Comparative Biochemistry and Physiology, Part A 192 (2016) 57–63

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Seasonal dietary shifting in yellow-rumped warblers is unrelated to macronutrient targets

Taylor J. Marshall *, Morag F. Dick, Christopher G. Guglielmo

Department of Biology, Advanced Facility for Avian Research, University of Western Ontario, London, ON, Canada

ARTICLE INFO

Article history:
Received 12 August 2015
Received in revised form 18 November 2015
Accepted 23 November 2015
Available online 25 November 2015

Keywords:
Dietary shift
Nutrient target
Migration
Songbirds
Yellow-rumped warbler
Geometric framework of nutrition

ABSTRACT

Dietary shifting, for example from insects to fruits, is a common mechanism used in migratory songbirds to accumulate fat to fuel migratory flights. We examined a potential underlying cause of dietary shifting in yellow-rumped warblers (*Setophaga coronata*) by comparing energy and protein intake goals of birds during fall migration and winter. We offered captive warblers pairs of three diets differing in macronutrient composition in both the fall and winter. Using the principles of the geometric framework of nutrition we evaluated protein and energy intake to determine if consumption of the diet pairs was adjusted to meet an energy or protein intake target, and if the target differed seasonally. Regardless of season, the warblers preferred the diet with the lowest protein content and highest carbohydrate content. Total energy intake was maintained relatively constant during migration, at around 60 kJ/day, regardless of diet combination, and at about 50 kJ/day during winter. This suggests that warblers consume macronutrients available to them without protein limitations to reach their total energy intake target. When the diet combination offered allows, the warblers mixed their diet intake to consume roughly 0.5 g/day of protein, regardless of season, which suggested a constant protein target. Our findings suggest that songbirds prefer to alter non-protein energy intake proportionally to meet changing energy demand, rather than an overall increase in macronutrient intake. Additionally, they have the ability to shift their diet based on availability, resulting in high flexibility in their macronutrient intakes to maintain energy intake.

1. Introduction

Migration is an energetically demanding process for birds, and accumulating fuel stores is crucial to migration success (Pond, 1978; McWilliams et al., 2004). Fat accounts for approximately 90% of the energy used for migratory flight, with protein contributing the remaining fuel (Jenni and Jenni-Eiermann, 1998). Fuel storage in preparation for migration is primarily achieved by increasing food intake prior to and during migration (McWilliams and Karasov, 2001). However, migrating songbirds also may use dietary shifting, where birds switch their primary food source, for example from insects to fruits to enhance fueling (Bairlein, 1990).

Many migratory songbirds shift from an insectivorous diet during breeding season to a frugivorous diet during fall migration (Parrish, 1997). Foraging for fruit may require less energy expenditure and expose birds to less predation risk compared with foraging for insects (Parrish, 1997). High fruit abundance at stopover sites allows for rapid energy intake while conserving energy due to opportune foraging (Parrish, 1997). Optimal diet theory usually assumes organisms always maximize their net rate of energy intake (MacArthur and Pianka, 1966), and therefore would support the preference for fruit. However, this focus on energy neglects other nutrients (Schaefer et al., 2001), such as protein, which may have the potential to limit consumption. High protein diets can lower caloric intake and promote satiety (Davidenko et al., 2013), which may reduce refueling rates by lowering the intake of other macronutrients.

Food preference, rather than food abundance or availability during fall migration, has been found to contribute to dietary shifting from insects to fruits, potentially allowing birds to be better able to seasonally balance their nutrient and energy intakes (Wheelwright, 1988; Bairlein, 1990). High protein-to-calorie ratio foods, such as insects, reduce adipose tissue build up and instead promote lean muscle mass growth (Rosebrough and McMurty, 1993). On the other hand, low protein-to-calorie ratio foods, such as fruits, promote adipose tissue accumulation (Rosebrough and McMurty, 1993). Smith and McWilliams (2009) observed that a high glucose diet promotes fat accumulation in migratory songbirds, regardless of protein or fat content. Migratory songbirds could switch to frugivory to promote fat accumulation rather than muscle growth in order to support the energetic demands of migratory flight. Stopover sites with more fruit available, leading to more fruit intake, had birds with significantly greater body masses and faster rates of body mass gain than stopover sites will little to no fruit availability (Thomas, 1979; Parrish, 1997). Conversely, eating a purely insectivorous

