

## The effect of water availability on fuel deposition of two staging *Sylvia* warblers

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In order to succeed in crossing extensive ecological barriers, migratory birds usually deposit fuel en route. High rates of fuel deposition may enable birds to shorten their total migration time and are therefore advantageous for time-minimizing migrants. Several studies have suggested that water provision may increase food utilization in non-migratory birds. The goal of this study was to test the influence of water availability on the fuel deposition of en route migratory passerines. We studied fuel deposition of blackcaps *Sylvia atricapilla* and lesser whitethroats *S. curruca* staging in a plantation of Mount Atlas gum-tree *Pistacia atlantica* in the northern Negev desert, Israel, during the autumns of 2000 and 2002. We manipulated water availability at the site and measured the effect of water supplementation on fuel deposition of birds of both species. We found that when water was available, blackcaps had higher fuel loads and higher fuel deposition rates than during control trials. However, water availability had no effect on fuel deposition of lesser whitethroats. Species-specific differences in adaptations to arid conditions, reflected in the species' winter habitat preferences, may be responsible for the between-species dissimilarity in responding to water provision. We suggest that water availability may have strong ecological and evolutionary consequences for birds migrating through arid environments, by its possible effect on bird behavior and physiology.

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Accumulation of large amounts of fuel is mandatory for migratory birds to ensure a successful journey across wide ecological barriers, such as large water bodies and deserts (Moreau and Dolp 1970, Pfister et al. 1998). Alerstam and Lindström (1990) argued that maximization of fuel deposition rates is adaptive for time-minimizing migrants that may benefit from e.g., arriving to their destination at an optimal time to occupy high quality territories (Price 1981, Hasselquist 1998, Kokko 1999). Hence, in addition to the total amount of accumulated fuel, the rate in which birds deposit fuel

(mainly fat) before and throughout their migratory journeys may also have an important effect on the fate of migratory birds.

Long-distance migratory birds in Europe and Western Asia usually migrate to Africa, south of the Sahara, and are thus bound to a bi-annual crossing of some 1,600 to 2,000 km of an extremely arid environment (Moreau 1972, Biebach et al. 1986). Migrants are compelled to prepare in advance for such a long cross-desert journey (e.g., Schaub and Jenni 2000) because they usually cannot gain energy while stopping over within deserts

(Biebach et al. 1986). Additionally, the extreme rarity of water sources in deserts, and to a large extent also in areas bordering deserts such as the Mediterranean zone (Ashbel 1950), prevents birds from water consumption over a much larger part of their route than mentioned above.

The importance of water to birds during migration is not clear. While some studies (Carmi et al. 1992, Klaassen 1996) suggested that the maintenance of a bird's water-balance may impose a serious constraint on the ability of birds to undertake long-distance migratory flights, others (Bruderer et al. 1995, Landys et al. 2000, Liechti et al. 2000) provided no empirical support for this hypothesis. Nevertheless, several studies, involving non-migratory bird species, found that water may improve food utilization and hence energy accumulation in birds (Yalda and Forbes 1995, Yalda and Forbes 1996, Kotler et al. 1998). Through its positive role in facilitating food utilization, this effect may be important for birds aiming to maximize their rate of energy accumulation. However, this remains to be demonstrated in migratory birds.

Water may facilitate energy intake of migrants by increasing the birds' food utilization. Kotler et al. (1998) reported a 50% increase in food patch utilization under water provision in Australian crows *Corvus coronoides*, a desert bird species. The authors suggested that birds in arid environments shun certain activities, including foraging, during some parts of the day, to avoid increased water loss. Water availability probably enabled these birds to extend their daily foraging duration and consequently to better utilize available food resources. In a different study, water provisioning to food was shown to substantially increase food digestibility in domestic hens (Yalda and Forbes 1995, 1996). Water supplementation was found to induce histo-morphological changes of the digestive tract (Yasar and Forbes 1999, 2000), which was argued to enable higher food digestibility by altering digestive tract functionality. These findings seem relevant for birds aiming to maximize their energy intake rate, as in the case of time-minimizing migrants (Lindström and Alerstam 1992). In particular, since ambient conditions may enhance water loss while foraging (Kotler et al. 1998), water availability may have a substantial effect on a bird's daily energy intake while staging in arid and hot environments.

