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# A ‘slow pace of life’ in Australian old-endemic passerine birds is not accompanied by low basal metabolic rates

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Running title: BMR in Australian passerines

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**Abstract** Life history theory suggests that species experiencing high extrinsic mortality rates allocate more resources toward reproduction relative to self-maintenance and reach maturity earlier ('fast pace of life') than those having greater life expectancy and reproducing at a lower rate ('slow pace of life'). Among birds, many studies have shown that tropical species have a slower pace of life than temperate-breeding species. The pace of life has been hypothesized to affect metabolism and, as predicted, tropical birds have lower basal metabolic rates (BMR) than temperate-breeding birds. However, many temperate-breeding Australian passerines belong to lineages that evolved in Australia and share 'slow' life-history traits that are typical of tropical birds. We obtained BMR from 30 of these 'old-endemics' and 10 sympatric species of more recently arrived passerine lineages (derived from Afro-Asian origins or introduced by Europeans) with 'faster' life histories. The BMR of 'slow' temperate-breeding old-endemics was indistinguishable from that of new-arrivals and was not lower than the BMR of 'fast' temperate-breeding non-Australian passerines. Old-endemics had substantially smaller clutches and longer maximal life spans in the wild than new arrivals, but neither clutch size nor maximum life span was correlated with BMR. Our results suggest that low BMR in tropical birds is not functionally linked to their 'slow pace of life' and instead may be a consequence of differences in annual thermal conditions experienced by tropical versus temperate species.

**Keywords** Australian passerines; basal metabolic rate; pace-of-life, life history, tropical vs. temperate

## Introduction

Biologists interpret life history traits as evolved solutions to ecological challenges that allow organisms to maximize their reproductive potential (Stearns 2000). Life history is shaped by intrinsic organismal properties (genetics, physiology, morphology, etc.) as well as by extrinsic ecological factors, both biotic (e.g., predation, competition) and abiotic (e.g., temperature, rainfall). Together with phylogenetic history, this complex selective matrix generates a strikingly diverse assemblage of phenotypes, but there are common features among animals that occupy particular regions of the life history continuum. For example, species with high rates of extrinsic mortality are selected to emphasize current reproduction over survival: they mature rapidly, reproduce early in life, show high fecundity, have low survival rates and maximum lifespan potential (MLSP), and are said to live a 'fast pace of life' (Ricklefs & Wikelski 2002). By contrast, species with low rates of extrinsic mortality are selected to favor survival over current reproduction to maximize lifetime reproductive success, and have slow maturation, low fecundity, high survival rates, and higher MLSP. Species with these life histories are said to have a 'slow pace of life' (Ricklefs & Wikelski 2002, Magrath et al. 2000).

The different emphasis on investing in fecundity versus survival as a function of the urgency of reproduction forms the basis of the physiology/life history nexus proposed by Ricklefs and Wikelski. They suggested that long-lived species should invest more in immune processes and other survival-promoting functions than species with short life spans, and some evidence indicates that immune responses do differ among birds and mammals with varying MSLP (Lee 2006, Prevital et al. 2012). They also predicted that long-lived and slow-paced animals should have relatively low basal metabolic rates. Basal metabolic rate (BMR) - the minimum energy cost of homeostatic existence in an endothermic animal - is probably rarely under direct selection (as by definition it is the cost of performing no growth, activity, or reproduction). However, it is mechanistically linked to traits that are likely to be 'seen' by selection, such as exercise or thermogenic capacity and field metabolic rate (the daily flux of energy through the animal; White & Seymour 2004; Hulbert & Else 2004). The idea that BMR should be lower in slow-paced animals was supported by a common-garden experiment with stonechats (*Saxicola torquata* and *S. rubicola*) obtained as nestlings from populations with contrasting life histories (Wikelski et al. 2003). Adults from a sedentary tropical population had lower metabolic rates than birds from a migratory north-temperate population. Similarly, two extensive comparative analyses showed that birds from Neotropical forests in Panama and Peru have lower BMR (Wiersma et al. 2007b; Londoño et al. 2015) and, in the Panamanian birds, lower maximal metabolic rates than species from temperate latitudes (Wiersma et al. 2007a). Given that tropical birds have smaller clutches, longer parental care, and higher juvenile and adult survival than their north-temperate counterparts [Moreau 1944; Skutch 1985; Martin 1996; Cardillo 2002; Russell et al. 2004)], these studies support the notion that a slow 'pace of life' engenders a slow 'pace' of energy metabolism (e.g., Pearl 1928). However, it is unclear if low BMR in the tropics is a functional necessity or byproduct of 'slow' life history, or instead is simply an outcome of living in warm, stable habitats with low requirements for thermoregulation, migration, or other energetically demanding activities (Wiersma et al. 2007a). One way to resolve this is to examine the metabolic rates of temperate-breeding birds sharing the same 'slow' life-history traits as tropical passerines, and compare them with sympatric passerines with 'fast' life-histories.

The Australian avifauna offers a good opportunity for such a test. Passerine species that breed in Australia include numerous 'old-endemic' species that evolved in relative isolation in Australia and New Guinea. A smaller number of 'new invaders' of Afro-Eurasian origin is thought to have colonized Australia much later. Additionally, a few north-temperate passerines were introduced by European settlers during the last two centuries (Rowley & Russell 1991; Keast 1981a). Of 338 passerine species that breed in Australia, 258 are old-endemics while 64 and 16 are ‘new invaders’ and introduced species, respectively (Keast 1981b). For simplicity we refer to the latter two groups as ‘new-arrivals’.