* Corresponding author at: Department of Biology, Advanced Facility for Avian Research, University of Western Ontario, London, ON N6G 4W4, Canada. Tel.: +1 705 330 2320; fax: +1 519 661 3935.
E-mail addresses: tmarsh8@uwo.ca, taylormarshall_4@hotmail.com (T.J. Marshall).

http://dx.doi.org/10.1016/j.cbpa.2015.11.014
1095-6433/

diet, or high protein diet, may limit the rate of fattening (Bairlein, 2002). The difference in macronutrient content of these diet items may influence intake. In mice, a low protein diet can promote an increased intake of carbohydrates and lipids, whereas a high protein diet can decrease caloric intake potentially due to satiety (Sørensen et al., 2008; Davidenko et al., 2013).

During migration, birds have an increased energy demand, but protein requirements do not increase proportionately (Langlois and McWilliams, 2010). Migratory birds have the same nitrogen excretion per day as non-migratory birds but consume more food overall, providing migrants with a more positive nitrogen balance which decreases the minimum dietary protein content required (Langlois and McWilliams, 2010). The dietary shift from an insectivorous diet to a frugivorous diet during fall migration could be a response to decreased dietary protein requirements, as migrant birds satisfy their protein requirements by eating a greater amount of lower protein food (Langlois and McWilliams, 2010).

An additional factor that may alter diet preference towards carbohydrates over protein during migration may be related to differences in nutrient absorption in the gut. Paracellular absorption of monosaccharides, amino acids and dipeptides occurs in the gut, but differ in the fractional absorption rates (Chediack et al., 2006). Monosaccharides have a higher rate of paracellular absorption compared to dipeptides, where peptide electroaffinity influences paracellular absorption (Chediack et al., 2006). This could influence the absorptions costs depending on diet composition. High protein diets, such as insects, increase transporter-mediated amino acid uptake in the small intestine (Afik et al., 1997a; Karasov and Levey, 1997). However, when fed a high carbohydrate fruit diet, no increase in transporter-mediated uptake capacity is observed (Afik et al., 1997a), while passive absorption of glucose is increased (Afik et al., 1997b). Passive absorption allows for higher absorption rates at lower energetic costs, which can be beneficial to fruit-eating migrating songbirds that need to accumulate fat stores quickly.

Migrating songbirds that shift their diet to fruit benefit from the greater energy efficiency to digest and utilize glucose, and this is aided by their ability to distinguish nutritional values of their food. Birds can detect subtle differences in nutritional values and select their diet accordingly (Wheelwright, 1988; Whelan and Willson, 1994), to the point of distinguishing between diets differing in carbohydrates by 1%, lipids by 2%, or cysteine by 4% (Schaefer et al., 2001). This precision for food nutrient evaluation allows birds to meet their macronutrient and energy goals by mixing the foods they consume.

The geometric framework of nutrition (GFN) is a graphical modeling approach used to assess how animals mix foods to meet their nutritional goals or targets (Simpson and Raubenheimer, 1994). By examining nutrient intakes within a nutritional space, the GFN allows visualization of the potential combinations of macronutrient and energy intakes an organism may choose to satisfy requirements. Each axis represents a nutrient of choice (e.g. protein, carbohydrate, or energy) (Simpson and Raubenheimer, 1994). Food consumption data can be plotted within the nutrient space created by different food options to evaluate potential nutrient targets, and to determine how animals consume their different food options to reach these targets. Nutrient or energy targets are the amount per day the animal is choosing to consume. The targets can be diet dependent or defended if different diet combinations lead to the same targets. The GFN analysis allows one to evaluate foraging goals of animals in their current physiological state, rather than minimum nutrient requirements or overall preference (Schaefer et al., 2001).

