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Communication

Fruit consumption in migratory passerines is limited by water ingestion rather than by body water balance

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Many insectivorous passerines become frugivorous during migration. Because water may facilitate the digestion of dry fruits, some passerines may benefit from staging in stopover sites that offer access to drinking water. In autumn, water consumption by blackcaps *Sylvia atricapilla* staging in Israel was found to induce a shift from insectivory to frugivory. We tested two alternative hypotheses concerning the mechanism facilitating consumption of the relatively dry fruits which are common in this region: 1) water intake facilitates the passage of fruits within the digestive tract when these two resources are simultaneously ingested, and 2) improved body water balance allows the consumption and ingestion of large amounts of dry fruits. Blackcaps were subjected to five treatments that included temporal separation of water and fruit consumption, as well as subcutaneous water injection to maintain balanced body water in water-deprived birds. Fruit consumption rate was measured daily. We found that only simultaneous provisioning of water and fruits significantly increased fruit consumption rate, implying that drinking water directly improves fruit digestion within the digestive system. Furthermore, the fuel deposition rate increased with increased fruit consumption rate. These results emphasize the importance of water availability for the ecology and conservation of migrating passerines.

Keywords: bird migration, blackcap, body water balance, frugivory, fuel loading

Introduction

Long distance migration is one of the most energy-demanding activities in the animal kingdom (Alerstam 1990). Subcutaneous lipids comprise the main energy source for long-distance migratory flight (Jenni-Eiermann and Jenni 1991). To accumulate these lipids, many migratory passerines increase their energy intake rate by diet shifting from insectivory to frugivory (Bairlein and Gwinner 1994, Pierce et al. 2005) during stopover (Bairlein and Simons 1995). Specifically, this diet shift allows birds to consume a food resource that is characterized by a rapid retention time (Afik and Karasov 1995), as well as high content of both unsaturated fatty acids and simple carbohydrates (Debussche et al. 1987, Bairlein and Gwinner 1994, Bairlein 2002, Smith et al. 2007).

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Consequently, fleshy fruits serve as a main energy source for many woodland migrants (Bairlein 2002, Sapir et al 2004a). In the Mediterranean region, there are many trees, bushes and vines bearing fruits that ripen during autumn (Izhaki and Safriel 1985, Shochat et al. 2002). Indeed, many of the trans-Sahara migratory passerines that stopover in this region consume large quantities of fruit while refueling (Shochat et al. 2002). Remarkably, the pulp of the Mt Atlas mastic tree's fruit (hereafter MAMT; *Pistacia atlantica*) is highly rewarding for woodland migrants (Sapir et al. 2004a), consisting of 53% fat by dry mass. The fruit contains a single, large, seed that is defecated by the birds after the ingestion of the fruit. These fruits are commonly consumed by the migrants and consequently MAMT groves have become important autumn stopover sites for many migratory passerines in Israel (Sapir et al. 2004b). The blackcap *Sylvia atricapilla* is one of the most abundant migratory passerine species in Israel (Shirihai 1996), breeding in Europe and Asia, and wintering predominantly south of the Sahara Desert (Snow and Perrins 1997). In general, blackcaps inhabit a large variety of environments, though during stopover they usually prefer woodlands (Bairlein 1983). Previous field and laboratory studies on migratory blackcaps have demonstrated that this species exhibits a high degree of seasonal frugivory (Sapir et al. 2004a, b) and that water consumption augments the consumption of the relatively water-poor MAMT fruits (34.5% water in the flesh of freshly picked fruit; Sapir et al. 2004b), resulting in increased fuel deposition rate (Tsurim et al. 2008). The increased consumption of fruits when water and fruits were simultaneously available did not result in higher digestive efficiency (Tsurim et al. 2008). To date, the mechanism by which water facilitates fruit consumption remains unclear.

