

# Summit metabolic rate exhibits phenotypic flexibility with migration, but not latitude in a neotropical migrant, *Parkesia noveboracensis*

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**Abstract** Physiology–life history interactions suggest that birds living with a fast ‘pace-of-life’ should have higher metabolic capacity to provision higher reproductive activity. Previous work supports this, but does not consider migration. We measured summit metabolism ( $\dot{V}O_2$  summit) in Northern Waterthrush (*Parkesia noveboracensis*) while wintering in the Republic of Panama, migrating northwards through eastern North America, and while breeding in northeastern North America.  $\dot{V}O_2$  summit is similar between breeding and overwintering (non-migratory) and is significantly elevated in migration. These data suggest that migration is a driver of phenotypic flexibility in these birds and that migration, like winter survival, may be an important determinant of connections between life history and physiology.

**Keywords** Phenotypic plasticity · Life history physiology · Northern Waterthrush

## Zusammenfassung

**Beim Uferwaldsänger, *Parkesia noveboracensis*, einem neotropischen Zugvogel, zeigen Stoffwechsel-Spitzenwerte phänotypisch Flexibilität bei Ortswechseln, aber nicht hinsichtlich der geographischen Breite**

Die Wechselwirkungen zwischen Physiologie und Lebensweise legen die Vermutung nahe, dass Vögel mit ihrem sehr

hohen Lebenstempo bei ihren intensiven Fortpflanzungsaktivitäten auch eine höhere Stoffwechselkapazität haben müssten. Frühere Untersuchungen unterstützen diese Annahme, haben aber die Vogelwanderungen nie berücksichtigt. Wir maßen die Stoffwechsel-Spitzen beim Uferwaldsänger (*Parkesia noveboracensis*) während seiner Überwinterung in der Republik Panama, während seiner Wanderung nach Norden durch das östliche Nordamerika und während seiner Brutperiode in Nordostamerika. Der Stoffwechsel während der Überwinterung ist dem in der Brutzeit ähnlich, während des Zugs aber signifikant erhöht. Die Ergebnisse legen nahe, dass der Vogelzug ein Treiber für die phänotypische Flexibilität dieser Vögel ist und dass der Zug, wie auch das Überleben im Winter, ein wichtiger, ausschlaggebender Faktor in der Wechselbeziehung von Lebensweise und Physiologie der Vögel sein könnte.

## Introduction

Life history traits of birds living at different latitudes are organized along a slow-to-fast continuum, or ‘pace of life’ such that ‘slow’ species have lower numbers of offspring, experience slower developmental rates, and have increased longevity compared to ‘fast’ species (Ricklefs and Wikelski 2002). This observation led Ricklefs and Wikelski (2002) to propose that physiological systems, including energy metabolism, also follow this slow-to-fast continuum. Supporting this hypothesis, both basal (Wiersma et al. 2007a), maximal (Wiersma et al. 2007b) and field (Wagner et al. 2013) metabolic rates of tropical birds were found to be lower than those of paired temperate species.

Life history predicts a fast pace-of-life for migratory birds, similar to temperate resident species. High-latitude

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breeding requires a relatively high reproductive rate in order to finish breeding in a narrow window of time. Thus, despite having lower clutch sizes and lower annual fecundity than temperate residents (Bohning-Gaese et al. 2000; Jetz et al. 2008), migrants have a high reproductive output relative to tropical residents. Alternatively, as migratory species avoid temperate winter environments throughout their annual cycle, one might predict migrants to resemble tropical residents.

The energetic demands of the migratory event necessitate higher metabolic rates (Swanson 1995). Migration entails a unique set of physiological challenges, notably extremely high energy expenditure during sustained flight over long distances, often with few stops. Phenotypic flexibility, defined as intra-individual and reversible phenotypic transformations (Piersma and Lindstrom 1997), permits migrants to adjust many physiological traits in response to the changing requirements of annual cycles (e.g., McWilliams and Karasov 2001). Similarly, metabolic capacity shows considerable flexibility in both temperate (Swanson 2010) and tropical residents (Wells and Schaffer 2012). Migratory birds are thus excellent organisms to examine the role of phenotypic flexibility of metabolic rate in the context of life history variation.

In the present study, we measure  $\dot{V}O_{2\text{ summit}}$  of the Northern Waterthrush (*Parkesia noveboracensis*), during tropical overwintering in Panama, migration through southwest Ohio, and while breeding in Maine. As metabolism is often reported to exhibit phenotypic flexibility (Swanson 2010), we hypothesize that Northern Waterthrush acclimatize to local environments, matching relatively low metabolic rates of tropical residents while overwintering and higher metabolic rates of temperate residents during breeding. Further, we predict the highest metabolic rates during migration.

