

# Drinking water boosts food intake rate, body mass increase and fat accumulation in migratory blackcaps (*Sylvia atricapilla*)

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**Abstract** Fat accumulation by blackcaps (*Sylvia atricapilla*) is a prerequisite for successful migratory flight in the autumn and has recently been determined to be constrained by availability of drinking water. Birds staging in a fruit-rich *Pistacia atlantica* plantation that had

access to water increased their body mass and fat reserves both faster and to a greater extent than birds deprived of water. We conducted a series of laboratory experiments on birds captured during the autumn migration period in which we tested the hypotheses that drinking water increases food use by easing limitations on the birds' dietary choices and, consequently, feeding and food processing rates, and that the availability of drinking water leads to improved digestion and, therefore, to higher apparent metabolizable energy. Blackcaps were trapped in autumn in the Northern Negev Desert, Israel and transferred to individual cages in the laboratory. Birds were provided with *P. atlantica* fruit and mealworms, and had either free access to water (controls) or were water-deprived. In experiment 1, in which mealworm availability was restricted, water-deprived birds had a fourfold lower fruit and energy intake rates and, consequently, gained less fat and total mass than control birds. Water availability did not affect food metabolizability. In experiment 2, in which mealworms were provided ad libitum, water availability influenced the birds' diet: water-restricted birds ate more mealworms, while control birds consumed mainly *P. atlantica* fruit. Further, in experiment 2, fat and mass gain did not differ between the two treatment groups. We conclude that water availability may have important consequences for fat accumulation in migrating birds while they fatten at stopover sites, especially when water-rich food is scarce. Restricted water availability may also impede the blackcap's dietary shift from insectivory to frugivory, a shift probably necessary for successful pre-migratory fattening.

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## Introduction

To undertake their annual long-distance journey, migratory birds must accumulate fat and protein for fuel. Birds lay down fuel reserves before the onset of migration and while staging at stopover sites (Lindström 2003). Storing fat before and during migration involves numerous behavioral and physiological mechanisms (Bairlein 1985; Moore and Kerlinger 1987; Pennycuick and Battley 2003; Karasov and McWilliams 2005), and the bird's morphology and physiology, as well as the environment in which it forages, limit its rate of fuel deposition (Lindström 2003). Theoretical studies of optimal migration in birds (Alerstam and Lindström 1990) revealed the importance of minimizing the duration of the migratory period by maximizing the rate of fuel deposition, which enables birds to arrive early in high-quality feeding and breeding areas at their destination (Price 1981; Gunnarsson et al. 2006). Thus, limitations on feeding by birds during migratory staging may have far-reaching consequences on their fitness (Pfister et al. 1998).

Fat accumulation by blackcaps (*Sylvia atricapilla*) migrating south in autumn has recently been found to be strongly constrained by water availability (Sapir et al. 2004b). Birds staging in a fruit-rich *Pistacia atlantica* plantation that had access to water increased their body mass ( $m_b$ ) and fat reserves to a greater extent and at a faster rate than birds without access to drinking water. The birds that had access to water were thus likely able to depart for their cross-Sahara journey (Moreau 1972; Biebach et al. 1986) earlier and in better body condition than birds without access to water. Sapir et al. (2004b) also found higher bird concentrations at their study site during water addition treatments.

At least two non-mutually exclusive explanations may clarify the water-induced fattening of blackcaps found by Sapir et al. (2004b). First, it is possible that the relatively low water content (only 35% water in the flesh of freshly picked fruit; Sapir 2002) of the fat-rich (53% of the fruit flesh dry mass; Sapir 2002), highly abundant *P. atlantica* fruit constrains mass gain. Based on a model of minimum water requirement, and supported by data on minimum water budgets, it seems highly unlikely that a bird could maintain, or gain mass on a diet comprising only 35% water (Karasov and Martinez del Rio 2007). Therefore, the birds may need to supplement their diet with water-rich foods, such as invertebrates (generally >50% water), that have low fat content. Second, water availability might affect the birds' food processing and digestive efficiency through its effects on food handling and swallowing, and on physiological properties of the digestive tract and biochemical processes within it (e.g. gut volume and enzyme activity; Yalda and Forbes 1995; Karasov and Martinez del

Rio 2007). For example, Yasar and Forbes (1999) suggested that dietary water content might affect digestive tract features and that water might enhance biochemical and, consequently, digestive processes by increasing enzyme penetration into food being digested (Yalda and Forbes 1996; Forbes 2003).

The goal of the present study was to investigate the effect of water availability on blackcap feeding and, consequently, on their fat accumulation and mass gain rates during migration. To this end, we used wild-caught migratory captive blackcaps under controlled laboratory conditions to test two non-mutually exclusive hypotheses. First, we hypothesized that the availability of drinking water affects mass gain and fat accumulation processes through its effect on food intake and/or metabolizability. We predicted that blackcaps with free access to drinking water will have higher rates of food intake and/or higher food metabolizability than birds deprived of drinking water. Second, we hypothesized that dietary preferences are affected by water balance considerations and, thus, water availability. We therefore predicted that when offered a free choice of diet, birds will shift from water-rich food (e.g. invertebrates) when deprived of water to water-poor, but fat-rich food (e.g. *P. atlantica* fruit) when free water is available.

