* it was observed that a wind-force of 4 m/s gives the same heat loss as a temperature reduction of 13° C (Walsberg 1983). This corresponds to an increase in energy expenditure of approximately 50%. Studies of how roosting sites are selected show that both Phainopepla *Phainopepla nitens* (Walsberg 1983) and Brambling *Fringilla montifringilla* (Jenni 1991) prefer sheltered localities and that the birds save energy by choosing these sites, even if they have to travel long distances daily between the roosting sites and the foraging areas.

Elkins (1988) states that the problems in foraging induced by low or medium wind-forces are few. Strong winds probably only puts an upper limit for how high up in the vegetation an individual is able to forage, because the wind-force decreases from the canopy and downwards.

The Bluethroat is a species which resides in the lower parts of the vegetation (Cramp 1988) and should according to the reasoning above only be moderately affected by a high wind-force. The fact that the number of netted Bluethroats was negatively affected by the wind in this study (Table 3) could be due to that the birds more easily avoid the nets under windy conditions. However, the fact that the birds' weight was negatively affected by the wind (Figure 3) despite that the number of insects was unaffected (Table 3), indicates that the birds lowered their activity and hence their foraging success at high wind-forces. This also explains why fewer birds were caught in strong winds.

The weight reduction of the Bluethroats with increasing wind-force could consequently be explained both by enhanced energy expenditure and lowered energy intake rate at high wind-forces.

Number of insects

Hutto (1985) showed that the density of breeding birds increases with increasing density of insects in the habitat, and that a bird spends a large proportion of time at the level in the vegetation where the density of insects is highest. In another study Hutto (1981) found that the diurnal activity of insectivorous birds was negatively correlated with the activity of insects.

The Bluethroats in Ammarnäs showed no correlation between number of captured birds and number of insects caught (Table 3). One interpretation of this is that the total activity, including foraging activity,

is independent of the number of insects. There was a tendency to a positive correlation between the change of weight of the birds and increasing number of insects which indicated that the foraging was more successful at high insect densities (Figure 4).

The number of insects caught decreased after periods of rainfall but did not correlate with any other abiotic factor. In later parts of the period the insect population showed a reduced ability to recover to previous number (Figure 2). This indicates that the precipitation and not *e.g.* the minimum temperature (as one may first consider because of the correlation of both the amount of insects and the minimum temperature with the progress of the season) could be the primary cause of the decreasing number of insects observed.

Conclusion

The moulting juvenile Bluethroats that stayed in the study area seemed unable to add any extra fat under natural conditions because of low energy intake rate and high energy expenditure. This was partly caused by: (1) decreased foraging activity and/or increased energy expenditure in high wind-forces, and (2) decreased amount of insects after rainy periods and with progress of the season. The wind-force had a direct effect on the condition of the birds whereas the precipitation affected them by indirectly lowering the food supply.

The overall low fat loads of the birds indicate that they performed a short-distance migration from the moulting areas, presumably to more favourable sites in terms of foraging conditions. Individuals that left early in the season were relatively old and in good condition and may have had better chance of reaching the stopover sites, as well as winter grounds, compared to others. Therefore, to be hatched early in the season presumably is important for Bluethroats in this area (cf. Perrins 1965; Arcese & Smith 1985).