## Materials and methods

Northern Waterthrush (*Parkesia noveboracensis*) were captured with mist nets at the Smithsonian Tropical Research Institute Bocas del Toro research station in the Republic of Panama (9°21'N, 82°15'W) from 21 to 25 February, 2009 and from 8 to 21 February, 2011 (tropical overwintering), at the Hueston Woods Biological Station in Hueston Woods State Park (39°34'N, 84°44'W) and at the Miami University Ecology Research Center (39°30'N, 84°45'W), both in southwest Ohio from 4 to 6 May, 2010 (migration), and in the Orono bog complex near Pushaw lake in Maine (44°53'N, 68°44'W) from 1 to 4 June, 2013 (breeding). All birds were caught between sunrise and early

afternoon,  $\dot{V}O_{2\text{ summit}}$  was measured within 2–3 h of capture (late morning to early afternoon) and the birds were released. A digital scale (Scout Pro; Pine Brook, NJ, USA) was used to measure the weight of each bird.

All work was approved by the Institutional Animal Care and Use Committee of Miami University (protocol #863), Ohio Dept. of Natural Resources (permit #15–9), Maine Dept. of Inland Fisheries and Wildlife (permit #2012–379), US Fish and Wildlife Services (permit #MB158451-2), and Republic of Panama Natural Resources Management agency (permit #SE/A-112-08).

Summit metabolism ( $\dot{V}O_{2\text{ summit}}$ ) was measured using indirect calorimetry (Rosenmann and Morrison 1974). Gas (21 % oxygen, balance helium) flowed at  $1.4\text{ l min}^{-1}$  through a mass flow meter (Sierra Instruments, Monterey, CA, USA) regulated by a flow controller (model MFC-2; Sable Systems, Las Vegas, NV, USA) and into a 1.0-l plastic chamber containing the animal before passing through a CO<sub>2</sub> analyzer (CA-10a or FoxBox Portable Oxygen Analysis System; Sable Systems, Las Vegas, NV, USA), a drierite column and an O<sub>2</sub> analyzer (FC-10a or FoxBox System; Sable Systems). For each measurement, the bird was enclosed in the metabolic chamber at room temperature for 15 min to allow equilibration. The chamber was then placed at a static temperature (Swanson et al. 1996) of 2 °C for 10–15 min during which steady state was reached for at least 5 min. We measured cloacal temperature for nearly every bird and all birds exhibited hypothermia during the challenge. Data were collected at 1 sample per second using Expedata (Sable Systems). Data were selected from the peak 1 min during the steady state period for average gas concentration values.  $\dot{V}O_{2\text{ summit}}$  was calculated using the equation from the Expedata manual (Sable Systems):

$$\dot{V}O_{2\text{ summit}} = \text{STP} \times \text{FR} \times ((F_iO_2 - F_eO_2) - (F_eO_2 \times (F_eCO_2 - F_iCO_2)) / (1 - F_eO_2))$$

where STP is standard temperature and pressure corrections, FR the flow rate,  $F_iO_2$  and  $F_eO_2$  the fractional content of oxygen in incurrent and excurrent air, respectively, and  $F_iCO_2$  and  $F_eCO_2$  the fractional content of carbon dioxide in incurrent and excurrent air, respectively.

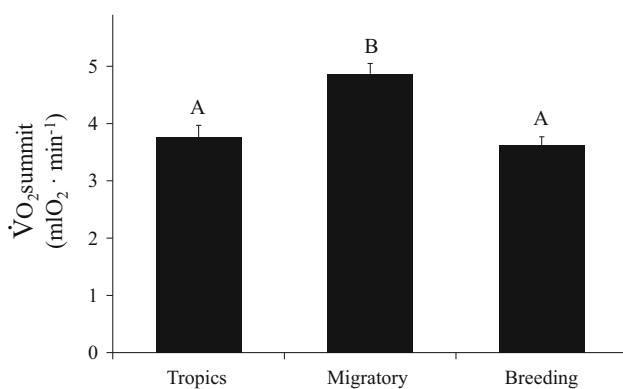
We analyzed the overall experimental effects for body weight and summit metabolism using an ANCOVA with body weight as a co-variate, followed by post hoc comparisons using the Tukey HSD method using R (v.3.1.1; R Core Team 2014). The level of significance was set at  $p < 0.05$  in all cases. All data are reported as mean  $\pm$  standard error. The number of observations is listed in the results.