## Materials and methods

The blackcap (*Sylvia atricapilla*) is an abundant migratory songbird in Israel (Shirihai 1996) and the Middle-East (Snow and Perrins 1998), wintering predominantly south of the Sahara Desert and breeding at temperate latitudes in Europe and Asia. Between 8 and 10 September 2003 we mist-netted 26 blackcaps in a 3-ha plantation of fruit-bearing *P. atlantica* trees in Lahav Forest in the Northern Negev, Israel (31°20'N, 34°50'E). Year-to-year variation in estimated fruit abundance in the plantation ranged from approximately 5.5 to approximately 9 million fruits during 1996–1999 and 2001, and was approximately 0.6 million in 2000 and approximately 1.5 million in 2002 (Sapir et al. 2004a, b). *Pistacia atlantica* is a common native tree in the area, with a wide distributional range in semi-arid regions between the Canary Islands and Morocco in the west and northwestern India in the east (Zohary 1952). As do many other autumn migratory song birds, blackcaps stage in the Lahav Forest (Shochat et al. 2002; Sapir et al. 2004a) before engaging in an approximately 1800 km-long journey across the Sahara Desert (Moreau 1972; Biebach et al. 1986). Many of the staging birds feed on the fat-rich fruits of *P. atlantica* that are locally plentiful during autumn (Shochat et al. 2002; Sapir et al. 2004a). There are no known water sources in a radius of <1 km of the site, a

distance beyond which we never re-trapped birds ringed at the study site (unpublished data).

## Experimental procedure

### *Preliminary treatment of birds*

We trapped birds between 0545 and 0930 hours, tagged each with an individually numbered aluminum leg ring, weighed it to  $\pm 0.1$  g with a digital balance (Ohaus CS-200) and evaluated its fat score on a 6-level visual scale following Helms and Drury (1960). This is a commonly used method for estimating body fat content in birds and has been found to correlate positively with body mass (Ellegren and Fransson 1992; Izhaki and Maitav 1998; Shochat et al. 2002; Redfern et al. 2004), body fat content (Kaiser 1993) and the concentration of free fatty acids in blood (Gannes 2001). Only lean, first-autumn birds scoring 0–2 on the visual fat scale were chosen for the experiment; however, we did not use birds with body mass  $< 14.0$  g in order to avoid accidental death by starvation. The birds were transferred to a temperature-controlled animal room at the Jacob Blaustein Institutes for Desert Research at Midreshet Ben-Gurion ( $30^{\circ}52'N$ ,  $34^{\circ}47'E$ ) and individually housed in metal cages (26.5 cm wide  $\times$  17.5 cm deep  $\times$  26.5 cm high), with a perch and containers for water and food. The birds were maintained at an air temperature of  $27.07 \pm 0.67^{\circ}C$  (mean  $\pm$  SD), which was measured every 15 min by a four-probe temperature-logger (MultiLog DB-526; Fourier Systems), and were under a 12:12-h (light:dark) photoperiod. These conditions approximate the ambient conditions encountered by migratory birds that pass through the region during this time of the year, with the exception of a reduced daily amplitude of air temperature, which oscillated between a minimum  $24.4^{\circ}C$  and a maximum  $28.5^{\circ}C$  in the animal room.

Blackcaps were provided with two types of food: mealworms (*Tenebrio molitor*; mean mass  $27.7 \pm 1.5$  mg individual $^{-1}$ ) and ripe *P. atlantica* fruits ( $93.1 \pm 2.2$  mg fruit $^{-1}$ ) that we harvested from trees at the trapping site and subsequently stored in plastic bags at  $4^{\circ}C$ . Under these storage conditions, pistachio drupes lose only  $0.16 \pm 0.13\%$  of their mass daily (unpublished data), while during the experimental sessions they lost  $12.2 \pm 0.26\%$  of their mass daily. Throughout this study, birds were weighed daily between 0915 and 1340 hours in random order, their visual fat score (VFS) was determined, orts (uneaten food), excreta and water left in the containers were collected and food and water were replenished as required by the experimental protocol.

During the first 4 days the blackcaps were in captivity, we did a preliminary experiment to determine the quantity of

mealworms required by blackcaps to maintain constant  $m_b$  while provided with *P. atlantica* fruits and water ad libitum. This period also served to habituate the birds to the ambient conditions and to the types of food used in the study. In the preliminary experiment, blackcaps were randomly assigned by sex to one of four experimental groups and provided with different numbers of mealworms daily: no mealworms (five birds), five mealworms (three birds), 15 mealworms (six birds) and 25 mealworms (six birds). During this preliminary experiment we released six birds that rapidly lost  $m_b$  to  $< 14$  g. We measured each bird's  $m_b$  change in relation to the number of mealworms consumed on the fourth day of the experiment, after controlling for the effect of the number of fruit consumed, and found that the number of mealworms eaten had a significant and positive effect on the birds' residual  $m_b$  gain [linear regression: residual  $m_b$  change =  $(-0.23) + 0.032 \times$  number of mealworms;  $n = 20$ ,  $R^2 = 0.25$ ,  $F = 6.08$ ,  $P = 0.024$ ]. Thus, in order to avoid excessive loss of  $m_b$  during the study, we provided a minimum of five mealworms (approx. 0.14 g) per day to a bird, regardless of its experimental treatment (see below).

### *Mealworm-limited feeding experiment*

Blackcaps were randomly assigned by sex and by experimental group in the preliminary experiment to one of two treatment groups: (1) control—six birds were offered pistachio fruit and drinking water ad libitum and provided with five mealworms per day for 2 days; (2) water-restricted—seven birds were provided with food exactly as with the control group, but they were deprived of drinking water for 1 day and then provided with water ad libitum on the second day. Four additional birds were assigned to the control group and three birds to the water-restricted group, but only for the first day of the 2-day-long experiment. Data from these additional birds were used in the analysis of the changes in VFSs, where we did not use parametric repeated measures tests and were therefore able to use the additional data when comparing the influence of water on VFS between treatment groups during the first day of the experiment. Bird  $m_b$  and VFS were determined daily, and orts, excreta and water left in the containers were collected.

