



Smaller beaks for colder winters: Thermoregulation drives beak size evolution in Australasian songbirds

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**Smaller beaks for colder winters: thermoregulation drives
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1 Abstract

2

3 Birds' beaks play a key role in foraging, and most research on their size and shape

4 has focused on this function. Recent findings suggest that beaks may also be

5 important for thermoregulation, and this may drive morphological evolution as

6 predicted by Allen's rule. However, the role of thermoregulation in the evolution

7 of beak size across species remains largely unexplored. In particular, it remains

8 unclear whether the need for retaining heat in the winter or dissipating heat in

9 the summer plays the greater role in selection for beak size. Comparative studies

10 are needed to evaluate the relative importance of these functions in beak size

11 evolution. We addressed this question in a clade of birds exhibiting wide

12 variation in their climatic niche: the Australasian honeyeaters and allies

13 (Meliphagoidea). Across 158 species, we compared species' climatic conditions

14 extracted from their ranges to beak size measurements in a combined spatial-

15 phylogenetic framework. We found that winter minimum temperature was

16 positively correlated with beak size, while summer maximum temperature was

17 not. This suggests that while diet and foraging behavior may drive evolutionary

18 changes in beak shape, changes in beak size can also be explained by the beak's

19 role in thermoregulation, and winter heat retention in particular.

20

21 **Introduction**

22

23 Many phenotypic traits are multifunctional, and thus understanding their
24 evolution in terms of adaptation and constraint can be a challenge (Gould and
25 Lewontin 1979; Wainwright 2007). Even if a trait is critically important for
26 maintaining one function, trait divergence among species may be driven by
27 selection on a second, sometimes less obvious, function (Cox et al. 2003; Ellers
28 and Boggs 2003). Bird beaks exhibit a stunning diversity in size and shape
29 (Cooney et al. 2017), and no doubt this diversity reflects the functional
30 importance of beaks in a variety of selective contexts (Willson et al. 1975; Gill
31 2007). Bird beaks are obviously critical for foraging, and the relationship between
32 beak size, shape and diet in Darwin's finches (Grant et al. 1976; Grant and Grant
33 2002) is now the cornerstone of many introductory lectures on natural selection.
34 However, beaks have also been shown to function as thermoregulatory
35 structures. They can function akin to radiators as they shed heat through
36 convection without losing water (Tattersall et al. 2009; Greenberg et al. 2012a),
37 an effect that can be augmented by vasodilation or reduced by vasoconstriction
38 (Hagan and Heath 1980). Thus a large beak may be adaptive in hot
39 environments, but present a problem for heat retention in cold environments
40 (Danner and Greenberg 2015). Given these different functions – heat radiation,
41 heat retention and foraging – it is unclear which factors are most responsible for
42 the evolution of bird beak size during diversification.

43

44 Thermal constraints are known to lead to large-scale variation in morphology. In
45 particular, Allen's rule (Allen 1877) is a classic ecogeographic pattern for

46 endothermic organisms that describes a gradient in extremity length varying with
47 climate. It predicts that selection will lead to individuals in higher elevations and
48 latitudes exhibiting relatively smaller extremities as a means of thermoregulation
49 (Lomolino et al. 2006). Researchers have long documented Allen's rule as a
50 geographic gradient in limb length among individuals of many bird and mammal
51 species (Yom-Tov and Nix 1986; Bried et al. 1997; VanderWerf 2012). While
52 Allen's Rule was earlier thought to be limited to local adaptation within species
53 (Mayr 1956), several studies have since established this pattern as one that
54 applies also across species (Cartar and Guy Morrison 2005; Nudds and Oswald
55 2007). However, these focused on limb length as the object of selection for
56 thermoregulation.

57
58 Examinations of Allen's rule in beak length have been rare until recently, as R.
59 Greenberg and colleagues have established the repeated adaptation of North
60 American sparrow species' beak size to salt marsh habitats (Greenberg and
61 Droege 1990; Grenier and Greenberg 2005). Both among and within salt marsh
62 sparrow populations, summer temperatures are good predictors of beak surface
63 area (Greenberg and Danner 2012; Greenberg et al. 2012b; Greenberg and
64 Danner 2013). However, it is apparent that winter temperatures can also
65 influence beak size, and a framework was presented by Greenberg et al. (2012;
66 Danner and Greenberg 2015) to test which season is the critical period for
67 thermoregulation. As with limb length, Allen's rule in beak size has recently been
68 extended as a pattern observed across species (Symonds and Tattersall 2010).

69 However, the key question remains: If thermal effects are important, is winter or
70 summer the critical season driving interspecific variation in beak size?

71
72 Australia provides a testing ground uniquely suited to disentangle the critical
73 season hypothesis, as its central arid and semi-arid zones exhibit challenging
74 high temperatures in summer and relatively low temperatures in winter. Thus, if
75 selection acts primarily on individuals unable to shed heat during summer, we
76 should expect to see larger beak sizes among species exposed to hot summers.
77 However, if selection acts primarily on individuals unable to conserve heat during
78 winter, we should expect to see smaller beak sizes among species exposed to cold
79 winters. To test these hypotheses, we focused on a diverse clade of Australasian
80 songbirds, the honeyeaters and allies (Meliphagoidea). These species are ideal for
81 such analyses, as they are widespread across Australasia, but largely confined to
82 it (Marki et al. 2017). Thus their in situ diversification across the different climate
83 regimes of Australasia (e.g. Miller et al. 2013) provides a natural experiment of
84 the effects of these regimes on beak morphology.

85
86
87

Methods

Measurements and Metrics

89 We used measurements taken from vouchered museum specimens of
90 Meliphagoidea at the Australian National Wildlife Collection (ANWC). We
91 measured beak length (culmen base to tip), beak depth (at distal end of nares),
92 and beak width (at distal end of nares). NRF performed all measurements,
93 sampling an average of 5 adult male specimens in breeding condition per

94 recognized species (estimated from skull pneumatization and gonad size), with
95 attempts to sample at least two individuals per subspecies group (Schodde and
96 Mason 1999). We included those species for which we were able to obtain data on
97 beak morphology, spatial distribution, and position on a multi-locus phylogeny.
98 This led to a taxonomic sampling of 94 species in Meliphagidae, 40 species in
99 Acanthizidae, and 24 species in Maluridae. We estimated beak surface area using
100 the conical equation described in (Danner and Greenberg 2015). Body mass was
101 included from measurements taken at the time of collection and reported in the
102 ANWC specimen database (Schodde and Mason 1999); in the few cases when
103 these were unavailable we used the median of estimates from the Handbook of
104 the Birds of the World (hereafter HBW; del Hoyo et al. 2007, 2008).

105

106 Most honeyeater species exhibit some degree of curvature in their beak,
107 potentially decreasing the conical estimate of beak surface area's accuracy. To
108 support the accuracy of our beak size and area estimates, we used 2D geometric
109 morphometric data from specimens photographed at the Natural History
110 Museum in Tring, UK to provide supplementary estimates of size and surface
111 area that account for curvature. We placed five landmarks and 19 semi-
112 landmarks around in the outline of each species' beak in *tpsDig* (Rohlf 2004)
113 using the arrangement shown in Figure 5. We used the R package *geomorph*
114 (Adams and Otárola-Castillo 2013) to measure the area of this shape and the
115 scaling factor of its Generalized Procrustes alignment as independent estimates.

116

117 *Climate*

118 We calculated climate averages for each species as the mean of all raster values
119 contained within a species' range (Birdlife International and NatureServe 2011)
120 using the R package *raster* (Hijmans 2015). As a measure of winter minimum
121 and summer maximum temperatures, we used bioclim data at a resolution of ten
122 minutes (bio5 and bio6 in Hijmans et al. 2005). These represent the maximum
123 temperature of a region's warmest month and the minimum temperature of its
124 coldest month, averaged across years from 1950 to 2000. For migratory species,
125 we used the breeding range to calculate summer climate variables, and the non-
126 breeding range to calculate winter climate variables. As the importance of
127 convective versus evaporative heat exchange is likely to change depending on the
128 availability of water during summer heat, we included a metric of aridity
129 (hereafter "summer heat stress"). For this metric, we extracted summer
130 precipitation (bio18 in Hijmans et al. 2005) to express "summer heat stress" as
131 its statistical interaction with summer maximum temperature (see below).