## Results

We measured body weight and summit metabolism ( $\dot{V}O_{2\text{ summit}}$ ) for 15 individuals during tropical overwintering in Panama, 8 during migration through Ohio, and 6 during their temperate breeding season in Maine. Mean body weights did not vary significantly ( $F_{2,26} = 1.73$ ;  $p = 0.197$ ) between the tropical overwintering ( $15.90 \pm 0.26$ ), migrating ( $16.49 \pm 0.40$ ) and breeding ( $15.51 \pm 0.25$ ) groups. Similarly, analysis of covariance showed no significant interaction between body mass and season ( $F_{2,23} = 1.14$ ;  $p = 0.336$ ). We then dropped body weight from the model. There was a significant effect of life history stage on  $\dot{V}O_{2\text{ summit}}$  ( $F_{2,25} = 6.29$ ,  $p = 0.006$ ).  $\dot{V}O_{2\text{ summit}}$  was highest during northern migration, while birds overwintering in the tropics and those breeding in temperate zones showed no significant difference in  $\dot{V}O_{2\text{ summit}}$  (Fig. 1). There was a similar effect of season when metabolic rate was calculated as mass-specific  $\dot{V}O_{2\text{ summit}}$  ( $F_{2,23} = 6.08$ ,  $p = 0.007$ ).

## Discussion

Similar to previous studies (Swanson 1995; Swanson and Dean 1999) that reported elevated  $\dot{V}O_{2\text{ summit}}$  during spring migration compared to temperate summer residency and fall migration, our expectation that metabolic capacity would be elevated during migration was supported. However, our data demonstrate that the metabolic rates of migratory populations did not differ while in the temperate breeding or tropical overwintering stages of the life cycle. This is the first report of this kind that we are aware of, and suggests that the efforts of breeding are not a major determinant for the



**Fig. 1** The maximal rate of oxygen consumption by Northern Waterthrush (*Parkesia noveboracensis*) during an acute cold challenge ( $\dot{V}O_{2\text{ summit}}$ ) is significantly higher during migration ( $n = 8$ ). Breeding birds ( $n = 6$ ) exhibit similar metabolic capacity as those overwintering in tropical habitat ( $n = 15$ ). Data are presented as mean  $\pm$  SEM. Different letters indicate significant differences following pair-wise comparisons

elevation of metabolic ceilings in migrant birds. We thus reject our hypothesis that phenotypic flexibility of metabolic capacity results in elevation while breeding or reduction while overwintering in the tropics.

Life history physiology data indicate that the faster pace-of-life in temperate bird species is associated with higher metabolic rates than tropical species (Wiersma et al. 2007a, b; Sgueo et al. 2012). While temperate species likely have higher activities in response to breeding demands, there are also clear differences in abiotic factors across habitats, most notably the seasonal temperature range experienced by temperate birds. Recent reports (Jetz et al. 2008; Swanson and Garland 2009; Swanson 2010) indicate that cold temperatures experienced during high-latitude winters are a more potent driver of metabolic capacity than migration. That observation also suggests that winter temperatures are more likely to drive the higher metabolic capacity of temperate birds than their more intense breeding behavior (see also Sgueo et al. 2012).

Our initial prediction that migrants would mirror the metabolic rates of temperate birds while breeding at high latitude and of tropical birds while overwintering was not supported. Instead, we see that the summit metabolic rate at either locale is intermediate to predicted values. For an average Northern Waterthrush of 16 g, the equations from Wiersma et al. (2007b) predict a  $\dot{V}O_{2\text{ summit}}$  of 1.01 W if a tropical resident and 1.54 W if a temperate resident. Our data, (converted to watts using the same assumptions as Wiersma et al. 2007b) are 1.26 ( $\pm 0.07$ ) W during tropical overwintering and 1.21 ( $\pm 0.05$ ) W during temperate breeding. Although included with temperate residents,  $\dot{V}O_{2\text{ summit}}$  data for migrants reported by Wiersma et al. (2007b) also tended to be lower than those of temperate residents. During migration, our birds had  $\dot{V}O_{2\text{ summit}}$  of 1.63 ( $\pm 0.06$ ) W, similar to a temperate resident during summer and less than one would predict during winter (at 2.02 W during winter, using the allometric equation provided in Swanson and Liknes 2006 for a winter-acclimated bird of 16 g). These values are in agreement with the observation of Swanson (2010) that migration is less of a stimulus for high metabolic capacity than winter survival. However, the degree of increase ( $\sim 32\%$ ) is similar for our Northern Waterthrush compared to the increases seen in temperate residents during winter (Swanson and Garland 2009), thus there may be species differences between migrants and residents that must be explored. Alternatively, migration may have less of a ‘carry-over’ effect on other seasons than temperate overwintering, explaining the lower metabolic capacity of migrants across all seasons.

The observation that seasonal residence in either tropical or temperate latitudes did not lead to differences in  $\dot{V}O_{2\text{ summit}}$  suggests that the evolution of divergent

physiology across latitudinal gradients may not be driven by life history variation. Instead, we suggest that higher metabolic rates in temperate and migrant birds may originate with extreme demands on energetic systems (winter survival or migration) that are then co-opted by evolution to facilitate higher reproductive rates. This interpretation is in agreement with the observations that temperate residents have higher metabolic rates during winter rather than while breeding (Swanson 2010; Sgueo et al. 2012). It may be that the demands of winter survival makes the high rates of energy expenditure of temperate breeding possible.

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