

1 **Metabolic rate is negatively linked to adult survival but does not explain latitudinal differences in**
2 **songbirds**

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25 fieldwork and performed analyses. AJB wrote the initial manuscript. BOW provided equipment and
26 training. All authors contributed to revisions of the manuscript.

27 **ABSTRACT**

28 Survival rates vary dramatically among species and predictably across latitudes, but causes of this
29 variation are unclear. The rate of living hypothesis posits that physiological damage from metabolism
30 causes species with faster metabolic rates to exhibit lower survival rates. However, whether increased
31 survival commonly observed in tropical and south temperate latitudes is associated with slower metabolic
32 rate remains unclear. We compared metabolic rates and annual survival rates across 46 species that we
33 measured, and 147 species from literature data across northern, southern, and tropical latitudes. High
34 metabolic rates were associated with lower survival but latitude had substantial direct effects on survival
35 independent of metabolism. The inability of metabolic rate to explain latitudinal variation in survival
36 suggests 1) that species may evolve physiological mechanisms that mitigate physiological damage from
37 cellular metabolism, and 2) a larger role of extrinsic environmental, rather than intrinsic metabolic, causes
38 of latitudinal differences in mortality.

39

40 **Key words:** physiology, adult survival, metabolism, life history theory, latitude, pace of life

41 INTRODUCTION

42 Adult survival rate varies extensively among species and is a major influence on fitness, demography and
43 life-history evolution (Ashmole 1963; Stearns 1977; Promislow & Harvey 1990; Martin 2015). The rate
44 of living hypothesis has been proposed as a physiological mechanism underlying variation in survival
45 rate. Production of damaging reactive oxygen species (ROS) from metabolism is thought to cause greater
46 oxidative damage and shorter life (Pearl 1928; Harman 1956; Balaban *et al.* 2005; Brys *et al.* 2007;
47 Monaghan *et al.* 2009). Yet, metabolism may be decoupled from senescence because mechanisms to
48 prevent or repair damage (e.g. endogenous antioxidants, mitochondrial membrane composition and
49 telomere dynamics) may coevolve with metabolic rate (Brand 2000; Monaghan & Haussmann 2006;
50 Hulbert *et al.* 2007; Costantini 2008; Salin *et al.* 2015; Skrip & McWilliams 2016; Vagasi *et al.* 2018).
51 Furthermore, survival rates may be unrelated to the accumulation of physiological damage entirely.
52 Extrinsic sources of mortality, such as harsh weather or predation, may be more important in shaping
53 variation in survival. Consequently, whether metabolic rate explains variation in adult survival across
54 species remains unclear (Costantini 2008).

55 Comparative studies show that metabolic rate is negatively correlated with maximum observed
56 lifespan (MLS) in birds and mammals at broad taxonomic scales (Trevelyan *et al.* 1990; Hulbert *et al.*
57 2007). However, the overriding influence of mass on both lifespan and metabolism obscures the
58 independent effect of metabolic rate on lifespan in such studies (Speakman 2005). Moreover, other
59 comparisons raise questions about this relationship. Bats and birds have higher metabolic rates but are
60 longer-lived than terrestrial mammals of similar size, suggesting that metabolism and lifespan can be
61 decoupled, at least across broad taxonomic groups (Holmes & Austad 1995; Holmes *et al.* 2001; Munshi-
62 South & Wilkinson 2010). Furthermore, measurements of MLS represent exceptional rather than an
63 average across individuals and are sensitive to variation in sample size, recapture probability and quality
64 of record keeping (Krementz *et al.* 1989; Promislow 1993). In addition, MLS is often based on captive
65 individuals that are well-fed and isolated from disease, predation and other extrinsic sources of mortality
66 that are ubiquitous in wild populations (i.e. de Magalhães & Costa 2009). Direct estimates of annual

67 survival rate are not susceptible to these issues.

68 Adult survival rates vary substantially across latitudes with tropical species generally exhibit
69 higher survival rates than south temperate or especially north temperate species. Yet evidence that
70 metabolic rate underlies variation in adult survival across latitudes is mixed. For example, lower
71 metabolic rates have been found in tropical songbirds (Wikelski *et al.* 2003; Wiersma *et al.* 2007;
72 Londoño *et al.* 2015) and because tropical species are generally longer-lived than temperate relatives
73 (Sandercock *et al.* 2000; Martin 2015; Martin *et al.* 2017), this pattern has been interpreted as evidence
74 that metabolic rate and adult survival are causally linked. However, other studies found no difference in
75 metabolic rates across latitudes in either adult birds (Vleck & Vleck 1979; Bennett & Harvey 1987) or
76 embryos (Martin *et al.* 2013). Furthermore, using latitude as a proxy for survival rate is problematic
77 because survival rates vary extensively among species within latitudes that yield overlap among species
78 between latitudes (reviewed in Martin *et al.* 2017). Metabolic rate and adult survival appeared to be
79 negatively correlated across latitudes in songbirds in one study (Williams *et al.* 2010). However, methods
80 used for estimating survival rates differed between latitudes, which can obscure patterns across sites
81 (Martin *et al.* 2017), and site effects were not included in a statistical test. Within sites, metabolic rate is
82 sometimes negatively linked to adult survival probability (Scholer *et al.* 2019) and sometimes unrelated
83 (Bech *et al.* 2016). Ultimately, studies that directly compare metabolic rates with robust estimates of adult
84 survival from wild populations are needed.