### *Unlimited mealworm feeding experiment*

Following the limited-mealworm feeding experiment, blackcaps were provided with food (both fruit and mealworms) and water ad libitum for 1 day and were then randomly assigned by sex and experimental group in the previous experiment to one of two new experimental groups: (1) control—nine birds that were fed ad libitum

with fruits and mealworms and had free access to water for 2 days; (2) water restricted—ten birds were fed ad libitum with pistachio fruit and mealworms and were deprived of drinking water for 2 days. As in the previous experiment, bird  $m_b$  and VFS were determined daily, and orts, excreta and water left in the containers were collected and measured. After completion of this experiment, the birds were provided with food and water ad libitum for 8 h and subsequently released at the trapping site.

## Data analysis

### Calculations of food use and metabolizability

At the end of each experimental day we weighed the orts (mealworms and *P. atlantica* fruits) and excreta to  $\pm 0.01$  g, dried the samples for 48 h at  $60^\circ\text{C}$  and weighed them again to  $\pm 0.01$  g. Excreta and samples of dried fruit and mealworms that were set aside were homogenized, and their energy density ( $\text{kJ g}^{-1}$ ) determined by adiabatic bomb calorimetry (semi-micro calorimeter: model 1425; Parr, Moline, IL). We used the set-aside samples of fruit and mealworms to estimate the proportion of dry matter in the food eaten and its energetic content. We calculated daily dry matter intake ( $\text{g day}^{-1}$ ) of fruit ( $Q_{i(\text{fruits})}$ ) and mealworms ( $Q_{i(\text{mealworms})}$ ) by subtracting the amount of orts from the amount of food supplied at the beginning of that day and then multiplying this difference by the estimated proportion of dry matter. We multiplied the daily dry matter intake of each food item by its respective energy density ( $\text{GE}_{i(\text{fruits})}$  and  $\text{GE}_{i(\text{mealworms})}$ ) and summed the products to obtain the gross energy content (kJ) of food eaten. Similarly, we estimated the gross energy content of excreta, but only in the mealworm-limited experiment, by multiplying the amount of excreta produced ( $Q_s$ ) by its energy density ( $\text{GE}_s$ ). We used this information to calculate the apparent metabolizable energy coefficient ( $\text{MEC}^*$ ; Kendeigh et al. 1977), defined as:

$$\text{MEC}^* = \frac{\text{GE}_i \times Q_i - \text{GE}_e \times Q_e}{\text{GE}_i \times Q_i}$$

This coefficient reflects digestive efficiency.

Apparent metabolizable energy coefficients are generally 1–3% below “true” metabolizable energy coefficients; they are more than 3% below “true” values when  $Q_i$  is well below the level required for maintenance (Karasov 1990), which was not the case in the present study.

### Statistical analysis

Fruit and mealworm mass, energy intake, apparent metabolizable energy coefficient and  $m_b$  change were

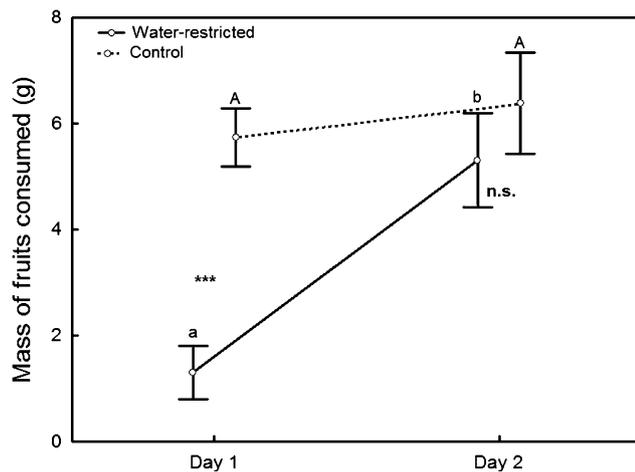
analyzed by repeated measures analysis of variance (ANOVA) according to two factors: treatment group (between-subject factor; control and water-restricted) and experimental day (within-subject factor; days 1 and 2). All tests were two-tailed and complied with the assumptions for parametric tests (normal distribution and homoscedasticity of variance). The statistical parameters for the main effects of the repeated measures ANOVAs are presented in the text with the relevant degrees of freedom as subscripts ( $F_{\text{effect, error}}$ ). Results for the interactions among the main effects are given only if they are statistically significant. Tests with statistically significant results were followed by planned comparisons to separate the overall effects by comparing the two treatment groups within each day and between experimental days within each treatment group. Visual fat score is a non-parametric factor and was analyzed using the Mann–Whitney  $U$  test to compare scores between treatment groups on the same experimental day, and by the Wilcoxon matched-pairs test to compare the response of each treatment group between experimental days. Results for these tests are presented as described above. Values are given as the mean  $\pm 1$  SE.

