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JLG conceived the study and with LJ designed the specimen sampling; RL, JS, JoS, KI, JLG collected the data and MRES, JLG, TA, AP designed the analysis; MRES, TA, JLG conducted the analysis; JLG wrote the manuscript and all authors contributed manuscript feedback and read and approved the final manuscript.

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39 exchange
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Abstract

Observed variation in the body size responses of endotherms to climate change may be explained by two hypotheses: size increases with climate variability (*The starvation resistance hypothesis*); size shrinks as mean temperatures rise (*The heat exchange hypothesis*). Across 82 Australian passerine species over 50 years, shrinking was associated with annual mean temperature rise exceeding $0.012^{o}C$ driven by rising winter temperatures for arid and temperate zone species. We propose *the warming winters hypothesis* to explain this response. However, where average summer temperatures exceeded $34^{o}C$, species experiencing annual rise over $0.0116^{o}C$ tended toward increasing size. Results suggest a broad-scale physiological response to changing climate, with size trends likely reflecting the relative strength of selection pressures across a climatic regime. Critically, a given amount of temperature change will have varying effects on phenotype depending on the season in which it occurs, masking the generality of size patterns associated with temperature change. Rather than phenotypic plasticity, and assuming body size is heritable, results suggest selective loss or gain of particular phenotypes could generate evolutionary change, but may be difficult to detect with current warming rates.

Introduction

Animal body size is predicted to decline in response to climate warming, in line with the global pattern of size variation known as Bergmann's Rule: smaller bodies tend to be associated with warmer, lower latitude climates and larger bodies with cooler higher latitudes [1], although the mechanisms underlying variation in body size remain contentious [2]. This relationship between body size and climate has also been observed across geological timeframes with reductions in body size associated with warming climates over millenia [3,4]. The nature and scale of these patterns have given rise to the prediction of pervasive

66   reduction in body size as the climate warms [4,5]. Because body size directly affects energy

67   and water requirements for thermoregulation, and rates of energy uptake and expenditure

68   [6,7,8], changes in body size have implications for thermal biology and energetics with

69   consequences for individual fitness and thus population dynamics.

70   Despite the prediction of declining body size, studies have reported considerable variation in

71   climate-related size trends over the last 50-100 years. While some species have declined in

72   size, others have increased or shown no change over time [reviews: 9-12]. Two hypotheses

73   have been advanced to explain this variation in endotherms. The heat exchange hypothesis

74   [sensu 13] suggests that smaller body sizes will be favoured in a gradually warming climate

75   because smaller bodies are more efficient at dissipating heat; this explanation relates to a

76   mechanistic link with thermoregulation, either in relation to increased capacity for heat

77   dissipation [14] or a reduction in the need for heat conservation [15].

78

79   The starvation resistance hypothesis (also known as the fasting endurance hypothesis)

80   suggests that unpredictable environments should favour larger-bodied individuals because

81   larger size increases resistance to starvation via capacity to carry more body reserves [8,16].

82   Energy stores increase with body size faster than does metabolic rate, so resistance to

83   starvation will increase with increasing body size [17]. In the context of climate change, [18]

84   suggested that observed increases in climate variability may reduce the predictability of

85   resources, with potential to increase starvation risk, hence selecting for increasing body size

86   with improved capacity to endure extreme events.

87

88   A special case of the starvation resistance hypothesis relates to the increase in frequency of

89   heatwaves that is associated with a warming climate [19]; more frequent and extreme

90   heatwaves are an important signature of current climatic variability [20]. Smaller individuals

91   exposed to heatwaves use disproportionately more energy and water to dissipate heat than

92   larger individuals (due to their greater surface area to volume ratio), while having

93   proportionately fewer reserves available [21,22]. Larger-bodied individuals are expected to

94   be favoured in such events, particularly when environmental temperatures exceed body

95   temperature and the only avenue for dissipating heat is via evaporative cooling [22, 23]. This

96   hypothesis implies climate-related hard selection via size-dependent mortality; smaller

97   individuals will be selected against in heatwaves leading to a mean increase in the body size

98   of populations over time. When ambient temperatures regularly exceed body temperature,

99   smaller body size ceases to be an advantage but becomes a liability.