Old-endemics and new-arrivals occur sympatrically in a variety of habitats, most of which are climatically temperate (warm summers, cool winters, large seasonal changes in rainfall and daylength). However, old-endemics have a ‘slow pace of life,’ with the small clutches, prolonged incubation and fledging care, and high survival rates that typify tropical birds (Magrath et al. 2000; Russell et al. 2004; Rowley & Russell 1991; Woinarski 1985; Yom-Tov 1987; Geffen & Yom-Tov 2000; Russell 2000). In contrast, new-arrivals have ‘fast’ life histories like those of temperate breeders from the Northern hemisphere. For example, clutch sizes average 2.7 in old-endemics and 4.7 in new-arrivals (Yom-Tov 1987). While the ecophysiology of Australian birds has received much attention (Astheimer & Buttemer 2002), no study has examined the energetics of Australian Passerines in the context of the ‘slow-fast’ contrast in their life histories. To determine if the BMR of old-endemics is indeed lower that that of new-arrivals, we measured BMR for 33 species from temperate climates, obtained BMR for several others from the literature, and used the combined dataset to compare BMR between ‘slow’ versus ‘fast’ life histories. To verify the postulated ‘slow-fast’ contrast in life history of our study species, we used information on clutch size and maximum lifespan (from banding data). To place our findings in a broader context, we compared our results to a global database of almost 500 temperate and tropical bird species (Londoño et al. 2015).

## Material and methods

### Bird capture and handling

We obtained most of the birds measured for this study near Wollongong, NSW (34.25˚S, 153.53˚E) or at the Fowlers Gap Research Station, NSW (31.09˚S, 141.70˚E). Wollongong-area birds were captured between October 1998 and August 1999 in urban areas, gardens, parks, and coastal eucalyptus woodland and temperate rainforest. Birds at Fowlers Gap were captured between September and November 2007 in eucalyptus and saltbush habitats. White-browed Babblers were caught at Back Yamma State Forest, NSW (33.33˚S, 148.21˚E) in May 1998 and held in large flight cages at the University of Wollongong. Birds were mist-netted between 15:00 and 17:00 local time and transported to the laboratory in individual cloth bags for metabolic measurements that night. Prior to the start of measurements, birds were caged individually with access to water but not food. Birds were released the following morning close to the site of capture (white-browed babblers were returned to flight cages). Each individual was used only once for determination of BMR.

Maximum life span data for wild birds were obtained from the Australian Bird and Bat Banding Scheme database (www.environment.gov.au/science/bird-and-bat-banding).

### Basal metabolism

We measured metabolism as rates of oxygen uptake ($\dot{V}O_2$). BMR trials started at approximately 1800 (local time) and continued for 12-14 h. Up to four birds were tested concurrently in individual chambers constructed from paint cans (2 or 5 L) equipped with air flow ports, a thermocouple, and a perch. Chambers were placed in an environmental cabinet maintained at 31.0 ± 1.0 °C, which we assumed to be within thermoneutrality for all species (in some species this was confirmed by measuring metabolism at several ambient temperatures). Separate mass flow controllers (Tylan; Bedford, Massachusetts, USA) maintained a constant flow of dry air to each chamber (500-2500 ml min$^{-1}$ STP depending on bird size). Mass flow controllers were calibrated by timing the rate of soap bubble travel in a precision burette, corrected to STP conditions. Excurrent air was subsampled at about 100 ml min$^{-1}$, scrubbed of $CO_2$ and water vapor, and routed to a two-channel $O_2$ analyzer (S3A-2; Applied Electrochemistry, Sunnyvale, California, USA) through a computer-controlled air stream selector (Respirometry Multiplexer

V2.0, Sable Systems, Las Vegas, Nevada, USA), such that two birds were measured simultaneously (one by each S3A channel). Birds were monitored for 42 minutes, followed by a 3-min reference reading, before switching to another individual. Accordingly, each bird was monitored approximately 47% of the time. The reference interval was sufficient for $O_2$ concentrations to reach stable, low values. Data were recorded on a Macintosh computer interfaced to a DataTaker 500 A/D converter (Data Electronics, Rowville, Victoria, Australia) with LabHelper software (www.warthog.ucr.edu). We computed $\dot{V}O_2$ as:

$$\dot{V}O_2 \text{ (ml } O_2 \text{ min}^{-1}) = F * (FiO_2 - FeO_2)/(1 - FeO_2)$$

where F is flow rate (ml $\text{min}^{-1}$ STPD), $FiO_2$ is incurrent fractional $O_2$ concentration and $FeO_2$ is excurrent fractional $O_2$ concentration. BMR was calculated as the lowest $\dot{V}O_2$ averaged over a continuous 10-minute interval when $\dot{V}O_2$ was low and stable. We converted $\dot{V}O_2$ to Watts using an oxycaloric value of 19.8 kJ $LO_2^{-1}$. Birds were weighed just prior to being placed in the respirometer chamber in the evening and again in the morning upon retrieval from the chamber, with the mean of the two values used as body mass ($M_b$).