## Results

### Mealworm-limited feeding experiment

#### Fruit consumption

Fruit consumption by blackcaps was significantly affected by the availability of drinking water (Fig. 1). The birds in the control group consumed a larger overall quantity of fruit than those in the water-restricted group ( $F_{1,11} = 9.8$ ,  $P = 0.01$ ). Also, more fruit was consumed on day 2, when both treatment groups were provided with water, than on day 1, when only the control group had access to water ( $F_{1,11} = 15.4$ ,  $P = 0.002$ ). The interaction between treatment and day of experiment was also statistically significant ( $F_{1,11} = 8.1$ ,  $P = 0.016$ ), indicating that the pattern of fruit consumption on the two experimental days varied between the two treatment groups. A breakdown of the main effects using planned comparisons (Fig. 1) reveals that on day 1 individual fruit consumption by the control group birds ( $5.74 \pm 0.81 \text{ g day}^{-1}$ ) was significantly higher ( $F_{1,11} = 35.3$ ,  $P < 0.001$ ) than that of the water-restricted group ( $1.30 \pm 0.09 \text{ g day}^{-1}$ ). The two treatment groups did not differ in terms of their fruit consumption on day 2, when both groups had free access to water ( $6.38 \pm 0.78$  and  $5.31 \pm 1.00 \text{ g day}^{-1}$  consumed by birds of the control and the water-restricted groups, respectively;  $F_{1,11} = 0.7$ ,  $P = 0.43$ ). Fruit consumption differed within the water-restricted group between day 1,

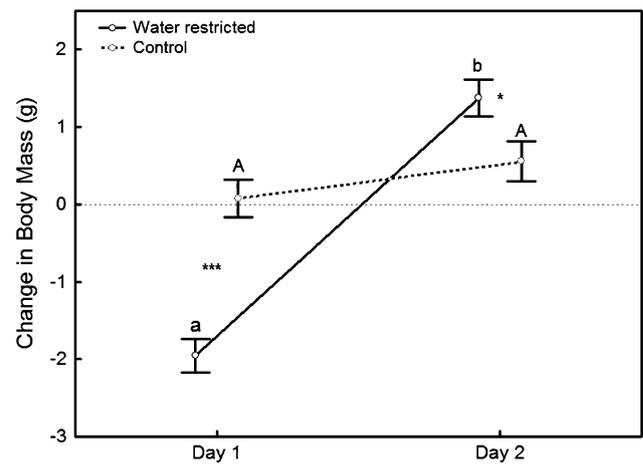


**Fig. 1** The relationship between fruit mass consumed by blackcaps (*Sylvia atricapilla*), water availability and day, as revealed by repeated measures analysis of variance (ANOVA) in the mealworm-limited feeding experiment. On day 1, control birds had access to drinking water, while a second group of birds was water-restricted. On day 2, both groups had access to drinking water. The average values of the 2 days for each group are connected by a *solid line* for the water-restricted birds and by a *hatched line* for the control birds. Error bars denote  $\pm 1$  SE. Different letters of the same case indicate statistically significant differences ( $P < 0.05$ ) between different days for the same experimental group. Asterisks indicate statistically significant differences ( $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ) between the different groups on the same day. *n.s.* Not significant

when birds were deprived of water, and day 2, when they had free access to water ( $F_{1,11} = 24.9$ ,  $P < 0.001$ ). There was no between-days difference in fruit consumption in the control group, which had free access to water on both days ( $F_{1,11} = 0.54$ ,  $P = 0.48$ ).

### Energy intake

Energy intake closely followed the pattern of fruit consumption with respect to water availability and experimental day ( $F_{1,11} = 8.9$ ,  $P = 0.012$  for between-treatment effects;  $F_{1,11} = 15.4$ ,  $P = 0.002$  for between-day effects;  $F_{1,11} = 8.1$ ,  $P = 0.016$  for the interaction between day and treatment). This was expected because the birds were provided with only five mealworms, while fruit accounted for most of the consumed food mass and energy. Planned comparisons indicated that the individual daily energy intake of the control group ( $132 \pm 18$  kJ day<sup>-1</sup>, of which mealworms constituted  $1.7 \pm 0.5$  kJ day<sup>-1</sup> and fruit  $130.7 \pm 12.5$  kJ day<sup>-1</sup>) was fourfold higher ( $F_{1,11} = 32$ ,  $P < 0.001$ ) than that of the water-restricted group ( $33 \pm 21$  kJ day<sup>-1</sup>, of which mealworms constituted  $3.3 \pm 0.5$  kJ day<sup>-1</sup> and fruit  $29.7 \pm 11.6$  kJ day<sup>-1</sup>) on day 1 when birds in the water-restricted group were deprived of water. Energy intake did not differ between the



**Fig. 2** The relationship between changes in body mass of blackcaps and water availability and day, as revealed by repeated measures ANOVA in the mealworm-limited feeding experiment. For details of the experimental procedures and symbols, see caption to Fig. 1

control ( $147 \pm 18$  kJ day<sup>-1</sup>, of which mealworms constituted  $1.7 \pm 0.5$  kJ day<sup>-1</sup> and fruit  $145.2 \pm 21.7$  kJ day<sup>-1</sup>) and water-restricted ( $124 \pm 23$  kJ day<sup>-1</sup>, of which mealworms constituted  $3.3 \pm 0.5$  kJ day<sup>-1</sup> and fruit  $120.8 \pm 20.1$  kJ day<sup>-1</sup>) groups on day 2, when both groups had free access to water ( $F_{1,11} = 0.58$ ,  $P = 0.46$ ). Energy intake increased within the water-restricted group from day 1, when the birds were water deprived, to day 2, when they had free access to water ( $F_{1,11} = 24.9$ ,  $P < 0.001$ ). Energy intake of the control group birds that had free access to water on both days did not differ between the days ( $F_{1,11} = 0.54$ ,  $P = 0.48$ ).

