

Article

Relative Water Economy Is a Useful Index of Aridity Tolerance for Australian Poephiline Finches

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Simple Summary: Zebra Finches (*Taeniopygia guttata*) are the most widespread Australian finches, occurring throughout much of Australia's semi-arid and arid zones. They have a similar physiology (body temperature, metabolic rate, evaporative water loss, thermal conductance) to other finches but differ in having a higher point of relative economy, the ambient temperature at which metabolic water production exceeds evaporative water loss. Overall physiological similarities of these species likely reflect evolutionary, ecological and behavioural factors. Our study highlights the utility of relatively water economy for evaluating integrated physiological adaptations to heat and aridity.

Abstract: We evaluate if the iconic Australian Zebra Finch (*Taeniopygia guttata*) has a unique physiology or if its metabolic, thermal and hygric physiology are similar to other Australian poephiline finches, by comparing it with three other species, the arid-habitat Painted Finch (*Emblema pictum*) and the mesic-habitat Double-barred (*Taeniopygia bichenovii*) and Red-browed (*Neochmia temporalis*) Finches. All physiological variables responded to ambient temperature as expected. There were no species differences for any of the standard physiological variables, consistent with the hypotheses that birds are pre-adapted to arid habitats, the recent development of Australian deserts has limited opportunity for physiological adaptation, and all four species share similar behavioural and ecological traits. Nevertheless, the ambient temperature where metabolic water production equals evaporative water loss (point of relative water economy) was highest for the Zebra (19.1 °C), lower for Double-barred (16.4 °C) and Painted (15.2 °C) and lowest for Red-Browed (4.1 °C) Finches, corresponding with their general patterns of habitat aridity. The point of relative water economy may be a sensitive index for assessing a species' tolerance of aridity because it integrates individual physiological variables. We conclude that the Zebra Finch is not a physiological outlier amongst Australian finches, but is at the end of a continuum of aridity tolerance for the four study species.

Keywords: poephiline finches; ambient temperature; body temperature; metabolism; evaporative water loss; thermal conductance; relative water economy; point of relative water economy



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1. Introduction

The Estrildidae is an old group of closely related, small, granivorous finches native to Africa, southern Asia and Australia [1–5]. Originating in Africa, there were likely three invasions of these finches to Australia, the subfamily Poephilinae (*Emblema*, *Neochmia*, *Taeniopygia*, *Poephila*, *Stagonopleura* and *Heteromunia*), its sister sub-family Lonchurinae (*Lonchura*), and subfamily Erythrurinae (*Erythrura*). These finches now occupy a wide range of habitats including deserts, mesic forests and the tropics [2,6,7]. The fact that these finches are all small and granivorous, with species widely distributed in a variety of arid and mesic

habitats, makes them useful subjects for comparative studies investigating environmental drivers of physiological traits [6,8,9].

The Zebra Finch is an iconic desert bird and as one of the most widely studied bird species worldwide [10,11] it has played an important role in avian physiological research, especially relating to tolerance of high ambient temperature (T_a) and limited water availability [6,12–17]; its adaptations to arid habitats are considered remarkable amongst birds [11]. Zebra Finches are found throughout the Australian interior, inhabiting open woodlands, shrublands and grasslands [4,7,18,19]. They can survive in the laboratory without water on a diet of air-dried seed [6,13] and drink saline water (0.5–0.8 M NaCl) [14,20,21]. In the field they are nomadic and eruptive [22–24] and can withstand ambient temperatures (T_a) in excess of 45 °C with no evidence of physiological stress [16], but are reliant on the availability of drinking water [2,15]. The physiology of other Australian finches has received much less attention, despite Bartholomew and Cade [8] recognising the potential contribution of this group to understanding avian water economy nearly 60 years ago. It is unclear if the physiological traits commonly associated with habitat aridity for Zebra Finches are unique amongst Australian estrildid finches or are associated with the group more generally.