132

133 *Spatial Distribution*

134 To visualize spatial distributions of beak size traits, we accounted for allometry
135 using residuals of their regression against body mass (these characters were not
136 used for comparative analyses described below). We used the *Spatial Analysis in*
137 *Macroecology* software package (Rangel et al. 2010) to estimate both species
138 richness and average trait values for each taxonomic family at every grid cell
139 ($0.5^{\circ} \times 0.5^{\circ}$). These grids were then trimmed to include only cells with at least
140 two species present. We used *QGIS* to produce choropleth figures describing

141 species richness and the spatial distribution of beak size traits (QGIS
142 Development Team 2015).

143

144 *Comparative Methods*

145 Correcting for phylogenetic non-independence is critical to the comparative
146 method. We conducted a separate analysis for each family by taking advantage of
147 their recent multi-locus phylogeny (Lee et al. 2012; Nyári and Joseph 2012;
148 Joseph et al. 2014). This approach has the advantage of both using high-quality
149 molecular phylogeny and at the same time assessing between-family
150 heterogeneity in evolutionary patterns. To estimate time-calibrated branch
151 lengths for these trees, we used penalized likelihood in *ape* to constrain branch
152 lengths by divergence time estimates in the references listed above (Paradis et al.
153 2004; Paradis 2013).

154

155 Just as closely related species are not phylogenetically independent, they are not
156 spatially independent either (Freckleton and Jetz 2009). Indeed, even when
157 using correction for spatial autocorrelation spurious correlations often result
158 from comparisons of species' climate variables and traits, apparently due to an
159 autocorrelation of ecology and historical biogeography (Tello and Stevens 2012;
160 Warren et al. 2014; Friedman and Remeš 2016). To avoid these pitfalls, we used a
161 Phylogenetic Generalized Least Squares framework that combines correction for
162 both phylogenetic and spatial relationships (Freckleton and Jetz 2009; hereafter
163 “spatial PGLS”). This model includes estimates of both a phylogenetic effect
164 parameter (λ) and a spatial effect parameter (Φ). Scripts to run this analysis in

165 the R programming environment are available from R. Freckleton upon request
166 as stated in the original publication (Freckleton and Jetz 2009). We used this
167 spatial PGLS method to test for significant relationships between morphological
168 characters and environmental factors in each family using a multivariate analysis.
169 In this analysis, we included winter minimum temperature, summer maximum
170 temperature and precipitation as predictors.

171

172 To correct for allometric scaling of beak size, we included body mass as a
173 covariate in each analysis. This approach is preferred among contemporary
174 phylogenetic comparative studies because the use of residuals may cause
175 collinearity issues (Freckleton 2009; Symonds and Tattersall 2010; Baab et al.
176 2014; Benson-Amram et al. 2015). To display allometric relationships outside the
177 context of our phylogenetically-corrected analyses, we used residuals from the
178 regression of \log_{10} beak size against \log_{10} body mass (for linear beak
179 measurements, body mass was raised to the 1/3 power; for beak surface area
180 body mass was raised to the 2/3 power).

181

182 To estimate the effect size of each predictor as the standardized regression
183 coefficient, we scaled each climate predictor by its standard deviation so that its
184 variance equaled 1. Below, we present results from bivariate analyses, as well as
185 analyses using multivariate models.

186

187 **Results and Discussion**

188

189 Our analyses illuminate the roles of different selection pressures in the evolution
190 of beak size in Australasian honeyeaters and allies. In particular, we found a
191 consistent evolutionary correlation between winter temperature and beak size
192 (Figure 1, Figure 2A). In areas with low winter minimum temperature, bird
193 species tend to have low beak surface area, length and width (Figure 2C; weaker
194 effects were observed for depth). The relationship between winter temperature
195 and beak size was consistent in its direction and was significant across each clade
196 examined in this study. In contrast, we found little evidence that beak size was
197 associated with summer maximum temperatures (Figure 2B,D).

198
199 Among multivariate analyses including summer heat stress (i.e., interaction
200 between summer maximum temperature and summer precipitation), beak size
201 measures were significantly correlated with winter minimum temperatures in
202 most models (Table 1). Five out of twelve comparisons, and at least one from each
203 clade we examined, showed significant relationships between low winter
204 temperatures and small beak sizes. In particular, winter temperatures were
205 associated with beak surface area and beak length in Meliphagidae and
206 Maluridae, and with beak width in Acanthizidae. On the contrary, summer heat
207 stress was not significantly associated with beak size in models that included
208 winter temperatures (Figure 3, Table 1). Maps of average beak sizes across
209 Australasia showed a similar pattern: species of each family tended to exhibit
210 relatively larger beaks in northern Australia and New Guinea, and smaller beaks
211 in central and southern Australia (Figure 4).

212

213 We observed the greatest effect of winter temperatures on beak length in
214 Meliphagidae and Maluridae, and on beak width in Acanthizidae (Figure 2C). The
215 relationship between winter temperature and beak surface area, the most
216 important beak characteristic in terms of thermoregulation, was consistent across
217 all families for univariate analyses. Furthermore, measurements of beak area and
218 scale accounting for curvature in Meliphagids showed similar results (Figure 5).
219 These results provide support for the evolutionary relationship between climate
220 and extremity length, particularly beak size (see also Campbell-Tennant et al.
221 2015; Gardner et al. 2016). Furthermore, our results show support for winter and
222 not summer temperatures driving beak size evolution across several clades
223 adapting to a broad range of climates. This pattern is not predicted by proximate
224 explanations for Allen's rule that rely on a direct effect of temperature on skeletal
225 development (Serrat et al. 2008; Burness et al. 2013), as developing songbirds
226 grow exceptionally fast and thus reach their adult size prior to the onset of winter
227 temperatures (Starck and Ricklefs 1998). However, birds can exhibit seasonal
228 variation in size of the keratin-based rhamphotheca, resulting in a slight increase
229 in beak length during the breeding season (Morton and Morton 1987; Greenberg
230 et al. 2012). In our study we measured specimens in breeding condition, thus we
231 can to some extent control for – but cannot describe – seasonal variation of the
232 rhamphotheca.

233

234 Among seasons, we found that winter temperatures were often significantly
235 correlated with beak size, while summer temperatures and summer heat stress
236 were never correlated with beak size. This suggests that selection in winter

237 produces the most detectable effect at a broad phylogenetic scale, not that
238 summer temperature has no impact on beak size. The evidence from North
239 American sparrows clearly supports a gradient in beak size driven by summer
240 heat stress (Greenberg et al. 2012b). However, this summer effect was observed
241 most prominently in coastal regions where winters are relatively mild (Danner
242 and Greenberg 2015). Similarly, we observed large beak sizes for species in
243 coastal northern Australia, where summers are hot and winters tend to be mild
244 (Figure 4). However, we observed small beak sizes for species in inland Australia,
245 where summers are still hot but winter temperatures can be harsh as well. While
246 selection on beak size in winter and summer appears to interact negatively across
247 Australia's broad aridity gradient, these effects may interact positively along
248 steep altitudinal gradients, where regions tend to be either hot or cool year-
249 round. This could explain the drastic contrasts in beak size we observed between
250 the central highlands and coastal lowlands of New Guinea in Meliphagidae and
251 Acanthizidae (Figure 4), as well as those observed in Hawaiian elepaios
252 (VanderWerf 2012). Path analysis studies (Hardenberg and Gonzalez-Voyer
253 2013) are needed to describe the effects of complex interactions between seasonal
254 climates and elevation on morphological evolution.

255

256 In this study we cannot rule out a major role for diet in the evolution of beak size
257 and shape in Meliphagoidea. While preferences for seeds, insects, or the nectar in
258 flowers are available in most species descriptions, these dietary categories may be
259 less important than the size of preferred items in driving the evolution of
260 divergent beak sizes (Grant et al. 1976). The manner in which these items are

261 procured (e.g., pursuit and hawking vs. probing and gleaning) and the substrate
262 they occupy likely also influence adaptive beak evolution (Miller et al. 2017). Such
263 detailed descriptions are typically unavailable for taxa in remote regions like
264 central Australia and New Guinea, making comparative studies difficult. Lastly,
265 particular food sources may increase or decrease in availability due to climate,
266 making it difficult to rule out diet in explaining differences in beak size between
267 regions. Thus, our results highlight the importance and need for thorough
268 descriptions of foraging niche at a broad taxonomic scale to better tease out the
269 relative roles of diet and thermoregulation in driving beak evolution.

270

271 It has long been clear that bird species employ a diverse range of specialized beak
272 shapes that are a close fit to their diets (Beecher 1951; Wooller and Richardson
273 1988). However, our results from a phylogenetic comparative study of
274 Australasian songbirds suggest that such structures likely also scale with the
275 demands of climate. Shorebirds provide an excellent example, where bill size has
276 dramatically increased with probing behavior (Barbosa and Moreno 1999). But
277 such species can be observed with their bills tucked into insulating plumage when
278 not in use, likely mitigating their thermoregulatory costs (Midtgård 1978).