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References

- Alerstam, T. 1982. *Fågelflyttning*. Signum, Lund.
- Arcese, P. & Smith, J. N. M. 1985. Phenotypic correlates and ecological consequences of dominance in Song Sparrows. *J. Anim. Ecol.* 54:817–830.
- Berthold, P. 1993. *Bird Migration*. Oxford Univ. Press, Oxford.
- Bosaeus, L. & Melin, C. 1988. *Årets väder*. ICA förlaget AB, Västerås.
- Cramp, S., ed. 1988. *Handbook of the Birds of Europe, the Middle East and North Afrika. The Birds of the Western Palearctic, Vol V*. Oxford Univ. Press, Oxford.
- Elkins, N. 1988. *Weather and bird behaviour*. Second edition. T & A D Poyser Ltd, Staffordshire.
- Hedenström, A. 1992. Flight performance in relation to fuel loads in birds. *J. Theor. Biol.* 158:535–537.
- Hutto, R. L. 1981. Temporal patterns of foraging activity in some wood warblers in relation to the availability of insect prey. *Behav. Ecol. Sociobiol.* 9:195–198.
- Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pp. 455–476 in *Habitat selection in birds* (Cody, M. L., ed.). Academic press, Orlando.
- Jenni, L. 1991. Microclimate of roost sites selected by wintering Bramblings *Fringilla montifringilla*. *Ornis Scandinavica* 22:327–334.
- Kendeigh, S. C., Dolnik, V. R. & Gavrilov, V. M. 1977. Avian energetics. Pp. 127–204 in *Granivorous birds in ecosystems, their evolution, populations, energetics, adaptations, impact and control* (Pinowski, J & Kendeigh, S. C., eds.). Cambridge University Press, Cambridge.
- Lindström, Å., Bensch, S. & Hasselquist, D. 1985. Höstflyttningsstrategier hos unga blåhakar *Luscinia svecica*. *Vår Fågelvärld* 44:197–206.
- Lindström, Å., Hasselquist, D., Bensch, S & Grahn, M. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. *Anim. Behav.* 40:456–461.
- Lindström, Å., Visser, G. H. & Daan, S. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiological Zoology* 66(4):490–510.
- Perrins, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* 34:601–647.
- Pettersson, J. & Hasselquist, D. 1985. Fat deposition and migration capacity of robins *Erithacus rubecula* and goldcrests *Regulus regulus* at Ottenby, Sweden. *Ringing & Migration* 6:66–76.
- Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*. Third ed. W. H. Freeman & Co. New York.
- Walsberg, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. *The Auk* 103:1–7.
- Whittow, G. C. 1986. Regulation of body temperature. Pp. 221–252 in *Avian Physiology*, fourth edition (Sturkie, P. D. ed.). Springer-Verlag, New York.
- Wiersma, P. & Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. *The Condor* 96:257–279.
- Wilkinson, L. 1987. *SYSTAT. The System for Statistics*. SYSTAT. Evanston, Ill.

Sammanfattning

Vädrets och födotillgångens inverkan på kondition och beteende hos unga blåhakar Luscinia svecica i norra Sverige

För att upprätthålla kroppstemperaturen förbrukar en fågel en energimängd motsvarande 40–60% av dess totala energiförbrukning, detta trots att fjäderdräkten ger en god isolering. Denna energiförbrukning påverkar möjligheten att fördela resurser till andra behov, såsom ruggning, fettupplagring och häckning. I tempererade områden krävs det att fåglarna innan flyttningen klarar av att lägga upp ett förråd av flygbränsle i form av fett. De som är mest tidspressade är de insektsätande arter som dessutom ruggar innan flyttningen. En sådan art är blåhaken.

Hur abiotiska faktorer, som låg temperatur, kraftig nederbörd och hög vindstyrka, fysiologiskt påverkar fåglar genom ökad energiförbrukning är väl studerat både empiriskt och teoretiskt medan dessa faktors påverkan på tättingars beteende är mindre väl undersökt.

I de norra delarna av Sverige kan vädret vara hårt och ofta går nattetemperaturen ner under noll grader under den period då fåglarna förbereder sig inför höstflyttningen. Dessa yttre förhållanden gör det lämpligt att studera hur en art som blåhaken under naturliga förhållanden fysiologiskt och beteendemässigt påverkas av väder och vind. Därför fångade och undersökte jag unga blåhakar i närheten av Ammarnäs (65°58'N, 16°07'E), beläget i Lappland, under perioden 25 juli till 17 augusti 1994. Fåglarna fångades under standardiserad nätfångst och individernas vikt, vinglängd, fettmängd och ruggningsstadium registrerades enligt standardiserade metoder. Det ruggningsstadium en individ befinner sig i är ett mått på hur utvecklad den är och används i denna uppsats som ett åldersmått. Vid detta tillfälle ringmärktes också fågel. Inom fångstområdet fångade jag insekter (även detta enligt en standardiserad metod). Insekterna bestämdes till ordning och antalet individer summerades per dag. Vid en annan lokal belägen ca 1 km från märkplatsen, skapade jag en riklig födokälla genom att erbjuda mjölmask i en skål under senare delen av studieperioden. Från denna födokälla kunde friflygande blåhakar hämta mat. Vid några tillfällen infångades dessa fåglar och

samma typ av data som vid ringmärkningstillfället insamlades.