100

101   Here, we test these hypotheses using a large dataset of body size measurements of 82 species

102   of Australian birds from the Infraorder Meliphagides [*sensu* 24], formerly Meliphagoidea, a

103   large and diverse radiation of Australasian passerines that include the honeyeaters, fairy-

104   wrens, pardalotes, thornbills and allies [25] (Table S1). We characterised changes in body

105   size for each species over the last ca 50 years (1958-2010), during a period of rapid climate

106   change, using 12,029 museum specimens sampled from multiple populations across the

107   distribution of each species (Fig. S1). We then calculated the change in annual mean

108   temperature, annual mean monthly rainfall and annual mean maximum summer temperature

109   in each species' distribution over the same 50-year period. We predicted that (1) body size

110   will tend to decrease over time more in species that have experienced larger increases in

111   mean ambient temperature over time (the heat exchange hypothesis); (2) body size will tend

112   to increase over time in environments with higher summer maximum temperatures that

113   regularly exceed body temperature (the starvation risk hypothesis).

114

115   **Methods**

116   *Study Species*

117   Our study focused on species from the Infraorder Meliphagides [*sensu* 24], formerly

118   superfamily Meliphagoidea), the largest radiation of Australasian passerines, consisting of

119   five families and some 276 species of which 145 are Australian; they comprise almost one

120   third of Australia's passerines [25]. The group comprising honeyeaters, fairy-wrens,

121   pardalotes, thornbills and allies, displays great diversity in life history, ecology and

122   morphology, spanning a wide range of body sizes (6-260 g) and climatic regions (from desert

123   to tropics), and together with their well-resolved phylogeny [25,26], they are an ideal group

124   for investigating responses to environmental change.

125

126   *Museum specimens*

127   Specimens examined from the major museums in Australia were collected between 1960 and

128   2010 (Table S1). Specimen localities spanned about 35° of latitude (10 to 45° S). We sampled

129   multiple populations across each species' range in Australia, including Tasmania (Fig. S1) in

130   order to minimise effects of local factors that can affect body size, such as predation pressure

131   and intraspecific competition. We aimed to quantify species-level responses to broad

132   environmental change, testing overaching hypotheses for causes. For each species, we

133   examined between 20 and 702 specimens (mean 146) (Table S1). We included 11 species

134   with <50 individuals because, although sample sizes are small, these species are relatively

135   well sampled for their small ranges (Table S1). Eight of the 11 species with the smallest

136   sample sizes also have some of the smallest ranges, and so are relatively well-sampled (Table

137   S1). The remaining 3 species (pied honeyeater, *Certhionyx variegatus*, black honeyeater

138   *Sugomel niger*, striped honeyeater, *Plectorhyncha lanceolata*) occur in relatively large

139   ranges. However, these species are nomadic and/or irruptive following good conditions so

140   their core range/distribution is smaller than the range maps would indicate (Fig. S1). All

141   occur in the more extreme (and remote) arid environments which are difficult to sample but

142   represent important species in the context of the questions we address.

143

144   *Body size measurement*

145   We measured the length of the flattened wing chord from the carpal joint to the tip of the

146   longest primary, recording to 0.5mm using a butt-ended ruler, as a measure of structural body

147   size. Each species was measured by a single observer. Among passerines, wing length is the

148   best linear predictor of body mass, and accordingly may be used as an index of body size

149   [27]. Some authors have used tarsus or culmen length as indices of body size because these

150   traits are less variable across an individual's life. However, both are subject to Allen's Rule,

151   which predicts a decrease in such traits with increasing latitude, opposite to Bergmann's Rule

152   [28]. This is because in warmer climates appendages of endotherms that play a role in

153   thermoregulation as a source of heat loss will be larger to allow for dissipation of heat loads

154   [29]. Thus, as temperatures rise, increases in bill and tarsus length are predicted and have

155   been demonstrated in several bird species [29, 30]. From the associated metadata we recorded

156   the sex, year of collection and location (latitude, longitude) at which each specimen was

157   collected. We estimated two additional parameters using Geographic Information Systems:

158   altitude, estimated from the latitude and longitude from each specimen, and nearest direct line

159   (orthodromic) distance to the coastline. We used distance to coast instead of longitude as a

160   measure of geographic location because individuals at the same longitude may experience

161   very different temperatures depending on their position relative to the coast. We assigned an

162   abrasion score of 1-12 based on month of capture, with 1 = new feathers assigned to birds

163   captured in March and 12 = old, abraded feathers for captures in February. This is based on

164   our knowledge of moult in Australian birds - most species moult Dec-March after breeding.