279

280 For decades, the evolution of beak size in Galapagos finches has been an
281 instructive model system for the study of adaptation, and findings using this
282 system have largely highlighted the importance of trophic processes in the
283 evolution of beak size (Grant et al. 1976; Grant and Grant 2002). However as
284 island endemics, these species are only subject to the climates present in a

285 narrow (if dynamic) geographic range (Grant and Boag 1980). We predict that if
286 our study were repeated in that clade it would be difficult to find a similar effect
287 of climate on beak size evolution; this contrast underscores the importance of
288 broad comparative studies in evolutionary research. In contrast, our study of
289 honeyeaters and allies across Australasia spans both tropical and temperate
290 zones including a continental gradient in precipitation and an extended range of
291 elevations up to above 4.5 km of elevation (Figure 4). We interpret our findings to
292 suggest that at greater spatial or temporal scales (Meliphagoidea originated 25-
293 30 Mya in early Oligocene; Moyle et al. 2016, Marki et al. 2017), the beak's
294 thermoregulatory role may explain a more considerable amount of evolutionary
295 change than previously thought. The relative importance of this mechanism
296 versus foraging niche divergence in explaining beak evolution will be an exciting
297 avenue of future research. Ultimately this finding highlights the diversity of
298 selective pressures acting on species morphological traits (Schluter et al. 1991)
299 and the contrasting patterns they may produce at different spatial and temporal
300 scales (Carroll et al. 2007).

301

302

303 **References**

304

305 Adams, D. C., and E. Otárola-Castillo. 2013. *geomorph*: An R package for the
306 collection and analysis of geometric morphometric shape data. *Methods*
307 *Ecol. Evol.* 4:393–399.

308 Allen, J. A. 1877. The influence of physical conditions in the genesis of species.
309 *Radic. Rev.* 1:108–140.

310 Baab, K. L., J. M. G. Perry, F. J. Rohlf, and W. L. Jungers. 2014. Phylogenetic,
311 ecological, and allometric correlates of cranial shape in malagasy

- 312 lemuriforms. *Evolution*. 68:1450–1468.
- 313 Barbosa, A., and E. Moreno. 1999. Evolution of foraging strategies in shorebirds:
314 an ecomorphological approach. *Auk* 116:712–725.
- 315 Beecher, W. J. 1951. Adaptations for food-getting in the American Blackbirds.
316 *Auk* 68:411–441.
- 317 Benson-Amram, S., B. Dantzer, G. Stricker, E. M. Swanson, and K. E. Holekamp.
318 2015. Brain size predicts problem-solving abilities in mammalian
319 carnivores. *Proc. Natl. Acad. Sci.* 133:2532-2537.
- 320 Birdlife International, and NatureServe. 2011. Bird species distribution maps of
321 the world. Birdlife International and NatureServe, Cambridge.
- 322 Bried, J., P. Jouventin, S. C. Loughheed, and T. E. Dowling. 1997. Morphological
323 and vocal variation among subspecies of the Black-faced Sheathbill.
324 *Condor* 99:818–825.
- 325 Burness, G., J. R. Huard, E. Malcolm, and G. J. Tattersall. 2013. Post-hatch heat
326 warms adult beaks: irreversible physiological plasticity in Japanese quail.
327 *Proc. Biol. Sci.* 280:20131436.
- 328 Campbell-Tennant, D. J. E., J. L. Gardner, M. R. Kearney, and M. R. E. Symonds.
329 2015. Climate-related spatial and temporal variation in bill morphology
330 over the past century in Australian parrots. *J. Biogeogr.* 42:1163-1175.
- 331 Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on
332 ecological time-scales. *Funct. Ecol.* 21:387–393.
- 333 Cartar, R. V., and R. I. Guy Morrison. 2005. Metabolic correlates of leg length in
334 breeding arctic shorebirds: the cost of getting high. *J. Biogeogr.* 32:377–
335 382.
- 336 Cooney, C. R., J. A. Bright, E. J. R. Capp, A. M. Chira, E. C. Hughes, C. J. A.
337 Moody, L. O. Nouri, Z. K. Varley, G. H. Thomas. 2017. Mega-evolutionary
338 dynamics of the adaptive radiation of birds. *Nature* 542:344–347.
- 339 Cox, R. M., S. L. Skelly, and H. B. John-Alder. 2003. A comparative test of
340 adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*.
341 57:1653–69.
- 342 Danner, R. M., and R. Greenberg. 2015. A critical season approach to Allen's
343 rule: bill size declines with winter temperature in a cold temperate

- 344 environment. *J. Biogeogr.* 42:114-120.
- 345 del Hoyo, J., A. Elliott, and D. A. Christie. 2007. Handbook of the Birds of the
346 World. Volume 12: Picathartes to Tits and Chickadees. Lynx Edicions,
347 Barcelona.
- 348 del Hoyo, J., A. Elliott, and D. A. Christie. 2008. Handbook of the Birds of the
349 World. Volume 13: Penduline-Tits to Shrikes. Lynx Edicions, Barcelona.
- 350 Ellers, J., and C. L. Boggs. 2003. The evolution of wing color: male mate choice
351 opposes adaptive wing color divergence in *Colias* butterflies. *Evolution.*
352 57:1100-6.
- 353 Freckleton, R. P. 2009. The seven deadly sins of comparative analysis. *J. Evol.*
354 *Biol.* 22:1367-1375.
- 355 Freckleton, R. P., and W. Jetz. 2009. Space versus phylogeny: disentangling
356 phylogenetic and spatial signals in comparative data. *Proc. R. Soc. B Biol.*
357 *Sci.* 276:21-30.
- 358 Friedman, N. R., and V. Remeš. 2016. Global geographic patterns of sexual size
359 dimorphism in birds: Support for a latitudinal trend? *Ecography.* 39:17-
360 25.
- 361 Gardner, J. L., M. R. E. Symonds, L. Joseph, K. Ikin, J. Stein, and L. E. B. Kruuk.
362 2016. Spatial variation in avian bill size is associated with humidity in
363 summer among Australian passerines. *Climate Change Responses* 3:1-11.
- 364 Gill, F. B. 2007. *Ornithology*. WH Freeman, New York, NY.
- 365 Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the
366 Panglossian paradigm: a critique of the adaptationist programme. *Proc. R.*
367 *Soc. B Biol. Sci.* 205:581-598.
- 368 Grant, P. R., and P. T. Boag. 1980. Rainfall on the Galápagos and the demography
369 of Darwin's finches. *Auk* 97:227-244.
- 370 Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of
371 Darwin's Finches. *Science.* 296:707-711.
- 372 Grant, P. R., B. R. Grant, J. N. Smith, I. J. Abbott, and L. K. Abbott. 1976.
373 Darwin's finches: population variation and natural selection. *Proc. Natl.*
374 *Acad. Sci.* 73:257-261.
- 375 Greenberg, R., V. Cadena, R. M. Danner, and G. J. Tattersall. 2012a. Heat loss

- 376 may explain bill size differences between birds occupying different
377 habitats. *PLoS One* 7:e40933.
- 378 Greenberg, R., R. Danner, B. Olsen, and D. Luther. 2012b. High summer
379 temperature explains bill size variation in salt marsh sparrows. *Ecography*.
380 35:146–152.
- 381 Greenberg, R., M. Etterson, and R. M. Danner. 2013. Seasonal dimorphism in the
382 horny bills of sparrows. *Ecology and Evolution*. 3:389–98.
- 383 Greenberg, R., and R. M. Danner. 2012. The influence of the California marine
384 layer on bill size in a generalist songbird. *Evolution*. 66:3825–35.
- 385 Greenberg, R., and R. M. Danner. 2013. Climate, ecological release and bill
386 dimorphism in an island songbird. *Biol. Lett.* 9:20130118.
- 387 Greenberg, R., and S. Droege. 1990. Adaptations to tidal marshes in breeding
388 populations of the Swamp Sparrow. *Condor* 92:393–404.
- 389 Grenier, J. L., and R. Greenberg. 2005. A biogeographic pattern in sparrow bill
390 morphology: parallel adaptation to tidal marshes. *Evolution*. 59:1588.
- 391 Hagan, A. A., and J. E. Heath. 1980. Regulation of heat loss in the duck by
392 vasomotion in the bill. *J. Therm. Biol.* 5:95–101.
- 393 Hardenberg, A. von, and A. Gonzalez-Voyer. 2013. Disentangling evolutionary
394 cause-effect relationships with phylogenetic confirmatory path analysis.
395 *Evolution*. 67:378–387.
- 396 Hijmans, R. J. 2015. raster: Geographic Data Analysis and Modeling. R package
397 version 2.4-20.
- 398 Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very
399 high resolution interpolated climate surfaces for global land areas. *Int. J.*
400 *Climatol.* 25:1965–1978.
- 401 Joseph, L., A. Toon, A. S. Nyári, N. W. Longmore, K. M. C. Rowe, T. Haryoko, J.
402 Trueman, and J. L. Gardner. 2014. A new synthesis of the molecular
403 systematics and biogeography of honeyeaters (Passeriformes:
404 Meliphagidae) highlights biogeographical and ecological complexity of a
405 spectacular avian radiation. *Zool. Scr.* 43:235–248.
- 406 Lee, J. Y., L. Joseph, and S. V Edwards. 2012. A species tree for the Australo-
407 Papuan Fairy-wrens and allies (Aves: Maluridae). *Syst. Biol.* 61:253–71.

