

# A feeding experiment on migratory fuelling in whitethroats, *Sylvia communis*

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**Abstract.** The influence of food abundance on whitethroats' behaviour when preparing for autumn migration was investigated in a feeding experiment on the island of Gotland in the Baltic. Whitethroats attracted to a feeding site during post-juvenile moult attained a stable body mass 1.4 g higher than birds in natural conditions. This fuel load is well below the maximum that whitethroats could deposit. After maintaining stable body mass during moult, the whitethroats started to gain mass and thereafter soon departed on migration. This shift was due to the birds increasing their gross food intake by about 70%. Both the average rate of fuel deposition (about 7% of lean body mass per day) and the average departure fuel load (over 50% of lean body mass) were much higher for birds at the feeding site than for birds in natural conditions. No correlation between rate of fuel deposition and departure fuel load was found at the feeding place. Larger departure fuel loads in late individuals suggest that departure decisions are affected by temporal cues. Comparisons with models of time-minimization during migration show that the lack of correlation between rate of fuel load and departure load contradicts the predictions in one model. In another model, where a finite distance is included, the relationship between rate of fuel deposition and departure fuel load is predicted to be step-wise. This means that within certain ranges of rate of fuel deposition the departure fuel load should not change, which is consistent with the result found in this study.

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Migrating birds require large amounts of fuel (e.g. Blem 1976, 1980; Klaassen 1996). Most often, depending on species and distances involved, fuel reserves have to be replenished at several intermediate stopover sites. The sites used might differ in several aspects, for example in food availability and predation risk (e.g. Graber & Graber 1983; Lindström 1990), which will affect rates of fuel deposition. Competitive interactions with conspecifics can also affect the opportunities an individual has to restore energy quickly (Rappole & Warner 1976; Lindström et al. 1990). For example, Lindström et al. (1990) showed that asymmetric competition based on size differences affected the rate at which bluethroats, *Luscinia svecica*, build up fuel loads.

Birds are capable of adjusting their fat reserves in response to environmental cues, for example foraging conditions and food availability (Ekman

& Hake 1990; Ekman & Lillendahl 1992) as well as predation risk (Gosler et al. 1995; Lillendahl 1997; Fransson & Weber 1997). The fact that fat reserves are often regulated at levels below physiological or environmental maxima has been used to argue that fat storage is costly (Witter & Cuthill 1993). In migratory birds the diminishing return of an increased fuel load on flight distance (Pennycuik 1975; Alerstam & Lindström 1990) should be important for determining fuel loads at departure. This relationship has also been used to model how a migratory bird should behave in situations where time, energy or mortality is to be minimized (Alerstam & Lindström 1990; Weber & Houston 1997). Alerstam & Lindström (1990) predicted that birds trying to minimize time on migration should be sensitive to the rate of fuel deposition, which should correlate positively with departure fuel load, while the departure fuel load should be independent of the rate of fuel deposition in birds minimizing cost of transport. Weber & Houston (1997) included a finite

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distance in their model of a time-minimizing migration and also predicted a positive relationship between rate of fuel deposition and departure fuel load, but the relationship was discontinuous and step-like with ranges of rates of fuel deposition where no variation in departure fuel loads were expected. When birds arrive at a new stop-over site they often initially lose mass (cf. Lindström 1995). This mass loss has been included in the models as a cost of stopover and is central for both approaches.

In this study I investigated how enhanced food availability affects whitethroats when they are preparing for their first flight stage during autumn migration, in terms of body mass during the preceding post-juvenile moult, rate of fuel deposition and departure fuel load. I compared the results with the predictions set out by the models. The whitethroat is a long-distance migrant: the European subspecies winters close to the southern border of the Sahara in Africa (Moreau 1972). Populations breeding in eastern Sweden migrate south-southeast in autumn, probably towards the central part of the winter range (Zink 1973; unpublished data). Adult birds have a complete (post nuptial) moult on their breeding grounds before autumn migration while at the same time first-year birds moult only their body feathers (Ginn & Melville 1983; Jenni & Winkler 1994).