Fruits contain large amounts of lipids and carbohydrates. Carbohydrates are hydrolyzed and transported across the intestinal gut wall to the bloodstream. Exogenous lipids, in their main form of triglycerides are absorbed in the small intestine and transported as portomicrons directly via the portal system to the liver (Stevens 2004). Several non-mutually exclusive mechanisms may explain the potential effect of water on the digestion process in migratory birds. Mizrahy et al. (2011) suggested that the renewal of the digestive tract, which is reduced during active migration, may be slower when water is limited. Yasar (1999) found that water often allowed a faster rate of passage of digesta through the tract, while also facilitating biochemical changes associated with the thickening of the gut wall, which facilitates absorption. Forbes (2003) suggested that a lack of drinking water can influence the rate of penetration by digestive enzymes and acids into food particles, which may consequently slow the digestion process. Empirical support for these mechanisms, however, is limited, and the extent to which they apply to migrating passerines is unknown because most studies were performed on domesticated chickens. Therefore, even basic information regarding the positive influence of water consumption on fruit intake and fuel loading is still largely unknown.

In this study, we tested two non-mutually exclusive hypotheses concerning the role of consumed water in the digestion of MAMT fruits in autumn-migratory blackcaps: 1) simultaneous consumption of MAMT fruits and water enhances lubrication, or dissolution of nutrients within the digestive system, or facilitates the penetration of digestive enzymes and acids into food particles, thus allowing the consumption of more fruits, and 2) water intake improves the body water balance which, in turn, indirectly improves nutrient absorption, energy assimilation, or biochemical processes within the digestive system, therefore facilitating the consumption of more fruits. We examined these two hypotheses using two approaches. The first approach was based on manipulating the consumption of water and fruits by segregating the time of water and MAMT fruits provisioning. The second approach relied on artificial maintenance of proper body water balance by subcutaneous infusion of fluids (Pare 1997). These two approaches allowed us to resolve whether fruit consumption is facilitated by the simultaneous consumption of water or through the maintenance of body water balance.

Methods

During October 2017, we performed an experiment testing the two aforementioned hypotheses regarding how water intake facilitates fruit consumption among autumn migrating blackcaps. Blackcaps were captured near Yerucham Lake (30°59′N, 34°53′E) and were transported to a temperature controlled room at the Univ. of Haifa, Israel (32°76′N, 35°02′E). The birds were individually housed in metal cages (30 cm wide × 23 cm long × 39 cm high) inside light controlled cabinets under a 12:12-h (light:dark) daily cycle. The room was maintained at an air temperature of 26.0 ± 1.9°C (mean ± SD) and relative humidity of 39.6 ± 12.3%, measured every 10 min by a temperature logger (WiFi-500 Sensor; MO Measurement Computing, Norton, MA, USA). These conditions approximate the average ambient conditions encountered by migratory birds passing through the Mediterranean region during this time of the year.

Birds were held in captivity for five to six days, and were released at the site of capture at the end of the experiment. During the first two days following capture, birds were acclimated to the housing conditions, and were provided with water and ad libitum ripe MAMT fruits, and mealworms *Tenebrio molitor*. Mealworms (mean ± SD body mass of 164.41 ± 22.70 mg, n = 15, weighed individually) are characterized by high protein, fat and water contents (Finke 2002, Siemianowska et al. 2013). Thereafter, birds were randomly assigned to one of five treatment groups in an experiment that lasted two to three days. Birds that were assigned to different treatments were housed together within the same cabinets. During this experiment the birds were provided with MAMT fruits and water as specified below, as well as five mealworms per day (Tsurim et al. 2008). The rationale behind selecting these treatment groups was to test whether maintaining balanced body water is sufficient for high consumption of fruits, or if only the simultaneous ingestion of water and fruits facilitates high fruit consumption. The five treatment groups included:

1) A group provided with ad libitum MAMT fruits for five hours each day (n = 6). For this group, a saline solution of 0.6 ml NaCl 0.9% (~3% of the warbler's body mass) was injected subcutaneously into the lateral flank area using a 25G needle (Pare 1997) once every day. Subcutaneous injection of NaCl is an alternative way for birds to receive water, which slowly absorbs into their circulatory system without involving the digestive system. The subcutaneous injection allows for exploration of whether birds that did not drink water, but otherwise maintained their body water balance, consumed more fruits than water-deprived birds (group 5 below). We also examined if birds in this treatment group consumed the same amount of fruits as birds that were provided with water and fruits simultaneously (group 2 below).
2) A group simultaneously provided with water and ad libitum MAMT fruits for five hours each day (n = 8). Half of the individuals in this group were punctured with a 25G needle without water injection, to test if the injection itself had any consequences on fruit consumption.
3) A group provided with drinking water for five hours and after a one-hour break, provided with ad libitum MAMT fruits for five hours (n = 6). This group represents birds with proper body water balance prior to fruit provisioning, but that were not able to ingest both fruits and water simultaneously.
4) A group provided with ad libitum MAMT fruits for five hours and after a one-hour break, provided with drinking water for five hours (n = 7). For this group, water was provided only after consuming fruit, and also in this case, the birds were not able to consume fruit and water simultaneously.
5) A water-restricted group that was provided with ad libitum MAMT fruits for five hours (n = 2). This group included only two birds due to ethical restrictions. These birds were held in captivity for only one day after acclimation period and were released after receiving ad libitum water and food for an additional day.

Each morning, at 07:00, birds were weighed to the nearest 0.1 g with a digital balance (Model A404; Brand Generic; China). Because warblers cannot digest MAMT seeds, examination of excreta at the bottom of the cage can reveal the number of fruits consumed by an individual bird. Seed count took place each morning. Thereafter, food and water were replenished according to the treatment group (above). Quantification of water consumption was not performed, but the birds were constantly observed feeding and drinking. Additionally, total body water was not assessed; however, injecting saline solution subcutaneously is a common practice to mitigate dehydration in avian veterinary medicine (Pare 1997).

Data analysis

To test for the effects of the treatment on daily fruit consumption rate in blackcaps, we used ANCOVA, followed by Tukey post-hoc tests, with treatment as the fixed explanatory variable and wing length and initial body mass as covariates. This analysis was also performed in order to test for differences between injected and non-injected individuals from treatment group 2.

To calculate individual fuel loads, we followed Sapir et al. (2004a). Specifically, we used their equation estimating an individual's size-specific lean body mass (hereafter LBM), based on bird body mass and wing length generated using a dataset comprised of 1137 blackcaps:

$$\text{LBM} = 0.12 \times \text{wing length} + 6.257 \tag{1}$$

We then calculated the fuel load of each individual using the following equation:

$$\text{Fuel load} = \frac{\text{Bird mass} - \text{LBM}}{\text{LBM}} \tag{2}$$

Fuel deposition rate (FDR) was calculated using the following linear equation:

$$\text{FDR} = \frac{FL_2 - FL_1}{t} \tag{3}$$

where FL_1 and FL_2 are the fuel loads of the focal individual during the first and last measurements, respectively, and t is the number of days between the two measurements.

To test for the effect of fruit consumption on FDR, we used a simple linear regression with FDR as the response variable, and the total number of consumed fruits as the explanatory variable. Because most of the variation in the fruit consumption rate was explained by the treatment, and because fruit consumption rate better explains the variation in fuel deposition rate, the feeding treatment was not included in this analysis. All tests were carried out using STATISTICA, ver. 12 (StatSoft, Inc., Tulsa, OK, USA) and were two-tailed, with a critical α of 0.05.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.qr45fs4> (Domer et al. 2019).

Results

ANCOVA revealed that the daily fruit consumption rate of blackcaps varied significantly among the five treatment groups ($F_{4,22} = 13.98$, $p < 0.001$, Fig. 1). When MAMT fruits