- 408 Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. Biogeography. 3rd Editio.
409 Sinauer Associates, Sunderland, MA.
- 410 Marki, P. Z., K. A. Jønsson, M. Irestedt, J. M. T. Nguyen, C. Rahbek, J. Fjeldså.
411 2017. Supermatrix phylogeny and biogeography of the Australasian
412 Meliphagides radiation (Aves: Passeriformes). Mol. Phylogenet. Evol.
413 107:516-529.
- 414 Mayr, E. 1956. Geographical character gradients and climatic adaptation.
415 Evolution. 10:105-108.
- 416 Midtgård, U. 1978. Resting postures of the Mallard *Anas platyrhynchos*. Ornis
417 Scand. 9:214-219.
- 418 Miller, E. T., A. E. Zanne, R. E. Ricklefs. 2013. Niche conservatism constrains
419 Australian honeyeater assemblages in stressful environments. Ecol. Lett.
420 16:1186-1194.
- 421 Miller, E. T., S. K. Wagner, L. J. Harmon, R. E. Ricklefs. 2017. Radiating despite a
422 lack of character: ecological divergence among closely related,
423 morphologically similar honeyeaters (Aves: Meliphagidae) co-occurring in
424 arid Australian environments. Am. Nat. 189:E14-E30.
- 425 Morton, M. L., and G. A. Morton. Seasonal changes in bill length in summering
426 mountain White-crowned Sparrows. Condor. 89:197-200.
- 427 Moyle, R. G., C. H. Oliveros, M. J. Andersen, P. A. Hosner, B. W. Benz, J. D.
428 Manthey, S. L. Travers, R. M. Brown, B. C. Faircloth. 2016. Tectonic
429 collision and uplift of Wallacea triggered the global songbird radiation.
430 Nat. Comm. 12709.
- 431 Nudds, R. L., and S. A. Oswald. 2007. An interspecific test of Allen's Rule:
432 evolutionary implications for endothermic species. Evolution. 61:2839-
433 2848.
- 434 Nyári, Á. S., and L. Joseph. 2012. Evolution in Australasian mangrove forests:
435 multilocus phylogenetic analysis of the *Gerygone* warblers (Aves:
436 Acanthizidae). PLoS One 7:e31840.
- 437 Paradis, E. 2013. Molecular dating of phylogenies by likelihood methods: a
438 comparison of models and a new information criterion. Mol. Phylogenet.
439 Evol. 67:436-44.

- 440 Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of Phylogenetics
441 and Evolution in R language. *Bioinformatics* 20:289–290.
- 442 QGIS Development Team. 2015. QGIS Geographic Information System.
- 443 Rangel, T. F., J. A. F. Diniz-Filho, and L. M. Bini. 2010. SAM: a comprehensive
444 application for Spatial Analysis in Macroecology. *Ecography*. 33:46–50.
- 445 Revell, L. J. 2009. Size-correction and principal components for interspecific
446 comparative studies. *Evolution*. 63:3258–3268.
- 447 Rohlf, F. J. 2003. TpsDig. Department of Ecology and Evolution, State University
448 of New York, Stony Brook, NY.
- 449 Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection pressures and
450 life history trade-offs. *Proc. R. Soc. B Biol. Sci.* 246:11–17.
- 451 Schodde, R., and I. J. Mason. 1999. *The Directory of Australian Birds: Passerines*.
452 CSIRO, Melbourne.
- 453 Serrat, M. A., D. King, and C. O. Lovejoy. 2008. Temperature regulates limb
454 length in homeotherms by directly modulating cartilage growth. *Proc.*
455 *Natl. Acad. Sci.* 105:19348–19353.
- 456 Starck, J. M., and R. E. Ricklefs. 1998. *Avian Growth and Development:*
457 *Evolution Within the Altricial-precocial Spectrum*. Oxford University
458 Press, Oxford, UK.
- 459 Symonds, M. R. E., and G. J. Tattersall. 2010. Geographical variation in bill size
460 across bird species provides evidence for Allen's rule. *Am. Nat.* 176:188–
461 97.
- 462 Tattersall, G. J., D. V Andrade, and A. S. Abe. 2009. Heat exchange from the
463 toucan bill reveals a controllable vascular thermal radiator. *Science*.
464 325:468–470.
- 465 Tello, J. S., and R. D. Stevens. 2012. Can stochastic geographical evolution re-
466 create macroecological richness-environment correlations? *Glob. Ecol.*
467 *Biogeogr.* 21:212–223.
- 468 VanderWerf, E. A. 2012. Ecogeographic patterns of morphological variation in
469 elepaio (*Chasiempis* spp.): Bergmann's, Allen's, and Gloger's Rules in a
470 microcosm. *Ornithol. Monogr.* 73:1–34.
- 471 Wainwright, P. C. 2007. Functional versus morphological diversity in

- 472 macroevolution. *Annu. Rev. Ecol. Evol. Syst.* 38:381–401.
- 473 Warren, D. L., M. Cardillo, D. F. Rosauer, and D. I. Bolnick. 2014. Mistaking
474 geography for biology: inferring processes from species distributions.
475 *Trends Ecol. Evol.* 29:572–580.
- 476 Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W.
477 Jetz. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's
478 birds and mammals. *Ecology* 95:2027.
- 479 Willson, M. F., J. R. Karr, and R. R. Roth. 1975. Ecological aspects of avian bill-
480 size variation. *Wilson Bull.* 87:32–44.
- 481 Wooller, R. D., and K. C. Richardson. 1988. Morphological relationships of
482 passerine birds from Australia and New Guinea in relation to their diets.
483 *Zool. J. Linn. Soc.* 94:193–201.
- 484 Yom-Tov, Y., and H. Nix. 1986. Climatological correlates for body size of five
485 species of Australian mammals. *Biol. J. Linn. Soc.* 29:245–262.

486
487

488 **Figure Titles**

489

490 Figure 1: Allometric plot of \log_{10} beak surface area against \log_{10} body mass, with
491 body mass raised to the $^{2/3}$ power to account for the dimensional difference
492 between area and volume. Minimum winter temperatures, averaged across
493 species ranges, are shown as the color of the points in the scatterplot, while
494 taxonomic families are depicted with different symbols. Ordinary least squares
495 linear models are shown to aid visualization of climate patterns relative to
496 allometry relationships, with lines colored by family. Most species in regions with
497 warm winters have large beaks for their body mass, whereas most species in
498 regions with cold winters have small beaks for their body mass.

499

500 Figure 2: (A-B) Comparisons of beak surface area, as residuals of the relationship
501 shown in Figure 1, to climate averages. (C-D) Effects of climate averages on four
502 measures of beak size, shown as effect sizes (standardized β) with 95% confidence
503 intervals. These effect sizes describe bivariate spatial PGLS models comparing
504 trait values across species and including body mass as a covariate to account for
505 allometry. Taxonomic families are represented by the symbols shown in the
506 legend in the upper right.

507

508 Figure 3: Comparison of model support across spatial PGLS analyses. Bar plots
509 show Akaike weights for models including combinations of predictor variables
510 that reflect a priori hypotheses. Models that include minimum temperature have
511 majority support in all analyses explaining beak surface area. Summer heat stress
512 (MaxTemp:Precip) models are a better fit as explanations of beak depth in
513 Acanthizidae and Maluridae. However, these associations with summer heat
514 stress were not statistically significant when winter minimum temperature was
515 included in multivariate analyses (Table 1).