The physiological traits of arid-habitat birds that are commonly interpreted as adaptations to xeric environments include thermoneutrality at higher T_a , lower metabolic rate, higher thermal conductance and lower evaporative water loss (EWL) compared to birds from mesic habitats e.g., [25–31]. However, other studies have failed to detect effects of habitat aridity on the basic physiology of birds e.g., [8,9,32–34]. Although the general bauplan of birds may pre-adapt them to exploit desert environments [8,35,36], it has been suggested that differing evolutionary histories explain these differences in physiological findings. For example, Williams and Tieleman [29,37] argue that New World birds have not had sufficient evolutionary time to adapt to geologically recent deserts.

One promising approach to examining the physiological propensity of endotherms to withstand conditions of heat and aridity is evaluating the relative water economy (RWE) [38,39]. It is calculated as the ratio of metabolic water production to evaporative water loss, measured under standardised laboratory conditions in the absence of drinking water and ignoring the relatively small contributions of urinary/faecal water loss [25,38]. As metabolic water production and EWL can account for the majority of a granivorous animal's water turnover [25,40], a bird is in positive water balance when $RWE > 1$ and can maintain water balance without drinking [25,38]. RWE integrates commonly-measured variables of metabolic rate, EWL and covers a range of T_a , incorporating potentially small and separately insignificant differences in each variable into a significant integrated index [41]. Since metabolic water production decreases and EWL increases with higher T_a [9], RWE decreases with T_a . The T_a at which metabolic water production is equal to EWL (or $RWE = 1$) is the point of relative water economy (PRWE). A high PRWE may result from either a high metabolic water production, a low EWL or a combination of both [9,25,26,42]. Endotherms with a higher PRWE are considered more economical with respect to water balance and better able to withstand arid environments than those with a lower PRWE [27,39,41,43,44].

Here we investigate the physiology, with particular attention to water economy, of the Zebra Finch in comparison to an additional arid and two mesic species of closely-related Australian poephiline finches, to evaluate if the iconic desert-adapted Zebra Finch has a specialised physiology or if its basic physiology is shared more generally with other Australian grass-finches. The Zebra Finch and the Double-barred Finch diverged about 5.5 million years ago (MYA) [5]. Double-barred Finches are found in open forests, woodlands and grasslands throughout tropical and temperate maritime climatic regions [7,18,19] and as such may be expected to have physiological traits associated with more mesic habitats (thermoneutrality at lower T_a , higher metabolic rate and EWL and lower thermal conductance) than the Zebra Finch. Painted Finches, which inhabit arid rocky hills, gullies and gorges in central and western parts of Australia's arid zone, diverged about 6.0 MYA from *Taeniopygia* and about 6.5 MYA from Red-browed Finches [5]. Red-browed Finches occupy undergrowth near

water courses in temperate forest, woodland, dense shrubland and grassland areas [7,18,19]. We expect Red-browed Finches to have traits more consistent with mesic-habitat birds than Painted and Zebra Finches. Consequently we assess the hypothesis that the Zebra Finch is an arid-adapted “outlier” [11] by comparing it with these other closely-related Australian grassfinches. We will also evaluate the utility of RWE as an index of adaptation to habitat aridity in comparison to more traditionally-reported thermal, metabolic and hygric variables [41].

2. Materials and Methods

Experimental birds were purchased from commercial aviculture dealers in Perth and were housed in sheltered, outdoor aviaries at the University of Western Australia, where they experienced natural conditions of photoperiod and temperature typical of Perth, Western Australia (31°57' S 115°52' E). Use of captive-bred birds from the same geographic location approximates a common garden design and consequently we can attribute the physiological characteristics we observe here to genetic species-specific traits rather than potential differences in developmental or acclimatory plasticity that may confound interpretation of studies of wild-caught birds. Birds were maintained on a diet of ad libitum millet seed and drinking water. Experiments were conducted during February and March (i.e., birds were summer acclimated) and each bird was measured at a single T_a per night. Six individual Double-barred Finches and seven individuals for the other three species were measured, although for logistical reasons not every variable could be measured for every individual at all three T_a .

