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Avian energetics: The passerine/non-passerine dichotomy

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ABSTRACT

Whether passerines collectively have a higher mean mass-independent basal rate of metabolism than the mean of other birds has been controversial. The conclusion that no difference exists was based on phylogenetic analyses. Higher basal rates, however, have been repeatedly seen in passerines and demonstrated by ANCOVA analyses. Several studies indicated that the mean mass-independent basal rate of passerines is >30% higher than the collective mean of other birds. Yet, at least three non-passerine orders of 25 have mean mass-independent basal rates equal to that of passerines. They are Anseriformes, Charadriiformes, and Procellariiformes, all characterized by an active lifestyle, including migratory and pelagic habits. In contrast, sedentary ducks endemic to islands have low basal rates. The high basal rates in temperate passerines correlate with migratory habits and life in cool to cold environments, the absence of these factors being partly responsible for the lower basal rates in most tropical passerines. The principal difference in energetics among non-passerines, between passerines and most non-passerines, and among passerines reflects the frequency of habits associated with high or low mass-independent energy expenditures, the habits correlating with body composition.

The mean mass-independent basal rate in tropical passerines is slightly lower than in temperate passerines which implies that the collective mean in passerines would be somewhat lower if tropical passerines were included in proportion to their diversity. However, their inclusion will not eliminate the difference presently seen between passerines and other birds because the difference between tropical and temperate passerines is less than that between passerines and other birds.

1. Introduction

Interest in the energetics of birds has been widespread for the last five decades and the many data gathered during this period have led to several controversies. One has been whether passerines have higher mass-independent basal rates of metabolism than the collective of other birds, the 'non-passerines.' Lasiewski and Dawson (1967), Aschoff and Pohl (1970), Kendeigh et al. (1977), Gavrilov (1999, 2000, 2014), Wiersma et al. (2007), and McNab (2009) based on ANCOVA analyses, maintained that the difference exists. Others (Reynolds and Lee, 1996; Rezende et al., 2002; McKechnie and Wolf, 2004; Wiersma et al., 2007) 'adjusting' for phylogeny, denied its existence. Londoño et al. (2015), using both methods, found that such a difference exists. The multifactorial analysis previously reported (McNab, 2009, 2015) is used here to explore the passerine/non-passerine dichotomy. It is based on ANCOVA, which is more appropriate than the phylogenetically based analysis when dealing with quantitative, physiological functions because it separates the quest for the physiological basis of a quantitative function from a description of the historical pattern of character evolution (McNab, 2012, 2015).

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2. The existence of the dichotomy in energetics

Many data demonstrate the existence of a difference between the mass-independent basal rates of passerines and non-passerines. Lasiewski and Dawson (1967) estimated that this difference equals 65% in 120 species. Aschoff and Pohl (1970) demonstrated that 14 passerines had basal rates that were 56% higher than found in 17 non-passerines during the resting period; it was 55% higher during the activity period. Passerines ($n = 41$) had basal rates that averaged 57% greater than non-passerines ($n = 30$) in summer, 70% in winter (Kendeigh et al., 1977). A mass analysis of the basal rates in 533 species of birds demonstrated that 274 passerines had a mean mass curve with a coefficient[1] that is ([0.130 kJ/h] / [0.089 kJ/h] = 1.46) 46% greater than that of 259 non-passerines ($P < 0.0001$) (McNab, 2009). But when the analysis included six ecological and behavioral factors and body mass, passerines had basal rates that averaged 32% greater than non-passerines, the difference with the mass analysis undoubtedly reflecting factor interaction among clade affiliation and the included factors. In a sample of 79 species in New Guinea, the basal rate of passerines averaged 75% greater than that of other birds with almost no overlap (McNab, 2013). Gavrilov (1999, 2000, 2014) found that boreal

[1] These coefficients are a in the equation: basal rate = $a(\text{mass})^b$, in this case, one for passerines (0.130 kJ/h) and one for non-passerines (0.089 kJ/h).

passerines have a collective mean basal rate that averages 30–40% greater than that of non-passerines. Wiersma et al. (2007), using ANCOVA techniques, concluded in 128 species that temperate species had basal rate that averaged ca. 17% greater than tropical species. Londoño et al. (2015) found in 488 species that the difference was 14 to 16%, this estimate derived from both an ANCOVA and a phylogenetic analysis. Why some estimates are much smaller than others is unclear unless it reflects the sample used, but that cannot be determined in Londoño et al. because the data were sequestered. The presence of the difference cannot be dismissed based on any "theoretical" argument.

