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# Patterns of migratory fuelling in Whitethroats *Sylvia communis* in relation to departure

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Whitethroats at a coastal autumn stopover site were supplied with mealworms *ad libitum* and their fuel accumulation rates were recorded by repeated weighings by means of a remote-controlled balance. This study focuses on two questions: (1) How does the daily fuelling rate change in relation to departure? (2) Is the decision to depart affected by weather conditions?
The fuelling rates were not constant during the fuelling period. A decreasing fuelling rate close to the departure was evident in both first-year and adult birds and as many as a fourth of the birds did not gain any body mass on the last day before departure. Among possible explanations for the observed pattern are mass-dependent costs, adverse weather conditions as well as physiological changes in preparation for the flight.
The decision to depart was not affected by local weather conditions (wind and cloudiness) and some individuals departed under head wind and overcast conditions. The frequency of strong head winds was, however, low during the period of departure. Weather data do not support the hypothesis that individuals that did not gain any body mass on the last day did so as a result of their departures being delayed as a consequence of adverse weather.

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Most birds must divide the migratory journey into several flight episodes, with periods of stopover in between when fuel stores are replenished. The time spent at stopover sites strongly affects the overall migration speed, which includes both time for refuelling and migratory flight (Alerstam and Lindström 1990). The stopover sites used might differ in many aspects and birds must adjust their behaviour to a variety of situations encountered. Passerine migrants have several times been found to respond to food availability at stopover sites (Carpenter et al. 1983, Lindström et al. 1990, Fransson 1998), and some of these responses indicate that birds try to minimise time on migration (Lindström and Alerstam 1992). During refuelling at stopover sites birds may also be exposed to an increased predation risk, both as a result of impaired flight performance due to an increased body mass, and as a result of intense foraging (e.g. Metcalfe and Furness 1984, Witter and Cuthill 1993, Hedenström 1992, Kullberg et al. 1996). Blackcaps *Sylvia atricapilla* perceiving an increased predation risk during an experimental stopover situation, were found to increase their initial food intake and seemed to shorten their stopover time (Fransson and Weber 1997). The decision when to depart can also be influenced by weather conditions, since much is to be gained by flying in favourable wind conditions (cf. Alerstam 1979, Richardson 1990, Liechti and Bruderer 1998).

In this study, data from a feeding experiment on migratory fuelling in Whitethroats *S. communis* were used to investigate the following questions: (1) How do the daily fuelling rates change in relation to the departure? (2) Is the decision to depart affected by weather conditions? I have earlier shown (Fransson 1998) that birds attracted to the feeding site have a higher fuel deposition rate and a much higher departure fuel load than birds under natural conditions in the surroundings. The Whitethroat is a long-distance migrant and populations breeding in Europe winter in Africa south of Sahara.

## Methods

The feeding site was situated in an old pasture at Sundre (56°56′N, 18°11′E) about 5 km from the southernmost point of the island of Gotland in the Baltic Sea. Meal worms *Tenebrio molitor* were supplied *ad libitum* between 1 August and about 15 September in 1990–1993. Whitethroats that started to use the feeding site were trapped, measured and individually marked with colour rings. The food was placed in a bowl on a remote-controlled balance making it possible to repeatedly measure the body masses of visiting individuals. Observations were conducted every evening, for at least 2 h between 1600 and 2000 hours. Individual evening body mass was calculated as the average of all weighings of a bird during an evening. Fuel loads were calculated by using size-specific lean body masses ranging between 13.0 and 13.9 g as estimated by Ellegren and Fransson (1992). One adult bird present at the feeder in more than one year was only included the first year, while another bird present both as a first-year and adult bird was included in both age-groups. When a bird disappeared after a period of body mass increase it was assumed to have departed on migration. In this analysis I have included individuals on which information on body mass was available from at least the last two days before departure, in total 28 individuals. When looking at a four-day period preceding departure, only individuals with data from all days were included which results in a smaller sample size.