Flow-through respirometry was used to measure metabolic rate and EWL after Withers [45]. A mass flow controller (Bronkhurst E5752AAA, Aalborg AFC2600 or Sierra 901C-PE) regulated the flow of compressed air at 200–500 mL/min STPD. Air was scrubbed of CO₂ and water vapour with Sodasorb and silica gel before entering a metabolic chamber consisting of a 1 L glass jar fitted with a perch. Excurrent air passed through a Vaisala HMI36 temperature and humidity probe, then through a column of Drierite before measurement of O₂ (Servomex 574, David Bishop 280 Combo or Taylor Servomex 184 analyser) and CO₂ (Qubit s152, David Bishop 280 Combo or Leybold-Heraeus Binos analyser). Analog voltage outputs of the O₂ and CO₂ analysers were interfaced to digital voltmeters (Thurlby 1905, Myoung YG77 or Autoplex) and their RS232 outputs, along with the RS232 output of the Vaisala HMI36, were recorded by a Visual Basic v6 data acquisition program (P. C. Withers and A. Roberts). Calibration was carried out weekly. Air flow rates were checked against an Alltech Digital Flow Check mass flow meter, O₂ analysers were calibrated using pure nitrogen (0% O₂) and air (20.95% O₂) and CO₂ and relative humidity (RH) analysers were calibrated using a liquid petroleum gas flame in the airstream [45]. Finches were measured at ambient temperatures of ~20, 30 and 32 °C.

A baseline of O₂ and CO₂ concentration and chamber RH was established before and after each experiment. Finches were weighed (± 0.1 g) using an electronic balance and then measured overnight for a period of 10–12 h. Finches were removed from the chamber the next morning and a cloacal temperature (T_b ; °C) immediately measured using a thermocouple connected to a RS Components 611.234 thermocouple meter. A custom-written Visual Basic v6 program (P. Withers) was used to calculate O₂ consumption (VO₂ mL O₂/g/h), CO₂ production (VCO₂ mL O₂/g/h) and EWL (mg/g/h) after Withers [45] for a period of at least 20 min where physiological variables were stable and minimal.

Measured data for VO₂, VCO₂, EWL and T_b were used to calculate additional variables. The respiratory exchange ratio (RER) was calculated as VCO₂/VO₂, wet thermal conductance (C_{wet} J/g/h/°C) as MHP/($T_b - T_a$), where metabolic heat production (MHP; J/g/h) was calculated from VO₂ using the appropriate joule equivalence interpolated for the measured RER [46], and dry thermal conductance (C_{dry} , J/g/h/°C) as (MHP - EHL)/($T_b - T_a$) where evaporative heat loss (EHL; J/g/h) was determined from EWL using the latent heat of vaporisation (2.4 kJ/g) [47]. Metabolic water production was calculated from the VO₂ using an RER-adjusted conversion factor [46] and was used to determine

relative water economy (RWE; mL O₂/mg H₂O) as MWP/EWL. The PRWE was calculated by extrapolating the regression line for RWE between the two lowest T_a to RWE = 1 for each species.

Statistical analyses were undertaken using R Studio and the R platform. We rendered metabolic rate, EWL and C_{wet} data independent of body mass prior to statistical analysis using their respective scaling exponents of 0.657, 0.653 and 0.522, with C_{dry} assumed to scale as for C_{wet} after Douglas et al. [48]. We used the lmer function in lme4 [49] to evaluate the effect of T_a and potential differences between species for each physiological variable with general linear models, with species and T_a as fixed factors; the Zebra Finch was the comparison group. Individual identity was included as a random factor to account for repeated measurement of birds at each T_a. We used the lmerTest package to examine the effect of individual as a random factor using the Likelihood Ratio Test (LRT) and Tukey tests with the emmeans package [50] to make pairwise comparisons between species. Values are presented as mean ± se, with N = number of individuals and n = number of measurements unless stated otherwise.

3. Results

Body mass of the finches ranged from 9.9 ± 0.24 g (N = 6, n = 17) for the Double-barred Finch to 10.7 ± 0.26 g (N = 7, n = 15) for Red-browed Finches, 12.3 ± 0.26 g (N = 7, n = 16) for Painted Finches and 12.4 ± 0.25 g (N = 7, n = 16) for Zebra Finches and (Supplementary Table S1). Body mass differed between species (F_{3,17} = 24.6, *p* < 0.001) with Red-browed and Double-barred significantly lighter than Zebra and Painted Finches (t_{16–18} > 4.13, *p* < 0.004). Individuals did not differ significantly with respect to mass (LRT₁ = 4.06, *p* = 0.083).