The goal of this study was to examine the influence of water availability on fuel deposition of migratory passerines about to cross the Sahara desert on their way to their wintering grounds, while staging at an en route site situated at a desert edge. First, we studied the effect of water provisioning on the distribution of fuel loads of staging bird populations and then examined whether water affected rates of fuel deposition in individual birds. We therefore examined whether changes in fuel load distribution of the population, when water

was available, could be attributed to the variation in the rates of fuel deposition of individual birds.

## Methods

### Study site and species

The study was conducted during the autumns of 2000 and 2002, in a 3-hectare plantation of *Pistacia atlantica*, bordering a large planted coniferous forest (Lahav Forest), located in the Northern Negev, Israel (31°20'N, 34°50'E). During autumn 2000, 10% of the trees in the grove bore fruits and total fruit abundance was estimated to be 558 000 fruits (Sapir 2002). During autumn 2002, 22% of the trees in the grove bore fruits and fruit abundance was estimated to be 1.5 million. Yet, during the course of the study only about 30% of these fruits were ripe at any one time and thus appropriate for consumption by birds (Sapir 2002). Many woodland passerine migrants concentrate in this site every autumn, just before they engage on a 1,800 km journey across the Sahara. For more details on the study site see Shochat et al. (2002) and Sapir (2002).

We studied two species of *Sylvia* warblers: the blackcap *Sylvia atricapilla*, and the lesser whitethroat *S. curruca*. Both species are abundant migrants in the area (Shirihai 1996), and have long migratory periods, spanning between the beginning of August to the end of October (Shochat 1999). Both species were found to consume *P. atlantica* fruits, with a 70% mean fruit volume in their feces (Sapir 2002). The birds digest the fruit's lipid-rich pulp (53% of dry content) and defecate the seed. Water comprises 34.5% of the pulp's wet-content (Sapir 2002). Sapir (2002) reported that the mean fuel deposition rates of these species at the study site during the autumns of 1995 to 1999, when fruit abundance ranged between 6 to 9 million fruits, were 3.97% and 3.49% for the blackcap and the lesser whitethroat, respectively.

### Experimental procedure

We conducted two experiments to study the effect of water availability on staging migratory passerines. The first experiment (hereafter PopExp) measured the response of the bird populations to water availability. In this experiment we examined the effect of water provisioning on the distribution of fuel loads and visual fat levels of the migrants. The second experiment (hereafter IndExp) measured the response of individual birds to water availability. In this experiment we examined the effect of water provisioning on rates of fuel deposition and on the rates of change in visual fat levels of individual birds.

PopExp took place between 7 August and 19 October 2000. During this period we conducted 13 constant-effort bird-trapping sessions, using a 96 m mist-nets array. Each trapping session started at first light and lasted 4 hours. In two sessions (15 and 23 September) we provided the birds with drinking water. Water was provided approximately 20 hours before the start of the trapping effort. The remaining 11 trapping sessions, in which no water was provided, served as controls. Experimental trials were interspersed between control trials (e.g., 8, 19 and 25 September).

IndExp was conducted during September 2002. During this experiment we conducted a total of 17 constant-effort bird-trapping sessions. Trapping sessions started on the 5 September and were then conducted daily from 8 to 23 September. In IndExp we used a mist-nets array of 141 m, again for the first 4 morning hours. Birds were trapped during three distinct periods (treatments), following each other. First, we trapped birds during 6 consecutive days (8 to 13 September), preceded by a single bird-trapping day (5 September). This period served as the first control trial and thus, water was not provided during this time. The second trapping period started immediately after the end of the first, and served as the water provision treatment. Water was provided throughout this period, starting 20 hours before the start of the first day's bird trapping session, and throughout for a total period of 5 days (14 to 18 September). This treatment was immediately followed by a third trapping period (19 to 23 September) in which water was again unavailable to the birds (water was removed at the end of the last bird trapping session of the preceding period). This last period served as a second control trial. Yet, due to small sample sizes (see Table 1) we had to pool the two control treatments for the purpose of statistical analyses.