165

166   *Data sets*

167   *(a) Body size*

168   We measured 12,667 individuals of 93 species from the Infraorder Meliphagides [*sensu* 24],

169   formerly superfamily Meliphagoidea) (Table S1). We excluded known juveniles and

170   immatures based on skull ossification recorded during specimen preparation and available

171   from the associated metadata, individuals for which there was no month of capture because

172   abrasion score could not be estimated and 545 individuals for which no sex was recorded

173   from gonads and the sexes were not dichromatic.

174

175   *(b) Climate data*

176   We extracted climate data for the distribution of each species. These data were generated

177   using the ANUClimate 1.0 spatial model [31]. This model produces monthly Australian

178   climate variables for the period January 1970 to December 2013 on a 0.01° longitude/latitude

179   grid interpolated from Australian Bureau of Meteorology national point climate data. We

180   collated monthly estimates of rain, minimum temperature and maximum temperature for the

181   years 1970 to 2012 (one raster for each month x year x climate variable combination). We

182   then extracted summary values for each raster from within each species range (we converted

183   the species range to a raster and used this as a mask for zonal statistics on the climate rasters).

184   These summary values were then tabulated to a .csv file for each species.

185

186   *(c) Climate variables*

187   We created climate variables as follows. Change in annual mean temperature: we calculated

188   the mean temperature for each year for each species, based on mean temperature for each

189   month, extracted for all cells in the distribution of each species. We then fitted annual mean

190   temperature as a response variable and year as an explanatory variable fitting models for each

191   species separately to extract the rate of change over time (year estimate), for use in

192   subsequent models. Models were fitted using the "lm" function in R. Mean monthly rainfall

193   was calculated by averaging mean rainfall for each month. Mean summer maximum

194   temperature was calculated by averaging mean maximum temperature for the hotter months

195   in each year, December, January, February. For our post-hoc analysis we calculated the

196   change in mean minimum winter temperature and change in mean maximum summer

197   temperature using the same procedure as described above for estimating change in mean

198   temperature. We defined winter as the months June, July, August and summer as December,

199   January, February.

200

201   (d) *Climate zones*

202   We calculated the proportion of each species' distribution that occurs in equatorial, arid or

203   temperate climate zones using the Köppen-Geiger climate classification (K-G GIS layer,

204   [32]). We classified species as arid/temperate if >70% of their distribution fell within arid or

205   temperate or arid and temperate zones; tropical species were those with >70% of their

206   distribution in the equatorial zone. Species that were widespread, occurring in both tropical

207   and arid/temperate zones were excluded from our post-hoc analysis.

208

209   *Statistical Analyses*

210   The analysis of the data was done in several steps. First, we estimated temporal change in

211   body size for each species. Then we used these species-specific rates of size change to test for

212   associations between changing climate and body size.

213

214   *(a) Patterns of year-to-year variation*

215   We used generalized additive models to describe patterns of year-to-year variation in body

216   size, using separate models for each species. The response variable was the wing length of

217   each specimen and the explanatory variables were the year of collection (with a smooth

218   function), latitude, altitude, distance to the coastline, abrasion score and sex of each

219   specimen. All the explanatory variables but the year of collection were centred before the

220   analysis. The models were fitted using the 'mgcv' package [33] in R version 2.15.2 [34]. We

221   assumed a normal distribution and identity link function and estimated the degree of

222   smoothness of the year function using the Generalized Cross Validation with $\gamma = 1.4$ to avoid

223   overfitting [33]. To avoid multicollinearity among the explanatory variables, we first

224   estimated pair-wise Pearson's correlation coefficients between the explanatory variables

225   (Table S2) and confirmed that correlations were not high for any of the combinations ($|r$

226    $|<0.65$).