516

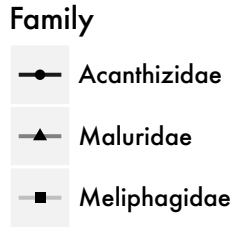
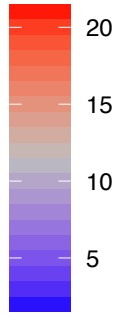
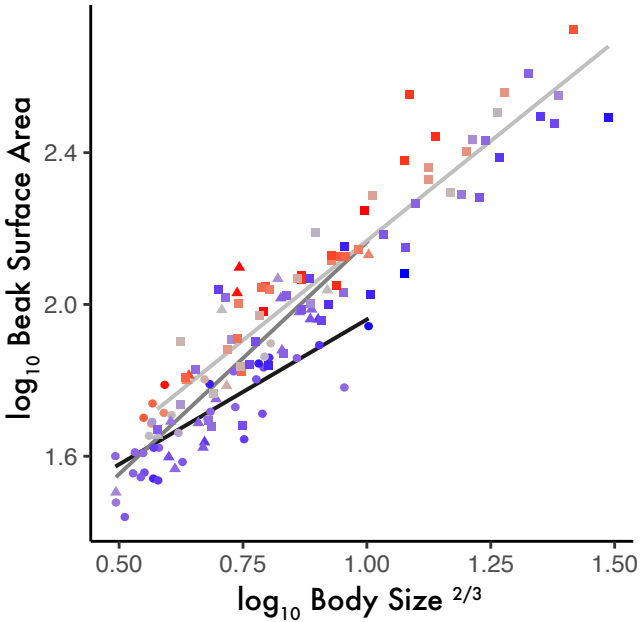
517 Figure 4: Geographic distribution of minimum winter temperature (a) and
518 maximum summer temperature (b) from the Bioclim dataset (Hijmans et al.
519 2005). Beak surface area averaged across species present in 0.5° grid cells (as
520 residuals of regression with body mass) for Meliphagidae (c), Acanthizidae (d)
521 and Maluridae (e). Larger beaks are shown in red and smaller beaks are shown in
522 blue. Cells with less than two species present were excluded (white).

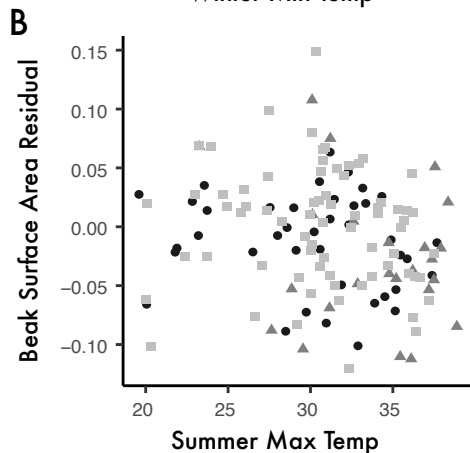
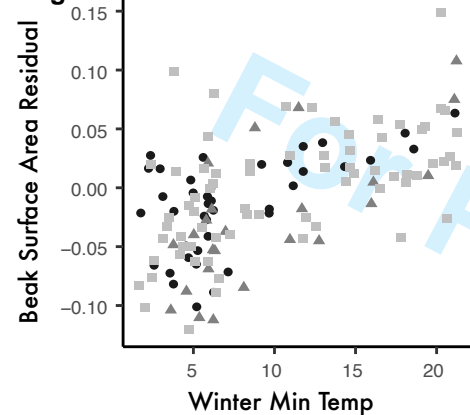
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524 Figure 5: At left, landmark (red) and sliding semi-landmark (magenta) positions
525 used in scoring beak area and size. Semi-landmarks were set at equal intervals
526 between landmarks. At right, effect sizes (standardized β) of spatial PGLS models
527 comparing climate predictor variables to landmark-based measures of beak area
528 and size; lines represent 95% confidence intervals.

529

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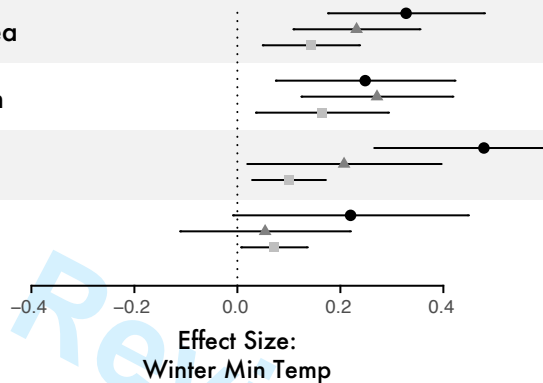
**C**S-PGLS w/ \log_{10} Body Mass Covariate

Surface Area

Beak Length

Beak Width

Beak Depth



Family

- Acanthizidae (n = 40 spp.)
- ▲ Maluridae (n = 24 spp.)
- Meliphagidae (n = 94 spp.)

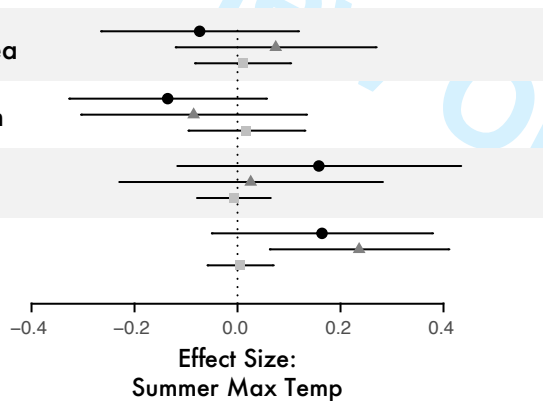
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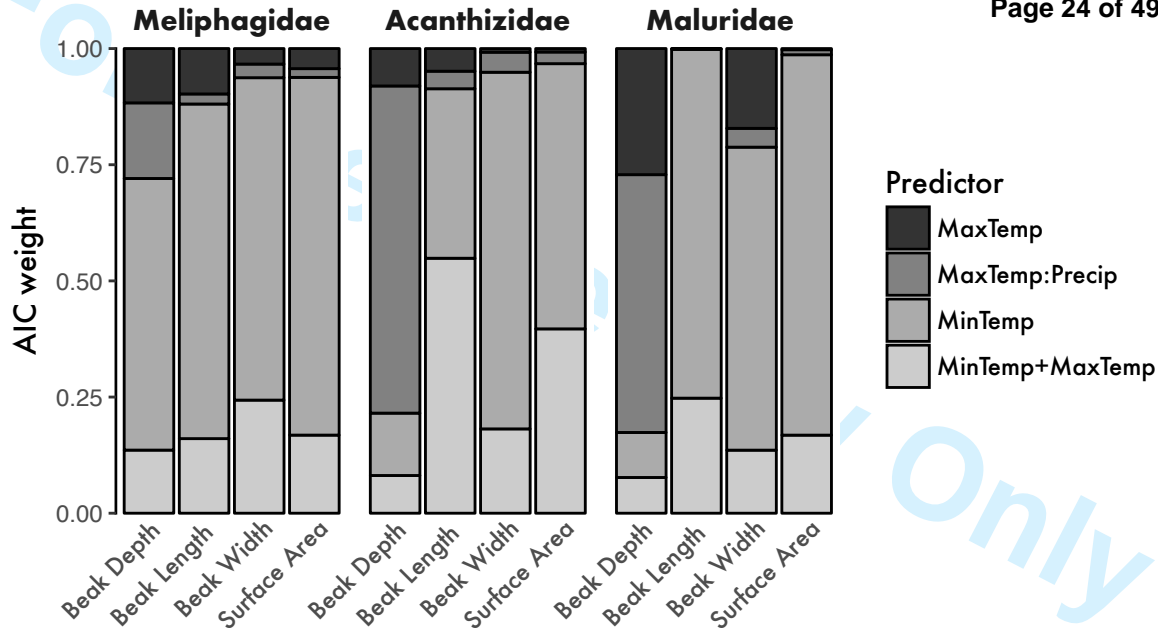
Surface Area

Beak Length

Beak Width

Beak Depth



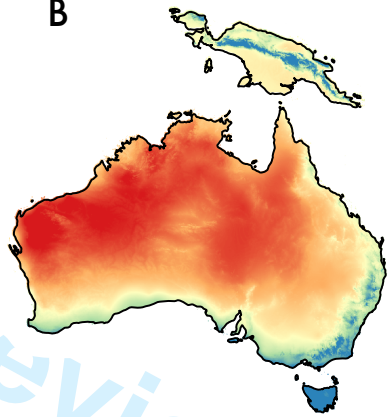
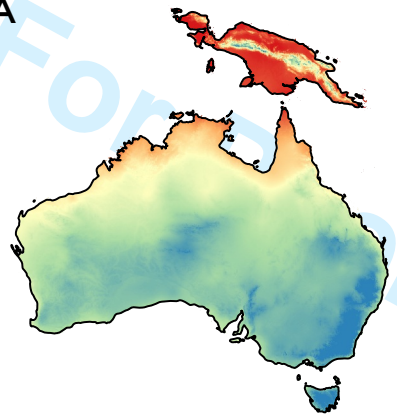
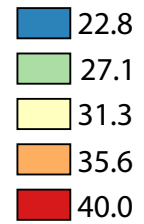
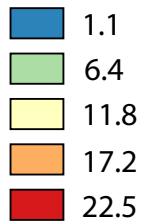