In both experiments, water was provided by using troughs placed underneath the canopies of *P. atlantica* trees, along the mist-net line and 5 meters from it. The

troughs (3 in PopExp and 10 in IndExp) were round-shaped, 60–70 cm in diameter, and were set in shallow depressions with their rims at ground level. The troughs were made of plastic sheets, and were superficially covered with gravel and stones. Each trough contained 5–10 liters of water and its water depth was about 30 cm when filled-up. During IndExp, when water treatment lasted several days, we constantly replenished the water to keep water level constant. Individuals of both species were often seen using the artificial water sources in both experiments.

We obtained the following measurements from all trapped birds: wing length (to the nearest 0.5 mm, using a wing-ruler), fat score (6-level visual fat index after Helms and Drury 1960), and body mass (to the nearest 0.1 g, using a Pesola mechanical balance in PopExp and an Ohaus CS-200 digital balance in IndExp). In addition, we calculated daily bird density by summing up all the individuals that were trapped during a daily constant trapping effort.

The design of the two experiments relies on the assumption that individual migrants are independent subjects. We therefore treated different individuals as independent replicates within a specific experimental session. It seems highly implausible that some other factors may have, by chance, coincided with the experimental manipulation in each of the two experiments.

### Fuel deposition calculations

To estimate individual bird fuel load and fuel deposition rate, we adopted the method proposed by Ellegren and Fransson (1992). First, we estimated an individual's size-specific lean body mass (hereafter LBM), based on bird body mass and size (wing length), using a dataset comprised of 1137 blackcaps and 877 lesser whitethroats, trapped in the area between 1995–2000 (reported in detail in Sapir 2002). The equations that were found to

Table 1. Sample sizes in PopExp (autumn 2000) and IndExp (autumn 2002). In IndExp, the numbers of birds re-trapped within the period of a certain experimental treatment are given in parentheses, and the average number of days, per treatment, from first trapping to last re-trapping of individual birds is given in brackets.

PopExp (autumn 2000)					
Species/treatment	Control	Water	Total		
Blackcap	43	61	104		
Lesser whitethroat	27	7	34		
IndExp (autumn 2002)					
Species/treatment	Control 1	Water	Control 2	Controls pooled	Total
Blackcap	72 (2) [3]	51 (6) [2.3]	60 (3) [1]	132 (5) [1.8]	183 (11)
Lesser whitethroat	71 (7) [3.4]	46 (5) [2]	40 (3) [1.3]	111 (10) [2.8]	157 (15)

describe each individual's estimated LBM, according to its species, are (mass is given in grams and wing length in millimeters):

$$\text{LBM}_{\text{blackcap}} = 0.12 \times \text{Wing length} + 6.257$$

$$\text{LBM}_{\text{lesser whitethroat}} = 0.115 \times \text{Wing length} + 2.756.$$

We then calculated each individual's fuel load by dividing the bird's actual mass beyond its estimated LBM, by the bird's estimated LBM to give:

$$\text{Fuel load} = \frac{\text{Bird mass} - \text{LBM}}{\text{LBM}}$$

A bird's fuel load is expressed in percentages of mass beyond and relative to its estimated LBM. Following Green (2001), we examined if our calculated fuel load variable corresponds to actual bird masses. In IndExp, when we studied re-trapped birds, we calculated the average daily fuel deposition rate as the difference between the birds' fuel loads in the second and the first trapping occasions, divided by the number of days between the two trapping dates. Fuel deposition rate is therefore expressed in percent fuel load increase per day. We also calculated the actual mass changes of each bird, in case our calculated fuel load variable would deviate considerably from the measure of the birds' body condition (Green 2001). Similarly, for each re-trapped bird we calculated the average daily change in its visual fat score between the second and the first trapping dates. For birds re-trapped more than once in a treatment during IndExp, we calculated these two variables using values obtained at the birds' first and last capture.