Information on weather conditions during the departure period (10 August–10 September) from the nearby weather station at Hoburg was received from the Swedish Meteorological and Hydrological Institute (SMHI). In this analysis I have used weather data from 2200 hours to reflect the conditions when Whitethroats start off on their nocturnal flights. Data included are wind speed (m $s^{-1}$), wind direction (divided on 12 directions) and cloudiness (from 0 = clear sky to 8 = total overcast). To get a combined value describing the wind conditions I calculated a tailwind component (F. Liechti pers. comm.). This was done according to a SSE-direction, which is the main migratory direction of Whitethroats breeding in eastern Sweden (own unpubl. data). To do this, I used the deviation in degrees (v) from NNW of the observed wind direction if the wind was from W to NE and the deviation from SSE if the wind was from SW to E. The component was calculated as follows: Wind component = cos (v) × observed wind speed (m $s^{-1}$). Wind observations from WSW and ENE resulted in a zero component while winds between E and SW were assigned negative values.

## Results

The departures of the Whitethroats included in this analysis were spread out over a period of about a month. Adults' departures tended to be more concentrated in time than those of first-year birds and all adults left between 20 August and 3 September.

The fuel deposition rate was not constant during the period of body mass increase. In 21 first-year birds, with data from the last two days, the average fuel deposition (as a proportion of lean mass) was 4.1% on the last day compared with 10.2% the day before (Wilcoxon signed-ranks test: $Z = 2.76$, $p < 0.01$). In seven adult birds, the trend was the same, 1.6% and 5.1% respectively, but without being significant (Wilcoxon signed-ranks test: $Z = 1.26$, $p = 0.21$). In nine first-year birds with data from the four days preceding departure, the average daily fuel deposition varied but was lowest on the last day (Fig. 1A). In six adult birds, the fuel deposition rate decreased continuously during the four days preceding departure and was on average very low on the last day (Fig. 1B). On the

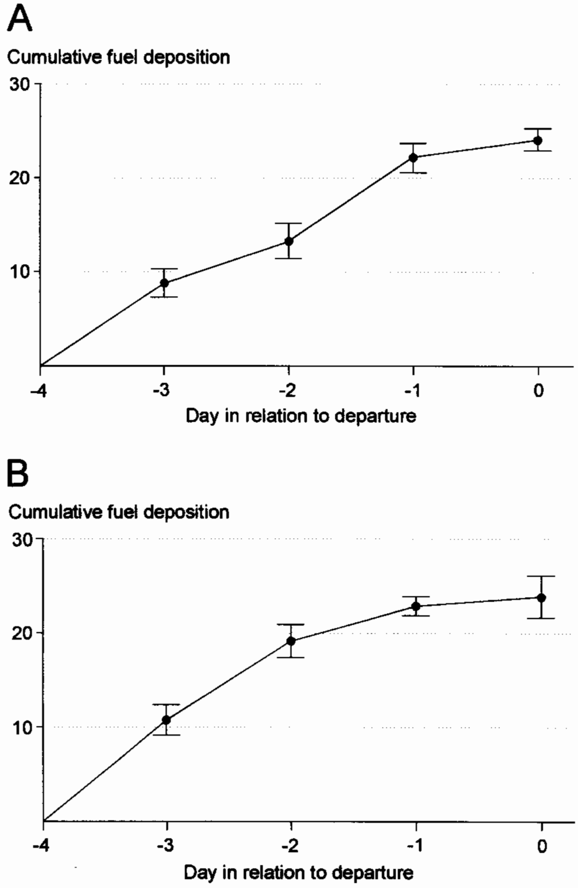


Fig. 1. Average cumulative fuel deposition (% of lean body mass ± SE) during four days before departure in (A) 9 first-year and (B) 6 adult Whitethroats attracted to a feeding place on southern Gotland.