### Body mass changes

Blackcap  $m_b$  gains were positively affected by the availability of drinking water (Fig. 2), both between treatment groups ( $F_{1,11} = 6.3$ ,  $P = 0.029$ ) and between experimental days ( $F_{1,11} = 65$ ,  $P < 0.001$ ). The interaction term between treatment and experimental day was also statistically significant ( $F_{1,11} = 36.2$ ,  $P < 0.001$ ), indicating that changes in bird  $m_b$  varied between the treatment groups on the two experimental days. Planned comparisons revealed that birds of the water-restricted group lost  $m_b$  during day 1 ( $-1.95 \pm 0.15$  g day<sup>-1</sup>), when they were deprived of water, and gained  $m_b$  during day 2 ( $1.38 \pm 0.25$  g day<sup>-1</sup>), when they had free access to water ( $F_{1,11} = 107.3$ ,  $P < 0.001$ ). Changes in  $m_b$  of the water-restricted birds on day 1 were generally negative and differed significantly from those of the control birds ( $F_{1,11} = 39.1$ ,  $P < 0.001$ ) that maintained a rather constant  $m_b$  ( $0.08 \pm 0.31$  g day<sup>-1</sup>). On day 2, however, when provided with drinking water, birds in the water-restricted group gained significantly

( $F_{1,11} = 5.4$ ,  $P = 0.04$ ) more  $m_b$  ( $1.38 \pm 0.25$  g day<sup>-1</sup>) than birds of the control group ( $0.56 \pm 0.25$  g day<sup>-1</sup>). There was no between-days difference in  $m_b$  gain in the control group ( $F_{1,11} = 1.9$ ,  $P = 0.19$ ).

#### Fat scores

Changes in VFS of the control group on day 1 ( $-0.2 \pm 0.25$  units day<sup>-1</sup>) were statistically different (Mann–Whitney  $U$  test,  $Z = -2.02$ ,  $P = 0.044$ ,  $n = 10$ ) from those of the water-restricted group ( $-0.90 \pm 0.18$  units day<sup>-1</sup>,  $n = 10$ ). However, the two groups did not differ in fat score on day 2 (Mann–Whitney  $U$  test,  $Z = -1.01$ ,  $P = 0.314$ ,  $n_{\text{control}} = 6$ ,  $n_{\text{water-restricted}} = 7$ ), when both groups had free access to water ( $0.67 \pm 0.42$  units day<sup>-1</sup> and  $0.29 \pm 0.18$  units day<sup>-1</sup> for the control and water-restricted groups, respectively). Changes in VFS of the water-restricted group differed significantly between day 1, when the birds were deprived of water, and day 2, when water was provided (Wilcoxon matched pairs test,  $Z = 2.20$ ,  $P = 0.028$ ,  $n = 7$ ). Changes in VFS of the control group did not differ between experimental days (Wilcoxon matched pairs test,  $Z = 1.28$ ,  $P = 0.2$ ,  $n = 6$ ).

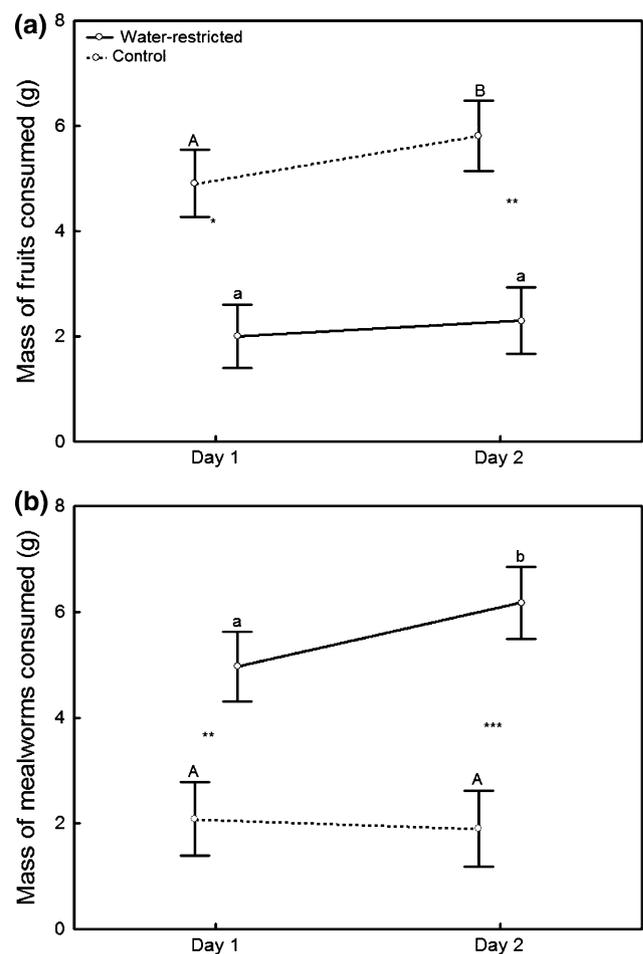
#### Food metabolizability

Neither the apparent metabolizable energy coefficient (MEC\*) of the control group on day 1 ( $0.282 \pm 0.015$ ) and day 2 ( $0.314 \pm 0.026$ ) nor the coefficients of the water-restricted group on day 1 ( $0.324 \pm 0.028$ ) and day 2 ( $0.331 \pm 0.021$ ) were affected by the treatment ( $F_{1,11} = 2.47$ ,  $P = 0.14$ ) or by the experimental day ( $F_{1,11} = 0.79$ ,  $P = 0.39$ ).