There were no significant interactions between species and T_a (F_{3,51–57} ≤ 1.68, *p* ≥ 0.182) and no significant differences between individuals (LRT₁ < 0.001, *p* > 0.999) for any of the physiological variables. Ambient temperature affected T_b (F_{1,55} = 5.25, *p* = 0.026; Figure 1) with a general increase from 20 to 32 °C, but T_b did not differ between species (F_{3,57} = 1.04, *p* = 0.384). Metabolic rates of the finches (Figure 1) changed with T_a (F_{1,55} = 73.4, *p* < 0.001), with a general pattern of a decrease as T_a increased from 20 °C to 30 °C and an increase above 30 °C, but there were no overall species differences (F_{3,55} = 0.857, *p* = 0.469). There was a gradual increase from T_a = 20 to 30 °C, and then a more dramatic increase above T_a = 32 °C for both wet and dry (F_{1,51} ≥ 33.8, *p* < 0.001) thermal conductance (Figure 2). There were again no species differences for either C_{wet} or C_{dry} (F_{3,51} ≤ 0.322, *p* ≥ 0.803).

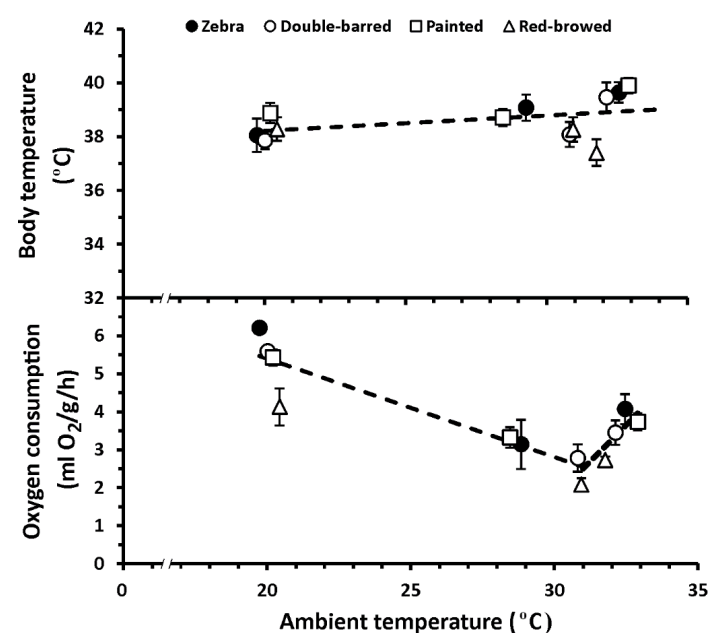


Figure 1. Body temperature and metabolic rate (oxygen consumption) of Australian poephiline finches

(symbols indicate species as per key; Zebra Finch *Taeniopygia guttata*, N = 7; Double-barred Finch *Taeniopygia bichenovii*, N = 6; Painted Finch *Emblema pictum*, N = 7; Red-browed Finch *Neochmia temporalis*, N = 7) at varying ambient temperatures. Dashed lines indicate the relationship determined from mixed model analysis. Values are mean \pm se.