85 Here, we test whether metabolic rate explains variation in adult survival probability across
86 latitudes. We directly measured resting metabolic rate (RMR) and estimated adult mortality probability
87 for songbirds at North temperate, tropical and South temperate field sites. We also compiled a global
88 database of basal metabolic rate (BMR) and adult survival data for 147 species from the literature. We
89 used phylogenetically-informed path analysis to test whether metabolic rate explained interspecific
90 variation in adult survival within and across latitudes.

91

92 **METHODS**

93 **Study species**

94 Passerine birds (songbirds) are a good group in which to examine these issues. Passerines are diverse (~
95 6,000 species) and show broad ecological and morphological variation (del Hoyo *et al.* 2017). They show
96 large interspecific variation in both metabolic rate (McKechnie & Wolf 2004; Wiersma *et al.* 2007;
97 Londoño *et al.* 2015; McKechnie 2015) and adult survival probability (Johnston *et al.* 1997; Sandercock
98 *et al.* 2000; Martin 2015; Martin *et al.* 2015, 2017).

99 **Field data**

100 Resting metabolic rate measurements and estimation of adult survival probability were conducted on
101 populations of passerine birds at Kinabalu Park, Sabah, Malaysia (6°N, 116°E), the Coconino National
102 Forest, Arizona, USA (35°N, 111°W) and the Koeberg Nature Reserve, Western Cape, South Africa
103 (34°S, 18°E). Metabolic measurements were performed during the breeding season at both sites
104 (Malaysia; February – June, 2013 – 2016, Arizona; May – July, 2015, South Africa; August – October
105 2016).

106 Birds were captured for metabolic measurements by both passive and targeted mist-netting.
107 Breeding females (based on presence of a brood patch) were excluded to minimize disruption of nesting
108 and because the extreme vascularization of the avian brood patch is likely to alter RMR. Birds were
109 transported to the lab and held for 1-2 hrs, depending on mass, to ensure they were post-absorptive during
110 measurements. Birds were watered before and after and returned to point of capture upon completion of
111 metabolic measurements.

112 Adult survival probability was estimated by banding, resighting and recapturing birds, using the
113 same long-term protocols at Malaysia and Arizona sites (Martin *et al.* 2015). Birds were captured by both
114 passive mist-netting and target-netting for six hours each day beginning at sunrise. Twelve nets were
115 deployed at each netting plot, which were distributed uniformly across accessible areas of each site. Each
116 plot was visited three times at equal intervals over the course of the field season. Birds were marked with
117 unique combinations of one alpha-numeric aluminum band and three color-bands to facilitate individual
118 identification via resighting. In addition to subsequent recaptures, birds were resighted opportunistically

119 each day for the duration of each field season. Similar mark-resight-recapture protocols were used in
120 South Africa (see Lloyd *et al.* 2014). Resulting estimates (see Statistical Analyses) are based on 10
121 consecutive years of mark-recapture-resighting effort in Borneo, 21 in Arizona, and 7 in South Africa.

122 **Metabolic measurements**

123 We measured RMR using an open-flow respirometry system similar to that described in Gerson *et al.*
124 (2015). We used 2 L and 5 L transparent plastic containers (Rubbermaid, Atlanta, GA, USA) as metabolic
125 chambers, depending on the size of the study species. These containers were modified to include incurrent
126 and excurrent air ports, with wire mesh platforms and plastic perches to allow the subject to rest
127 comfortably. The bottom of the chamber contained a 2cm layer of mineral oil to trap moisture and gas
128 associated with feces. Containers were placed inside a large cooler, which was modified to hold an
129 integral peltier device (model AC-162, TE Technology, Traverse City, MI), connected to a temperature
130 controller (Gerson *et al.* 2015) to regulate chamber air temperature. Incurrent air was provided by a high
131 capacity pressure/vacuum pump (model DAA-V515-ED, Gast Manufacturing, Benton Harbor, MI, USA),
132 and was routed through a coil of copper tubing prior to entering the inner chamber to facilitate rapid
133 temperature equilibration. Air flow rates were regulated by mass-flow controllers (Alicat Scientific,
134 Tucson, AZ) with an accuracy of < 2% of the reading and their calibration was checked annually against a
135 factory five-point calibration Alicat mass flow meter used only for this purpose. Flow rates were varied
136 from 2-15 L/min depending on temperature and mass of the study species. Incurrent and excurrent air
137 were both subsampled at rates between 250 and 500 ml/min and CO₂ and H₂O were measured using a
138 portable gas-analyzer (LI-COR model LI-840a, Lincoln, NE, USA) zeroed and then spanned against a gas
139 with a known CO₂ concentration (1854±0.2 ppm). These data were sampled every second and recorded
140 using Expedata (Sable Systems, Las Vegas, NV, USA).

141 Humidity of incurrent air was regulated using a dew-point generator constructed of three Nalgene
142 bottles connected in series. Air was bubbled through water in the first two bottles, and the third was empty
143 and served as a water trap. The entire device was then submerged in a water bath kept at approximately
144 10°C by the addition of small ice-packs. This device prevented rapid fluctuations in humidity due to either

145 ambient air temperature or ambient humidity and also prevented condensation occurring in the system. By
146 adjusting water bath temperature and incurrent air pressure, we maintained relative humidity between 50
147 and 70%, which is within the range of normal conditions at both sites during the breeding season.

148 Each individual was sampled at multiple temperatures as part of a concurrent study of thermal
149 tolerance. We subsetted data for analysis by selecting the longest continuous period of resting behavior
150 after chamber temperature had reached equilibrium for at least 30 minutes. Subject activity was monitored
151 in real-time via an infrared security camera connected with an external LCD screen. If no period of
152 complete rest greater than two minutes was observed, no data were analyzed for that temperature. We
153 pooled measurements from 27, 30, and 33°C, which are within the thermoneutral zone of most passerines
154 (McKechnie & Wolf 2004; McNab 2009) and selected the lowest measurement for each individual as
155 RMR.