A difference in energy expenditure between passerines and other birds raises the question of what characteristics found in the heterogeneous collection of non-passerines might set their basal rates lower than that of passerines, or what distinctive characteristic found in passerines might lead to higher rates. The identification of the change in the dichotomy is needed to clarify the basis for the difference in energetics that exists between passerines and other birds (McNab, 2015). All appreciable dichotomies must be grounded in some biologically important reorganization of behavior and function, not simply some vague non-functional division. A fundamental difficulty with phylogenetic analyses is that they are satisfied with noting where and when an evolutionary dichotomy occurred without any concern for its basis and consequences.

3. A potential basis for the dichotomy in energetics

The correlation of the dichotomy in energy expenditure with a phylogenetic dichotomy potentially reflects the correlation of various character states with both dichotomies. For example, a correlation of energy expenditure with food habits might be attributed to the phylogenetic dichotomy because of a correlation of food habits with the branches of a dichotomy. To explore this possibility, a comparison is made between passerines and other birds that have a shared food habit, frugivory. Is there still a difference in basal rate between passerine and non-passerine frugivores?

Frugivorous passerines ($n = 18$) have a mean metabolism/mass curve based on ANCOVA that is ([0.189 kJ/h] / [0.122 kJ/h] = 1.55) 55% greater than 27 non-passerine frugivores ($P < 0.0001$) (McNab, 2015), although two parrots and a cuckoo have "passerine" basal rates

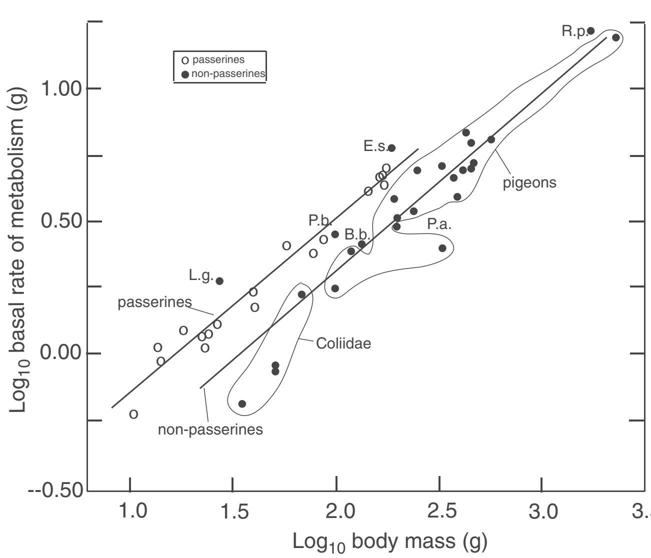

Fig. 1. Log_{10} basal rate of metabolism as a function of log_{10} body mass: 27 non-passerine and 18 passerine frugivores (modified from McNab (2012)). Some non-passerines are individually identified: *R.p.*, *Rhyticeros plicatus* (Bucerotidae), *E.s.*, *Eudynamys scolopacea* (Cuculidae), *P.a.*, *Pteroglossus aracari* and *B.b.*, *Baillonius bailloni* (Rhamphasidae), and *P.b.*, *Psittacella brehmii* and *L.g.*, *Loriculus galgulus* (Psittacidae).