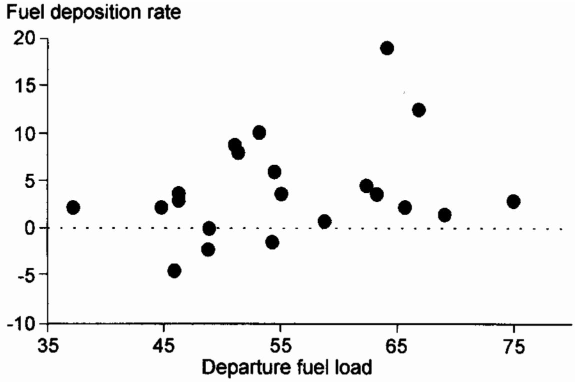


Fig. 2. Fuel deposition rate (% of lean body mass) during the last day before departure in relation to the departure fuel load (% of lean body mass) in first-year Whitethroats ($r = 0.31$, $p = 0.18$, $n = 21$).

last day, seven out of 28 individuals (4 first-year and 3 adult birds) showed no increase or even decreased in body mass. In first-year birds there was no correlation between the departure fuel load and the fuel deposition on the last day (Fig. 2). By contrast, in the group of adult birds a negative correlation was found between the departure fuel load and the fuel deposition rate on the last day (Fig. 3). The amount of fuel deposited on the last day was not affected by time of season in either first-year ($R = 0.28$, $p = 0.21$, $n = 21$) or adult birds ($R = 0.11$, $p = 0.97$, $n = 7$).

Information on wind conditions during the departure period in 1990–1993 shows that head and tail winds occurred in almost equal frequency and that strong winds were relatively rare (Fig. 4A). The distribution of wind conditions on the evenings when the 28 individuals departed (Fig. 4B) does not show any significant difference from the overall wind distribution (Mann-Whitney U-test: $Z = -1.53$, $p = 0.13$). One possible explanation why some individuals did not gain any

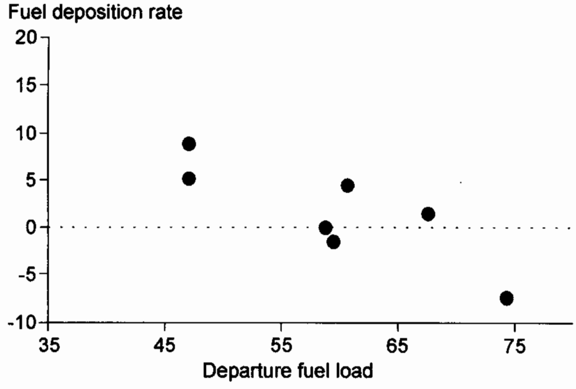


Fig. 3. Fuel deposition rate (% of lean body mass) during the last day before departure in relation to the departure fuel load (% of lean body mass) in adult Whitethroats ($r = -0.84$, $p = 0.018$, $n = 7$).

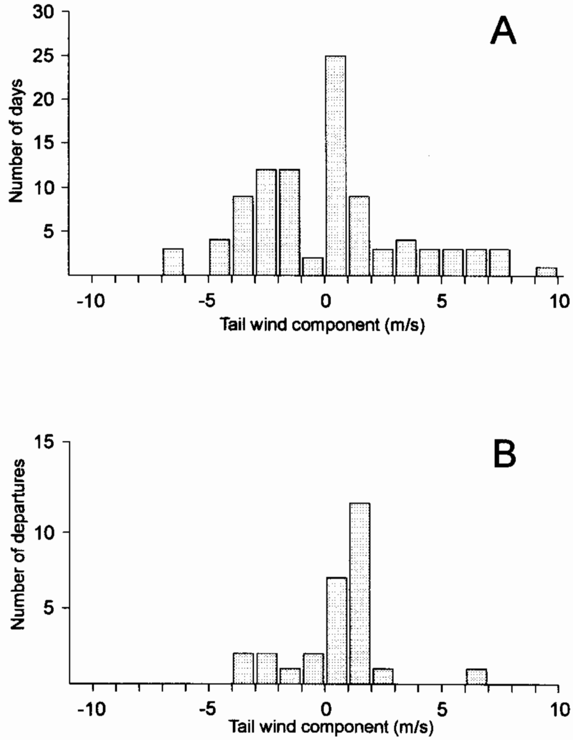


Fig. 4. (A). Distribution of daily tail wind conditions during the period 10 August–10 September in 1990–1992 ($n = 96$) based on observations made at 2200 hours. (B). Distribution of tail winds on evenings when Whitethroats departed from southern Gotland ($n = 33$). Negative values mean that birds experience head wind conditions (see text for further details).