### Literature and unpublished data

We measured BMR in 33 free-living Australian passerine species (24 old-endemics, four new invaders and five introduced species). In addition, we included published BMR for seven old-endemics and two new-arrivals. We used only data that conformed to requirements for true BMR (Mckecknie & Wolf 2005) and excluded data from long-term captives (white-browed babblers were held in large flight cages and were recent captures). When dual measurements were available we used mean values, for a total of 40 species (Table 1).

BMR for additional species were obtained from Londoño et al. (2015). To avoid confounding analyses, we excluded the Australian species from that study that we had measured ourselves (N=9).

## Statistics

Analyses are based on species means. Both $M_b$ (in grams) and BMR (in Watts) were $\log_{10}$-transformed to account for allometric scaling. Where necessary, a further Box-Cox transformation was applied to achieve normal distributions.

For 12 of the Australian species, data were available for only one or two individuals. Given these low sample sizes (N), we performed two sets of analyses, one including only species for which $N > 2$ (28 species) and the other including all 40 Australian species. There were very few differences between the two analyses. Accordingly, we show results derived from the complete dataset~~,~~ except when there were qualitative differences in significance; these instances are noted in the Results section.

Phylogenetic signal (a measure of the statistical dependence among species' trait values due to their phylogenetic relationships; Blomberg et al. 2003) was estimated for BMR, $M_b$, and residuals of regressions between BMR and $M_b$ (Revell 2010) with Pagel's lambda (Pagel 1999) using 'phytools' (Revell 2002). Since significant phylogenetic signal was present (see below), we made between-group comparisons with phylogenetic analyses performed in R (R Core Team 2013), based on trees derived from the avian 'tree of life' (Londoño et al. 2015;Jetz et al. 2012; Hackett et al. 2008; Fig. 1; Supplemental Fig. 1). Phylogenetic Independent Contrasts (PIC; Felsenstein 1985) were used to estimate correlations between BMR and $M_b$ ('ape' package; Paradis et al. 2004). To compare BMR and $M_b$ across origins (old-endemic and new-arrivals), orders, and geographic locations, we performed Phylogenetic Generalized Least Squares (PGLS) with 'nlme' (Pinheiro et al. 2013). We evaluated five models of evolution for the correlation structure (Londoño et al. 2015; Revell 2010; Blomberg et al. 2003; Grafen 1989; Martins & Hansen 1997). Akaike Information Criterion tests ('qpcR' [39]) indicated that Pagel's model was the best fit for Australian Passerines and for temperate-tropical and Passerine-non-Passerine comparisons. The Grafen model was the best fit for comparisons between Australian and non-Australian Passerines. For life span comparisons between old-endemic and new-arrival Australian passerines, the Ornstein-Unlenbeck model was the best fit.

Since the use of phylogenetically-aware statistical models remains controversial (McNab 2015) we also performed conventional analyses (ordinary least squares; OLS), using JMP Pro 11 (SAS institute, Cary, North Carolina, USA).

Unless stated otherwise, all data are reported as mean ± standard error.

## Results

Tests revealed significant phylogenetic signal in $M_b$, BMR, and their residuals ($P < 0.006$ for all groups), and there were significant effects of $M_b$ on BMR in all groups (Tables 2A and 2B).

### Maximum life span

OLS ANCOVA of maximum free-living life span (body mass as covariate) revealed that the old-endemic species in our dataset have maximum life spans (MLS) 62% longer than those of new arrivals (13.8 ± 0.8 years versus 8.5 ± 1.5 years, respectively; $F_{1,37} = 10.0$, $P = 0.0031$; Supplemental Fig. 1). Maximum life span increased with $M_b$ in old endemics ($t = 2.76$, $P = 0.010$), but the relationship was not statistically significant in the smaller sample of new arrivals ($P = 0.95$). Results were similar if the species with the shortest MLS was discarded (*Eremiornis carteri;* 1 year, possibly an artifact of low sample size): old endemics live longer than new arrivals (13.8 ± 0.8 years versus 9.4 ± 1.4 years, respectively; $F_{1,36} = 6.9$, $P = 0.0125$).

Phylogenetic analysis (PGLS) yielded qualitatively similar results: old endemics have maximum life spans longer than those of new arrivals ($F_{1,37} = 6.66$, $P = 0.0139$), and larger species have longer MLS than small birds ($F_{1,37} = 4.90$, $P = 0.033$).

## Seasonal effects on BMR

Seasonal changes in avian BMR are well known (McKechnie & Swanson 2010) and could bias comparisons. Most (but not all) of our data were obtained in the spring and summer (September – March; Supplemental Table 1), as were the BMR data for northern hemisphere passerines (April-July; Wiersma et al. 2007). Capture dates (±30 days for literature sources) were available for 37 of the 40 Australian species in our study. The remaining 3 species were sampled in the spring and summer (September –February; Vitali et al. 1999). For most species, all individuals were captured and tested within intervals of 60 days; for these we computed a mean capture date (day of the year). Seven species were captured in two discrete periods separated by more than 60 days; for these we computed mean values and capture dates for each of the two periods. Since capture date could not be normalized, we used nonparametric tests. For all 37 species for which we had dates, there was no significant influence of capture date on BMR ($P = .119$, Kendall's $\tau$; $P = .135$, Spearman's $\rho$). Similarly, in the seven species sampled within two distinct periods, there was no significant effect of capture date ($P = .154$, Kendall's $\tau$; $P = .253$, Spearman's $\rho$).