## METHODS

I offered whitethroats mealworms *ad libitum* at Sundre (56°56'N 18°11'E) on the southernmost point of the island of Gotland in the Baltic. The feeding site was situated about 5 km from the coast in an old pasture, surrounded by a mixture of arable and pasture land. Mealworms were supplied between 1 August and about 15 September in three consecutive years (1990–1992) in a small bowl placed on a remote-controlled balance (see Carpenter et al. 1983 and Lindström et al. 1990 for comparable methods). Individuals that started to use the feeding site were trapped, measured and individually marked with colour rings. For birds trapped both at the feeding site and in the surrounding area, I measured wing length (Svensson 1992), body mass and fat score (Pettersson & Hasselquist 1985). I also classified the post-juvenile moult on a scale from 0 to 6 (Lindström et al. 1985; Bensch & Lindström

1992), where 0 denotes a bird in juvenile plumage with primaries not fully developed and 6 denotes a bird with the post-juvenile moult completed. I recorded the body masses of birds visiting the bowl to the nearest 0.1 g. Since the balance was tared to zero including the mealworms, before each bird's arrival, body masses did not include the food birds consumed on visits. I could then measure the amount of food eaten as the net decrease given by the balance when the individual left. When many birds used the feeding site simultaneously, complete information was sometimes impossible to gather. Occasionally other bird species, especially red-backed shrikes, *Lanius collurio*, started to use the feeding site, but they were trapped and displaced. I carried out observations at the feeding site every evening, at least 2 h between 1600 and 2000 hours, and sometimes also in the morning (between 0500 and 0800 hours). Morning observations were conducted more regularly during 1990.

I calculated morning and evening body mass for individuals as the average of all weighings of the bird recorded during that morning or evening. I calculated individual mean daily mass gain of birds at the feeder as the body mass recorded on the last evening that the bird was present divided by the number of days on which the bird gained body mass. In a few cases when the body mass decreased on the last day, I still included it in the period of mass gain. In birds also present during a period of stable body mass, I confined calculations of daily mass gain to the period of body mass increase. Since increases in body mass during migration involve both fat and non-fat components, throughout this paper I use the term fuel load (see Lindström & Piersma 1993 for a review). When calculating individual fuel loads, I used a size-specific lean body mass varying between 13.0 and 13.9 g estimated by Ellegren & Fransson (1992). Birds that disappeared after a period of body mass increase were assumed to have departed on migration, and I then calculated departure fuel loads from individual mass measurements taken on the last evening of presence. Birds caught as adults and present in more than 1 year are included only in their first year (two individuals, one of them was present all 3 years). I included one bird that was present both in its first year and as an adult the following year in both age-groups. As some of the individuals disappeared before they had gained weight (presumably

for reasons other than migration), and some individuals started to increase in body mass as soon as they arrived, the numbers of birds involved in the different calculations differ somewhat.

I compared the results with data from whitethroats in natural conditions, trapped in mist-nets in the surrounding area. Since this trapping took place in the mornings, certain comparisons with feeder data are restricted to 1990 when regular observations at the feeder were also carried out in the morning. Some of the trapping data were collected by the Sundre Bird Ringing Group during the standard bird ringing programme at Hoburgen, about 7 km from the feeding site. During 1989–1993 2580 whitethroats were trapped on southern Gotland in autumn. Out of the individuals trapped in the surrounding area, I compared only birds in moult stage 4 with the individuals at the feeding site. This stage represents the last active part of the post-juvenile moult (Bensch & Lindström 1992). I estimated the migratory body mass increase in natural conditions from recaptures of individuals in 1988–1993 (sufficient data were available only for first-years). Since most recaptures included birds in post-juvenile moult, which do not put on fuel for migration, I confined calculations to 'control' birds present for less than 10 days that were putting on migratory fuel (showing a body mass gain of more than 1 g). I estimated individual average daily mass gain from the total mass increase divided by the number of days between the first and last trapping. The method used might tend to overestimate the daily body mass gain but, if all retraps were included, the daily gain would be greatly underestimated. On the other hand, some individuals might not have started to gain mass until some days after the first trapping, giving an underestimated value. It is possible that those two biases counteract and that the estimated value represents natural conditions fairly well.