156 We corrected mass flow rates of humid air, and calculated CO₂ and H₂O production using
157 equations in Lighton (2008). Metabolic rate (W) was calculated as in Walsberg and Wolf (1995). CO₂
158 production was converted to metabolic energy using a respiratory quotient (RQ) value of 0.71, as
159 suggested for post-absorptive, non-granivorous birds (Gessaman & Nagy 1988).

160 **Literature data**

161 We compiled basal metabolic rate (BMR) data from the literature, drawing primarily from four
162 manuscripts that use large BMR datasets to investigate allometric and latitudinal variation in avian BMR
163 (McKechnie & Wolf 2004; Wiersma *et al.* 2007; Londoño *et al.* 2015; Bech *et al.* 2016). Estimates of
164 annual adult survival probability were compiled by searching the literature, and were greatly aided by
165 manuscripts containing large literature (Martin 1995; Martin & Clobert 1996) and field (Scholer *et al.*
166 2019) datasets. Where multiple estimates of either BMR or adult survival probability for a single species
167 were present in the literature, we chose the estimate based on the most recent study.

168 **Statistical Analyses**

169 For our Malaysia and Arizona field data, we employed Cormack-Jolly-Seber models to estimate apparent
170 annual adult survival (ϕ) and detection probability (p) for each species based on live encounters in an

171 open population using program MARK (White & Burnham 1999; Burnham & Anderson 2002). A suite of
172 models were built for each species, allowing parameters to vary based on sex and/or age-structure (time
173 since marking; Pradel *et al.* 1997). Top models were selected based on Akaike's information criterion
174 (AICc) adjusted for small sample size. Estimates used here are an updated subset of those presented in
175 Martin *et al.* (Martin *et al.* 2015, 2017), where additional methodological details are provided. For our
176 South Africa data, we similarly fit Cormack-Jolly-Seber models but survival was held constant and year
177 was treated as a random effect. Estimates used here are from Lloyd *et al.* (2014).

178 We used simple linear regression to examine the expected allometric relationship between species
179 mean body mass and metabolic rate for both field RMR and literature BMR datasets. We log-transformed
180 RMR (W), BMR (W), and body mass (g).

181 We used phylogenetic path analysis (PPA) to examine the causal relationships between mass,
182 metabolic rate, apparent adult survival, and latitude (Hardenberg & Gonzalez-Voyer 2013). PPA uses the
183 d-separation method to test the plausibility that a causal model created the observed data and to compare
184 the relative support of multiple models. We developed six possible models (Fig. 1) that varied in the
185 depictions of how latitude and metabolic rate influence survival and how latitude influences metabolic
186 rate. We tested the conditional independencies of each model using phylogenetic least-squares regression
187 (PGLS), implemented in the package 'ape' (Paradis *et al.* 2004; Popescu *et al.* 2012). We then tested the
188 plausibility of each causal model using Fisher's C statistic. We used the C statistic Information Criterion
189 with a correction for small sample sizes (CICc) to rank and compute the probability of each causal model
190 given the data and the candidate model set (CIC weight). We then used model averaging to estimate
191 standardized path coefficients for all plausible models ($p > 0.05$; Anderson *et al.* 2000; Hardenberg &
192 Gonzalez-Voyer 2013). We log-transformed RMR (W), BMR (W), and body mass (g). We followed
193 identical procedures for analysis of both our field RMR data and literature BMR data.

194 Phylogenetic trees were acquired from birdtree.org (Jetz *et al.* 2012) using the Hackett backbone
195 (Hackett *et al.* 2008). We sampled a distribution of 1000 trees for each analysis and produced majority-
196 rules consensus trees using Mesquite (Maddison & Maddison 2011). In one case (*Troglodytes aedon*), we

197 include both a tropical (*T. a. musculus*) and temperate (*T. a. aedon*) subspecies in our literature BMR
198 dataset. To facilitate phylogenetic analysis in which duplicate estimates for a single species are
199 problematic, we assigned one estimate to a closely related congener (*T. cobbi*) for tree construction.

200 Finally, we combined field and literature datasets and tested for differences in allometric
201 relationships between RMR and BMR using a simple linear model. All analyses were performed in R (R
202 Core Team 2015).

203

204 **RESULTS**

205 We obtained field-based estimates of adult mortality probability and resting metabolic rate for 47
206 species; 14 in Arizona, 16 in Malaysia, and 17 in South Africa. We measured RMR in a total of 237
207 individuals with an average of 5.0 individuals per species (Table 1). Body mass explained the majority of
208 variation in metabolic rates ($R^2 = 0.94$, $P < 0.01$, Fig. 2A). The allometric scaling exponent was 0.64,
209 which is consistent with known values for birds (Bennett & Harvey 1987; McKechnie & Wolf 2004). The
210 only plausible model that explained relationships was the full model (Fig. 1F) which described direct
211 causal relationships between RMR and survival, latitude and survival, and latitude and RMR (Fig. 2C,
212 3A). Adult survival declined with RMR, but was higher in tropical and south temperate species compared
213 with north temperate relatives after accounting for RMR (Fig. 2C, 3A). RMR was slightly lower in
214 tropical species, but higher in the south temperate when compared to north temperate species (Fig. 2C,
215 3A).