## Australian passerine BMR

An OLS ANCOVA of the BMR of 40 Australian passerines including $M_b$, origin (old-endemic versus new arrival) and clutch size showed strong effects of $M_b$ ($F_{1,38} = 262$, $P < 0.0001$) and origin ($F_{1,38} = 6.5$, $P = 0.0155$;), with old-endemics having about 12% higher BMR than new arrivals. There was also an origin X $M_b$ interaction ($F = 4.7$, $P = 0.0376$), but no effect of clutch size on BMR. Removal of clutch size from the model did not change the qualitative results. Clutch size was independent of $M_b$ ($F_{1,38} = 0.05$, $P = .82$) but was significantly higher in new arrivals than in old endemics (3.62 ± .21 and 2.68 ± .12, respectively; $F = 15.3$, $P = 0.0004$).

There was no effect of maximum life span on BMR, after accounting for $M_b$ and origin ($F_{3,36}$ = 0.3, P = .58).

Results from phylogenetically-aware analyses were similar. Regressions describing PIC of $M_b$ and PIC of BMR were not affected by origin ($F_{1,38}$ = 0.15, P = .70; Group-PIC $M_b$ interaction = 0.324 in a GLM; Fig. 2). PGLS revealed a strong dependence of BMR on $M_b$ ($F_{1,38}$ = 448.3, *P* < 0.0001), but no $M_b$ X origin interaction ($F_{1,38}$ = 0.15, *P* = 0.70). Clutch size was independent of $M_b$ and BMR (P > .75 for both) but was significantly higher in new-arrivals than in old-endemics (3.61 ± 0.20 and 2.68 ± 0.11 respectively, P = 0.0011). Maximum life span did not significantly affect BMR after accounting for $M_b$ and origin (PGLS; $F_{1,36}$ = 0.091, P = .76).

**Comparison of Australian to Northern Hemisphere Temperate-breeding Passerines**

In an OLS ANCOVA of 129 temperate-breeding passerines (40 Australian plus 89 Northern Hemisphere species), $M_b$ was strongly correlated to BMR ($F_{2,126}$ = 444, P < 0.0001), origin was also significant ($F_{2,126}$ = 5.10, P = 0.0074) and there was a significant origin X $M_b$ interaction ($F_{2,126}$ = 5.23, P = 0.0066). Post-hoc comparisons (Tukey-Kramer) showed no difference between new arrivals and either north-temperate breeders (P = .77) or old-endemics (P = 0.064), but 11% higher BMR in old-endemics than in north-temperate breeders (P = 0.0095).

In phylogenetically-aware tests, there was no $M_b$ X origin interaction (PGLS; $F_{2,126}$ = 1.66, *P* = .20). As expected, BMR and $M_b$ were strongly correlated ($F_{2,126}$ = 624, *P* < 0.0001), with a slope (mass exponent) of 0.71 ± 0.04 (SE). However, BMR differed between Australian and north-temperate passerines ($F_{2,126}$ = 7.73, *P* < 0.0001), with BMR of Australian species averaging 7.7% lower. Most of the difference stemmed from new-arrivals, which had BMR 21.5 % less than that of north-temperate passerines, whereas the BMR of old-endemics was only 3.1 % lower. When analysis was restricted to the 28 Australian species for which sample size was greater than 2 individuals, there was no effect of origin (Australian vs. north-temperate) on BMR ($F_{2,114} = 2.67$, $P = .105$).

### *Temperate/tropical and passerine/non-passerine comparisons*

In 519 bird species (40 Australian passerines plus data from 5 datasets in Londoño et al. 2015), OLS ANCOVA found significantly lower BMR in tropical than temperate species ($F_{1,517} = 9.36$; $P = 0.0023$), significantly lower BMR in passerines than in non-passerines, a significant effect of dataset ($F_{5,513} = 9.68$, $P < 0.0001$), a significant dataset X $M_b$ interaction ($F_{5,513} = 6.90$, $P = 0.0001$), but no $M_b$ X latitude or $M_b$ X order interactions ($F_{1,517} = 1.60$, $P = .21$ and $F = 1.29$, $P = .26$, respectively). As expected, BMR was strongly correlated with $M_b$ ($F_{1,517} = 2049$, $P < 0.0001$) with a slope (mass exponent) of 0.678 ± 0.015 (SE). On average, the BMR of temperate species was 12% higher than that of tropical species and the BMR of passerine birds averaged 19.5% higher than that of non-passerines.

Phylogenetically-aware tests (PGLS) also indicated that tropical birds have lower BMR than temperate birds ($F_{1, 517} = 17.53$, $P < 0.0001$) and that Passeriformes have higher BMR than non-Passeriformes ($F_{1, 517} = 86.02$, $P < 0.0001$) with a strongly positive overall correlation between $M_b$ and BMR ($F_{1, 517} = 2368$, $P < 0.0001$). There were significant interactions between $M_b$ and taxonomic order ($F_{1, 517} = 8.54$, $P = 0.0038$), latitude ($F_{1, 517} = 15.58$, $P = 0.0001$) and dataset ($F_{5, 513} = 3.69$, $P = 0.0013$). Restricting the PGLS analysis to the 28 Australian species for which N>2 resulted in similar overall findings, although there was no Mb X taxonomic order interaction ($F_{1,505} = 0.02$, $P = .88$).

