

# **Global variation in avian metabolic rates and the slow pace of life of tropical birds**

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Efforts to identify mechanistic links between the rates at which birds use energy and their ecology and evolution have often focused on metabolic rates measured under standardized conditions, most notably basal metabolic rate (BMR). It has long been recognized that birds inhabiting tropical regions generally have lower BMR than their temperate-zone counterparts. Two alternate hypotheses have been advanced to explain this difference. On the one hand, the low BMR of tropical species may arise directly from living in warm environments, with modest demands for metabolic thermogenesis and activity reflected in low rates of baseline energy expenditure. This notion is supported by two recent analyses that found negative correlations between BMR and air temperature (White *et al.* 2007; Jetz, Freckleton & McKechnie 2008). The second possibility is that the low BMR of tropical species is instead mechanistically linked to their generally slow

pace of life and lower investment in reproduction (Ricklefs & Wikelski 2002). According to this view, the more modest investments in reproduction by tropical birds compared to fast-breeding, highly fecund temperate-zone species result in lower overall energy demands, which translate into lower BMR via mechanisms such as lower masses and/or mass-specific metabolic rates of organs (Wiersma *et al.* 2007; Williams *et al.* 2010).

Measurements of avian BMR date back to early in the 20<sup>th</sup> Century (Benedict & Fox 1927; Brody & Proctor 1932; Riddle, Smith & Benedict 1932), and the species for which BMR measures exist now number well over 500 (McNab 2009). Although several researchers have gone to considerable effort to measure BMR in tropical species (e.g., Hails 1983; McNab 2001; McNab 2005; Wiersma *et al.* 2007), data for low-latitude species remain disproportionately sparse, particularly when viewed in light of the enormous diversity of tropical avifauna. This paucity of tropical data has severely limited global analyses of avian BMR, particularly those seeking to investigate the roles of life history *versus* climate in driving latitudinal metabolic variation.

In this issue of *Functional Ecology*, Londoño *et al.* in (press) present a global analysis of avian BMR based, in part, on new measurements for over 250 tropical species. This study not only greatly increases the number of species for which BMR estimates are available, but also goes a long way towards remedying the latitudinal imbalance in our knowledge of this important metabolic trait. Most of Londoño *et al.*'s data were collected at three field stations at 13 °S in Peru, spanning a 2,600 m altitudinal gradient from lowland rainforest to montane cloud forest. The study took place over a three-year period and covered phylogenetically diverse taxa, including tinamous, doves, nightjars,

hummingbirds, toucans, woodcreepers, elaenias, manakins, thrushes, euphonias, and flowerpiercers.

The variation in altitude and hence temperature among the study sites provided the basis for testing the influence of climate on avian metabolic rate. Despite the highest of the three sites being on average 12 °C colder than the lowest, BMR did not vary significantly with altitude. This finding suggests that the low BMR of tropical species is not directly linked to temperature but instead represents a characteristic of tropical birds in general, supporting the hypothesis that low BMR is mechanistically linked to a slow pace of life.

However, the nature of these links between BMR and life history remain unclear. One obvious potential link concerns the relationship between BMR and field metabolic rate (FMR), the total amount of energy a bird uses on a daily basis. Relatively few FMR estimates exist for tropical birds, and those that are available do not provide a clear picture. For instance, an analysis of latitudinal variation in avian FMR found that the handful of low-latitude species in which it has been measured often have FMRs comparable to those of species from temperate regions (Anderson & Jetz 2005). In contrast, the FMR of spotted antbirds (*Hylophylax naevioides*) in Panama measured via heart rate telemetry was much lower than allometrically predicted values (Steiger *et al.* 2009). Many more measurements of FMR in tropical species are needed to examine the potential link to low BMR.

In addition to providing important new insights into global patterns in avian energetics, Londoño *et al.* (in press) also reignite a long-standing debate concerning phylogenetic variation in avian BMR. Several early workers noted that BMR in the order Passeriformes, which includes more than half all extant

bird species, is consistently higher than in non-passerines (Lasiewski & Dawson 1967; Zar 1968; but see also Prinzinger & Hänssler 1980). However, with the advent of phylogenetically independent comparative methods (Felsenstein 1985) the higher BMR of passerines was found to reflect phylogenetic inertia, with no significant difference compared to non-passerines once patterns of evolutionary relatedness were taken into account (Reynolds & Lee 1996; Garland & Ives 2000).

Reynolds and Lee, and others who reached the same conclusion, used the avian phylogeny proposed by Sibley & Ahlquist (1990). However, a radically different model of avian phylogenetic relationships was recently proffered (Hackett *et al.* 2008). This phylogeny identified falcons and parrots as the closest relatives of the passerines, a finding subsequently supported by other lines of evidence (Suh *et al.* 2011). In addition to significantly expanding the currently-available avian BMR data set, Londoño *et al.* (in press) present the first major analysis based on the Hackett *et al.* (2008) phylogeny. Their analysis brings the passerine *versus* non-passerine debate full circle, by revealing significantly higher BMR in passerines compared to non-passerines.