## RESULTS

### Appearance and Behaviour at the Feeder

The majority of the whitethroats arriving at the feeding site started to use it regularly, even though some individuals disappeared after a few days. The number of birds using the feeder increased from day to day during the first part of the study period and thereafter decreased, mainly as a result

of birds departing on migration. As an example, during 1990, when the largest number of birds was present, the number of feeding birds increased steadily up to 22 August and then quickly decreased again (Fig. 1). After a small temporary increase, the number continued to decrease after 4 September.

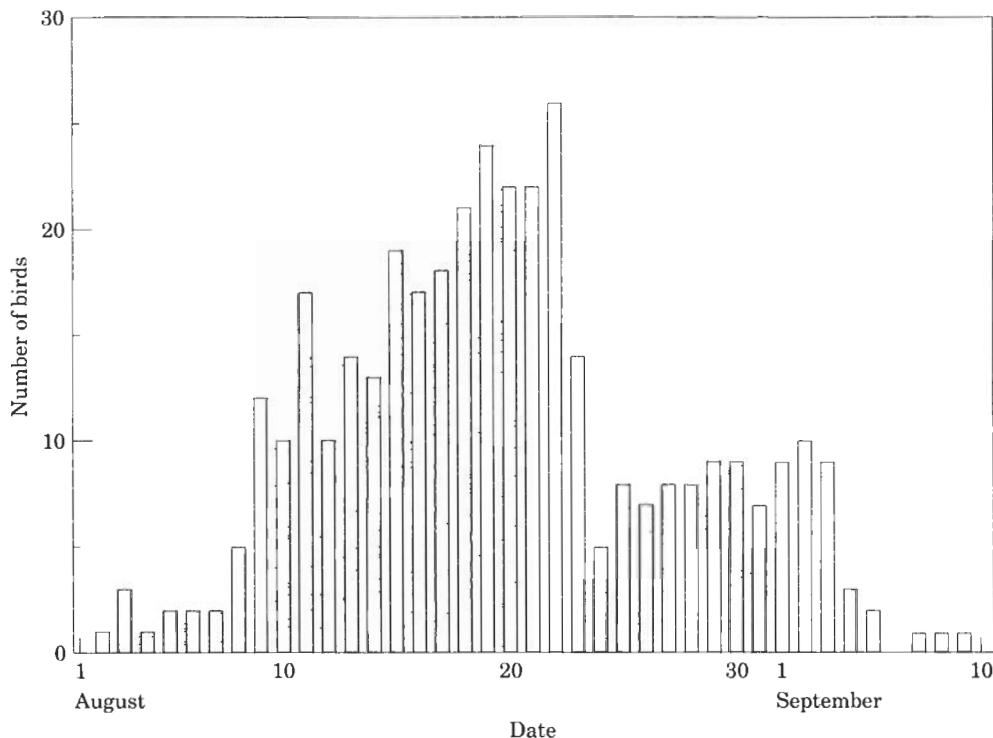
On a few occasions, newly arrived individuals were aggressive to other visitors to the feeder, but otherwise the whitethroats showed very little aggression towards each other.