## Discussion

The addition of our findings for Australian species does not change the conclusions of analyses showing lower BMR in tropical-breeding birds than in temperate-breeding species (Wiersma et al. 2007b; Londoño et al. 2015) and higher BMR in passerines than in non-passerine orders (Londoño et al. 2015). However, in the context of metabolism and life history, our most interesting findings are that the BMR of temperate-zone, old-endemic Australian passerines is indistinguishable from that of new-arrivals inhabiting the same region, and that BMR is not affected by clutch size or by maximum life span. This lack of differentiation was unexpected, as both old-endemics and tropical forest passerines have a 'slow pace of life' but new-arrivals are 'faster.' In the Australian species we sampled, clutch size was 35% higher in new-arrivals than in old endemics, and for a much broader sampling of Australian passerines it was >70% higher in new-arrivals (Yom-Tov 1987). Maximum life span was 62% longer in the old endemics in our sample, also consistent with this group having a 'slow' life history. If life history and energy metabolism were coupled, then BMR and clutch size should be positively correlated whereas BMR and MLS should be negatively correlated after accounting for body mass, and in general, old-endemics should have low BMR compared to new-arrivals. None of these predictions was supported by our data.

Our comparison of Australian passerines to north-temperate passerines also did not reveal low BMR in the old-endemics (in fact, it may be higher than that of 'fast' north-temperate passerines, as suggested by OLS post-hoc tests). Moreover, the new-arrivals have maintained similar clutch sizes in Australia as their conspecifics in Europe (Yom-Tov 1987), again showing lack of correlation between BMR and reproductive 'pace of life'.

Seasonal variation in some bird species, particularly those from high latitudes, is well documented (e.g., Mckechnie & Swanson 2010), so if our comparisons of old endemics, new arrivals, and north-temperate passerines were based on data obtained in contrasting seasons, results could be biased. Many of the north-temperate species were sampled in spring and summer (April –July; Wiersma et al. 2007b), and most of the Australian samples were obtained in the same season (September –February). The Australia data also contained some samples obtained outside that period, but we found no significant effect of sampling date on BMR, either for all Australian species combined or within a subset of species with data spanning several months. A previous study of superb fairy-wrens (Lill et al. 2006) also found no effect of seasonality on BMR. Therefore we do not believe our intergroup comparisons were confounded by sampling in contrasting seasons.

Of the old-endemics we sampled, only the Pomatostomidae (babblers), which are relatively weak flyers with clutch sizes averaging 3 eggs, had consistently low BMR (Table 1). The two old-endemic families with the highest BMR included the one with the lowest average clutch size (honeyeaters; Meliphagidae; 2.3 eggs) and the Pardalotidae (pardalotes, scrubwrens, thornbills), which averaged 3 eggs per clutch (Table 1). While clutch size is only one minor component of total reproductive effort in birds, it is a fundamental life history trait and the basis of other, larger investments in fecundity (e.g., incubation and especially parental care). The independence of clutch size and BMR in Australian passerines suggest that the difference in BMR between temperate and Neotropical birds found by Wiersma et al. (2007b) and Londoño et al. (2015) may not result from a linkage between the reproductive 'pace of life' and metabolism. Instead, it may derive from latitudinal contrasts in temperature or other factors separate from life history *per se* (Wiersma et al. 2007a).

At variance with that suggestion is the lack of effect of a 2.6 km altitude gradient on BMR in Andean birds in Peru, despite a 12 °C difference in environmental temperature between lowland and highland habitats (annual means 23 °C and 11 °C, respectively; Londoño et al. 2015). Such temperature differences should strongly affect rates of energy use for thermoregulation, especially for small birds, which typically have lower critical temperatures of 25-28 °C (unpublished data). However, some recent analyses indicate that variation in BMR across bird species is best explained not only by average ambient temperature, but also by its annual variation (White et al. 2007; Jetz et al. 2008). Hence, seasonal stability, despite differing average temperatures, may explain the across-altitude similarity of BMR among Peruvian species (Londoño et al. 2015); in contrast, the large seasonal variation in temperate latitudes may engender high BMR. Birds expend more energy thermoregulating in cool habitats than in warmer regions and hence may have greater demand on muscular thermogenesis and digestive functions. Wiersma and colleagues found that Panamanian birds have lower maximal metabolic rates than temperate birds during forced exercise and shivering thermogenesis, as well as lower BMR (Wiersma et al. 2007a). They suggested that the reduced aerobic capacity might derive from lower demands for flight performance in tropical forests, where most birds are non-migratory and many are relatively sedentary; this, as well as low BMR (Vezina et al. 2006; Daan et al. 1990; Chappell et al. 1999) is consistent with data showing relatively small pectoral muscle and organs (heart, lung, liver, kidney, liver, pancreas) in tropical species (Wiersma et al. 2012).

Overall, we found that BMR and two indices of the 'pace of life' -- reproductive investment (indicated by clutch size) and maximum life span -- are not linked in Australian passerines. Our findings are more consistent with the idea that low BMR in tropical birds is a consequence of living in a benign and relatively aseasonal climate rather than to having a 'slow' set of life-history traits, as predicted by the 'physiology-life history nexus' concept (Ricklefs and Wikelski 2002). To further test this interpretation, characterization of BMR in Australian old-endemic species living in temperate versus tropical regions is an obvious opportunity.