Min Winter Temp (°C)

Max Summer Temp (°C)

A

B

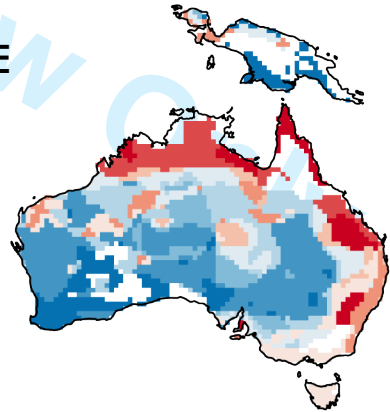
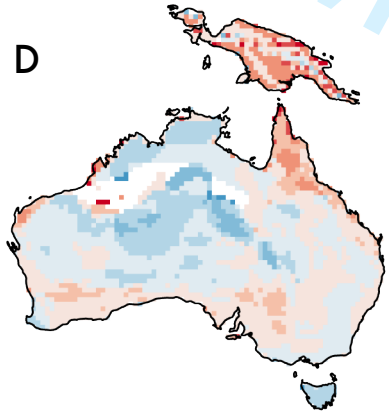
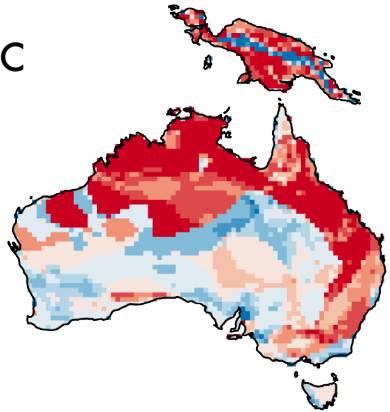
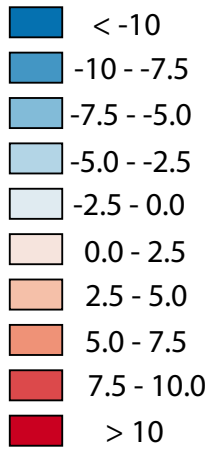


Beak Surface Area (Body Mass Residual)

C

D

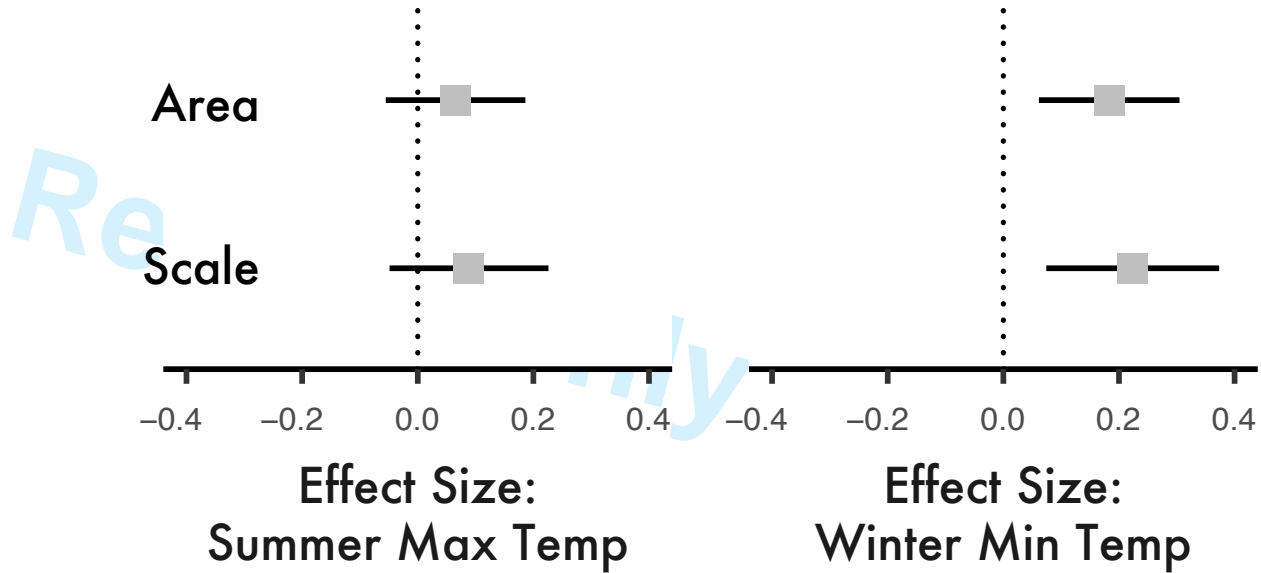
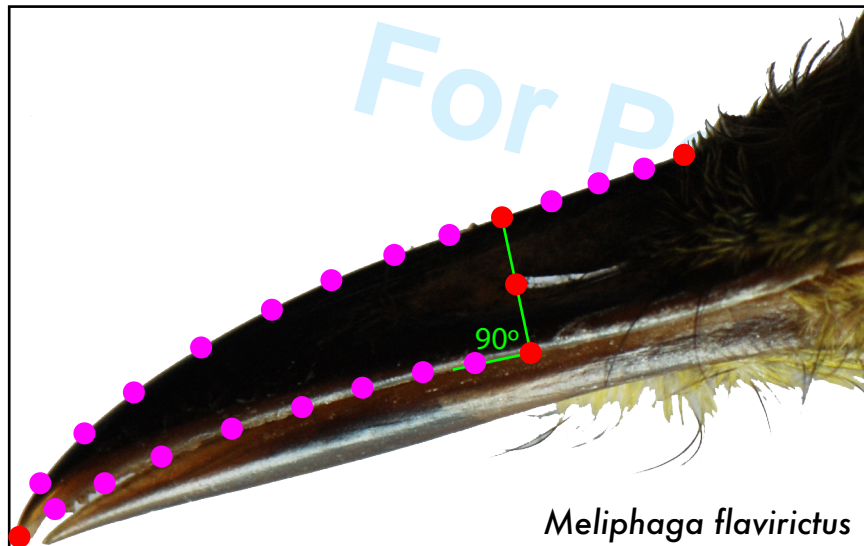
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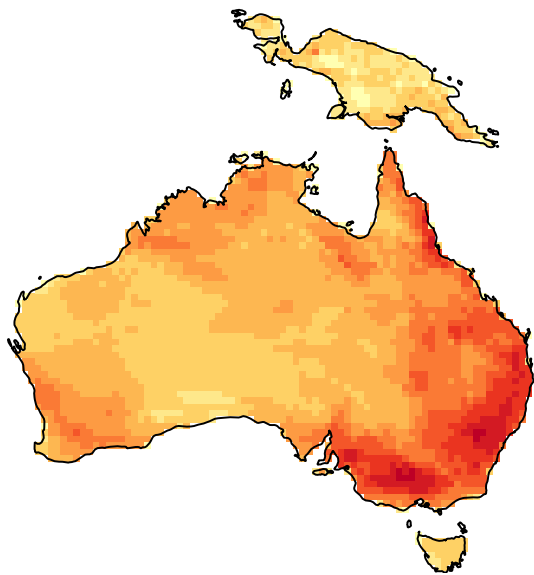
Meliphagidae

Acanthizidae

Maluridae



Meliphagidae



Species Richness

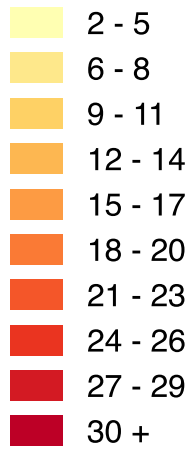
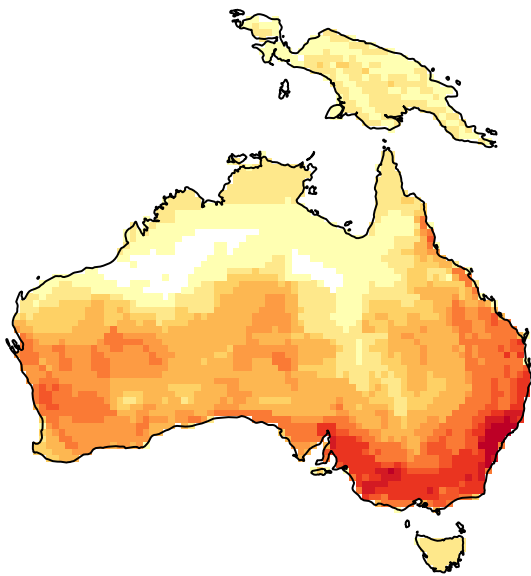
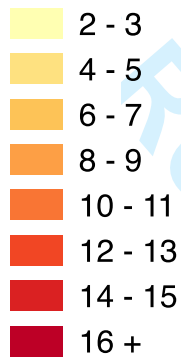


Figure S1: Species richness of three Australasian songbird clades, estimated from the sampling used in this study. Note that this sampled richness may differ from estimates of species richness assembled from all recognized taxa, particularly in New Guinea.