216 Our compiled literature data for BMR and adult survival probability included 62 temperate, 64
217 tropical, and 21 south temperate species (Supplementary Table 1). Similar to our field data, body mass
218 explained extensive variation in metabolic rates ($R^2 = 0.86$, $P < 0.01$, Fig 2B). The allometric scaling
219 exponent was 0.66, nearly identical to our RMR estimate above. Four models could have plausibly
220 created the observed BMR and survival data from the literature (Fig. 1, 3B). Among these, a direct effect
221 of latitude on adult survival was strongly supported (CICc weight = 1.0). A negative relationship between
222 BMR and survival also had some support (CICc weight = 0.505), as well as latitudinal differences in

223 BMR (CICc weight = 0.463). Adult survival declined with BMR and was higher in tropical and south
224 temperate species than north temperate relatives after accounting for BMR (Fig. 2D, 3B). BMR was
225 slightly lower in tropical and south temperate species than in north temperate species (Fig. 2D, 3B).

226 RMR was 14.7% higher than BMR ($P < 0.01$), but the allometric relationship between mass and
227 metabolism did not differ for (RMR) and basal (BMR) metabolic rates ($P = 0.51$, Fig. 7).

228

229 **DISCUSSION**

230 Broad tests of metabolism and annual survival probability across diverse species have been lacking,
231 despite a long history of their possible association ((Pearl 1928; Harman 1956; Balaban *et al.* 2005; Brys
232 *et al.* 2007; Monaghan *et al.* 2009) that has been challenged by cross-taxa comparisons (i.e., Holmes &
233 Austad 1995; Holmes *et al.* 2001; Munshi-South & Wilkinson 2010). Our field data on RMR and those
234 from the literature on BMR included 193 species across the world and yielded results that were largely in
235 agreement between the two datasets. In particular, the results suggest that metabolic rate is associated
236 with adult survival, but most of the variation in adult survival probability among latitudes is independent
237 of metabolic rate (Fig. 2, 4). Our results provide some support for a possible role of the rate-of-living
238 hypothesis within latitudes. However, more significantly, our results parallel those of comparisons across
239 taxonomic groups (i.e., Holmes & Austad 1995; Holmes *et al.* 2001; Munshi-South & Wilkinson 2010) in
240 suggesting that metabolic rate is not the primary driver of broader global patterns of survival probability.

241 We found that while metabolic rates were reduced in tropical compared with north temperate
242 species, results were mixed when comparing south temperate to north temperate species (Fig. 2A-B, 3).
243 Lower metabolism in tropical species fits with results of previous studies (Wiersma *et al.* 2007; Londoño
244 *et al.* 2015). However, the difference in metabolism across latitudes is only a small, statistical difference
245 (as also found by Wiersma *et al.* 2007, Fig 1; Londono *et al.* 2015), whereas adult survival probability
246 shows a consistently large difference between the north temperate and tropical latitudes (Martin *et al.*
247 2017). The small difference in metabolism and larger difference in survival fits with our results that much
248 of the difference in survival probabilities between latitudes is not related to metabolism.

249 Consideration of metabolism and survival in south temperate regions has been limited (but see
250 Bech *et al.* 2016). However, inclusion of this region provides critical additional insight. Our field dataset
251 indicated higher resting metabolic rate in South African species compared with Arizona, but support for
252 the significance of this relationship was relatively weak (Fig. 3A). Nonetheless, the resting metabolic
253 rates do not fit the pace-of-life hypothesis given that the Southern African species have substantially
254 higher survival rates than Arizona species (Peach *et al.* 2001; Lloyd *et al.* 2014). In contrast, BMR was
255 reduced in south temperate compared with north temperate species based on literature data (Fig. 3B), and
256 this relationship was strongly supported. The high survival rates of south temperate species (Lloyd *et al.*
257 2014) taken together with their lower BMR rates then fits with the pace-of-life hypothesis (Wiersma *et al.*
258 2007; Healy *et al.* 2019). This inconsistency between RMR and BMR together with earlier work in both
259 adult birds (Vleck & Vleck 1979; Bennett & Harvey 1987) and embryos (Martin *et al.* 2013) that show no
260 latitudinal difference in metabolism, suggests that metabolic rate is a minor influence on latitudinal
261 variation in survival rates relative to other factors associated with latitude.

262 Latitudinal variation in avian mortality rates may be driven primarily by differences in extrinsic
263 mortality probability. Extrinsic mortality is thought to account for 80-95% of all mortality for birds with
264 total annual mortality rates similar to those in our study (Ricklefs 1998). Thus, variation in extrinsic
265 mortality is likely to have a much larger effect on total mortality rates than intrinsic physiological
266 differences. However, reduced metabolic costs to survival should be favored in populations with low
267 extrinsic adult mortality, meaning extrinsic and intrinsic mortality rates should be correlated (reviewed in
268 (Charlesworth 1994, 2000). Indeed, actuarial (Promislow 1991; Ricklefs 1998, 2000) and experimental
269 (Stearns *et al.* 2000) studies across taxa suggest intrinsic mortality rate increases with extrinsic mortality
270 rate (e.g. weather, predation). However, the proportion of deaths from intrinsic sources are greater when
271 overall mortality rates are low, suggesting that adaptations to slow the rate of aging are limited, such that
272 extrinsic and intrinsic rates may become increasingly decoupled as extrinsic mortality declines (Ricklefs
273 & Scheuerlein 2001). Furthermore, the onset of senescence is commonly delayed until well after the age
274 of maturity (Promislow 1991), suggesting that intrinsic and extrinsic mortality rates may also be unrelated

275 when extrinsic mortality is very high. Ultimately, high adult mortality rates in temperate birds may reflect
276 high rates of extrinsic mortality imposed by abiotic factors (MacArthur 1972) that better explain
277 latitudinal differences in survival (Martin 2002, 2015; Martin *et al.* 2015).