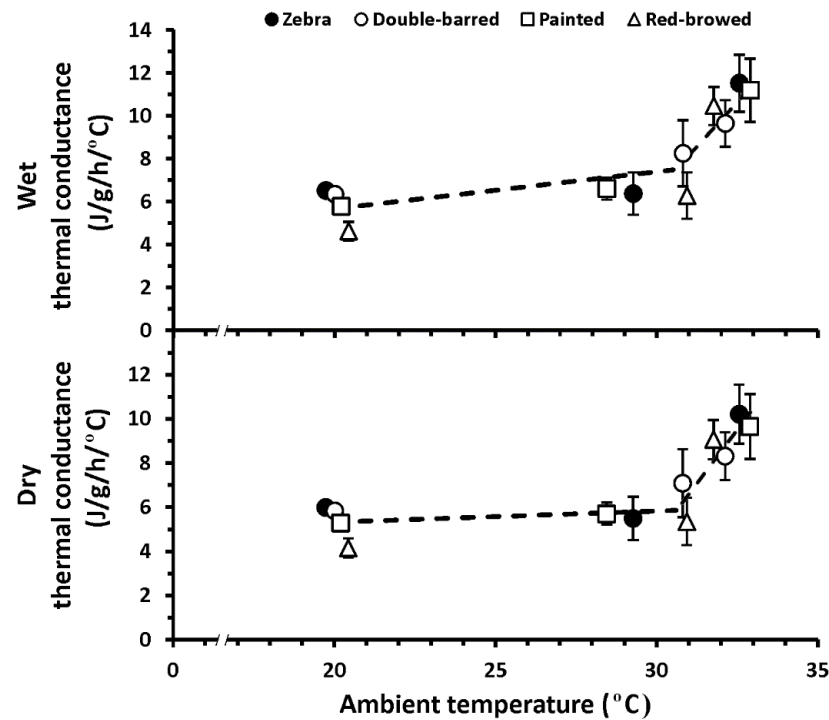


Figure 2. Wet and dry thermal conductance of Australian poeophiline finches (symbols indicate species as per key; Zebra Finch *Taeniopygia guttata*, N = 7; Double-barred Finch *Taeniopygia bichenovii*, N = 6; Painted Finch *Emblema pictum*, N = 7; Red-browed Finch *Neochmia temporalis*, N = 7) at varying ambient temperatures. Dashed lines indicate the relationship determined from mixed model analysis. Values are mean \pm se.

Evaporative water loss was independent of T_a ($F_{1,39} = 0.095$, $p = 0.760$; Figure 3) and did not differ between species ($F_{3,43} = 0.486$, $p = 0.694$) or individuals ($LRT_1 = 2.60$, $p = 0.107$). However, there was a highly significant temperature effect for RWE ($F_{1,37} = 67.5$, $p < 0.001$; Figure 4) with no species differences ($F_{3,41} = 1.86$, $p = 0.151$; Figure 4). The PRWE was 19.1 °C for the Zebra Finch and declined to 16.4 °C for the Double-bar Finch, 15.2 °C for the Painted Finch and finally 4.1 °C for the Red-browed Finch.

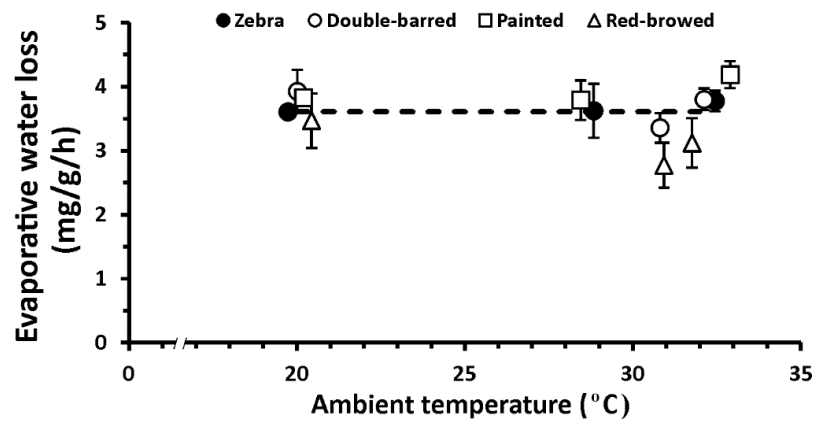


Figure 3. Evaporative water loss of Australian poeophiline finches (symbols indicate species as per key;

Zebra Finch *Taeniopygia guttata*, N = 7; Double-barred Finch *Taeniopygia bichenovii*, N = 6; Painted Finch *Emblema pictum*, N = 7; Red-browed Finch *Neochmia temporalis*, N = 7) at varying ambient temperatures. The dashed line indicates the relationship determined from mixed model analysis. Values are mean \pm se.