## Data analyses

In analyzing PopExp data, we used group t-tests to examine within species differences in fuel loads between the treatments (after examination of the data by Kolmogorov-Smirnov tests for normal distribution and by Levene's tests for homogeneity of the variance, as required by the assumptions of the test). In this experiment we examined individuals trapped only on a single occasion throughout the period in which the study was conducted. Likelihood ratio  $\chi^2$ -test was used to examine whether blackcaps of the two treatments differed in their fat scores. Due to sample size considerations, we could not perform  $\chi^2$ -test on the lesser whitethroats' fat score data. We therefore used the Fisher's exact probability test. In addition, we conducted Polytomous Logit Universal Models ordinal regression analyses, using SPSS® (SPSS Inc. 1999), with the treatment as the independent variable and the fat scores as the dependent variable, to test the effect of water availability on the fat score distribution of the blackcap,

the lesser whitethroat and of the two species combined (in the latter case, bird species was another independent variable). The results of the lesser whitethroat ordinal regression analysis were uncertain due to the small sample size, and hence were not included hereafter. We also used Wilcoxon's non-parametric tests (Siegel and Castellan 1988) to examine whether bird densities (of each species) differed significantly between control and water-provisioning treatments. Spearman's correlation tests were applied to examine the relationships between capture date and the fuel load of the birds, and to examine the relationships between fuel loads and fat scores. Pearson correlation tests were applied to investigate the relationships between calculated fuel loads and the body mass of the birds. All tests were two-tailed.

When analyzing IndExp data, we used the Wilcoxon's non-parametric test to examine the effect of water supplementation on fuel deposition rates, on mass change rates and on the daily changes in the fat score of birds trapped and subsequently re-trapped during a single experimental treatment. The same test was applied to examine if water affected bird density and to determine if during their first trapping occasion fuel loads of birds in the two treatments (in each species) were different from each other. The latter tests were conducted in order to rule out the possibility that the birds' fattening rates were related to their energetic states at first capture. Spearman's correlation tests were applied to examine the relationships between the daily average fuel deposition rate, the daily rate of mass change and the daily average change in the bird's fat score. All tests were two-tailed.

## Results

### PopExp (autumn 2000)

#### *The effect of water provisioning on fuel level distributions within a population of migrants*

The number of birds trapped in each treatment in PopExp is given in Table 1. The daily average fuel loads in the control sessions did not correlate with the number of days from the first trapping session in either blackcap or lesser whitethroat (Spearman's correlations;  $n = 11$ ,  $r_s = -0.387$ ,  $P = 0.24$  for blackcap and  $n = 6$ ,  $r_s = -0.187$ ,  $P = 0.35$  for lesser whitethroat; note that lesser whitethroats were trapped only in 6 of the 11 control trapping sessions). Nor did it correlate with the number of days from the mid-season date, which was determined arbitrarily as the mean date between the first and last trapping occasions (Spearman's correlation;  $n = 11$ ,  $r_s = -0.02$ ,  $P = 0.93$ , only for blackcap, as the sample size for lesser whitethroat was too small to be tested). These results suggest that fuel loads of both species were unrelated to the capture date during the season. Fuel

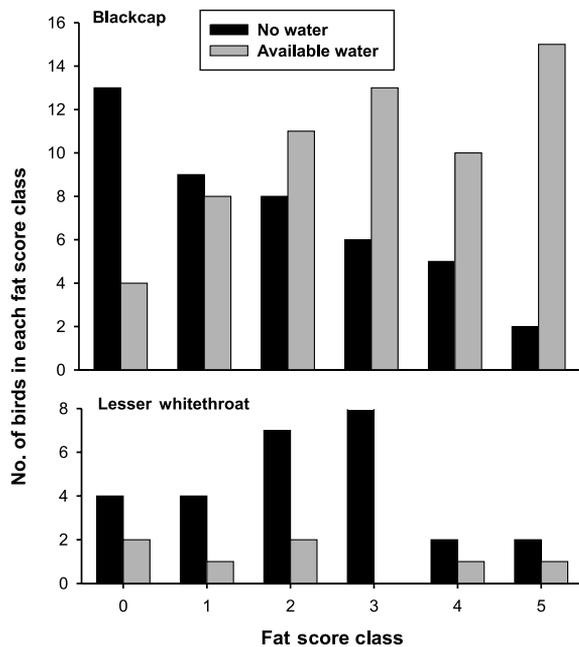


Fig. 1. Frequency distribution of visual fat scores of blackcaps (upper part) and lesser whitethroats (lower part), in relation to treatment in PopExp (autumn 2000).

load data for each species was, therefore, pooled for all control sessions. The same was done for the two water sessions.