#### Unlimited mealworm feeding experiment

##### Fruit consumption

Fruit consumption by blackcaps (Fig. 3a) was affected by both treatment ( $F_{1,17} = 14.1$ ,  $P = 0.002$ ) and experimental day ( $F_{1,17} = 4.8$ ,  $P = 0.043$ ). Planned comparisons revealed that fruit consumption by the control group ( $4.91 \pm 0.82$  and  $5.82 \pm 0.93$  g day<sup>-1</sup> for days 1 and 2, respectively) was more than twofold higher than fruit consumption by the water-restricted group ( $2.00 \pm 0.39$  and  $2.30 \pm 0.25$  g day<sup>-1</sup> for days 1 and 2, respectively;  $F_{1,17} = 10.8$ ,  $P = 0.004$  for day 1 and  $F_{1,17} = 14.8$ ,  $P = 0.001$  for day 2). Additionally, the control group birds consumed more fruits on day 2 than on day 1 ( $F_{1,17} = 5.13$ ,  $P = 0.037$ ). There was no between-day



**Fig. 3** The relationship between the mass of fruit (a) and mealworms (b) consumed by blackcaps and water availability and day during the unlimited mealworm feeding experiment, as revealed by repeated measures ANOVA. Both treatment groups were provided with mealworms and fruits ad libitum, but only the control group had access to water. The average values of the 2 days of each group are connected by a solid line for the water-restricted birds and by a hatched line for the control birds. Error bars denote  $\pm 1$  SE. Different letters of the same case indicate statistically significant differences ( $P < 0.05$ ) between days for the same group on different days. Asterisks indicate statistically significant differences ( $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ) between the different groups on the same day

difference in fruit consumption by the water-restricted group ( $F_{1,17} = 0.6$ ,  $P = 0.45$ ).

##### Mealworm consumption

Mealworm consumption was affected by treatment ( $F_{1,17} = 14.5$ ,  $P = 0.001$ ), but not by experimental day ( $F_{1,17} = 3.7$ ,  $P = 0.07$ ; Fig. 3b). However, the statistically significant interaction term between the two variables ( $F_{1,17} = 6.8$ ,  $P = 0.019$ ) suggests that the two groups varied in their mealworm consumption between the two

experimental days. This is further supported by planned comparisons, which revealed that the control group consumed fewer mealworms ( $2.09 \pm 0.58$  and  $1.9 \pm 0.79$  g day<sup>-1</sup> for days 1 and 2, respectively) than birds of the water-restricted group ( $4.97 \pm 0.75$  and  $6.17 \pm 0.62$  g day<sup>-1</sup> for days 1 and 2, respectively;  $F_{1,17} = 9.05$ ,  $P = 0.008$  for day 1 and  $F_{1,17} = 18.38$ ,  $P < 0.001$  for day 2) and that birds in the water-restricted group consumed more mealworms on day 2 than they did on day 1 ( $F_{1,17} = 10.74$ ,  $P = 0.005$ ). There was no between-day difference in mealworm consumption by the birds in the control group ( $F_{1,17} = 0.23$ ,  $P = 0.64$ ).

### Energy intake

Overall energy intake, summed for all fruit and mealworms consumed by the birds, differed between experimental days ( $F_{1,17} = 9.9$ ,  $P = 0.006$ ). Planned comparisons revealed that this results from a higher energy intake by the water-restricted birds on day 2 than on day 1 ( $F_{1,17} = 9.8$ ,  $P = 0.006$ ), while there was no such difference in the control-group birds ( $F_{1,17} = 1.8$ ,  $P = 0.19$ ).

Overall energy intake was affected by neither the experimental treatment ( $F_{1,17} = 0.31$ ,  $P = 0.59$ ) nor by the interaction between the day in the experiment and the experimental treatment ( $F_{1,17} = 1.4$ ,  $P = 0.26$ ). Planned comparisons revealed that the overall energy intake per control bird ( $162 \pm 19$  and  $178 \pm 17$  kJ day<sup>-1</sup> for days 1 and 2, respectively) did not differ statistically from that of the water-restricted birds ( $165 \pm 17$  and  $201 \pm 19$  kJ day<sup>-1</sup> for days 1 and 2, respectively;  $F_{1,17} = 0.02$ ,  $P = 0.89$  and  $F_{1,17} = 0.82$ ,  $P = 0.38$  for days 1 and 2, respectively).

### Body mass changes

All water-restricted birds gained  $m_b$  ( $0.41 \pm 0.24$  and  $0.63 \pm 0.17$  g day<sup>-1</sup> on days 1 and 2, respectively), as did all control birds ( $0.6 \pm 0.27$  and  $0.43 \pm 0.17$  g day<sup>-1</sup> on days 1 and 2, respectively). Neither treatment ( $F_{1,17} < 0.01$ ,  $P \sim 1$ ) nor experimental day ( $F_{1,17} = 0.02$ ,  $P = 0.88$ ) had a significant effect on the changes in  $m_b$ .

### Visual fat score changes

Changes in VFS did not differ between the control ( $-0.22 \pm 0.22$  units day<sup>-1</sup> and  $0.44 \pm 0.18$  units day<sup>-1</sup> on days 1 and 2, respectively) and water-restricted ( $-0.30 \pm 0.30$  units day<sup>-1</sup> and  $0.20 \pm 0.25$  units day<sup>-1</sup> on days 1 and 2, respectively) groups (Mann–Whitney  $U$

test,  $n_{\text{control}} = 9$ ,  $n_{\text{water-restricted}} = 10$ ;  $Z = -0.13$ ,  $P = 0.90$ , for day 1 and  $Z = 0.63$ ,  $P = 0.53$  for day 2). Changes in VFS also did not differ between experimental days in both treatment groups (Wilcoxon matched pairs test,  $Z = 1.01$ ,  $P = 0.31$ , for the control group and  $Z = 1.78$ ,  $P = 0.076$  for the water-restricted group).