227

228   To account for model selection uncertainty, we adopted a multi-model inference approach

229   based on AIC (Akaike Information Criterion) [35]. For each species, we first generated a

230   candidate set of models with all possible parameter subsets, which were then fitted to the data

231   and ranked by ΔAIC values (the difference between each model's AIC and AIC$_{min}$, the value

232   of the "best" model). Models with ΔAIC < 2 are usually considered to have substantial

233   support [35]. We considered species to show important inter-annual variation in body size if

234   they have a smoothed year term in, at least, one of the models with ΔAIC < 2 (Fig S2). For

235   the visual inspection of the estimated smoothed function, we used the result based on the

236   model with the smallest AIC that included the smoothed year term.

237

238   *(b) Rates of temporal size change*

239   For species showing linear or near linear change in body size across time (effective degrees

240   of freedom < 3 in the full model; edf shows the flexibility of the smoothed function) we

241   calculated the annual rate of size change. After removing 11 species with edf >3, the final

242   data set contained 82 species (Table S1). We fitted separate linear regression models for each

243   species with body size (wing length) as the response variable and year as the explanatory

244   variable, while controlling for sex, age, altitude, latitude and distance to coast when identified

245   in the generalized additive models as important. Residual plots and normal probability plots

246   were used to check for deviations from normality among residuals. All models were fitted

247   using the lm function in R.

248

249   (c) *Comparative analysis*

250   We used Phylogenetic Generalised Least Squares (PGLS) to test for associations between

251   climate and changes in body size over the last 50 years for 82 species of Meliphagides. This

252   approach controls for the phylogenetic relatedness between species by applying a

253   phylogenetic variance-covariance matrix to the linear regression [36]. The analysis was

254   implemented through the R package, *caper* [37]. The phylogeny employed was taken from

255   the maximum likelihood tree produced for the Meliphagides [25], with the tree made

256   ultrametric using the chronoPL function in the ape package [38]. To account for model

257   selection uncertainty, we adopted a multi-model inference approach based on AIC (Akaike

258   Information Criterion) as described above.

259

260   We used the slope of the relationship between body size and year for each species (estimated

261   as described above in 'Rates of temporal size change') as the response variable and fitted the

262   climate variables (change in mean temperature, mean monthly rainfall, and mean summer

263   maximum temperature, and 2 two-way interactions - change in mean temperature : mean

264   summer maximum temperature, and change in mean temperature : mean monthly rainfall) as

265   explanatory variables, controlling for phylogenetic relatedness. All variables were *z*-

266   standardised prior to analysis. Because the response variable comprised single point estimates

267   of the relationship between body size and year without acknowledging the error in those

268   estimates, we also conducted a second analysis where the response variable was a random

269   value taken from the normal distribution with mean equal to the observed estimate, and

270   standard deviation equal to the standard error around that estimate. The final model estimates

271   here were the mean of the estimates derived from 1000 simulations.

272

273   (d) *Post-hoc analyses*

274   To test whether the declines in body size we observed (see results) were associated with rates

275   of warming in winter versus summer, we undertook the following post-hoc analysis. We used

276   the slope of the relationship between body size and year as the response variable and fitted

277   climate variables (change in winter temperature, change in summer temperature, mean

278   summer maximum temperature, mean winter minimum temperature) and two interactions

279   (between mean winter temperature and mean change in winter temperature; and between

280   mean summer temp and mean change in summer) as explanatory variables. We included only

281   arid and temperate species, and controlled for phylogenetic relatedness as in the main

282   analysis. As above, we also repeated the analyses using repeat simulations of the response

283   variable. There were only 8 tropical species in our dataset, too few to detect an effect.

284

285   **Results and Discussion**

286   Annual mean temperature has increased over the last 50 years in 81 of the 82 species'

287   distributions we considered (Fig. 1). In contrast, patterns of mean rainfall showed

288   considerable variation across distributions with some showing increases in mean rainfall and

289   others declines or no change (Fig. 1).

290

291   Change in mean temperature, rather than summer temperature or rainfall, showed the

292   strongest association with estimates of body size changes across species, and was the only

293   climate variable included in all top models (Table 1). Similar estimates to those in Table 1

294   were derived from 1000 model simulations where errors in the estimates of body size change

295   were taken into account, providing strong support for this result (Table S3). Declines in body

296   size start to be observed in cases where the rate of mean temperature change within a species'

297   distribution exceeded 0.012°C per year (1.2°C per 100 years), consistent with the heat

298   exchange hypothesis (Fig. 2). Given the diversity of species and habitats included in our

299   analyses, the identification of a rate of temperature change beyond which declines in body

300   size were observed suggests a broad-scale physiological response to changing climate.