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**Table 1.** Body mass and BMR (in ml $O_2$/min) in Australian old and new endemic passerine birds (n = number of individuals). Clutch sizes (numbers of eggs) are averages or ranges (Yom-Tov 1987; Higgins et al. 2001, 2006; Higgins and Peter 2002). Maximum life span (MLS; in years) is from Australian Bird and Bat Banding Scheme data (www.environment.gov.au/science/bird-and-bat-banding).

| **Species** | **Common name** | **Grou** | **n** | **Mass (g)** | **BMR** | **MLS** | **Clutch** | **Source**[B] |
|---|---|---|---|---|---|---|---|---|
| **Maluridae** | | | | | | | | |
| *Malurus cyaneus* | Superb Fairy-wren | Old | 10 | 8.7 ± 0.5 | 0.53 ± 0.08 | 10.4 | 3.1 | This study (Woll) |
| *Malurus cyaneus* | Superb Fairy-wren | Old | | 9.2 | 0.45 | | | Lill et al. 2006[C] |
| *Malurus lamberti* | Variegated Fairy-wren | Old | 7 | 7.8 ± 0.4 | 0.55 ± 0.03 | 11 | 2.8 | This study (FG) |
| **Meliphagidae** | | | | | | | | |
| *Acanthagenys rufogularis* | Spiny-cheeked Honeyeater | Old | 7 | 43.4 ± 4.4 | 1.90 ± 0.21 | 13.6 | 2.2 | This study (FG) |
| *Manorina flavigula* | Yellow-throated Miner | Old | 5 | 41.1 ± 3.7 | 1.83 ± 0.22 | 12.1 | 3.2 | This study (FG) |
| *Meliphaga lewinii* | Lewin’s Honeyeater | Old | 7 | 36.2 ± 3.0 | 1.60 ± 0.10 | 15.9 | 2.2 | This study (Woll) |
| *Lichenostomus virescens* | Singing Honeyeater | Old | 12 | 25.0 | 1.03 | 12 | 2.2 | Collins et al. 1980 |
| *Lichenostomus virescens* | Singing Honeyeater | Old | 4 | 20.7 ± 0.8 | 1.06 ± 0.05 | | | This study (FG) |
| *Lichenostomus penicillatus* | White-plumed Honeyeater | Old | 9 | 17.7 ± 1.3 | 0.97 ± 0.06 | 15.9 | 2.3 | Buttemer & Astheimer 2000 |
| *Melithreptus lunatus* | White-naped Honeyeater | Old | 11 | 14.3 ± 0.6 | 0.74 ± 0.01 | 12.3 | 2.7 | Vitali et al. 1999 |
| *Lichmera indistincta* | Brown Honeyeater | Old | 15 | 9.0 | 0.55 | 13.2 | 1.9 | Collins et al. 1980 |
| *Lichmera indistincta* | Brown Honeyeater | Old | 6 | 10.1 ± 0.7 | 0.63 ± 0.03 | | 2 | Vitali et al. 1999 |
| *Phylidonyris pyrrhoptera* | Crescent Honeyeater | Old | | 14.6 | 0.96 | 10.9 | 2.1 | Weathers et al. 1996 |
| *Phylidonyris novaehollandiae* | New Holland Honeyeater | Old | | 17.3 | 0.95 | 14.4 | 2.2 | Weathers et al. 1996 |
| *Phylidonyris melanops* | Tawny-crowned Honeyeater | Old | 13 | 18.8 ± 0.7 | 0.87 ± 0.03 | 4.9 | 2.0 | Vitali et al. 1999 |
| *Acanthorhynchus tenuirostris* | Eastern spinebill | Old | 7 | 11.3 ± 0.9 | 0.83 ± 0.07 | 15.5 | 2.2 | This study (Woll) |
| *Acanthorhynchus tenuirostris* | Eastern spinebill | Old | | 9.7 | 0.74 | | | Weathers et al. 1996 |
| **Pardalotidae** | | | | | | | | |
| *Pardalotus punctatus* | Spotted Pardalote | Old | 2 | 7.8 | 0.66 | 4 | 3-4 | This study (Woll) |
| *Sericornis citreogularis* | Yellow-throated Scrubwren | Old | 3 | 16.9 ± 0.5 | 1.09 ± 0.08 | 15.6 | 2.5 | This study (Woll) |
| *Sericornis frontalis* | White-browed Scrubwren | Old | 11 | 13.2 ± 0.8 | 0.96 ± 0.10 | 17.6 | 2.8 | This study (Woll) |
| *Sericornis magnirostris* | Large-billed Scrubwren | Old | 1 | 8.7 | 0.61 | 15.3 | 3 | This study (Woll) |
| *Smicrornis brevirostris* | Weebill | Old | 1 | 5.9 | 0.49 | 7.4 | 2.6 | This study (FG) |
| *Acanthiza pusilla* | Brown Thornbill | Old | 6 | 6.4 ± 0.7 | 0.67 ± 0.07 | 17.7 | 2.9 | This study (Woll) |
| *Acanthiza uropygialis* | Chestnut-rumped Thornbill | Old | 2 | 6.6 | 0.53 | 12.7 | 3.3 | This study (FG) |
| *Acanthiza chrysorrhoa* | Yellow-rumped Thornbill | Old | 8 | 8.3 ± 0.6 | 0.67 ± 0.07 | 13.1 | 3.2 | This study (FG) |
| **Pomatostomidae** | | | | | | | | |
| *Pomastostomus superciliosus* | White-browed Babbler | Old | 4 | 36.1 ± 0.7 | 1.03 ± 0.06 | 14.4 | 2.6 | This study (Woll) |
| *Pomastostomus ruficeps* | Chestnut-crowned Babbler | Old | 8 | 45.4 ± 2.5 | 1.32 ± 0.11 | 8.3 | ca. 4 | This study (FG) |
| *Acanthiza lineate* | Striated Thornbill | Old | 1 | 7.3 | 0.48 | 23.5 | 2.9 | This study (Woll) |
| **Petroicidae** | | | | | | | | |
| *Eopsaltria australis* | Eastern Yellow Robin | Old | 7 | 19.2 ± 2.3 | 1.05 ± 0.10 | 14.6 | 2.3 | This study (Woll) |
| **Cinclostomatidae** | | | | | | | | |
| *Psophodes olivaceus* | Eastern Whipbird | Old | 1 | 61.0 | 2.12 | 12.3 | 2-3 | This study (Woll) |
| **Pachycephalidae** | | | | | | | | |
| *Pachycephala pectoralis* | Golden Whistler | Old | 4 | 24.0 ± 0.3 | 1.08 ± 0.06 | 18 | 2.2 | This study (Woll) |
| **Dicruridae** | | | | | | | | |
| *Rhipidura fuliginosa* | Grey Fantail | Old | 1 | 8.9 | 0.49 | 9.7 | 2.7 | This study (Woll) |
| **Artamidae** | | | | | | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Cracticus torquatus* | Grey Butcherbird | Old | 2 | 93.7 | 2.13 | 20.2 | 3.2 | This study (Woll) |
| *Strepara graculina* | Pied Currawong | Old | 1 | 306.7 | 5.65 | 24.1 | 3.1 | This study (Woll) |
| **Passeridae** | | | | | | | | |
| *Passer domesticus* | House Sparrow | New | 35 | 23.0 ± 2.0 | 0.94 ± 0.11 | 7.5 | 4.1 | This study (Woll) [D] |
| *Taeniopygia guttata* | Zebra Finch | New | 8 | 11.7 ± 0.6 | 0.64 ± 0.05 | 4.2 | 4.4 | This study (FG) |
| *Neochmia temporalis* | Red-browed Firetail | New | 2 | 9.6 | 0.53 | 7.4 | 5 | This study (Woll) |
| **Pycnonotidae** | | | | | | | | |
| *Pygnonotus jacosus* | Red-whiskered Bulbul | New | 2 | 32.9 | 1.07 | 11.1 | 3.2 | This study (Woll) |
| **Sylviidae** | | | | | | | | |
| *Eremiornis carteri* | Spinifexbird | New | 23 | 11.6 ± 0.2 | 0.56 ± 0.02 | 1 | 2-3 | Ambrose et al. 1996 |
| **Zosteropidae** | | | | | | | | |
| *Zosterops lateralis* | Silvereye | New | 6 | 10.4 ± 0.4 | 0.63 ± 0.04 | 18.7 | 2.8 | This study (Woll) |
| *Zosterops lateralis* | Silvereye | New | 9 | 11.8 ± 1.5 | 0.48 ± 0.08 | | | Maddocks & Geiser 1997 |
| **Muscicapidae** | | | | | | | | |
| *Zoothera lunulata* | Bassian Thrush | New | 2 | 113.2 | 3.07 | 3.4 | 2-2.5 | This study (Woll) |
| **Turdidae** | | | | | | | | |
| *Turdus merula* | Eurasian Blackbird | New | 3 | 85.1 ± 2.74 | 2.88 ± .03 | 9.4 | 3.5 | This study (Woll) |
| **Sturnidae** | | | | | | | | |
| *Sturnus vulgaris* | Common Starling | New | 8 | 57.5 ± 3.1 | 1.76 ± 0.23 | 14.1 | 4.6 | This study (Woll) |
| *Acridotheres tristis* | Common Myna | New | 4 | 102.3 ± 2.9 | 2.65 ± 0.25 | 12.2 | 3.7 | This study (Woll) |