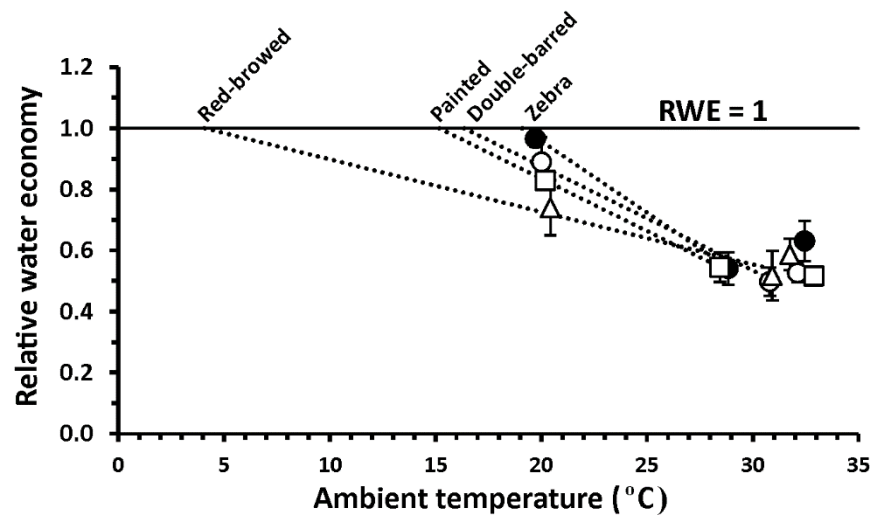


Figure 4. Relative water economy of Australian poeophiline finches (Zebra Finch *Taeniopygia guttata*, N = 7; Double-barred Finch *Taeniopygia bichenovii*, N = 6; Painted Finch *Emblema pictum*, N = 7; Red-browed Finch *Neochmia temporalis*, N = 7) at varying ambient temperatures. The horizontal line depicts relative water economy = 1, and the dashed lines for each species indicate the linear relationship for data at the two lowest ambient temperatures, extrapolated to the point of relative water economy (PRWE) where RWE = 1. Values are mean \pm se.

4. Discussion

All four finch species conformed to the expected endothermic physiological response of a bird to a range of moderate T_a [31,51]. We found little evidence that the standard physiology of the Zebra Finch was unique amongst Australian grassfinches. None of the finches achieved a positive water economy at $T_a \geq 20^\circ\text{C}$ and so would presumably require drinking water at even these moderate to warm T_a , although the Zebra Finch came closest to achieving water balance during the study with a PRWE of 19.1°C . We suggest that the PRWE may have greater utility than standard physiological variables for assessing species tolerance of heat and aridity as it integrates small differences in thermal and hygric physiology into a single index.

The patterns of response to T_a that we observed for the Zebra and other finches were generally consistent with previous data for Zebra Finches although Calder [13] and Cade et al. [6] found that Zebra Finches didn't increase metabolic rate until $T_a \geq 40^\circ\text{C}$. Our value for metabolic rate of Zebra Finches of $3.1 \pm 0.65 \text{ mL O}_2/\text{g/h}$ at $T_a = 28^\circ\text{C}$ was within the range of $2.1\text{--}3.6 \text{ mL O}_2/\text{g/h}$ previously reported for basal metabolic rate [6,13,16,17,52–55] for this species despite being measured slightly below thermoneutrality. Evaporative water loss below the thermoneutral zone ($3.6 \pm 0.42 \text{ mg/g/h}$) was also within the previously reported range of $2.3\text{--}9.7 \text{ mg/g/h}$ [6,13,16,17,56]. The considerable range of estimates of basal metabolic rate and especially EWL presumably results from a combination of bird condition (e.g., hydrated or dehydrated, wild caught, wild-derived captive, or domestic) and measurement protocol (e.g., experimental duration and timing, T_a , sampling protocol, continuous vs gravimetric measurement), all of which can impact the estimation of physiological variables of this and other species e.g., [14,16,57–60].

The PRWE of 19.1°C that we calculated for hydrated Zebra Finches is consistent with observations of finches surviving without drinking at room temperature [6,8,14] but being in negative water balance at higher T_a [16,17]. We calculated a PRWE of 15.7°C from Cade et al.'s [6] Zebra Finch data which is lower than our estimate of 19.1°C due to their higher

EWL. A PRWE of -60 to -70 °C for Zebra Finches estimated from the data of Calder [13] is clearly unrealistic and a consequence of excessively high EWL values that presumably result from gravimetric measurement and experimental timing and duration (e.g., [59,60]).