278 The absence of a strong relationship between metabolic rate and adult survival across latitudes
279 does not discount the possibility that physiological damage from cellular metabolism contributes to adult
280 survival rates and life-history tradeoffs. On the contrary, a causal relationship between metabolism and
281 survival was supported (Fig. 3) and the predicted negative associations were observed within most
282 regions using both RMR and BMR datasets. Moreover, increased investment in mechanisms to mitigate
283 damage, such as endogenous production of antioxidants (Parolini *et al.* 2017) or mitochondrial membrane
284 composition (Hulbert *et al.* 2007), can reduce damage from cellular metabolism. If tropical species invest
285 in these mechanisms with allocation costs for growth or reproduction, such a tradeoff could explain the
286 longer life and slower life-history strategies of tropical species despite broadly similar metabolic rates
287 across latitudes. Yet, ultimately, investment in such mechanisms only makes sense if extrinsic mortality is
288 low.

289 BMR and RMR are the most easily measured and comparable metrics of energy expenditure in
290 wild organisms. However, these measures only encompass minimal energy expenditure to sustain life and
291 thus exclude energy allocated to essential activities such as reproduction, thermoregulation, locomotion
292 and digestion. Physiological damage from metabolism may be more tightly linked to measures of total
293 energy expenditure that describe all energetic expenditures in free-living organisms. Measurements of
294 total energy expenditure, such as field metabolic rate (FMR) or daily energy expenditure (DEE) are
295 comparatively rare in the literature, especially for tropical species (McKechnie 2015), but do show a
296 relationship with adult survival probability in the temperate zone (Martin 2014). BMR and RMR are
297 strongly correlated with each other (Fig. 4), and with measures of total energy expenditure across species
298 (Daan *et al.* 1990; Auer *et al.* 2017), making BMR and RMR reasonable but imperfect proxies for total
299 energy expenditure. Future studies should examine the relationship between FMR and adult survival
300 within and across latitudes.

301 Our study provides support for some role for the rate-of-living hypothesis within latitudes while
302 also suggesting that it is only explains a small amount of the variation in survival within latitudes and is
303 unable to explain differences between latitudes. This contradiction provides obvious opportunity for
304 future studies. South temperate and tropical birds have longer developmental periods and parents invest
305 more energy per-offspring compared with temperate species (Martin 1996, 2015; Martin *et al.* 2011; Gill
306 & Haggerty 2012). These differences may facilitate longer life in tropical species if they facilitate greater
307 investment in physiological adaptations to combat oxidative damage in the face of similar metabolic rates.
308 Quantifying interspecific and latitudinal variation in physiological mechanisms capable of mitigating
309 oxidative damage may reveal how tropical and south temperate species maintain low adult mortality
310 without a major reduction in basal metabolic rate. Mortality rate differences among latitudes may also be
311 due to variation in extrinsic mortality but quantifying latitudinal differences in cause-specific mortality
312 are necessary to test this hypothesis. Overall, our results suggest an urgent need to carefully examine
313 alternative physiological and ecological mechanisms shaping global variation in demographic rates and
314 life histories.

315

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484

485 **Table 1.** Mean (\pm SE) values of mass, resting metabolic rate (RMR) and annual mortality probability for species in our field studies. N (sample
 486 size) values represent the number of unique individuals measured for metabolic rate and the number of unique individuals marked for annual
 487 mortality probability.

Species	Metabolism			Survival Probability					
	Mass (g)	SE	RMR (W)	SE	N	Rate (Yr ⁻¹)	SE	N	
Arizona									
<i>Empidonax occidentalis</i>	11.72	0.34	0.277	0.019	5	0.601	0.034	674	
<i>Parus gambeli</i>	11.65	0.16	0.326	0.019	5	0.511	0.033	709	
<i>Certhia americana</i>	7.47	0.26	0.227	0.011	4	0.549	0.072	408	
<i>Sitta canadensis</i>	10.38	0.24	0.291	0.015	6	0.472	0.058	547	
<i>Sitta carolinensis</i>	17.67	0.34	0.41	0.019	4	0.426	0.057	164	
<i>Sialia mexicana</i>	23.68	0.55	0.44	0.017	3	0.477	0.096	73	
<i>Catharus guttatus</i>	29.07	0.39	0.571	0.01	7	0.535	0.023	1,875	
<i>Turdus migratorius</i>	73.11	2.75	0.944	0.111	3	0.519	0.035	655	
<i>Pipilo chlorurus</i>	30.25	0.75	0.575	0.025	6	0.56	0.088	158	
<i>Junco hyemalis</i>	21.99	1.14	0.448	0.01	7	0.57	0.014	1,885	
<i>Vermivora celata</i>	8.98	0.17	0.267	0.013	7	0.565	0.027	976	
<i>Dendroica coronata</i>	12.67	0.21	0.345	0.028	8	0.551	0.038	1,008	
<i>Cardellina rubrifrons</i>	9.99	0.63	0.266	0.015	6	0.587	0.051	694	
<i>Piranga ludoviciana</i>	28.3	0.71	0.512	0.023	5	0.615	0.035	728	
Malaysia									
<i>Pachycephala hypoxantha</i>	22.99	0.43	0.399	0.007	7	0.76	.029	309	
<i>Rhipidura albicollis</i>	12.18	0.15	0.309	0.008	8	0.654	.043	230	
<i>Alophoixus ochraceus</i>	49.12	1.3	0.76	0.032	9	0.817	.037	111	
<i>Orthotomus cuculatus</i>	7.13	0.15	0.225	0.012	5	0.676	.067	77	
<i>Urosphena whiteheadi</i>	10.4	0.17	0.299	0.012	6	0.717	.069	66	
<i>Yuhina everetti</i>	13.81	0.23	0.365	0.002	2	0.751	.019	459	