### Body Mass during Post-juvenile Moulting

In 1990, the average morning body mass at the feeding site ( $\bar{X} \pm \text{SE} = 16.1 \pm 0.12$  g,  $N=21$ ) was 1.4 g higher than the corresponding morning body mass in moulting birds in natural conditions ( $14.7 \pm 0.08$  g,  $N=159$ ) in the surrounding area ( $t_{178}=6.7$ ,  $P<0.001$ ). The body mass of the majority of birds attracted to the feeding site remained fairly stable for several days. The average change in the evening body mass, compared with the first day of visit, was 0.02 g in 17 birds after 5 days and 0.14 g in seven of these after 10 days. In neither case was the change in average body mass significant ( $t_{16}=0.30$ , NS and  $t_6=0.80$ , NS, respectively). This maintenance of a stable body mass coincided with body moult. During this period of stable body mass, all birds were carrying a relatively large amount of visible subcutaneous fat (fat score;  $\bar{X} \pm \text{SE} = 4.3 \pm 0.27$ ,  $N=11$ , range 3–6). Birds in active post-juvenile moult in natural conditions had less visible fat (in 1990;  $\bar{X} \pm \text{SE} = 1.66 \pm 1.12$ ,  $N=159$ ). The evening body mass in 1990 was on average 3.3 g higher ( $N=20$ ) than the size-specific lean body mass, representing an average individual fuel load  $\pm \text{SE}$  of  $24.0 \pm 1.1\%$  of lean body mass.

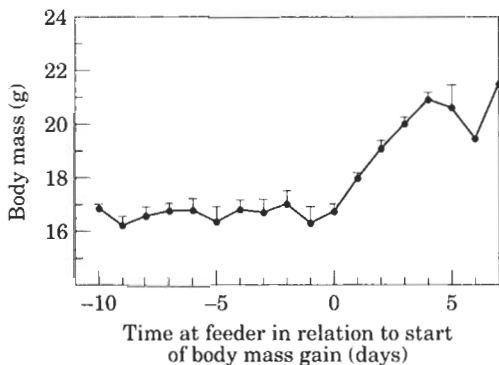
### Feeding Behaviour

After the period of stable body mass, individuals very abruptly began to gain body mass (Fig. 2). The period between arriving at the feeding site and the start of body mass gain varied, and some birds started to gain body mass as soon as they arrived. A few birds caught and observed close to this shift still had a lot of body feathers growing. In 11 individuals, the frequency of visits to the site tended to be higher during the mass build-up period than before (Wilcoxon



**Figure 1.** Daily numbers of whitethroats present at a feeding site on southern Gotland in the Baltic during the autumn of 1990. Not all individuals were individually marked but some of the unmarked birds were possible to separate by their body mass.

signed-ranks test:  $Z = -1.87$ ,  $P = 0.06$ ). Eight of the 11 individuals visited the bowl more frequently during the build-up period. The average interval between visits decreased from 38.5 min during the stable period to 30.2 min during the build up. Furthermore, the amount of food eaten when the birds visited the bowl was larger during the period of body mass gain in eight out of 10 individuals studied (Wilcoxon signed-ranks test:  $Z = -2.09$ ,  $P < 0.05$ ). The average amount of food eaten each visit increased from 0.42 to 0.56 g, which represents an approximate change from four to five or six mealworms eaten. Combining the probabilities for the tests of visiting rate and food intake, the whitethroats clearly increased their total food intake during the period of body mass gain ( $\chi^2_4 = 12.22$ ,  $P < 0.02$ ; Sokal & Rohlf 1981, page 623). The gross food intake per unit time increased by about 70% when birds shifted from stable body mass during moult to the period of body mass gain.



**Figure 2.** Average daily body mass ( $\pm$ SE) in 12 whitethroats present at a feeding site during both a period of stable body mass and a period of mass gain. The time has been standardized in relation to the day when individuals started to gain mass. Since birds were not present for the same number of days, fewer birds are included at either end of the graph. During the last 2 days of mass gain, information is available from only one and two individuals, respectively.