(Fig. 1). No 'adjustment' of these data can obscure this difference, the data conforming to the criteria that define basal rate, namely that the measurements were made in thermoneutrality, the individuals being inactive during the inactive period, post-absorptive, and regulating their normal body temperature (McNab, 1997).[2] Shared food habits, at least frugivory, cannot account for the difference in basal rate between passerines and other birds (Fig. 1).

A clue to the basis of the difference in energy expenditure between passerines and other birds was found in the analysis of 533 species (McNab, 2009). Three out of 25 non-passerine orders had mean mass-independent basal rates that were indistinguishable from that of passerines. They are the Anseriformes (ducks, geese, swans; $n = 30$; $P = 0.20$), Procellariiformes (shearwaters, petrels, albatrosses; $n = 13$; $P = 0.26$), and Charadriiformes (shorebirds, gulls, terns; $n = 25$; $P = 0.81$). Miller and Eadie (2006) also found that waterfowl had basal rates similar to those of passerines. Furthermore, a sample of 21 parrots (Psittaciformes) had a mean mass-independent basal rate that is marginally lower than that of passerines ($P = 0.041$) (McNab, 2009), but when a larger sample becomes available, their collective mean rate, reflecting high levels of activity, may not differ from that of passerines. Notice the high basal rates in two parrots (Fig. 1).

The three orders are characterized not only by high basal rates, but also by high mobilities, seasonal migration, and a pelagic existence in Procellariiformes. Yet, nine ducks in New Zealand, six endemic, two of which are flightless, have mass-independent rates of metabolism that average 70% of the mean of 18 migratory ducks in the Northern Hemisphere ($P < 0.0001$, McNab, 2003b) (Fig. 2). Preliminary measurements indicate that two ducks endemic to Hawaii and two endemic to Madagascar have basal rates as low as the New Zealand species (pers. obs.).

Daan et al. (1990) demonstrated that mass-independent variation in the basal rate of birds correlated with mass-independent variation in heart and kidney masses, i.e., in organs directly involved with sustaining energy expenditure. New Zealand's ducks have smaller pectoral muscle masses than continental ducks in the Northern Hemisphere (McNab, 2003b). The low mass-independent basal rates of metabolism of fruit pigeons of the genus *Ducula* endemic to intermediate and small islands in the South Pacific (McNab, 2000) correlate with smaller pectoral muscle masses in contrast to the higher rates and larger pectoral masses found in *Ducula* resident on New Guinea ($n = 8$, $P = 0.0018$) (McNab, 2013). Similar differences in basal rate and pectoral muscle mass occur between volant and flightless rails (McNab and Ellis, 2006). Flightless birds also have small hearts (McNab, 1994). However, shorebirds have rather large flight muscles (23–32% of body mass) and hearts (1.1 to 1.5%), which correlate with their high basal rates and migratory habits. A similar pattern (flight muscles 29 to 32% [pectoral masses 19 to 21%] and hearts 1.2%) is seen in migratory anatids (Hartman, 1961). With regard to parrots, they have flight muscles between 19 and 24% and heart masses between 1.2 and 1.6% (Hartman, 1961).

If this analysis accounts for high basal rates in the three non-passerine orders and the low rates in the other orders, why do passerines collectively have higher basal rates than other birds and why do temperate passerines tend to have higher basal rates than tropical species? There are two answers to this question, physiological and

[2] The addition of another criterion, requiring that at least 3 individuals of a species be measured (McKechnie and Wolf, 2004), is arbitrary and permits many more data from non-passerines to be discarded. If 3, why not 5 or 7? Many individuals are always desirable, but the number of individuals available is often dictated by a species' rarity or protected status. For example, of three species of kiwis (*Apteryx*) measured, two had only two individuals measured, but the measurements on individuals in a species were in agreement (McNab, 1996). Two individual Takahe (*Porphyrio mantelli*), a highly endangered, flightless gallinule, once thought to be extinct, were also measured and in agreement (McNab and Ellis, 2006). Why should these data be ignored? Do we only study common species? The characteristics of some species, including their energetics, may give insight into their endangered status. Measurements on one Dodo (*Raphus cucullatus*) would be priceless!