<i>Zosterops atricapilla</i>	8.49	0.15	0.235	0.017	7	0.759	.053	319
<i>Stachyris nigriceps</i>	15.67	0.56	0.344	0.023	7	0.749	.014	607
<i>Trichastoma pyrrogenys</i>	18.97	0.4	0.392	0.011	5	0.849	.032	118
<i>Napothera crassa</i>	27.79	0.69	0.459	0.03	4	0.849	.025	103
<i>Rhinomyias gularis</i>	25.58	0.46	0.461	0.035	6	0.853	.023	171
<i>Brachypteryx montana</i>	20.27	-	0.448	-	1	0.835	.047	96
<i>Enicurus leschenaulti</i>	35.69	-	0.609	-	1	0.81	.065	38
<i>Myophonus borneensis</i>	116.25	4.66	1.411	0.109	4	0.822	.061	43
<i>Ficedula hyperythra</i>	8.44	0.19	0.23	0.011	5	0.658	.027	207
<i>Aethopyga siparaja</i>	6.01	0.77	0.176	0.019	2	0.766	.079	46

South Africa

<i>Cossypha caffra</i>	29.99	1.01	0.653	0.043	6	0.903	0.02	83
<i>Erythropygia coryphaeus</i>	21	0.47	0.402	0.019	6	0.777	0.02	364
<i>Pycnonotus capensis</i>	34.36	1.28	0.786	0.035	7	0.786	0.04	45
<i>Prinia maculosa</i>	9.19	0.23	0.338	0.036	6	0.706	0.02	212
<i>Apalis thoracica</i>	11.49	0.07	0.307	0.006	7	0.764	0.02	134
<i>Zosterops pallidus</i>	10.87	0.22	0.407	0.048	5	0.742	0.04	41
<i>Sphenoeacus afer</i>	28.05	1.41	0.474	0.02	3	0.838	0.05	21
<i>Sylvietta rufescens</i>	11.57	0.36	0.327	0.022	6	0.788	0.04	41
<i>Sylvia subcaerulea</i>	13.20	0.34	0.374	0.018	4	0.810	0.03	62
<i>Serinus flaviventris</i>	16.05	0.39	0.399	0.044	6	0.596	0.04	95
<i>Serinus albogularis</i>	30.50	1.41	0.640	0.013	4	0.670	0.07	24
<i>Emberiza capensis</i>	19.90	0.31	0.469	0.023	6	0.623	0.07	25
<i>Colius colius</i>	45.21	1.19	0.725	0.069	6	0.721	0.08	62
<i>Telophorus zeylonus</i>	67.65	-	1.138	-	1	0.785	0.07	13
<i>Cisticola subruficapilla</i>	10.15	-	0.298	-	1	0.629	0.05	54
<i>Anthoscopus minutus</i>	6.90	0.24	0.223	0.009	3	0.337	0.06	53
<i>Nectarinia chalybea</i>	8.08	0.2	0.298	0.031	5	0.794	0.03	55

489 **Figure Legends**

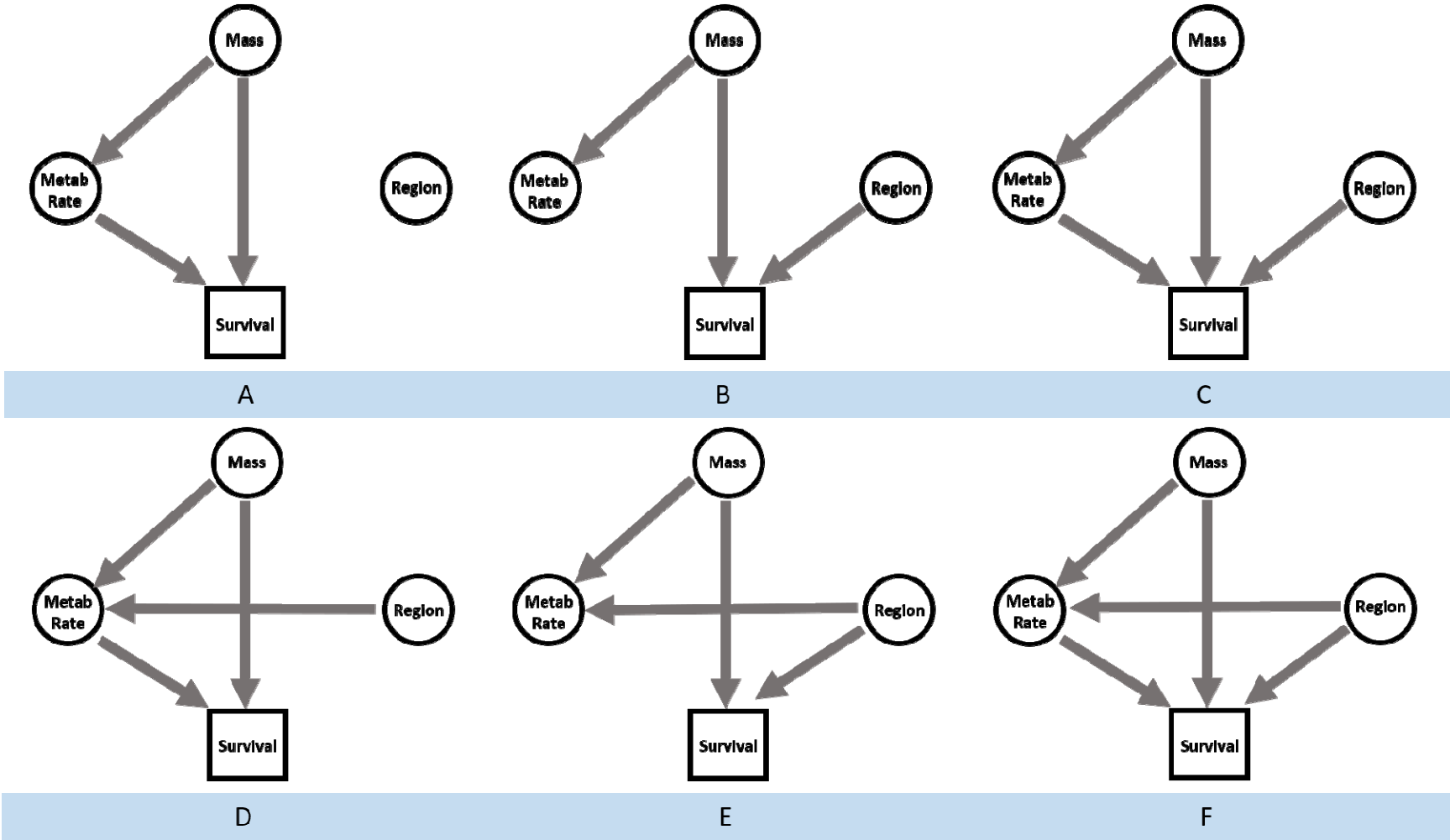
490 **Figure 1.** Our candidate model set (A-F) for phylogenetic path analysis. Models visually describe
491 possible causal relationships between body mass, metabolic rate, survival probability and site/region.
492 Metabolic rate is resting metabolic rate (RMR) for field studies and basal metabolic rate (BMR) for
493 literature data.