## Migratory Fuelling

First-year birds in natural conditions gained less migratory body mass than those at the feeder. Ten individuals recaptured within 10 days (range 3–9 days) in natural conditions had an average mass gain  $\pm$  SE of  $0.43 \pm 0.07$  g/day (range 0.20–0.97 g/day) compared with  $1.01 \pm 0.07$  g/day ( $N=28$ ) for first-year birds at the feeder ( $t_{36}=4.63$ ,  $P<0.001$ ). The daily increase in body mass in adult birds at the feeder was, on average  $\pm$  SE,  $0.86 \pm 0.09$  g/day ( $N=8$ ), not significantly different from that of first-year birds ( $t_{34}=1.0$ , NS). The body mass gain in proportion to lean body mass was on average 7% per day ( $N=28$ ) in first-year birds and 6% per day ( $N=8$ ) in adults. There was no correlation between individual size (represented by wing length) and increase in body mass within first-year birds ( $r=-0.03$ ,  $N=28$ , NS); nor was there any seasonal effect on the rate of fuel deposition ( $r=0.29$ ,  $N=28$ , NS). The total increase in body mass ranged between 1.9 and 6.3 g.

The rate of increase in body mass was not constant during the period of gain in body mass. In 22 first-year birds, with data from the last 2 days, the average gain in body mass on the last day was 0.57 g/day compared with 1.38 g/day the day before (Wilcoxon signed-ranks test:  $Z=2.80$ ,  $P<0.01$ ). On the last day, body mass even declined in three birds. The pattern was the same for adults: out of six birds the mass of two declined on the last day at the feeder. Estimates of the period of gain in body mass differed slightly between first-year birds ( $\bar{X} \pm \text{SE}=4.0 \pm 0.32$  days,  $N=23$ ) and adults ( $5.0 \pm 0.73$  days,  $N=6$ ), but not significantly so ( $t_{27}=1.04$ , NS).

## Fuel Loads and Time of Departure

To estimate departure body mass in natural conditions I used the heaviest 25% of first-year birds trapped in the surrounding area with post-juvenile moult completed ( $N=309$ ) (see Alerstam & Lindström 1990, for the logic behind this). The average body mass within this group was 17.8 g (range 16.6–20.4 g). The time of capture varied between 7 August and 24 September with a median date of 20 August. The average body mass of the 10 individuals recaptured while they were putting on fuel for migration was  $17.2 \pm 0.41$  g (range 15.7–19.3 g) on the last trapping occasion. Combining both these estimates, and correcting

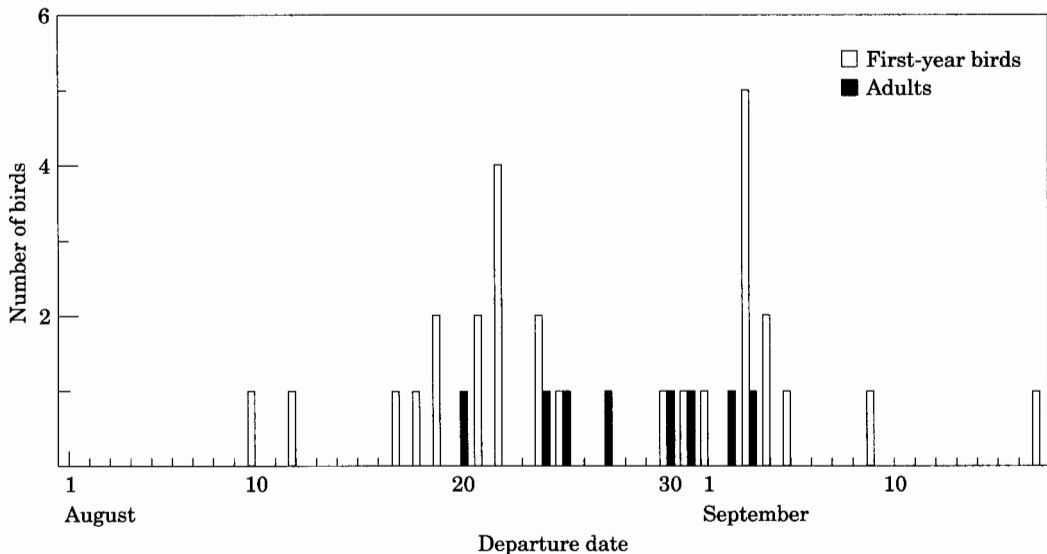
for birds being trapped before noon, suggested that the average evening departure body mass in natural conditions was somewhere between 18.0 and 18.5 g, representing a fuel load of about 35%.