body mass on the last day might be that weather conditions were bad for departure the day before, and that they stayed for another day without gaining any mass. However, wind conditions the evening preceding the day of departure give no support for this explanation (Fig. 5). There was no indication that the cloudiness affected birds' departure, and the overall cloudiness scores did not differ from those when birds departed (Mann-Whitney U-test: $Z = -0.66$, $p = 0.51$). The largest number of birds (57%) departed when the

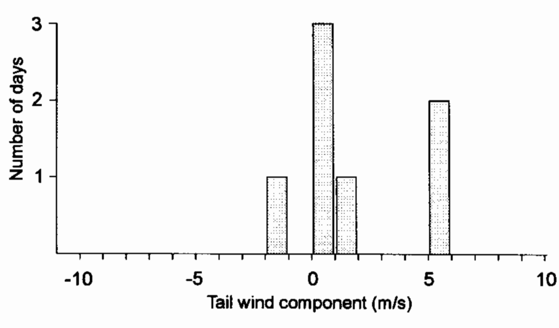


Fig. 5. Tail wind condition on the evenings preceding the departure day of Whitethroats showing no mass gain on the day of departure ($n = 7$).

sky was almost clear, but a number of birds also departed when it was overcast and one individual even left in rain.

## Discussion

The results of this study clearly show that Whitethroats preparing for autumn migration have a lower body mass gain close to the departure than earlier during the fuelling period. This reduced body mass gain was evident even though birds were fed *ad libitum* and hence not restricted by food availability. The individual variation in fuel deposition on the last day includes as many as a fourth of the birds which did not gain any mass at all.

Detailed temporal data on fuel deposition in relation to departure are rare and in most cases hard to obtain because it is most often not possible to know exactly when birds are about to depart. Information is, however, available from a few studies. From a feeding experiment with Bluethroats *Luscinia svecica*, Lindström and Alerstam (1992) conclude that there were no consistent indications that mass gain changed during the fuelling period as a whole. From graphs in Klaassen and Lindström (1996), however, where the same Bluethroats are shown, it is evident that about half of the birds show a clearly lower fuel deposition rate during the last day before departure than earlier during the period of fuelling. In a study of Rufous Hummingbirds *Selasphorus rufus* under natural conditions, however, there were no indications of a lower fuel deposition rate close to the departure (Carpenter et al. 1983). It is interesting to note that in several studies of migratory fuelling in captivity, body mass gain has been found to slow down at the end of the experimental period (e.g. Klaassen and Biebach 1994, Fransson and Weber 1997). It is, however, not possible to know if the decreased fuelling rate observed is a result of the birds being unable to depart or whether the observation is representative for natural conditions or not.

If a lower fuel deposition rate close to departure is a common pattern, what is the explanation for it? Several explanations have been proposed that may account for a lower body mass increase when a bird gets heavier close to the departure. Klaassen and Lindström (1996) proposed that extra resting metabolic and transport costs associated with an increased fuel load should result in a decrease in fuel deposition rate with time. Birds might also, as a result of mass-dependent predation risk (see Witter and Cuthill (1993) for a review), be more cautions foragers as they get heavier and hence have lower food intake rate and, as a consequence, a lower fuel deposition rate. Both these explanations predict that the body mass increase should be negatively correlated with the actual fuel load. Such a correlation was found between the fuel deposition rate during the last day and the departure fuel load in adult Whitethroats but not in first-year birds.

The decision to depart might also be affected by weather conditions, since a migrant bird has much to gain by choosing to depart when it has wind assistance. There were no indications that the Whitethroats in this study took the wind conditions at ground level under consideration when deciding to depart, but this might be explained by the fact that strong head winds were rare during the period of departure. It is also obvious that those occasions when individuals did not gain any body mass during the last day cannot be explained as delayed departures as a result of adverse wind conditions.