301

302   Although there was no association between body size and mean maximum temperature *per*

303   *se*, a shift in the extent and direction of size change was observed for species experiencing

304   both high levels of warming and high summer temperatures (Table 1). Fig. 2b indicates that

305   above about 34°C, no decreases in body size are predicted, regardless of amount of

306   temperature change experienced (all of the model predictions > 0), and for species

307   experiencing greater than 0.0116°C (the point at which the regression lines intersect in Fig

308   2c), body size may even increase in warmer climates (interaction Tmax x Tmean; Fig. 2;

309   Table 1, Table S3). Increasing body size to increase body reserves as climate variability

310   increases is consistent with the starvation resistance hypothesis in the context of heatwaves.

311   Our result is unlikely to be an artefact of sampling because the species included in the

312   analysis covered the entire range of these two variables: 67% of species (55/82 species)

313   experienced >0.01166°C per year change, with 38 species experiencing mean maximum

314   summer temperatures below 34°C and 17 species exceeding 34°C (Fig. 2). When

315   environmental temperatures exceed body temperature (ca. 40°C) the only avenue for birds to

316   dissipate body heat is via evaporative cooling, with small bodied individuals particularly

317   vulnerable to dehydration and mortality because of their disproportionately large surface

318   areas [21,22]. Smaller individuals thus face twin costs under heatwave conditions: lower

319   energy and water reserves, and disproportionately high rates of water loss. Accordingly, the

320   benefit of smaller body size is plausibly outweighed by the costs of exposure to extreme

321   temperatures during heatwaves.

322

323   Recent work by [39] examined evaporative cooling capacity and heat tolerance in 5 passerine

324   species in Australia's arid zone, including two of the species in this study (yellow-plumed

325   and spiny-cheeked honeyeaters). They confirmed the reliance of these species on evaporative

326   heat loss via panting at high air temperatures, consistent with studies of other Australian

327   passerines. When air temperatures exceeded 38°C rates of evaporative water loss (EWL)

328   increased rapidly and linearly to 7-fold (670-860%) above basal rates [39]. Moreover, rates of

329   EWL scaled negatively with body mass with smaller-bodied individuals more vulnerable to

330   dehydration, consistent with our result. This work accords with recent studies showing that a

331   body temperature of 45°C is the upper limit to physiological function in most birds [39]. In

332   contrast, increase in metabolic rate associated with the onset of panting varied considerably

333   among species, suggesting that dehydration rather than energy balance represents the greatest

334   threat to species in heatwaves [23]. Thus, although our results are consistent with the

335   starvation risk hypothesis, they also suggest the significance of maximizing resistance to

336   dehydration in the face of increasing heatwaves.

337

338   Empirical studies of wild populations identify air temperatures in the mid-30s as potentially

339   harmful, with individuals unable to maintain body condition following prolonged exposure to

340   such temperatures, sometimes leading to size-dependent mortality [40,41]. In a population of

341   Australian white-plumed honeyeaters, *Ptilotula penicillata*, repeated exposure to daily

342   maxima >35°C in a semi-arid region was associated with increases in mean body size over a

343   time scale of decades, apparently via the loss of small individuals from the population [42].

344   This effect appeared to be mediated by size-dependent effects of weather on body condition;

345   smaller individuals lost more mass when exposed to high temperatures and were less likely to

346   survive to the following spring [41]. Our observed mean summer temperature threshold of

347   about 34°C, at which no decrease in body size is predicted, is remarkably consistent with

348   empirical studies that identify prolonged exposure to air temperatures >35°C as harmful, and

349   is also consistent with hard selection because the observed change in avian body size aligns

350   with known physiological tolerances associated with fitness [21,22, 23].