We are unaware of physiological data for other Australian poephiline finches, but the Australian Gouldian Finch (*Chloebia gouldiae*; subfamily Erythrurinae) [5] has a similar basal metabolic rate of about 2.4 mL O₂/g/h but higher T_b and EWL [52,61] compared to the poephiline species that we measured. We calculated an unlikely PRWE of -32 °C from the metabolic rate and EWL data of Burton and Weathers [61] who unfortunately did not measure their Gouldian Finches under standardised conditions (they were measured during the active phase with measurement durations as short as 1 h), so it is impossible to meaningfully compare their physiological variables with the other four species of finch [34,60,62]. There is a similar pattern of comparable basal metabolic rates of ~ 2.7 mL O₂/g/h but higher EWL of ~ 7.2 mg/g/h for non-Australian lonchurine finches (sister subfamily to Poephilinae) [52,63–67] and other estrildids of ~ 3.2 mL O₂/g/h for basal metabolic rate and EWL of 7–12 mg/g/h [6,52,66,68–71]. These data suggest similar metabolic and thermal physiology and potentially lower rates of EWL for Australian poephiline finches including the Zebra Finch, but methodological differences between studies make this interpretation difficult, especially considering that it is EWL of endotherms that is most impacted by methodology [59,60,72,73]. It would be interesting to formally compare physiological variables of all of these estrildid finches in a phylogenetic and ecological context, but this would be premature given variation in available data that can be ascribed to methodological differences [74], the limited number of species studied for each subfamily, and the relatively recent divergence dates for these estrildid lineages (5).

We might not expect large differences in the basic physiological bauplan of these Australian finches due to their relatively recent phylogenetic divergence and the view that birds are pre-adapted to desert environments [8,32,35,36]. The general ecology of these Australian poephiline finches is remarkably similar despite their varied habitats. They are all morphologically similar, small, granivorous birds found close to water. They are generally resident and sedentary with migratory or nomadic movements driven by food and especially water availability [18]. Despite the arid habitats of both the Zebra and Painted Finches they exploit natural (pools, waterholes, rockholes) and anthropogenic (dams, troughs, wells, buckets, taps, gardens) free water sources throughout their range [1,18]. Painted Finches are restricted to rocky gullies, gorges and outcrops where waterholes are more permanent [18]. Even the Zebra Finch is synonymous with water availability [1,75,76] despite being considered an iconic desert species. Both of these desert species drink throughout the day from water sources as required [15,77–79]. A common reliance on drinking water and seed and the mobility to meet these requirements, together with typical avian traits of high T_b and low urinary and faecal water loss, may negate strong drivers of physiological adaptation of desert finches in comparison with their mesic counterparts.

Although the Australian continent is one of the hottest, driest and most arid worldwide [37,80] its deserts are comparatively recent. Initial drying commenced during the Late Tertiary period, with phases of aridity occurring from 10 MYA and well underway by 2.5 MYA. However, the major changes toward a more arid environment occurred during the Quaternary, with a series of significant drying events from 25,000 YA and peak aridity as recently as 16,000 YA [80]. The various groups of poephiline finches diverged about 6.5 MYA, with Red-browed Finches diverging about 6.5 MYA, Painted Finches about 6.0 MYA, and *Taeniopygia* diverging about 5.5 MYA [5]. This is early in the gradual transition to widespread aridity and before current patterns of desertification were firmly established. In contrast, Old World deserts are >10 and in some cases >20 million years old, so desert birds in these regions have had longer to adapt to arid conditions and it is in these species that physiological divergence of arid and mesic species is most apparent [29,37,81]. In contrast, adaptation to arid environments is less apparent amongst New World birds; North American birds from geologically more recent ($<11,000$ years) deserts show little evidence of physiological adaptation to arid habitats [8,29,37,81,82]. Our data suggest

a similar lack of specific physiological adaptation to aridity in Australian poeophilines, including the iconic Zebra Finch, which, together with the Painted Finch differs little from its more mesic counterparts and remains water-dependent despite inhabiting some of the most extreme deserts on Earth.