Jag använde de minimi- och maximitemperaturer samt nederbördsmätningar, utförda av SMHI, som fanns tillgängliga från väderstationen i Ammarnäs. Dessutom bokförde jag vindstyrkan var tredje timma under dygnets ljusa timmar.

Resultat och diskussion

Tidigt på säsongen hade blåhakar som kom att återfångas en signifikant lägre vikt vid nymärkningstillfället jämfört med de som inte återfångades. Under slutet av säsongen skilde sig däremot inte dessa kategorier åt. De individer som kom att återfångas visade en trend mot att vara yngre än de som inte återfångades (Tabell 1). Fåglar som stannade i området var således både lättare och yngre än de som lämnade området. Då det erbjöds rikligt med mat ökade däremot fåglarnas vikt och fettvärde signifikant med i snitt 2,9 g respektive 3,1 fettsteg, vilket visar att den naturligt förekommande födointagshastigheten var alltför låg för att viktökning och fettackumulering skulle kunna ske.

Fångsten av insekter och således insekts- och födotillgången i området minskade efter dagar med regn (Figure 2) men korrelerade dock inte med någon annan väderparameter (Tabell 3). Mot slutet av säsongen hade insektspopulationen inte förmågan att återhämta sig efter regn (Figure 2) och uppvisade därför ett starkt negativt samband med säsongen (Tabell 2). Fångsten av blåhakar korrelerade med vindstyrkan så att färre fåglar fångades i hårda än i svaga vindar, men däremot påverkades den inte av någon annan väderparameter (Tabell 3). Om man ser till enskilda individers viktökning mellan olika dygn så uppvisar även denna en negativ korrelation med vindstyrkan (Tabell 4; Figure 3). Dessutom observerades en tendens till positiv korrelation mellan individernas viktökning och insekt-

stillgången (Tabell 4; Figure 4). Vindens påverkan skulle kunna förklaras med att blåhakarna minskade sin aktivitet i blåsigt väder, möjligen för att söka lä och på detta sätt minska sin energiförbrukning eller genom att födosöksframgången förmodligen är låg i sådant väder.

Att blåhakarna inte kunde visas vara påverkade av andra väderfaktorer än vinden är anmärkningsvärt. Exempelvis har det visats i andra studier att temperaturen har stor påverkan på ett djurs energiförbrukning och således borde en viktvariation kunna registreras i förhållande till olika nätters temperaturförhållanden. Om man däremot tillför information från andra källor som visar att även insektsaktiviteten påverkas av temperaturen och att detta sker omvänt mot ett djurs energiförbrukning, kan man tänka sig att individen korrigerar för det ökade energiutlägg som en kall natt och morgon innebär med ett ökat födointag p.g.a. att mindre aktiva byten är mer lättfångade. Detta skulle kunna förklara varför individerna viktmissigt sett inte påverkades negativt av kalla nätter i denna studie.

Resultaten tyder på att de unga ruggande blåhakarna i Ammarnäs inte kunde lägga på sig fett p.g.a. lågt energiintag och höga energiutgifter. Detta kan bl.a. bero på (1) låg födosöksaktivitet och/eller hög energiåtgång under kraftiga vindförhållanden och (2) minskad insektstillgång efter regn och mot slutet av säsongen. Vindstyrkan påverkade fåglarnas kondition direkt medan nederbörden påverkade indirekt genom att födotillgången minskade. Fåglarnas överlag låga fettvärden indikerar att de som lämnade lokalen utförde en kortdistansflyttning, förslagsvis till andra platser mer fördelaktiga ur födosökssynpunkt. Intressant nog var individer som lämnade området tidigt på säsongen i relativt god kondition och hade därför antagligen större chans att nå rastplatserna och även övervintringsområdet jämfört med andra.