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[A] 'Old' indicates old-endemics, while 'new' includes both new invaders and introduced species

[B] Woll = Wollongong, FG = Fowlers Gap

[C] Mean values for three seasons (winter, spring and summer; no seasonal differences were found)

[D] In part published in Chappell et al. (1999).

**Table 2A.** Allometric equations for BMR in several groups of birds, based on ordinary least squares regression, for the relationship between body mass and BMR, where BMR (watts) = a * $M_b^b$ (in grams). Slope (b) is shown ± SE. In all cases, F > 200 and P < .0001.

| Group | *N* | *a* | *b* | $r^2$ |
|---|---|---|---|---|
| Old-endemic | 30 | 0.0547 | 0.602 ± .033 | .92 |
| New-arrivals | 10 | 0.0327 | 0.722 ± .030 | .98 |
| North-temperate passerines | 89 | 0.0329 | 0.739 ± .036 | .83 |
| Temperate breeders[A] | 203 | 0.0425 | 0.644 ± .012 | .94 |
| Tropical breeders[A] | 316 | 0.0482 | 0.592 ± .014 | .85 |
| Passerines [A] | 376 | 0.0438 | 0.637 ± .017 | .79 |
| Non-passerine orders [A] | 143 | 0.0351 | 0.659 ± .015 | .93 |

[A] Data from Londoño et al. 2015.