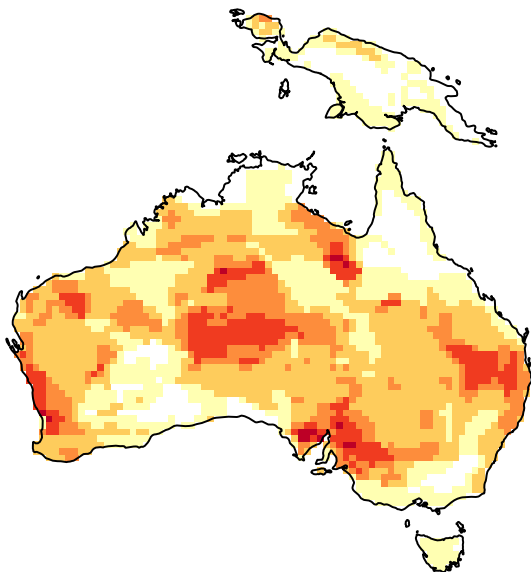
Acanthizidae



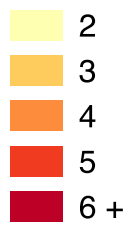
Species Richness



Maluridae



Species Richness



Review Only

1 | ~~R. R.~~ **Abstract**

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2
3 | Birds' beaks play a key role in foraging, and most research on their
4 | ~~morphology~~ size and shape has focused on this function. Recent findings suggest
5 | that beaks may also be important for thermoregulation, and this may drive
6 | morphological evolution as predicted by Allen's rule. However, the role of
7 | thermoregulation in the evolution of beak size ~~during diversification~~ across
8 | species remains largely unexplored. In particular, it remains unclear whether the
9 | need for retaining heat in the winter or dissipating heat in the summer plays the
10 | greater role in selection for beak size. Comparative studies are needed to evaluate
11 | the relative importance of these functions in ~~the beak size~~ evolution of beak size.
12 | We addressed this question in a clade of birds exhibiting wide variation in their
13 | climatic niche: the Australasian honeyeaters and allies (Meliphagoidea). Across
14 | 158 species, we compared species' ~~climate~~ climatic conditions extracted from their
15 | ranges to beak size measurements in a combined spatial-phylogenetic
16 | framework. We found that winter minimum temperature was positively
17 | correlated with beak size, while ~~broad dietary categories were~~ summer maximum
18 | temperature was not. This suggests that while diet and foraging behavior may
19 | drive evolutionary changes in beak shape, changes in beak size can also be
20 | explained by the beak's role in thermoregulation, and winter heat retention in
21 | particular.

22

23 Introduction

24

25 Many phenotypic traits are multifunctional, and thus understanding their

26 evolution in terms of ~~selection~~adaptation and constraint can be a challenge

27 (Gould and Lewontin 1979; Wainwright 2007). Even if a trait is critically

28 important for maintaining one function, trait divergence ~~and variation~~ among

29 species may be driven by selection on a second, sometimes less obvious, function

30 (Cox et al. 2003; Ellers and Boggs 2003). Bird beaks exhibit a stunning diversity

31 in size and shape, (Cooney et al. 2017), and no doubt this diversity reflects the

32 functional importance of beaks in a variety of selective contexts (Willson et al.

33 1975; Gill 2007). Bird beaks are obviously critical for foraging, and the

34 relationship between beak size, shape and diet in Darwin's finches (Grant et al.

35 1976; Grant and Grant 2002) is now the cornerstone of many introductory

36 lectures on natural selection. However, beaks have also been shown to function as

37 thermoregulatory structures. They can function akin to radiators as they shed

38 heat through convection without losing water (Tattersall et al. 2009; Greenberg

39 et al. 2012a), an effect that can be augmented by vasodilation or reduced by

40 vasoconstriction (Hagan and Heath 1980). Thus a large beak may be adaptive in

41 hot environments, but present a problem for heat retention in cold environments

42 (Danner and Greenberg 2015). Given these different functions – heat radiation,

43 heat retention and foraging – it is unclear which factors are most responsible for

44 the evolution of bird beak size during diversification.

45

46 Thermal constraints are known to lead to large-scale variation in morphology. In

47 particular, Allen's rule (Allen 1877) is a classic ecogeographic pattern for

48 endothermic organisms that describes a gradient in extremity length varying with
49 climate. It predicts that selection will lead to individuals in higher elevations and
50 latitudes exhibiting relatively smaller extremities as a means of thermoregulation
51 (Lomolino et al. 2006). Researchers have long documented Allen's rule as a
52 geographic gradient in limb length among individuals of many bird and mammal
53 species (Yom-Tov and Nix 1986; Bried et al. 1997), ~~and most recently in Hawaiian~~
54 ~~elepaio~~ (VanderWerf 2012). While Allen's Rule was earlier thought to be
55 limited to local adaptation within species (Mayr 1956), several studies have since
56 established this pattern as one that applies also across species (Cartar and Guy
57 Morrison 2005; Nudds and Oswald 2007). However, these focused on limb
58 length as the object of selection for thermoregulation.

59
60 Examinations of Allen's rule in beak length have been rare until recently, as R.
61 Greenberg and colleagues have established the repeated adaptation of North
62 American sparrow species' beak size to salt marsh habitats (Greenberg and
63 Droege 1990; Grenier and Greenberg 2005). Both among and within salt marsh
64 sparrow populations, summer temperatures are strong predictors of beak
65 surface area (Greenberg and Danner 2012; Greenberg et al. 2012b; Greenberg
66 and Danner 2013). However, it is apparent that winter temperatures can also
67 influence beak size, and a framework was presented by Greenberg et al. (2012;
68 Danner and Greenberg 2015) to test which season is the critical period for
69 thermoregulation. As with limb length, Allen's rule in beak size has recently been
70 extended as a pattern observed across species (Symonds and Tattersall 2010).

71 ~~However, several key questions remain: 1) Is the effect of climate on beak size~~

72 | ~~detectable during evolutionary diversification?~~ 2) However, the key question
73 | remains: If thermal effects are important, is winter or summer the critical season
74 | driving interspecific variation in beak size?

75 |
76 | Australia provides a testing ground uniquely suited to disentangle the critical
77 | season ~~hypotheses~~ hypothesis, as its central arid and semi-arid zones exhibit
78 | challenging high temperatures in summer and relatively low temperatures in
79 | winter. Thus, if selection acts primarily on individuals unable to shed heat during
80 | summer, we should expect to see larger beak sizes among ~~arid-adapted~~ species
81 | exposed to hot summers. However, if selection acts primarily on individuals
82 | unable to conserve heat during winter, we should expect to see smaller beak sizes
83 | among ~~arid-adapted~~ species exposed to cold winters. To test these hypotheses, we
84 | focused on a diverse clade of Australasian songbirds, the honeyeaters and allies
85 | (Meliphagoidea). These species are ideal for such analyses, as they are
86 | widespread across Australasia, but largely confined to it- (Marki et al. 2017). Thus
87 | their in situ diversification across the different climate regimes of Australasia
88 | (e.g. Miller et al. 2013) provides a natural experiment of the effects of these
89 | regimes on beak morphology.

90 | **Methods**

91 | *Measurements and Metrics*

92 |
93 | We used measurements taken from vouchered museum specimens of
94 | Meliphagoidea at the Australian National Wildlife Collection (ANWC). We
95 | measured beak length (culmen base to tip), beak depth (at distal end of nares),
96 |

97 and beak width (at distal end of nares). NRF performed all measurements,
98 sampling an average of 5 adult male specimens in breeding condition per
99 recognized species (estimated from skull pneumatization and gonad size), with
100 attempts to sample at least two individuals per subspecies group (Schodde and
101 Mason 1999). We included those species for which we were able to obtain data on
102 beak morphology, ~~diet~~, spatial distribution, and position on a multi-locus
103 phylogeny. This led to a taxonomic sampling of 94 species in Meliphagidae, 40
104 species in Acanthizidae, and 24 species in Maluridae. We estimated beak surface
105 area using the conical equation described in (Danner and Greenberg 2015). Body
106 mass was included from measurements taken at the time of collection and
107 reported in the ANWC specimen database; (Schodde and Mason 1999); in the few
108 cases when these were unavailable we used the median of estimates from the
109 Handbook of the Birds of the World (hereafter HBW; del Hoyo et al. 2007,
110 2008).