The authors note several gaps in our current knowledge that are highlighted by their study, such as whether species in tropical regions exhibit seasonal variation in BMR as is the case for species from temperate and subtropical latitudes (Smit & McKechnie 2010; Swanson 2010). Similarly, the extent to which latitudinal variation in metabolic rates arises via phenotypic plasticity *versus* hardwired genotypic differences reflecting physiological adaptation remains unclear (Wikelski *et al.* 2003). Londoño *et al.*'s paper represents a significant advance in our understanding of global avian metabolic diversity, and

serves to remind us of the many fundamental questions concerning avian physiology and ecology that remain to be answered.

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### **References**

Anderson, K.J. & Jetz, W. (2005) The broad-scale ecology of energy expenditure of endotherms. *Ecology Letters*, **8**, 310-318.

Benedict, F.G. & Fox, E.L. (1927) The gaseous metabolism of large birds under aviary life. *Proceedings of the American Philosophical Society*, **66**, 511-534.

Brody, S. & Proctor, R.C. (1932) Growth and development, with special reference to domestic animals. XXIII. Relation between basal metabolism and mature body weight in different species of mammals and birds. *Missouri University Agricultural Experimental Station Research Bulletin No.*, **166**, 89-101.

Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1-15.

Garland, T. & Ives, A.R. (2000) Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist*, **155**, 346-364.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt,

- C.C. & Yuri, T. (2008) A phylogenomic study of birds reveals their evolutionary history. *Science*, **320**, 1763-1768.
- Hails, C.J. (1983) The metabolic rate of tropical birds. *Condor*, **85**, 61-65.
- Jetz, W., Freckleton, R.P. & McKechnie, A.E. (2008) Environment, migratory tendency, phylogeny and basal metabolic rate in birds. *PLoS One*, **3**, e3261.
- Lasiewski, R.C. & Dawson, W.R. (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor*, **69**, 13-23.
- Londoño, G.A., Chappell, M.A., del Rosario Castañeda, M., Jankowski, J.E. & Robinson, S.K. (in press) Basal metabolism in tropical birds: latitude, altitude, and the “pace of life”. *Functional Ecology*.
- McNab, B.K. (2001) Energetics of toucans, barbets and a hornbill: implications for avian frugivory. *Auk*, **118**, 916-933.
- McNab, B.K. (2005) Food habits and the evolution of energetics in birds of paradise (Paradisaeidae). *Journal of Comparative Physiology B*, **175**, 117-132.
- McNab, B.K. (2009) Ecological factors affect the level and scaling of avian BMR. *Comparative Biochemistry and Physiology A*, **152**, 22-45.
- Prinzinger, R. & Hänsler, I. (1980) Metabolism-weight relationship in some small nonpasserine birds. *Experientia*, **36**, 1299-1300.
- Reynolds, P.S. & Lee, R.M. (1996) Phylogenetic analysis of avian energetics: passerines and non-passerines do not differ. *American Naturalist*, **147**, 735-759.
- Ricklefs, R.E. & Wikelski, M. (2002) The physiology/life history nexus. *Trends in Ecology and Evolution*, **17**, 462-468.

- Riddle, O., Smith, G.C. & Benedict, F.G. (1932) The basal metabolism of the mourning dove and some of its hybrids. *American Journal of Physiology*, **101**, 206-267.
- Sibley, C.G. & Ahlquist, J.E. (1990) *Phylogeny and classification of birds*. Yale University Press, New Haven.
- Smit, B. & McKechnie, A.E. (2010) Avian seasonal metabolic variation in a subtropical desert: basal metabolic rates are lower in winter than in summer. *Functional Ecology*, **24**, 330-339.
- Steiger, S.S., Kelley, J.P., Cochran, W.W. & Wikelski, M. (2009) Low metabolism and inactive lifestyle of a tropical rain forest bird investigated via heart-rate telemetry. *Physiological and Biochemical Zoology*, **82**, 580-589.
- Suh, A., Paus, M., Kiefmann, M., Churakov, G., Franke, F.A., Brosius, J., Kriegs, J.O. & Schmitz, J. (2011) Mesozoic retroposons reveal parrots as the closest living relatives of passerine birds. *Nature Communications*, **2**, 443.
- Swanson, D.L. (2010) Seasonal metabolic variation in birds: functional and mechanistic correlates. *Current Ornithology*, pp. 75-129.
- White, C.R., Blackburn, T.M., Martin, G.R. & Butler, P.J. (2007) The basal metabolic rate of birds is associated with habitat temperature and precipitation, not productivity. *Proceedings of the Royal Society B*, **274**, 287-293.
- Wiersma, P., Muñoz-Garcia, A., Walker, A. & Williams, J.B. (2007) Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 9340-9345.
- Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A. & Gwinner, E. (2003) Slow pace of life in tropical sedentary birds: a common-garden experiment on

four stonechat populations from different latitudes. *Proceedings of the Royal Society of London B*, **270**, 2383-2388.

Williams, J.B., Miller, R.A., Harper, J.M. & Wiersma, P. (2010) Functional linkages for the pace of life, life-history, and environment in birds. *Integrative and Comparative Biology*, **50**, 855-868.

Zar, J.H. (1968) Standard metabolism comparisons between orders of birds. *Condor*, **70**, 278.