When changing from feeding to flying during migration, some bird species have been shown to rapidly decrease the size of their digestive machinery, which has been interpreted as an adaptive loss of a tissue that is expensive to maintain (e.g. Hume and Biebach 1996, Piersma and Lindström 1997). Hume and Biebach (1996) found in experimental Garden Warblers *S. borin*, exposed to a starvation period (mimicking migratory flight) after a period of fuelling, that the dry tissue mass of the digestive tract decreased considerably during starvation. If the lower fuel deposition rate close to departure observed in the Whitethroats in this study can be attributed to the fact that some of the physiological changes shown in Garden Warblers take place before, rather than after departure remains to be shown. If some physiological changes takes place before departure, however, there might be a balance between keeping the digestive tract functional as long as possible (especially if the departure should be postponed) and the cost of maintaining it during the initial flight. Another question is whether the observed pattern could have been an effect of the birds having access to an unrestricted food source. More detailed temporal data on fuel deposition from migratory passerine birds under natural as well as manipulated conditions would be of great interest.

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## References

Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. – In: Gwinner, E. (ed.). Bird Migration: The Physiology and Ecophysiology. Springer Verlag, Berlin, pp. 331–351.

Alerstam, T. 1979. Wind as a selective agent in bird migration. – Ornis Scand. 10: 76–93.

Carpenter, F. L., Paton, D. C. and Hixon, M. A. 1983. Weight gain and adjustment of feeding territory size in migrant

hummingbirds. – Proc. Natl Acad. Sci. USA 80: 7259–7263.
Ellegren, H. and Fransson, T. 1992. Fat loads and estimated flight-ranges in four *Sylvia* species analysed during autumn migration at Gotland, South-East Sweden. – Ring. Migr. 13: 1–12.
Fransson, T. 1998. A feeding experiment on migratory fuelling in whitethroats, *Sylvia communis*. – Anim. Behav. 55: 153–162.
Fransson, T. and Weber, T. P. 1997. Migratory fuelling in blackcaps (*Sylvia atricapilla*) under perceived risk of predation. – Behav. Ecol. Sociobiol. 41: 75–80.
Hedenström, A. 1992. Flight performance in relation to fuel load in birds. – J. theor. Biol. 158: 535–537.
Hume, I. D. and Biebach, H. 1996. Digestive tract function in the long-distance migratory garden warbler *Sylvia borin*. – J. Comp. Physiol. B. 166: 388–395.
Klaassen, M. and Biebach, H. 1994. Energetics of fattening and starvation in the long-distance migratory garden warbler, *Sylvia borin*, during the migratory phase. – J. Comp. Physiol. B. 164: 362–371.
Klaassen, M. and Lindström, Å. 1996. Departure fuel loads in time-minimizing migrating birds can be explained by the energy costs of being heavy. – J. theor. Biol. 183: 29–34.
Kullberg, C., Fransson, T. and Jakobsson, S. 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). – Proc. R. Soc. Lond. B. 263: 1671–1675.
Liechti, F. and Bruderer, B. 1998. The relevance of wind for optimal migration theory. – J. Avian Biol. 29: 561–568.
Lindström, Å., Hasselquist, D., Bensch, S. and Grahn, M. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. – Anim. Behav. 40: 453–461.
Lindström, Å. and Alerstam, T. 1992. Optimal fat loads in migrating birds: A test of the time-minimization hypotheses. – Am. Nat. 140: 477–491.
Metcalfe, N. B. and Furness, R. W. 1984. Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. – Behav. Ecol. Sociobiol. 15: 203–206.
Piersma, T. and Lindström, Å. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. – Trends Ecol. Evol. 12: 134–138.
Richardson, W. J. 1990. Wind and orientation of migrating birds: A review. – Experientia 46: 416–425.
Witter, M. S. and Cuthill, I. C. 1993. The ecological costs of avian fat storage. – Phil. Trans. R. Soc. Lond. B. 340: 73–92.