### Discussion

Water availability had a strong positive effect on the amount of fruit consumed by the birds and, consequently, on their energy intake when mealworms were limited in quantity. Under such conditions, variations in the birds'  $m_b$  and fat accumulation rate were tightly linked to the pattern of fruit consumption, as water deprivation constrained the birds' food intake and thus their fat accumulation. Similar circumstances in which fruits are abundant but invertebrate prey is scarce are likely encountered by the birds in their natural environment because by the time autumn migrants reach staging sites along the northern edges of the Sahara Desert, where water is largely unavailable, invertebrate abundance has already passed its peak (Bodenheimer 1935). Indeed, based on field experiments, Sapir et al. (2004a, b) reported that under natural conditions arthropods represented only about 31% of the birds' diet and that under such conditions, the birds'  $m_b$  and fat gain rates were significantly lower than when water was artificially provided. In the present study, when mealworms were provided ad libitum, water availability had no effect on the birds'  $m_b$  and fat accumulation rates; however, water availability did determine the birds' diet. The diet of birds with free access to water consisted predominantly of fruit (approx. 73% of the total dry matter by mass and approx. 80% of total gross energy ingested), while the diet of water-restricted birds consisted chiefly of mealworms (approx. 71% of the total dry matter, accounting for approx. 45% of the gross energy ingested). It is likely that the relatively higher water content of the mealworms (62%; Finke 2002), compared to that of *P. atlantica* fruit flesh (35%; Sapir 2002), enabled water-restricted birds to compensate for their water losses by switching from a fruit-based water-poor diet to a mealworm-based water-rich diet. Differences in metabolic water production would not be able to compensate birds on a water-restricted diet to any useful extent because, based on an analysis of nutrient composition, catabolism of the fruit and mealworms would yield similar quantities of metabolic water per unit energy (0.025 and 0.024 g water/kJ, respectively) (Bell 1990; Karasov and Martinez del Rio 2007). These findings suggest that, under certain circumstances, migrating birds without ready access to water may be able to maintain their rate of fat and  $m_b$  gain by adjusting their dietary

composition, at least as long as water-rich foods are available. Our data also concur with recent hypotheses that the high plasticity of bird foraging repertoires during migration is an important component of their success at migratory stopovers (e.g. Loria and Moore 1990). However, the birds we studied achieved relatively high compensation by consuming over 5 g of mealworms per day (corresponding to approx. 71% of their diet). This amount is far higher than that known from blackcap fecal analysis at our field site (Sapir et al. 2004a) and may represent an improbably large quantity of insect food, for an autumn migrant at a stopover at the northern edge of the Sahara desert.

We tested two, non-mutually exclusive hypotheses to explain the positive effect of drinking water on mass gain and fat accumulation in migratory blackcaps.

(1) *Limitation on food processing and water balance.* A lack of drinking water may limit a bird's ability to consume water-poor foods, such as *P. atlantica* fruits, because such food does not contain enough water to compensate for the bird's daily water losses. To achieve the latter, the bird must consume water-rich foods, such as invertebrates. We predicted that drinking water will facilitate higher overall food intake, resulting in higher fat deposition and  $m_b$  gains. Indeed, in the limited mealworm experiment, blackcaps provided with water ate significantly more (>fourfold) fruit and had higher rates of fat deposition ( $-0.2$  units  $\text{day}^{-1}$  and  $0.67$  units  $\text{day}^{-1}$  for the control group, on days 1 and 2, respectively, and  $0.29$  units  $\text{day}^{-1}$  for the water-restricted group on day 2, when provided with water) and  $m_b$  gains ( $0.08$  and  $0.56$  g  $\text{day}^{-1}$  for the control group on days 1 and 2, respectively, and  $1.38$  g  $\text{day}^{-1}$  for the water-restricted group on day 2, when provided with water) than birds deprived of water ( $m_b$  and fat loss of  $1.95$  g  $\text{day}^{-1}$  and  $0.9$  units  $\text{day}^{-1}$ , respectively). These results are comparable to those of Sapir et al. (2004b), where birds in the field offered supplementary water gained  $m_b$  at an average of  $1.11$  g  $\text{day}^{-1}$ , while birds that were not given water lost  $0.76$  g  $\text{day}^{-1}$ .

In the unlimited mealworm feeding experiment, blackcaps shifted, as predicted, from a fruit-rich diet, when water was freely available, to an invertebrate-rich diet, when water-restricted. The overall dry matter ingestion and energy intake of birds with access to drinking water did not differ from those of the water-restricted birds, leading to similar fat deposition and  $m_b$  gains. These results are not fully consistent with our predictions, because we predicted that water restricted birds would have lower food intake and thus lower fat and  $m_b$  gains. However, such complete compensation is unlikely under natural conditions at the field study site as well as at most autumn stopover sites that precede the Sahara traverse, since insect food availability is unlikely to suffice.