At the feeder, the departure fuel load of first-year birds ( $\bar{X} \pm \text{SE}=55.2 \pm 2.0\%$ ,  $N=28$ ) was higher than that observed in natural conditions. Adults at the feeder departed with a fuel load not different from that of first-year birds ( $58.3 \pm 3.4\%$ ,  $N=8$ ;  $t_{34}=0.77$ , NS). The individual departure fuel load varied between 37.2 and 75.0% of lean body mass (body mass range: 18.9–23.8 g). A maximum fuel load of 82% (24.8 g) was recorded for an adult the day before departure. The time of departure of the earliest and the latest first-year birds from the feeding site varied by more than a month (10 August–17 September) with 24 August as the median date (Fig. 3), which is in accordance with the period when first-year birds with completed moult were trapped in the surrounding area. The adult birds' departures were more concentrated, all leaving within a 2-week period (20 August–3 September). The median date, 27 August, was, however, not significantly different from that of the first-year birds (Mann–Whitney  $U$ -test:  $Z=-0.27$ ,  $N_{\text{ad}}=8$ ,  $N_{\text{first year}}=28$ , NS). I was able to follow 12 first-year birds during a period of moult and the period of increase in body mass. These individuals left between 12 August and 17 September. Both rate of fuel deposition and departure fuel load were higher in those birds with access to extra food than in those in natural conditions, but there was no correlation between rate of fuel deposition and departure fuel load (Fig. 4). The departure fuel load increased with time of season (Fig. 5), but, even controlling for the seasonal effect, no correlation could be found between fuel deposition rate and departure fuel load ( $t_{10}=0.73$ , NS; partial correlation controlling for seasonal effect). The higher fuel loads in late individuals were a result of longer periods of increase in body mass ( $r=0.6$ ,  $N=12$ ,  $P<0.05$ ).

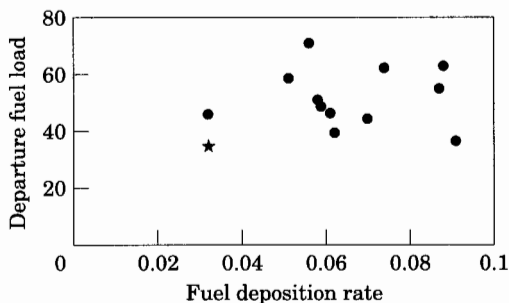
## DISCUSSION

### Influence of Food Abundance on Migratory Fuelling

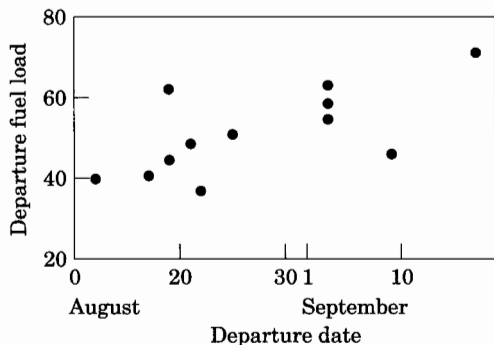
My results show that whitethroats preparing for autumn migration adjust (1) their body mass during moult, (2) the rate of migratory fuel deposition and (3) the departure fuel load in response



**Figure 3.** Departure time of first-year and adult birds from a feeding site on southern Gotland in the Baltic during the autumns of 1990–1992.



**Figure 4.** Rate of fuel deposition (given as the daily gain in fuel mass relative to lean body mass) and departure fuel load (% of lean body mass) in 12 whitethroats attracted to a feeding place ( $r=0.001$ , NS). \*: the estimated average rate of fuel deposition and departure fuel load in birds in natural conditions on southern Gotland.



**Figure 5.** Departure fuel load (% of lean body mass) in 12 whitethroats attracted to a feeding site in relation to departure date ( $r=0.67$ ,  $P<0.05$ ).

to the abundance of food. They also indicate that whitethroats can be attracted to a super-abundant food source and use it as the main food supply for a period of time before departure.