351

352   Although recent attention has mainly focused on spring and summer temperatures in

353   mediating size changes under global warming, declining body size may also be associated

354   with reduced selection pressures on small individuals experiencing warmer autumns and

355   winters, leading to their higher survival. Winter is considered a challenging time, and can

356   cause direct mortality via cold stress, reductions in immune function, or energetic constraints

357   as a result of resource shortages [43,44]. Indeed, energetic costs of thermoregulation in

358   winter during periods of low food availability can exceed those during the breeding season

359   [43]. Moreover, winter mortality is often observed to be size-dependent with the smallest

360   individuals suffering higher mortality, contributing in part to the widely accepted rule for

361   positive viability selection on body size [45]. Accordingly, reduced selection pressures

362   associated with warming winters may increase the survival of smaller individuals leading to

363   an incremental decrease in mean body size over time; hence we propose "the warming

364   winters hypothesis". Because animals are acclimatized to local conditions and winter

365   represents the harshest conditions in temperate environments, a release from selection

366 pressures associated with a given level of temperature rise (here 1.2°C/100 years) is likely to

367 have similar effects across all populations, in this case favouring smaller individuals,

368 regardless of the severity of winter conditions experienced.

369

370 By comparison, the decrease in body size we observed across species is less likely to relate to

371 warming summers because the same rate of warming will have different effects on body size

372 depending on the thermal tolerances of individual species and the summer conditions each

373 experiences [7,21]. Only if rising temperatures push individuals beyond the upper bound of

374 the thermoneutral zone (TNZ) - the range of air temperatures where no additional energy and

375 water are specifically allocated to maintain homeostasis - will the adaptive significance of

376 body size change. Because the location of the TNZ varies among species due to differences

377 in body size and shape [7, 23] and phylogeny [46], a given degree of temperature change is

378 likely to affect species differently. Indeed, our post-hoc analysis found that declining body

379 size was associated with increasing winter, but not summer, temperatures for arid and

380 temperate species in line with our warming winters hypothesis (Table 2, Table S4).

381

382 Analysis of long-term data sets of wild populations provide some of the strongest evidence

383 that temporal declines in body size may be associated with a release from winter stress. In

384 Soay sheep, *Ovis aries*, warmer winters have led to higher survival of smaller individuals,

385 leading, in part, to a decline in body size over the last 30 years [47]. A similar pattern was

386 observed in a much milder climate in Western Australia where winters do not generally

387 involve sub-zero temperatures. Warmer winter conditions were associated with higher

388 survival of smaller individuals in two small passerine species monitored over 39 years [48].

389 Although most evidence suggests that shifts in body size are climate related, density-

390 dependent effects (e.g. competition for food) are also likely to be important and drive

391   complex size patterns. However, such effects are likely to be site specific so unlikely to

392   account for the broad scale patterns observed.

393

394   In contrast to species in temperate climates, relaxation in selection pressure is unlikely to

395   account for temporal declines in endotherm body size in the tropics which experience low

396   seasonality and limited temperature range. As temperatures rise, selection pressures in the

397   tropics are more likely associated with increasing costs of keeping cool, favouring smaller

398   body sizes with increased capacity for heat dissipation. James [14] argued that selection for

399   smaller body size is particularly strong in the tropics because high temperatures coincide with

400   high humidity which reduces the gradient driving evaporation, thereby limiting heat loss.

401   Smaller bodies with relatively larger surface areas are therefore advantageous [49]. In

402   addition, the capacity for acclimatization is likely limited for tropical species because they

403   experience narrow daily and seasonal temperature range [50], so a given increase in

404   temperature is likely to impose greater costs on tropical compared with temperate species.

405   Thus, although a warming climate might favour smaller body sizes in both the tropics and

406   temperate regions, the underlying mechanisms may differ. Our dataset included only 8

407   tropical species, and so lacked the necessary power to test for an effect.

408

409   Overall, our study suggests that avian body size is indeed responsive to climate change

410   [contra 12,51], and that climate-driven changes in body size are both temperature-related and

411   founded in a physiological response to changing conditions. Temperature-related effects may

412   account for global patterns of changing body size in the absence of extreme events, (both

413   summer and winter), and regardless of rainfall patterns which have previously been suggested

414   as important in driving selection [52] even though water availability differs between northern

415   and southern hemispheres [53] and rainfall patterns are highly variable at regional scales

416   [54]. We found no evidence that rainfall directly underlies body size trends at the species

417   level; rainfall and its interaction with mean temperature were included in the top model, but

418   their effects were weak (Table 1). Nevertheless, rainfall can mediate responses to

419   temperature, in both hot and cold conditions, as well as affect foraging behavior and food

420   availability [55,56]. Rainfall is therefore likely to be integrally linked with climate-driven

421   changes in physiology at the level of populations.