*Pistacia atlantica* fruits contain a large non-digestible seed and, therefore, a larger proportion of indigestible matter than mealworms. Digestible material and energy content of *Pistacia* fruit flesh average  $0.023$  g  $\text{fruit}^{-1}$  and  $531$  J  $\text{fruit}^{-1}$ , respectively, and account for approximately 25% of the fruit's dry mass and gross energy content, suggesting that there is less digestible material in *P. atlantica* fruit than in mealworms. Why then did our experimental blackcaps prefer eating *P. atlantica* fruits over mealworms, and why did mass and fat accumulation not differ between the fruit- and mealworm-based diets? First, *P. atlantica* fruit are superabundant (Sapir et al. 2004a) and may require less effort to pick from the tree, handle and swallow than catching invertebrates (Snow and Snow 1988; Bairlein 2002), which are mobile and relatively less abundant (Bodenheimer 1935). Second, the nutritional content, especially the fatty acid composition, of *P. atlantica* fruit is probably more beneficial to migratory birds during fattening periods than those of invertebrates (see Bairlein 2002; Pierce and McWilliams 2005; Pierce et al. 2005). A dietary shift towards frugivory, associated with periods of accelerated fattening has been documented for various avian and mammalian taxa facing prolonged fastening or enduring periods of physical exertion (Bairlein 2002). Moreover, it has also been shown that birds prefer diets of a particular nutrient composition; for example, yellow-rumped warblers prefer diets rich in long-chain, mono-unsaturated fatty acids to diets rich in saturated and poly-unsaturated fatty acids (McWilliams et al. 2002). These dietary preferences may be reflected in the seasonal switch from mostly insectivory to mostly frugivory that is observed in many migrating passerines. This dietary shift is probably induced by endogenous processes related to the circannual rhythm of the animal, rather than by the ecological conditions in a certain habitat (Bairlein 2002).

(2) *Bird food assimilation.* Water consumption may facilitate higher energy assimilation from the digested food in the gut through histo-morphological alterations of the digestive tract (Yasar and Forbes 1999) or by influencing biochemical processes in the gut (Forbes 2003). Consequently, we predicted that water-restricted blackcaps will have a lower digestive efficiency than birds with access to drinking water. Our data do not support this prediction.

The reconstruction of the digestive organs during migration, after prolonged migratory flights, occurs mainly during the first few days at the stopover site (Karasov and Pinshow 2000; Gannes 2002; Bauchinger et al. 2005). Our birds were allowed a 4-day habituation period in which they were provided with water and food, before the start of the experiments. These birds probably rebuilt their digestive organs during that period (Karasov et al. 2004) and, therefore, the effects of water on food metabolizability, which might occur through histo-

morphological changes in the digestive tract, were less likely to be detected. The ability of the birds to consume large amounts of fruit from the outset of the experiment supports this reasoning, as this is a characteristic of staging birds that have already adjusted their digestive system for intense feeding (Gannes 2002; Karasov et al. 2004). Hence, our conclusion that water does not affect digestive efficiency is limited to the possible effect of water on biochemical processes in the gut, as the experimental design of the present study does not permit investigation of possible histo-morphological alterations of the digestive tract. These findings conform with those of Karasov and Pinshow (2000), who found that increased food assimilation by staging blackcaps resulted from hyperphagia rather than from increased assimilation efficiency of the ingested food.

Our results imply that water enhances fat and mass gains of staging blackcaps by facilitating higher food intake rates, specifically when eating a fat-rich and water-poor fruit-based diet. Furthermore, our results indicate that water availability may constrain the birds' diet, so that shifts from insectivory to frugivory, supposedly a prerequisite for the pre-migratory fattening process (Bairlein 2002), are hampered when water is unavailable (Sapir et al. 2004b).

The specific mechanisms underlying this phenomenon may be complex. Sapir et al. (2004b) demonstrated that artificial provision of water at a stopover site had a strong positive effect on the rates of fat deposition and  $m_b$  gains of migratory blackcaps. In addition, these authors suggested that positive effect may result through an extension of the daily foraging time and by the induction of certain physiological alterations in the birds' digestive tract (see also Yasar and Forbes 1999). Karasov and Martinez del Rio (2007) proposed that the consumption of desiccated food, specifically of plant origin, may be constrained by the animal's water requirements. Karasov and Martinez del Rio (2007) also proposed that secondary metabolites, common in foods of plant origin, including many fleshy fruits, may also elevate the bird's water requirements. Other food processing and dietary constraints specifically related to a fruit-based diet, such as gut capacity and mechanical function (Kersten and Visser 1996; Karasov and McWilliams 2005) and food handling and swallowing (Fritz et al. 2001; Jeschke et al. 2002; Durant et al. 2003), may also be affected by water intake. The effects of these mechanisms may be entwined and hard to separate. For example, physical constraints on food intake, such as swallowing, may be related to the bird's water balance, and so water-deficient birds will have more difficulty handling or swallowing food than birds with access to drinking water. It is also possible that water-restricted birds have slower digestive processing that limits assimilation rate

without altering efficiency, which we measured. However, our data are insufficient to differentiate between the original "digestion efficiency" and the "slower digestive processing" hypotheses, as in the time frame of our measurements the two hypotheses have similar predictions with respect to the collected data.

To conclude, the availability of drinking water to staging blackcaps during their autumn migration resulted in increased fat and  $m_b$  accumulation rates when invertebrate food was limited. This occurred through increased fruit consumption, but probably not through improved food assimilation in the gut. When invertebrates (mealworms) were available ad libitum, water availability brought about a diet shift from invertebrates to fruit, but it did not affect fat and  $m_b$  accumulation rates. This result implies that fruit are a preferred food during the autumn migration but that their consumption is constrained by water availability. We suggest that fruits are an important food resource for autumn migrating blackcaps, probably due to their availability or their nutritional content. Consequently, the availability of drinking water has important fitness consequences to migratory blackcaps by enabling increased fruit consumption during "en route" refueling periods.

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