The GFN differs from the optimal diet theory, as it considers physiological state in the analysis. The optimal diet theory lacks this physiological perspective, and therefore may produce misleading results, for example, concluding that migratory birds switch to a fruit diet strictly due to fruit abundance and energy costs rather than a change in nutritional targets. Previous studies of migratory bird nutrition have evaluated diet complementation, and seasonal changes in diet based on nutritional reward and requirements (Moore and Simm, 1985; Wheelwright, 1988; Whelan and Willson, 1994; Parrish, 1997). However, seasonal diet shifting and changes in preference may be related to changing protein and energy targets during migration.

Our objective was to examine protein and energy targets of a migratory songbird, the yellow-rumped warbler (*Setophaga coronata*), during fall migration and winter using the GFN, and to understand how this relates to diet preference. Yellow-rumped warblers shift their diet seasonally, consuming insects and other small invertebrates during the spring breeding season, and eating a mixture of insects and fruit, and sometimes exclusively fruit during fall migration and winter (Hunt and Flaspohler, 1998). We hypothesized that yellow-rumped warblers would have different nutrient targets depending on their migratory condition. Overall, we predict higher energy intake during migration. Additionally, we predicted that protein requirements would decrease when the warblers were in a migratory condition, and high protein intake would lower total energy intake due to potential satiation.

2. Material and methods

2.1. Animals and housing

We used 12 yellow-rumped warblers (11 juveniles: 5 females, 1 male and 5 unknown sex; and 1 adult female). The warblers were caught from late September to early October 2014, at Long Point, Ontario, and housed at the Advanced Facility for Avian Research at the University of Western Ontario. Animal collection and care protocols followed the Canadian Council on Animal Care guidelines and were approved by the University of Western Ontario's Animal Care and Use Sub-Committee (protocol 2010–216), and by the Canadian Wildlife Service (permit CA 0256).

During the feeding trials, the birds were housed individually in cages measuring 70 cm wide by 50 cm deep and 50 cm height. Upon arrival in the fall, the birds were maintained on a natural fall photoperiod (12 h light: 12 h dark), and switched to a short day winter photoperiod (8 h light: 16 h dark) in late November (over one month prior to the winter feeding trial period). To ensure that the warblers were in the appropriate physiological state during each feeding trial, the birds were filmed overnight using infrared cameras, and we confirmed the presence of migratory restless behavior (Gwinner, 1986) during the fall and its absence during the winter trial.

2.2. Diets and feeding trials

The experiment consisted of two 15-day feeding trial periods; a fall migratory feeding trial period ran from October 15–November 1, and a winter feeding trial period ran from December 28–January 12. To reduce any potential food preferences based on familiarity, the warblers were fed a different synthetic diet to the experimental diets and mealworms before and between the feeding trial periods. In both feeding trial periods, we fed the warblers three experimental diets: a high carbohydrate diet (HC), a high protein diet (HP), and an intermediate diet (I) (Table 1). The diets varied in the amount of casein, the primary protein source, and dextrose, the primary carbohydrate source, to achieve the varied macronutrient compositions. All other ingredients were kept consistent between the three different diets (Table 1).

During each feeding trial period, the warblers were rotated through a series of three different diet combinations, with two different diets offered together in each rotation ((i) high carbohydrate diet and intermediate diet (HCI), (ii) high protein diet and intermediate diet (HPI), (iii) high protein diet and high carbohydrate diet (HCHP)). The placement of the dishes in the cage was random each day to reduce a side bias for food selection. The warblers were randomly assigned into three groups of four warblers, with each group rotating through the combination in a different sequence. Each combination was fed ad libitum for five days, with the first day being excluded from data