The fuel loads of blackcaps trapped at the two water-treatment trapping days ( $n = 61$ ,  $\text{mean} \pm \text{S.E.} = 22.4\% \pm 2.12$ ) were significantly higher (group t-test,  $t = 3.177$ ,  $P = 0.002$ ) than the fuel loads of blackcaps trapped during the eleven control sessions ( $n = 43$ ,  $\text{mean} \pm \text{S.E.} = 11.95\% \pm 2.5$ ). The fat scores of blackcaps trapped during the water provisioning sessions ( $\text{mean} = 3.02$ ) were significantly higher (Likelihood ratio  $\chi^2$ -test,  $\chi^2_3 = 18.01$ ,  $P = 0.003$ ; Ordinal regression,  $df = 1$ , Wald  $\chi^2_1 = 15.28$ ,  $P < 0.001$ ) than those of the blackcaps trapped during control sessions ( $\text{mean} = 1.7$ ). As illustrated in Fig. 1, blackcaps of the control group tended to have a high frequency of low fat scores, while an opposite trend was found in the water-treatment group. The blackcaps' fat scores and fuel loads were positively and significantly correlated (Spearman's correlation,  $n = 104$ ,  $r_s = 0.83$ ,  $P < 0.001$ ). Also, fuel loads and body masses of blackcaps were found to be strongly and positively correlated (Pearson correlation,  $n = 104$ ,  $r = 0.995$ ,  $P < 0.001$ ). Furthermore, blackcap densities were significantly higher (Wilcoxon's test,  $n = 13$ ,  $W = 66$ ,  $P = 0.028$ ) when water was provided ( $n_{\text{water}} = 2$ ,  $\text{mean}_{\text{water}} \pm \text{S.E.} = 31 \pm 2$  birds/trapping effort), relative to control sessions ( $n_{\text{control}} = 11$ ,  $\text{mean}_{\text{control}} \pm \text{S.E.} = 3.6 \pm 0.8$  birds/trapping effort).

The fuel loads of lesser whitethroats trapped at the two water treatment sessions ( $n = 7$ ,  $\text{mean} \pm \text{S.E.} =$

$21.77\% \pm 8.23$ ) were somewhat higher but not significantly different (group t-test,  $t = 0.54$ ,  $P = 0.59$ ) from the fuel loads of lesser whitethroats trapped during the eleven control sessions ( $n = 27$ ,  $\text{mean} \pm \text{S.E.} = 19.35\% \pm 3.72$ ). Lesser whitethroats' fat scores (Fig. 1) were not significantly different (Fisher's exact probability test,  $P = 0.67$ ) between control ( $\text{mean} = 2.2$ ) and water ( $\text{mean} = 2$ ) sessions. We found that when we tested the effects of water availability and bird species on the birds' fat score, by using ordinal regression analysis, water was not found to be significant ( $df = 1$ , Wald  $\chi^2_1 = 0.26$ ,  $P = 0.61$ ), and bird species was insignificant as well ( $df = 1$ , Wald  $\chi^2_1 = 3.01$ ,  $P = 0.083$ ). However, the interaction term between these two effects was found to be significant ( $df = 1$ , Wald  $\chi^2_1 = 5.07$ ,  $P = 0.024$ ), implying that the two bird species reacted differently to the treatment, with regard to their fat score distribution. The lesser whitethroats' fat scores and fuel loads were positively and significantly correlated (Spearman's correlation,  $n = 34$ ,  $r_s = 0.8$ ,  $P < 0.001$ ). Fuel loads and body masses of lesser whitethroats were found to be strongly and positively correlated (Pearson correlation,  $n = 34$ ,  $r = 0.99$ ,  $P < 0.001$ ). We did not have enough data to statistically compare densities of lesser whitethroats between control ( $n = 6$ ), and water sessions ( $n = 2$ ), but their densities appear to be similar, with means ( $\pm \text{S.E.}$ ) of  $4.5 \pm 1.47$  birds/trapping effort and  $3.5 \pm 2.5$  birds/trapping effort for control and water treatments, respectively.