There was only a little apparent aggression between individual at the feeder. In bluethroats, studied in similar situations, individuals were very aggressive and tried to defend a feeding site at a stopover site as a territory; individuals in post-juvenile moult, however, became less aggressive at a feeding site when they had gained mass

(Lindström et al. 1990). The use of territories during stopover periods has been reported in several cases as an important factor in fuel deposition (Rappole & Warner 1976; Carpenter et al. 1983). It is not clear if the lack of aggression is typical of whitethroats, or if the cost of defending the resource was too large in my study (cf. Myers et al. 1981). That some newly arrived individuals were aggressive indicates that the latter might be the case. Thomas (1979) similarly observed no signs of intraspecific competition between garden warblers, *S. borin*, feeding on figs in Portugal.

They were rather passive towards each other and waited their turn to visit a particularly ripe fruit, which closely resembles the behaviour of whitethroats at the feeder in this study.

Whitethroats using the feeding site while undergoing post-juvenile moult attained a much higher stable body mass than those in natural conditions. Almost identical results, found in a feeding experiment with bluethroats in Swedish Lapland, have been interpreted as a response to a poor food supply in the subalpine birch forest (Lindström et al. 1990). Whether whitethroats face a poor food supply at this time of year is not known, but it is possible that their main food source (insects) is fairly common but dispersed so that searching time most often constrains total food intake. Since the stable body mass achieved at the feeder was higher than in moulting birds in natural conditions but far below the maximum fuel loads they could deposit, and since migration is obviously suppressed, it is reasonable to suppose, as Lindström et al. (1990) pointed out in the bluethroat study, that this fuel reserve provides security for unpredictable foraging success. The fact that the fuel reserve is regulated at a certain level might be a result of the trade-off between the costs and benefits of fuel storage (Witter & Cuthill 1993). An increased fuel reserve might, for example, impair manoeuvrability and increase predation risk (e.g. Lima 1986; McNamara & Houston 1987; Hedenström 1992; Witter et al. 1994). Evidence from both field observations and experiments have also indicated that birds adjust their body mass to a lower level in response to a perceived predation risk (Gosler et al. 1995; Lilliendahl 1997). After a period of stable body mass, whitethroats quickly changed to a period of increase in body mass. Since the majority of birds trapped in this period had a lot of growing body feathers, this shift may not seem to be connected with the completion of moult. It is, however, possible that all of the old feathers had been shed and the last new feathers were growing out. Since moult is energetically demanding (cf. Lindström et al. 1993) one possible explanation for the observed abrupt shift from stable to increasing body mass might be that less energy is used for feather synthesis after the moult and so more energy could be relocated to fuel deposition. Both the time between the visits and the amount of food eaten at each visit indicate, however, that the shift is more likely to be a result of a behavioural

change, increasing the total food intake. It also seems obvious that the start of migration is suppressed during the main moult period, even if the birds have plenty of food.

Whitethroats at the feeding site had a significantly higher rate of fuel deposition and a much higher departure fuel load than birds in natural conditions in the neighbouring area. The fact that individuals in natural conditions sometimes came close to the values observed at the feeding site indicates, however, that good feeding opportunities can sometimes be encountered elsewhere.

No differences in rate of fuel deposition, duration of mass gain and departure fuel load were observed between first-year birds and adults attracted to the feeder, which corresponds to results found in a detailed study of the mountain white-crowned sparrow, *Zonotrichia leucophrys oriantha* (Morton & Pereyra 1994). Ellegren (1991) found no difference in rate of fuel deposition between first-year and adult bluethroats at a stopover site in eastern Sweden, but adults departed after a shorter time. Since they did not show any initial mass loss they were also departing with a larger fuel load than first-year birds. In some other studies adult birds have also been found to be heavier on migration than first-year birds (Murray 1979; Veiga 1986).