**Table 2B.** Regression of Phylogenetic Independent Contrasts (PIC) of body mass versus PIC of BMR, where PIC BMR = a + b * PIC mass. Slope (b) is shown ± SE. In all cases, F > 190 and P < .0001.

| Group | *N* | *a* | *b* | $r^2$ |
|---|---|---|---|---|
| Old-endemics | 30 | 0.0007 | 0.678 ± .07 | 0.82 |
| New-arrivals | 10 | -0.004 | 0.757 ± .04 | 0.98 |
| North-temperate passerines [A] | 89 | -0.002 | 0.737 ± 0.05 | 0.69 |
| Temperate breeders [A] | 203 | -0.002 | 1.033 ± 0.04 | 0.75 |
| Tropical breeders[A] | 316 | 0.0005 | 0.981 ± 0.03 | 0.58 |
| Passerines [A] | 376 | 0.0002 | 0.876 ± 0.04 | 0.52 |
| Non-passerine orders [A] | 143 | -0.0008 | 1.095 ± 0.05 | 0.76 |

[A] Data from Londoño et al. 2015.

**Figure 1.** Phylogenetic tree for Australian passerines used in the present study. species.

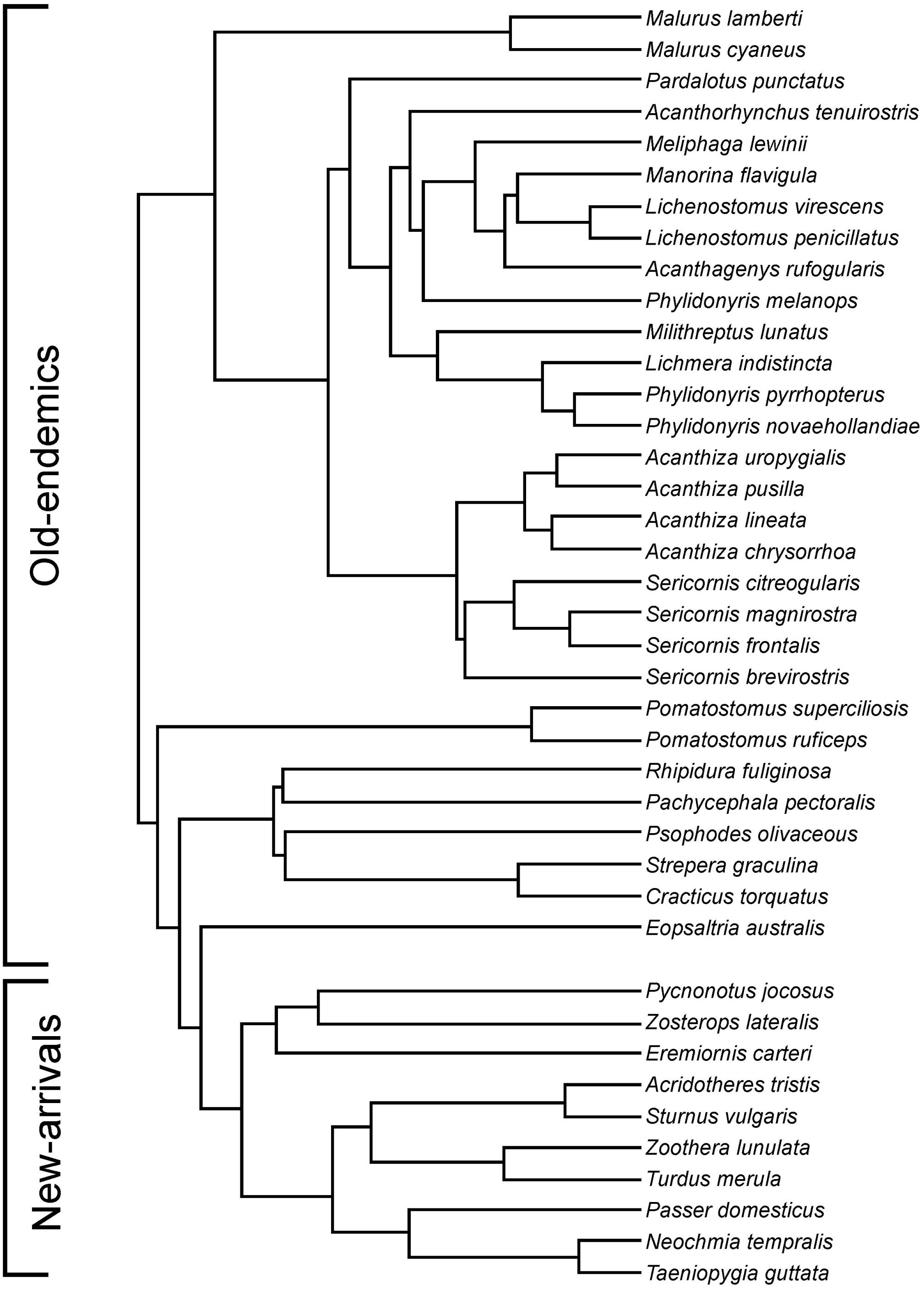

**Figure 2.** Phylogenetically independent contrast (PIC) of BMR against PIC of body mass for 40 species of Australian passerines (old-endemics and new-arrivals) and 89 species of temperate-breeding passerines from the Northern Hemisphere (individual data points not shown for clarity). The latter was based on data in Wiersma et al. (2007b) and Londoño et al. (2015). See text for statistics.