## IndExp (autumn 2002)

### *The effect of water provisioning on fuel deposition rates of individual migrants*

The number of birds trapped in each treatment, the number of re-trapped birds and the average number of days between the first and last captures in IndExp, are given in Table 1. Without available water (control treatment), the average fuel deposition rate of individual blackcaps was  $-4.9\%/day$  (range  $-10.3$  to  $-1.3$ ,  $n = 5$ ). Under the water provision treatment, blackcaps significantly increased their fuel load (Wilcoxon's test,  $n = 11$ ,  $W = 15$ ,  $P = 0.006$ ) at an average rate of  $7.2\%/day$  (range  $3.7$  to  $10.9$ ,  $n = 6$ ; Fig. 2a). The average daily change in the birds' visual fat score was also significantly different between the two treatments (Wilcoxon's test,  $n = 11$ ,  $W = 15$ ,  $P = 0.004$ ), with an average of  $-0.2$  units/day (range  $-1$  to  $0$ ) in the control birds, and an average of  $0.8$  units/day (range  $0.3$  to  $1$ ) in the water provisioned birds (Fig. 2b). The birds' daily mass change was also significantly different between the two experimental groups (Wilcoxon's test,  $n = 11$ ,  $W = 15$ ,  $P = 0.006$ ), with water treated birds exhibiting a mean mass gain of  $1.11$  g/day (range  $0.57$  to  $1.8$ ) and control group

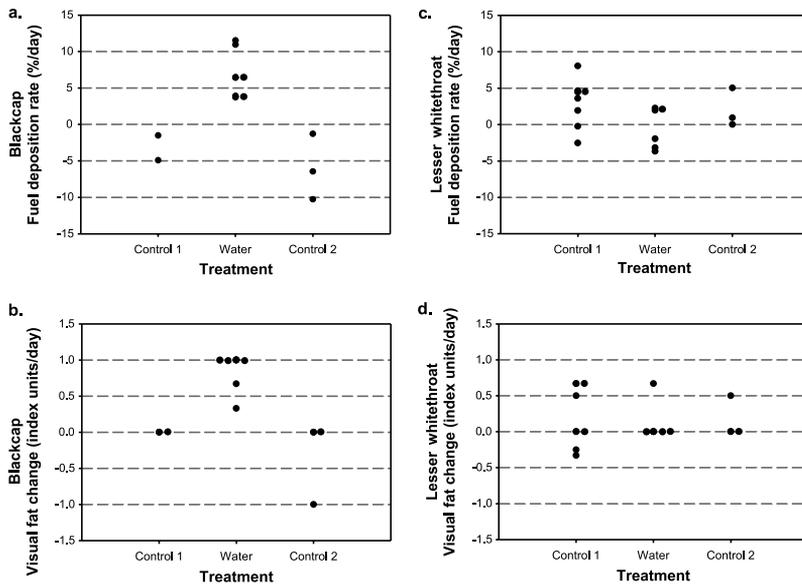


Fig. 2. The effect of treatment on the daily average fuel deposition rates of re-trapped blackcaps (a) and lesser whitethroats (c), and on the daily average changes of visual fat scores of blackcaps (b) and lesser whitethroats (d), in IndExp (autumn 2002). Control 1 treatment was conducted before water supplementation and Control 2 was performed after the experimental treatment. Overlapping points were moved sideways.

birds showing the opposite trend, with a mean rate of  $-0.76$  g/day (range  $-1.6$  to  $-0.2$ ). Fuel deposition rate and daily change in fat score were found to be significantly and positively correlated (Spearman's correlation,  $n = 11$ ,  $r_s = 0.86$ ,  $P = 0.001$ ), and the same was found for fuel deposition rate and the mean daily change in body mass (Spearman's correlation,  $n = 11$ ,  $r_s \approx 1$ ,  $P < 0.001$ ). Fuel loads of blackcaps in the two treatments were statistically indifferent at the birds' first capture (Wilcoxon's test,  $n = 11$ ,  $W = 33$ ,  $P = 0.58$ ), with average values between  $10.6\%$  (range  $-7.1$  to  $36.8$ ) and  $6.1\%$  (range  $-4.7$  to  $26.8$ ) in the control and water treatment birds, respectively.