494
495 **Figure 2.** Allometric scaling of resting metabolic rate (A) and basal metabolic rate (B) and body mass for
496 our field and literature datasets. The relationship between resting (C) and basal (D) metabolic rate and
497 adult survival for species in our field and literature datasets. Both variables are residual values controlled
498 for body mass. Each point represents mean values for an individual species. Throughout the plots, north
499 temperate species are in black, tropical species in yellow and south temperate species in blue.

500
501 **Figure 3.** Visual and tabular representation of the causal relationships between body mass, latitude,
502 metabolic rate and adult survival probability for our field and literature datasets. Blue lines represent
503 positive relationships and negative relationships are in red. Arrows point in the direction of causality
504 (from cause to effect). The width of each arrow is proportional to the effect size in number of standard
505 deviations in variation explained according to weighted model averaging. Arrows are only present for
506 relationships present in a subset of plausible models. Bolded models in CIC_c tables are those which are
507 plausible given the data ($\alpha = 0.05$).

508
509 **Figure 4.** Allometric scaling relationships of RMR and BMR. Each point represents individual species-
510 mean values for body mass and metabolic rate. RMR measurements are in yellow, BMR points are in
511 black.

512 Fig 1



513

Fig 2

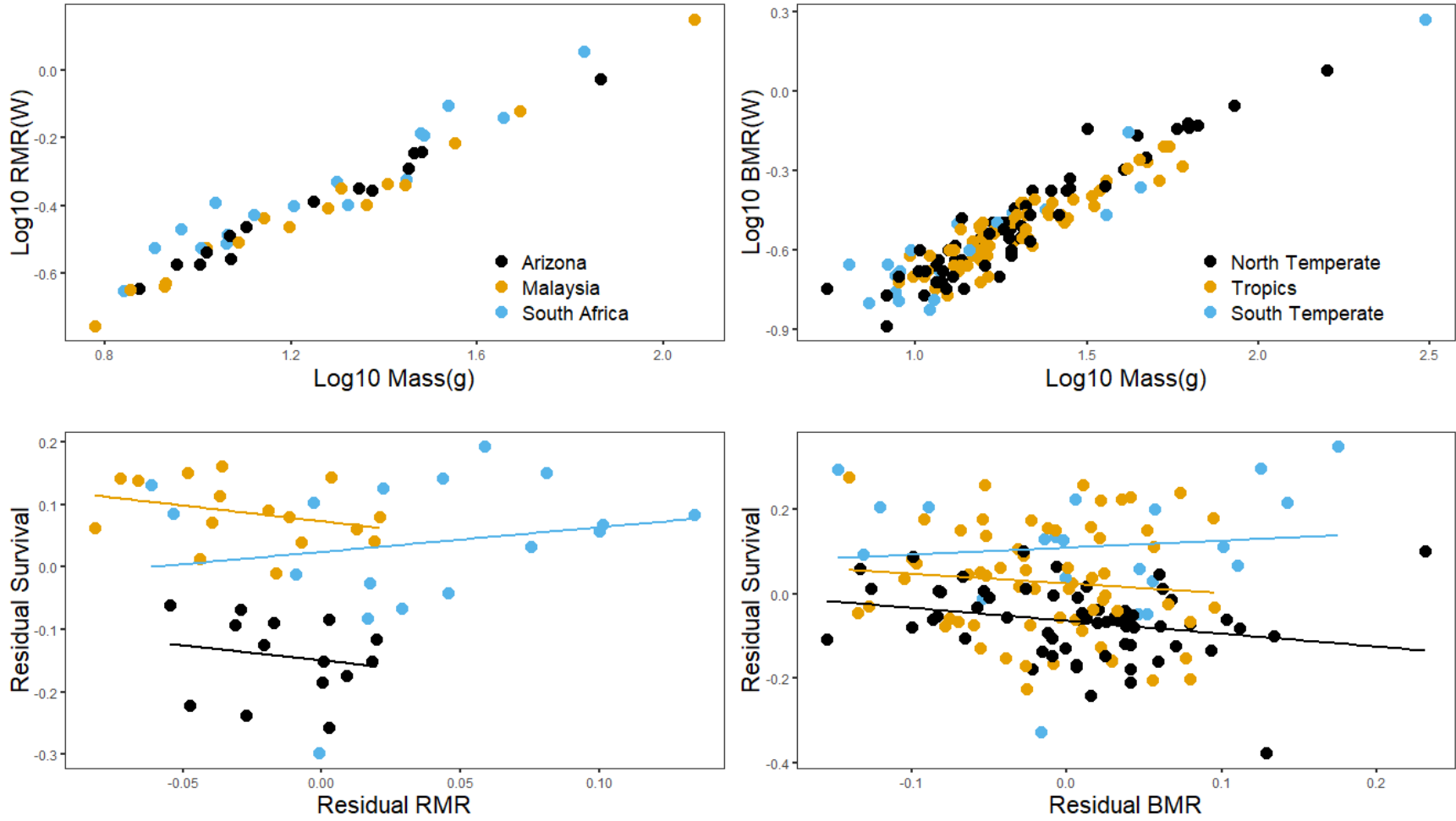
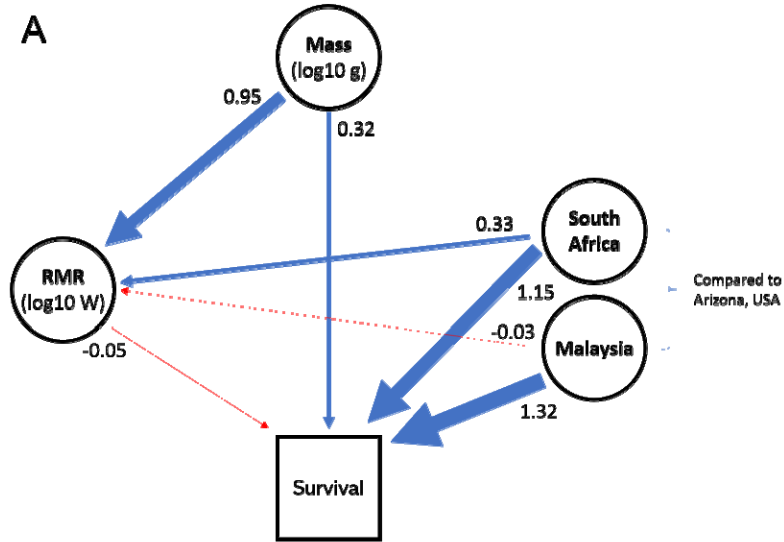
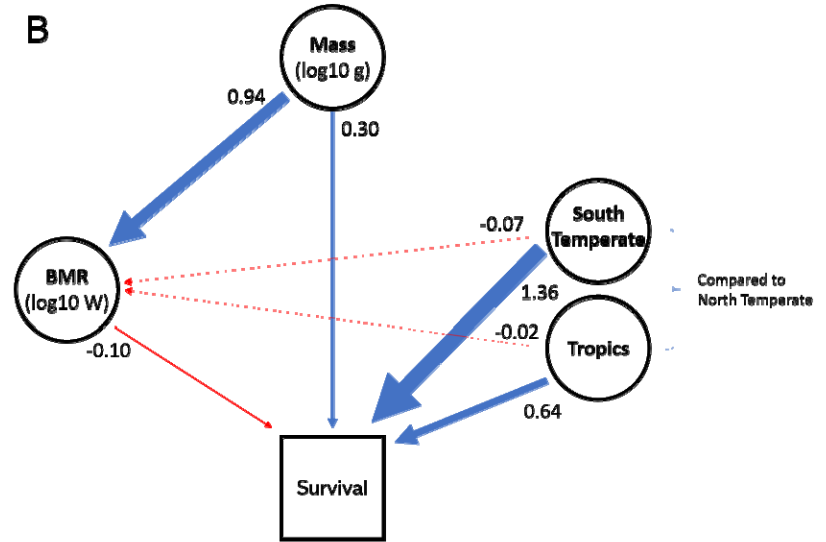


Fig 3



Model	k	C	p	CIC _c	Δ CIC _c	weight
F	1	0.059	0.971	22.924	0	0.999
D	2	18.102	0.001	37.891	14.968	0.001
E	2	18.102	0.001	37.891	14.968	0.001
B	3	25.864	<0.001	42.735	19.812	0
C	2	25.49	<0.001	45.279	22.355	0
A	3	43.533	<0.001	60.404	37.481	0

Relationship	Σ weight
RMR → Survival	0.999
Site → Survival	0.999
Site → RMR	0.999



Model	k	C	p	CIC _c	Δ CIC _c	weight
C	2	2.655	0.617	19.698	0	0.272
B	3	4.946	0.551	19.751	0.053	0.265
F	1	0.694	0.707	20.008	0.309	0.233
E	2	2.985	0.56	20.028	0.33	0.23
A	3	32.66	<0.001	47.465	27.767	0
D	2	30.699	<0.001	47.742	28.044	0

Relationship	Σ weight
BMR → Survival	0.505
Latitude → Survival	1
Latitude → BMR	0.463

Fig 4