Although we were unable to quantify any significant differences in specific physiological variables between the Zebra Finch and other Australian poeophilines, they nevertheless live in extremely disparate habitats so some divergence may be expected, despite similar evolutionary histories and behavioural and ecological compensations. Calculation of RWE, and extrapolation to the PRWE, can provide a more sensitive evaluation of physiological propensity for survival of heat and aridity than examining physiological variables independently, because PRWE integrates hygric, thermal and metabolic responses [41]. Consequently PRWE has been used previously to evaluate adaption to habitat aridity for dasyurid and phalangerid marsupials [44,83] and to assess potential impacts of climate change and translocation for pseudocheirid possums and other folivorous marsupials [41]. Here we describe a similar utility of PRWE for evaluating response to habitat aridity for Australian poeophiline finches, with the Zebra Finch having the highest PRWE (19.1 °C) consistent with its broad hot, arid distribution and observed responses to water deprivation in the laboratory, and the Red-browed Finch the lowest (4.1 °C), consistent with its cooler, very mesic habitat. Painted and Double-barred Finches had intermediate PRWE (15.2 °C and 16.3 °C respectively) representing their intermediate exposure to a combination of temperature and aridity. We propose that the PRWE can provide a more powerful separation of resistance to potential heat and aridity than assessing potentially small differences in individual standard physiological variables, as the index magnifies any small differences in metabolic and hygric physiology and their response to T_a . The PRWE may prove particularly useful for evaluating the suitability of current and future habitats for birds in the face of global warming and other anthropogenic environmental change (as for mammals) [41,83] and therefore may contribute to conservation and management. For example it highlights the necessity of water availability for the survival of all these species at typical daytime temperatures within their distribution and suggests that reduction in free water within their habitats, as predicted by some authors [84], may negatively impact their distribution. However, calculations of RWE do require standardised measurement protocols; the unrealistic prediction of -60 to -70 °C we calculated for PRWE of Zebra Finches from the data of Calder [13], and an unlikely -32 °C for the Gouldian Finch [61] are examples of the consequence of excessively high EWL measurements that clearly underestimate dehydration tolerance compared to the consistency achieved between predictions and direct observations for our standardised data. As McKechnie and Wolf [74] point out, “good predictions need good data”.

Overall, we conclude that the physiological profile of Zebra Finches differs very little from other Australian poeophiline finches and find little evidence that it has a unique physiology compared to some of its close relatives, despite some authors considering it to be an ecological outlier amongst desert birds [11]. All Australian finch species responded to T_a in a similar way and there were no significant differences for any of the physiological variables examined despite considerable differences in the aridity of their distributions [7,19], presumably due to similarities in morphology, ecology and water dependence. Further studies of these four species over a broader range of T_a , particularly above the thermoneutral zone to evaluate their heat tolerance, and data for additional species of estrildid finch would allow for more detailed evaluation of the physiology of the Zebra Finch in comparison to other species, and the utility of finches for assessing environmental drivers of avian physiological traits. However, it was clear from our data that the PRWE was a systematic difference between the species constant with the aridity of their geographical distribution, with the Zebra Finch having the highest PRWE and the Red-browed Finch having the lowest. The limited published data for ecophysiological measures of estrildid finches is compounded by varying methodologies and experimental design. This was particularly obvious for measurements of EWL, which were generally much higher than expected,

reflecting limitations in measurement methodology and short experimental durations. This is especially unfortunate because EWL is a critical component of RWE and PRWE, which appears to be one of the few ecophysiological differences between finch species.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/birds3020012/s1>, Table S1: Summary of data for four species of poephiline finches at varying ambient temperatures.

Author Contributions: Conceptualisation, methodology, software and resources P.C.W.; Formal Analysis P.C.W., C.E.C. and A.N.L.; Investigation and data curation C.E.C. and A.N.L.; Writing—Original Draft Preparation C.E.C. and A.N.L.; Writing—Review & Editing, P.C.W., C.E.C. and A.N.L.; Visualization, Supervision, Project Administration, Funding Acquisition P.C.W. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: Experiments followed the Australian Code of Practice for the care and use of animals for scientific purposes, approved by the Animal Ethics Committee of the University of Western Australia (approval number 0506008E60).

Data Availability Statement: Data are available as Supplementary Table S1.

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