Unlike the blackcap case, fuel deposition rates (Fig. 2c) and daily changes of fat score (Fig. 2d) of lesser whitethroats were not statistically different between control and water treatments (Wilcoxon's test,  $n = 15$ , fuel deposition rates:  $W = 26$ ,  $P = 0.96$ ; rate of change in visual fat score:  $W = 40$ ,  $P \approx 1$ ). Average fuel deposition rates were  $2.6\%/day$  (range  $-2.6$  to  $8$ ) and  $-0.9\%/day$  (range  $-3.2$  to  $2.3$ ) in the control and water treatments, respectively. Average daily change of fat score was  $0.2$  units/day (range  $-0.3$  to  $0.7$ ) and  $0.1$  units/day (range  $0$  to  $0.7$ ) in the control and water treatments, respectively. Mass changes of lesser whitethroats were not statistically different between the two experimental groups (Wilcoxon's test,  $n = 15$ ,  $W = 25.5$ ,  $P = 0.075$ ), with the control group tending towards higher rates of mass gains (mean  $= 0.27$  g/day, range  $-0.27$  to  $0.85$ ) than the water-treated group (mean  $= -0.1$  g/day, range  $-0.4$  to  $0.23$ ). Fuel deposition rate and daily change in fat score were found to be significantly and positively correlated (Spearman's correlation,  $n = 15$ ,  $r_s = 0.63$ ,

$P = 0.012$ ) and the same was found for fuel deposition rate and mean daily change in bird body mass (Spearman's correlation,  $n = 15$ ,  $r_s \approx 1$ ,  $P < 0.001$ ). Fuel loads of control and water treated lesser whitethroats were not statistically different in the birds' first capture (Wilcoxon's test,  $n = 15$ ,  $W = 78$ ,  $P = 0.81$ ), with average values of  $13.2\%$  (range  $-12.1$  to  $46.3$ ) and  $11.4\%$  (range  $-0.6$  to  $15.0$ ) for birds of the control and water treatments, respectively.

Density of blackcaps was not statistically different between the two treatments (Wilcoxon's test,  $W = 96$ ,  $P = 0.2$ ), with means  $\pm$  S.E. of  $8.9 \pm 3.17$  birds/constant trapping effort (range  $1$  to  $42$ ,  $n = 12$ ) and  $10 \pm 1.9$  birds/constant trapping effort (range  $3$  to  $14$ ,  $n = 5$ ) in the control and water treatments, respectively. The same was found for the lesser whitethroat ( $W = 100.5$ ,  $P = 0.43$ ), with means  $\pm$  S.E. of  $8.17 \pm 1.54$  birds/constant trapping effort (range  $2$  to  $21$ ,  $n = 12$ ) and  $9 \pm 1$  birds/constant trapping effort (range  $6$  to  $12$ ,  $n = 5$ ) in the control and water treatments, respectively.

## Discussion

Fuel loads of migratory blackcaps at an en route stopover habitat were substantially higher when water was available at the site, during autumn 2000 (PopExp). This could have resulted from two different, not necessarily mutually exclusive, processes: (1). Concentration of blackcaps around water sources that might have altered the composition of the population at the site to include more birds that were characterized by high fuel loads, and consequently shifting the population's

fuel-load distribution towards higher values. This might have occurred if birds exhibited state dependent habitat selection to high-quality sites, including such with available water (*sensu* Alerstam and Lindström 1990). (2). Individual birds might have actually increased their fuel deposition under the influence of water supplementation.