422

423   More broadly, the suggestion that changes in food availability driven by climate-related

424   changes in primary production underlie observed temporal trends in body size across species

425   [12, 52] seems unlikely on the basis of our results. With the exception of the relatively small

426   alpine zone, primary productivity on the Australian continent is regulated and constrained by

427   rainfall and plant water availability rather than temperature *per se* [54], and climate change

428   impacts on rainfall regimes are varying greatly at regional scales [57]. Accordingly, body size

429   trends we observed across species that inhabit different climatic zones and regions are

430   unlikely to be associated primarily with rainfall-related variation in primary productivity. To

431   further address this issue, we re-ran our main model replacing mean monthly rainfall with

432   change in rainfall (estimated using the same method as for change in mean temperature).

433   Models with rainfall change were a poorer fit to the data compared with the equivalent

434   models using mean rainfall (best model with rainfall change included AIC: 235.0 versus

435   231.7 for best model with mean rainfall), and the top model did not include rainfall change,

436   (and was the same as model 3 in Table 2), supporting our conclusion. Moreover, in the

437   northern hemisphere, primary production is associated primarily with temperature not rainfall

438   [58], so it seems unlikely that changing primary production underlies global trends in body

439   size if the drivers of productivity differ between hemispheres.

440

441   Our findings have important implications. We provide strong evidence for changes in body

442   size as a response to climate change, with multiple mechanisms likely to underlie species'

443   responses. Temporal trends in body size are likely to reflect the relative strength of selection

444   pressures at different times of the year and different phases of a climatic regime, including

445   release from winter conditions as well as increased pressure from summer extremes [e.g. 59].

446   To date, most studies have focused on the negative consequences of extreme events but our

447   results also highlight the potential importance of relaxation in winter conditions. Given the

448   importance of temperature extremes in this context, birds might indeed be considered the

449   'canaries in the coalmine' because they are likely to be more responsive to changing climate

450   than are mammals, being diurnal, with small body sizes, and limited in their capacity to store

451   body reserves because of the demands of flight. This may explain, in part, the finding that

452   mammals are less likely to show temporal size change than birds [12].

453

454   When analyzing size trends, studies should consider the rate of temperature change

455   experienced, given that our results suggest that declines in body size are triggered only when

456   increasing mean temperature exceeds 0.012°C per year. Studies that include climate variables

457   as predictors often fit static measures, omitting rates of change, and critically ignore the

458   season (window) in which the temperature change has occurred. A recent study by [60]

459   concluded that there was no evidence that warmer mean temperatures are associated with

460   selection for smaller body size. However, our results suggest that a given amount of (mean)

461   temperature change will result in differing effects on phenotype depending on the season in

462   which the temperature change occurs. For example, a given mean temperature change that

463   occurs in winter might be associated with declining size, but not when it occurs in spring.

464   Similarly, selection on body size associated with rising summer temperatures will only be

465   detectable in species where the given increase in mean temperature occurs in summer, and

466   pushes the species beyond its TNZ thereby changing the selection pressure. Attempts to find

467   associations between selection gradients for size and mean temperature change are therefore

468   unlikely to succeed. This is especially the case where selection gradients are derived from

469   differing, often short, timeframes [60], making it even more difficult to detect patterns.

470

471   We agree with [12] that more data are needed on how climatic factors shape selection

472   pressures and the adaptive nature of temporal size trends in relation to climate change.

473   Nevertheless, although most evidence to date suggests that shifts in body size are the result of

474   phenotypic plasticity, our results raise the possibility that change in the composition of a

475   population via the selective appearance or disappearance of particular phenotypes could

476   generate evolutionary change, assuming body size is heritable [61]. However, detecting such

477   shifts may be difficult if rising temperatures are only now reaching levels at which changes in

478   selection pressures may occur, and the translation from effects on individuals to population-

479   level changes in mean body size are likely to be incremental. This may account for difficulty

480   thus far in detecting microevolutionary responses to climate change [62].