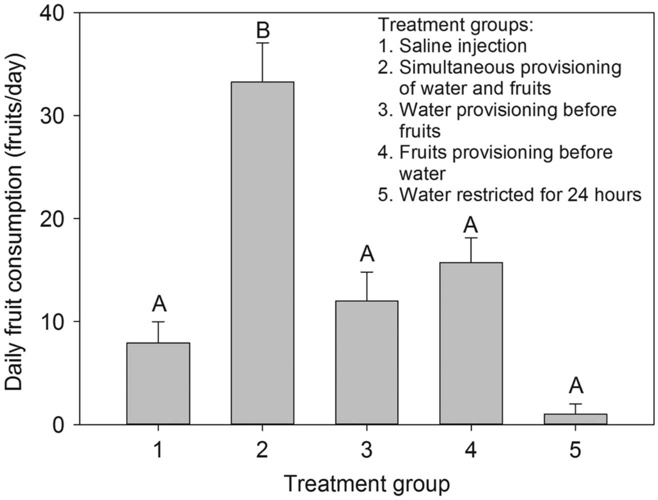

Figure 1. The number of fruits consumed by blackcaps per day in each of the five treatment groups. Only simultaneous provisioning of water and fruits (treatment 2) resulted in a statistically significant increase in fruit consumption ($F_{4,22} = 13.98$, $p < 0.001$), implying that the simultaneous ingestion of water and fruits facilitates fruit processing in the gut. Different letters indicate significant differences among treatment groups, derived from a Tukey post-hoc test. Bars and lines represent mean ± SE.

and water were provided simultaneously (treatment group 2), the daily fruit consumption rate (fruits day^{-1}, mean ± SE) was 33.25 ± 3.82 (n = 8). This daily fruit consumption rate was 4-fold higher than that of the saline injected group (treatment group 1; 7.92 ± 2.07, n = 6; Tukey post-hoc test: $p < 0.001$; Fig. 1), 3-fold higher than that of birds first provided water and then fruits (treatment group 3; 12.0 ± 2.81, n = 6; Tukey post-hoc test: $p < 0.001$; Fig. 1), and 2-fold higher than that of birds first provided fruits and then water (treatment group 4; 15.71 ± 2.42, n = 7; Tukey post-hoc test: p = 0.002; Fig. 1). Fruit consumption in the water-restricted group (treatment group 5) was extremely low (1.0 ± 1.0; n = 2; Tukey post-hoc test: $p < 0.001$; Fig. 1). ANCOVA revealed no differences between punctured and non-punctured individuals pertaining to treatment group 2 ($F_{1,4} = 2.40$, p = 0.196).

A linear regression indicated that FDR was positively related to the cumulative number of fruits consumed during the entire experimental period (p = 0.010, adjusted $R^2 = 0.190$, $F_{1,27} = 7.655$, Fig. 2). The residuals of this linear regression were normally distributed (Shapiro–Wilk test, p = 0.304). The body masses of the birds at the beginning and end of the experiment are presented in Supplementary material Appendix 1 Table A1 in relation to their treatment group.

Discussion

Herein, we examined two non-mutually exclusive hypotheses related to the role drinking water plays in facilitating the consumption of MAMT fruits by autumn migrating blackcaps: 1) drinking water enhances lubrication or dissolution of nutrients within the digestive system or facilitates the penetration of digestive enzymes and acids into food particles, allowing birds to consume more fruits, and 2) water intake improves the birds' body water balance which, in turn, indirectly improves nutrient absorption, energy assimilation, or biochemical processes in the digestive system, therefore facilitating the consumption of more fruits. Consistent with the first hypothesis, fruit consumption rate was 2–4 folds higher when water and fruits were simultaneously provided (Fig. 1), implying that the presence of consumed water in the digestive tract facilitates fruit processing in the gut. Retention time was not measured in this work; previous studies on frugivorous passerines have revealed relationships between retention time and fruit characteristics such as secondary metabolites, seed and fruit size and seed weight (Wahaj et al. 1998, Fukui 2003), but no relationship with fruit water content was found (Fukui 2003). Nonetheless, it is possible that water consumption also reduced the retention time of fruits within the gut.

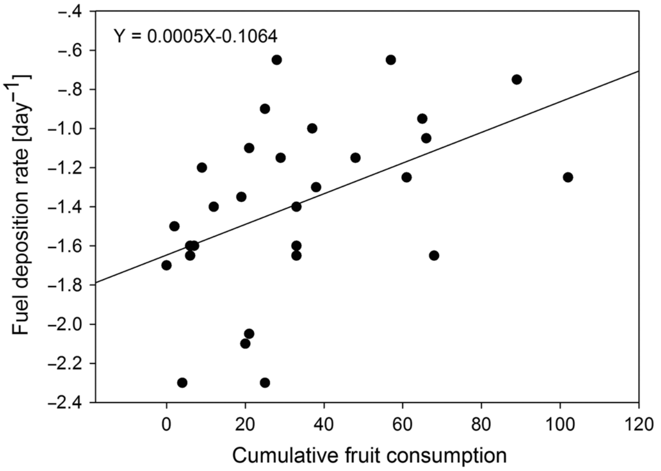

Figure 2. The relationship between the cumulative number of fruits consumed by captive blackcaps during the entire experimental period and their fuel deposition rate (p = 0.010, adjusted $R^2 = 0.190$; n = 29). Fuel deposition rate was positively correlated with the total number of fruits consumed by blackcaps during the entire experimental period. Fuel deposition rate was calculated as described in Sapir et al. (2004a); for more details, see Methods.