The autumn 2002 results (IndExp) clearly demonstrate, for the first time, that water provision had a strong positive effect on fuel deposition rates of individual migratory blackcaps. State-dependent concentrations of birds at the site may therefore be an additional, but certainly not the only, process explaining the findings of PopExp. The IndExp (autumn 2002) results show that water provisioned birds increased in mass and in visual fat levels, while individuals that staged at the site when water was not available decreased in mass and their visual fat levels decreased or remained constant. Though it is clear that not all of the variation in the body mass could be attributed to fat level changes, and ingested water may by itself contribute to the increase in the birds' body mass, the positive correlation between the average daily changes of visual fat levels and the calculated fuel deposition rates indicates that deposition of fuel (mainly fat; Lindström and Piersma 1993), can account for a substantial portion of the variation in the body mass changes. Therefore, by encountering water sources in an arid environment, and consequently increasing their fuel stores, individual birds may shorten their stopover time, which should be advantageous for time-minimizing migrants.

The behavioral mechanism suggested by Kotler et al. (1998), in which water availability may lead to an expansion of the daily foraging duration, is one possible explanation for the observed variation in fuel deposition rates. This is so, because the longer daily foraging duration may markedly increase migratory birds' daily rate of energy accumulation (Kvist and Lindström 2000). The physiological mechanism suggested by Yalda and Forbes (1995, 1996) and by Yasar and Forbes (1999, 2000), in which water may enhance certain physiological alterations in the birds' digestive tract that enable the birds to increase their food utilization, is another possible explanation that may account for the observed variations in fuel deposition rates. The digestive systems of migratory birds are known to be very flexible. Birds are able to substantially reduce their digestive tract mass during flight (Piersma and Lindström 1997, Karasov and Pinshow 1998, Piersma 1998, Lindström et al. 2000), presumably in order to decrease energy costs of transport. The opposite may happen during en route staging periods, while the birds efficiently utilize a variety of food types (Bairlein 1996, Lepczyk et al. 2000). The specific role of the two non-mutually exclusive mechanisms for facilitating higher fuel deposition rates of water-treated blackcaps is yet to be discovered.

Contrary to the blackcaps, we found no effect of water provision on the fuel deposition of lesser whitethroats that co-occurred with the blackcaps in the staging habitat. These two species share important ecological attributes, such as diet, habitat selection, predation avoidance tactics and migration timing, while stopping over at this particular site (Sapir 2002). However, the relationships between the birds' fuel load distribution and the habitat's food abundance differed considerably between the species. While blackcaps were having much higher fuel loads in food-rich habitats (*P. atlantica* fruits), fuel loads of the lesser whitethroats were similar in patches that differed in their food abundance by one to two orders of magnitude. Thus, it may be possible that lesser whitethroats are doing equally well in a very wide range of habitats, while blackcaps are able to deposit fuel only in a narrow range of habitats, characterized by certain feeding conditions. The control blackcaps in the 2002 experiment may have thus lost mass because the habitat was relatively poor compared with other years in which the habitat was much more fruit-rich. As this was also the case during the autumn of 2000, it is possible that water may affect blackcaps only at the extreme part of their stopover habitat range.

It might be worth mentioning that some differences exist in the types of habitat occupied by the two species during their African winter period. While the blackcap was reported to inhabit mainly humid forests in various parts of western, central and eastern Africa, the lesser whitethroat settles in drier habitats, some of which are comprised of only bushes or tall grass, in areas bordering the Sahara Desert (Moreau 1972, Snow and Perrins 1998). Maybe due to its adaptations to such semi-arid environments, where water is rare, the lesser whitethroat is able to successfully forage and utilize food in habitats where food and water are scarce. On the contrary, foraging and food utilization of the blackcap might have evolved to be influenced by the availability of water, which is readily available in many of the species' wintering habitats.

What then are the possible ecological and evolutionary consequences of the relationships between water availability and fuel accumulation in the blackcap, and possibly in other songbirds? By facilitating energy accumulation, water availability may influence habitat selection of long-distance migrants staging in arid and semi-arid areas along their migratory route. For staging birds that are sensitive to migration timing, gain of high water-induced energetic rewards during stopover may have an important influence on the birds' migratory strategy with respect to energy and time savings, and may consequently determine the success of birds throughout their route and at their destination. Future studies of a wider range of taxa and under diverse ecological circumstances are required to understand the

generality of the phenomenon, and the behavioral and physiological mechanisms underlying it.

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