481

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660   **Figure Legends**

661

662   **Fig. 1**. Temporal trends in (a) body size (wing length) and (b) mean annual temperature and

663   (c) mean summer maximum temperature and (d) mean monthly rainfall across 50 years (1970

664   – 2010) for 82 species of passerine bird in the Meliphagides. Each line represents a single

665   species, and the order of species is the same in each panel. We calculated mean temperature,

666   mean summer maximum temperature and mean monthly rainfall for each year for each

667   species, based on values for each month, extracted for all cells in the distribution of each

668   species. Solid green dots represent significant change in body size; green circles indicate

669   trends.

670

671   **Fig. 2**. Association between the change in structural body size (wing length) and change in

672   mean annual temperature, given mean maximum summer temperature for 82 species of

673   passerine bird from Meliphagides [*sensu 24*], formerly superfamily Meliphagoidea). (a) 3D-

674   representation of the phylogenetic generalised least squares model predicted relationship; (b)

675   2D-representation showing species data points, PGLS regression lines for the relationship

676   between change in body size and mean summer maximum temperature showing species that

677   experience different degrees of temperature change with PGLS model regression lines for 0,

678   0.004, 0.008, 0.012, 0.013, 0.014. 0.015 and 0.016 °C increase in mean temperature; (c)

679   similar representation of relationship between change in body size and change in mean

680   annual temperature showing species that experience different mean summer temperatures:

681   model lines represent relationship at 18, 23, 28, 33 and 38 °C (colours as represented in

682   legend).

683

684   **Table 1**. Top phylogenetic generalized least squares models (ΔAIC<2) predicting body size

685   changes over time in 82 species of Meliphagides. Predictors are ΔT_{mean}: mean temperature

686   change (°C / year), T_{max}: mean summer maximum temperature (°C), Rain: mean monthly

687   rainfall (mm), and all interaction terms. Response variable is the regression slope estimate of

688   body size over time for the species. All variables were standardised and model estimates

689   (with standard errors) are shown for each model (larger estimates are therefore larger effects).

690   W_i = Akaike weight of the model. Parameter estimates in the models that were statistically

691   significant (at α = 0.05) are indicated in bold.

692

Model	ΔT_{mean}	T_{max}	Rain	ΔT_{mean}:T_{max}	ΔT_{mean}:Rain	R^2	ΔAIC	w_i
1	**-0.904** (0.248)	-0.133 (0.154)	-0.338 (0.180)	**0.548** (0.211)	0.317 (0.182)	0.149	0	0.254
3	**-0.682** (0.217)	-0.229 (0.144)	**-0.361** (0.181)	**0.403** (0.198)		0.114	0.879	0.164
4	-0.169 (0.110)					0.029	1.729	0.107

693

694   **Table 2.** Top phylogenetic generalized least squares models (ΔAIC<2) predicting body size

695   changes over time for 64 temperate and arid zone species of Meliphagides. Predictors are

696   mean minimum winter temperature (T_{winter}), mean summer maximum temperature (T_{summer}),

697   and the mean change over time (°C / year) for both measures (ΔT_{winter} and ΔT_{summer}, for winter

698   and summer temperatures respectively). Response variable is the regression slope estimate of

699   body size over time for the species. All variables were standardized and model estimates

700   (with standard errors) are shown for each model (larger estimates are therefore larger effects).

701   W_i = Akaike weight of the model. All parameter estimates in the models that were statistically

702   significant (at α = 0.05) and are indicated in bold.

703

Model	T_{winter}	T_{summer}	ΔT_{winter}	ΔT_{summer}	R^2	ΔAIC	w_i
1	**1.354** (**0.535**)	**-1.803** (**0.547**)	**-0.978** (**0.340**)	0.510 (0.292)	0.349	0	0.187
2	0.837 (0.469)	**-1.294** (**0.492**)	**-0.592** (**0.277**)		0.257	0.493	0.146
3					0	0.573	0.140
4		-0.540 (0.298)	-0.610 (0.298)		0.136	0.963	0.116
5			-0.178 (0.186)		0.032	1.911	0.072

704