As one may expect, fuel deposition rate was positively correlated with the cumulative number of fruits birds consumed (Fig. 2). Other methods that are based on physiological measurements, such as plasma triacylglycerol concentration in the blood, may provide more accurate data regarding the state of the individual and its lipid deposition (Jenni-Eiermann and Jenni 1994), compared with the fuel deposition rate estimated in this study. However, using this estimated fuel deposition rate is still valid and has been used in many other studies (Bayly et al. 2012, Schmaljohann et al. 2013, Gómez et al. 2017) to give an overall gross estimate of the change in bird state over the duration of an experiment. The use of this gross estimate combined with other factors such as the stress level of the captive birds may explain why, although significant, the statistical model explained only ~20% of the variance in FDR.

Because the amount of energy expended by passerines during stopover is two times higher than that expended during migratory flight (Wikelski et al. 2003), it is reasonable to claim that water is a factor with high impact on passerines during stopover. In some regions, migrating birds tend to aggregate in specific stopover sites where water is available (Bonter et al. 2009). The availability of drinking water may allow animals to increase daily foraging duration (Kotler et al. 1998), which, for staging migrants, may result in high FDR. In addition to energy stores, water availability can significantly affect the decision of migrating birds to depart a stopover site, by limiting fuel deposition. For instance, Skrip et al. (2015) illustrated that dehydrated birds had a higher tendency to leave stopover sites (reflected by restlessness), regardless of their body condition. Our results reveal that on top of increased FDR, water availability at a stopover site has an impact on diet composition of passerines.

Our study focused on a single fruit type as it relates to one passerine species. In the future, it would be important to understand whether our findings are applicable to other types of fruits, including those that are characterized by higher water content and that contain more carbohydrates and less lipids. Several studies have documented behavioral differences between the mesophilic blackcap and the xerophilic lesser whitethroat *Sylvia curruca* in their responses to variation in water availability. Specifically, the lesser whitethroat is more abundant in relatively xeric stopover sites with sparse vegetation where no surface water is available, whereas blackcaps are more common in moist oases, gardens and woodlands (E. Shochat, unpubl.). In addition, Sapir et al. (2004b) have demonstrated that supplying drinking water during autumn at a stopover site located on the desert edge increased the number of blackcaps stopping over, but did not change the quantities of lesser whitethroats. Their study also revealed that water availability significantly increased FDR in blackcaps but not in lesser whitethroats. Moreover, lesser whitethroats staging at this stopover site demonstrated a lesser extent of frugivory (Domer et al. 2018). Given all these findings, it would be interesting to directly test if and how the differences in MAMT fruit consumption between lesser whitethroat and blackcap change as a function of water availability and whether fruit consumption is affected by similar factors in these two species, as well as in additional frugivorous species.

In conclusion, our results support the notion that drinking water availability may influence seasonal diet selection and hyperphagia in blackcaps (also suggested by Mizrahy et al. 2011), facilitating the diet shift necessary for accumulating fuel while stopping over during migration. These findings could be relevant to a broad range of migratory species in different parts of the world where seasonal frugivory is common (Bairlein 1990, Afik and Karasov 1995, Parrish 1997, Smith and McWilliams 2010). On a broader perspective, due to the influence of water availability on fruit digestion, one should expect stopover site selection among mesophilic species during migration to be influenced by water availability.

Permits – All required permits and approvals for bird trapping in the field and laboratory experimentation were obtained from Israel's Nature and Parks Authority (permit number 2017/41775), and from the Institutional Animal Care and Use Committee (IACUC; permit number 521/17).

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Supplementary material (available online as Appendix jav-02021 at <www.avianbiology.org/appendix/jav-02021>). Appendix 1.