Lindström et al. (1990) interpreted a positive correlation between individual size and increase in body mass in bluethroats at a feeding site as a result of asymmetric competition over food resources. Among the whitethroats in this study, where little aggression was observed, no correlation between size and increase in body mass was found. The observed average daily rates of fuel deposition of 6–7% in relation to lean mass are close to the approximately 5% predicted to be the average population maximum rates of fuel deposition for passerine birds of this size, based on metabolic considerations (Lindström 1991). This indicates that some of the individuals using the feeder might have reached their upper limit of metabolizable energy intake. The temporal pattern of the departure fuel load indicates that individuals adjusted their behaviour in response to temporal cues. A larger fuel load (caused by a prolonged period of fuel deposition) in late individuals suggests that these individuals, through a higher departure fuel load and a longer potential flight range, try to compensate for the delay. A higher migration speed in individuals migrating

late has also been shown for this and several other bird species (Ellegren 1993; Fransson 1995).

### Comparisons with Models of Optimal Migration

In an optimality approach, Alerstam & Lindström (1990) analysed how a migratory bird should behave depending on which selection criteria (time, energy or predation risk) operate. One of the predictions they made is that a bird trying to minimize time spent on migration, rather than transport costs, should be sensitive to the rate of fuel deposition and increase the departure fuel load with increasing rate of fuel deposition. Qualitative agreement with the time-minimization hypothesis was found with data from bluethroats and rufous hummingbirds, *Selasphorus rufus* (Lindström & Alerstam 1992). The whitethroats at the feeder in the present study had both a higher rate of fuel deposition and a higher departure fuel load than birds feeding elsewhere, which is in agreement with the time-minimization hypothesis but not with the energy minimization hypothesis, in which no response to the rate of fuel deposition should be found (cf. Lindström 1995). The expected correlation between deposition rate and departure fuel load was, however, absent within the range of observed rates of fuel deposition at the feeder. One possible explanation for this may be that the whitethroats had reached their upper fuel-carrying capacity. This seems unreasonable, however, since small migratory birds of this size are supposed, and have been observed in the field, to be able to carry fuel loads of about 80–100% of lean body mass (Hedenström & Alerstam 1992). When testing the time-minimization hypothesis, Lindström & Alerstam (1992) found a lower slope in the relationships between rate of fuel deposition and departure fuel loads than their model predicted. They believed that a possible source of the discrepancy is that the expected speed might increase along the route, which would lead birds to depart with smaller fuel loads than predicted. There are no indications, however, that white-throats increase the speed of autumn migration with distance (Fransson 1995).

Weber & Houston (1997) developed an optimality model for time-minimization during migration in which they included a finite distance. In this model they also predicted a positive overall relationship between rates of fuel deposition and departure fuel loads. The relationship should,

however, be step-wise with ranges of rate of fuel deposition where the departure fuel load does not change, which might be in agreement with my results. Both of these models include the assumption that there is some cost connected with each stopover period. This cost is measured in units of time and might be associated with the time required for search/settling at the new stopover site and/or a physiological effect when changing to a period of high food intake and lipid deposition (Alerstam & Lindström 1990; Weber & Houston 1997). In the present study, carried out when autumn migration was about to start, it was not possible to identify any such cost in terms of a delayed start of fuel deposition. It is, however, possible that some kind of physiological decision (e.g. changing of the digestive system and the liver), not indicated by any change in body mass, exists a day or two before the body mass starts to increase.

According to Lindström & Alerstam (1992) a time-selected migrant should depart from a favourable stopover site with a higher fuel load if the expected speed of migration decreases along the route. The observed temporal response with higher departure fuel loads in late whitethroats may be a result of stopover sites further south in Europe and in the Mediterranean deteriorating in the autumn, but this contradicts the idea that the quality of the stopover sites might increase along the route towards more southerly latitudes (cf. Lindström & Alerstam 1992). Another possibility is that the selective forces acting on migratory birds might vary and that early birds, for example, are not subject to the same need to minimize time, and therefore take other considerations (for example mass-dependent predation risk) into account.

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