111
112 Most honeyeater species exhibit some degree of curvature in their beak,
113 potentially decreasing the conical estimate of beak surface area's accuracy. To
114 support the accuracy of our beak size and area estimates, we used 2D geometric
115 morphometric data from specimens photographed at the Natural History
116 Museum in Tring, UK to provide supplementary estimates of size and surface
117 area that account for curvature. We placed five landmarks and 19 semi-
118 landmarks around in the outline of each species' beak in *tpsDig* (Rohlf 2004)
119 using the arrangement shown in Figure 5. We used the R package *geomorph*

120 (Adams and Otarola-Castillo 2013) to measure the area of this shape and the
121 scaling factor of its Generalized Procrustes alignment as independent estimates.

122



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123 *Diet*

124 ~~To formulate broad descriptions of species' diets, we used reports of species'~~
125 ~~feeding habits from HBW (del Hoyo et al. 2007, 2008). The coarse nature of~~
126 ~~those data requires that we interpret them with caution and as a first~~
127 ~~approximation only. We established seven food type categories that matched~~
128 ~~those reported for species in HBW: "plant material", "fruit", "nectar", "seeds",~~
129 ~~"insects and other invertebrates", "fish", and "other vertebrates" (equivalent to~~
130 ~~estimates in Wilman et al. 2014). We scored species' diet by assigning the~~
131 ~~proportion of each category used in the diet according to text descriptions, such~~
132 ~~that the sum of all category values for any species was equal to five. This~~
133 ~~approach enabled us to convert information in the text according to predefined~~
134 ~~and fixed terminology into a proportional use of diet categories. To test whether~~
135 ~~axes of diet variation affected beak size, we performed a phylogenetically~~
136 ~~corrected PCA (Revell 2009) of diet scores (Figure S1).~~

137

138 *Climate*

139 We calculated climate averages for each species as the mean of all raster values
140 contained within a species' range (Birdlife International and NatureServe 2011)
141 using the R package *raster* (Hijmans 2015). As a measure of winter minimum
142 and summer maximum temperatures, we used bioclim data at a resolution of ten
143 minutes (bio5 and bio6 in Hijmans et al. 2005). These represent the maximum

144 | temperature of a region's warmest month and the minimum temperature of its
145 | coldest month, averaged across years from 1950 to 2000. For migratory species,
146 | we used the breeding range to calculate summer climate variables, and the non-
147 | breeding range to calculate winter climate variables. As the importance of
148 | convective versus evaporative heat exchange is likely to change depending on the
149 | availability of water during summer heat, we included a metric of aridity
150 | (hereafter "summer heat stress"). For this metric, we extracted summer
151 | precipitation (bio18 in Hijmans et al. 2005) to express "summer heat stress" as
152 | its statistical interaction with summer maximum temperature (see Results below).

153

154 | *Spatial Distribution*

155 | To visualize spatial distributions of beak size traits, we accounted for allometry
156 | using residuals of their regression against body mass (these characters were not
157 | used for comparative methods analyses described below). We used the *Spatial*
158 | *Analysis in Macroecology* software package (Rangel et al. 2010) to estimate both
159 | species richness and average trait values for each taxonomic family at every grid
160 | cell (0.5° x 0.5°). These grids were then trimmed to include only cells with at
161 | least two species present. We used *QGIS* to produce choropleth figures describing
162 | species richness and the spatial distribution of beak size traits (QGIS
163 | Development Team 2015).

164

165 | *Comparative Methods*

166 | Correcting for phylogenetic non-independence is critical to the comparative
167 | method, ~~and requires accurate and complete information on phylogenetic~~

168 ~~relationships among species. Among avian lineages, the honeyeaters and allies~~
169 ~~are among the most phylogenetically under-sampled. Consequently, it was~~
170 ~~necessary to conduct. We conducted~~ a separate analysis for each family ~~to take by~~
171 ~~taking~~ advantage of their ~~most~~ recent multi-locus phylogeny (Lee et al. 2012;
172 Nyári and Joseph 2012; Joseph et al. 2014). ~~This approach has the advantage of~~
173 ~~both using high-quality molecular phylogeny and at the same time assessing~~
174 ~~between-family heterogeneity in evolutionary patterns.~~ To estimate time-
175 calibrated branch lengths for these trees, we used penalized likelihood in *ape* to
176 constrain branch lengths by divergence time estimates in the references listed
177 above (Paradis et al. 2004; Paradis 2013).

178

179 Just as closely related species are not phylogenetically independent, they are not
180 spatially independent either (Freckleton and Jetz 2009). Indeed, even ~~when~~
181 using correction for spatial autocorrelation spurious correlations often result
182 from comparisons of species' climate variables and traits, apparently due to an
183 ~~autocorrelations~~ ~~autocorrelation~~ of ecology and historical biogeography (Tello and
184 Stevens 2012; Warren et al. 2014; Friedman and Remeš 2016). To avoid these
185 pitfalls, we used a Phylogenetic Generalized Least Squares framework that
186 combines correction for both phylogenetic and spatial relationships (Freckleton
187 and Jetz 2009; hereafter "spatial PGLS"). This model includes estimates of both a
188 phylogenetic effect parameter (λ) and a spatial effect parameter (Φ). ~~A series of~~
189 ~~scripts for~~ ~~Scripts to run this analysis in~~ the R programming environment ~~to run~~
190 ~~this model~~ are available from R. Freckleton upon request as stated in the original
191 publication (Freckleton and Jetz 2009). We used this spatial PGLS method to test

192 for significant relationships between morphological characters and
193 environmental factors in each family using a multivariate analysis. In this
194 analysis, we included ~~diet~~, winter minimum temperature ~~and~~, summer maximum
195 temperature and precipitation as predictors.

196
197 To correct for allometric scaling of beak size, we included body mass as a
198 covariate in each analysis. This approach is preferred among contemporary
199 phylogenetic comparative studies because the use of residuals may cause
200 collinearity issues (Freckleton 2009; Symonds and Tattersall 2010; Baab et al.
201 2014; Benson-Amram et al. 2015). To display allometric relationships outside the
202 context of our phylogenetically-corrected analyses, we used residuals from the
203 regression of \log_{10} beak size against \log_{10} body mass (for linear beak
204 measurements, body mass was raised to the 1/3 power; for beak surface area
205 body mass was raised to the 2/3 power).

206

207 To estimate the effect size of each predictor as the standardized regression
208 coefficient, we scaled each climate predictor by its standard deviation so that its
209 variance equaled 1. Below, we present results from bivariate analyses, as well as
210 analyses using multivariate models.

211

212 **Results and Discussion**

213

214 Our analyses illuminate the roles of different selection pressures in the evolution
215 of beak size in Australasian honeyeaters and allies. In particular, we found a
216 ~~strong and~~ consistent role of evolutionary correlation between winter temperature

217 | ~~in and~~ beak size ~~evolution~~ (Figure 1, Figure 2A). In areas with low winter
218 | minimum temperature, bird species tend to have low beak surface area, length
219 | and width (Figure 2C; weaker effects were observed for depth). The ~~effect~~
220 | ~~of relationship between~~ winter temperature ~~on and~~ beak size was consistent in its
221 | direction and was significant across each clade examined in this study. In
222 | contrast, we found little evidence that beak size was associated with summer
223 | maximum temperatures ~~or diet~~ (Figure 2B,D; ~~Figure S1~~).
224 |
225 | Among multivariate analyses including ~~diet~~ summer heat stress (i.e., interaction
226 | between summer maximum temperature and summer ~~heat stress, precipitation)~~,
227 | beak size measures were significantly correlated with winter minimum
228 | temperatures in most models (Table 1). Five out of twelve comparisons, and at
229 | least one from each clade we examined, showed significant relationships between
230 | low winter temperatures and small beak sizes. In particular, winter temperatures
231 | were associated with beak surface area and beak length in Meliphagidae and
232 | Maluridae, and with beak width in Acanthizidae. ~~Neither~~ On the contrary,
233 | summer heat stress ~~nor diet~~ was not significantly associated with beak size in
234 | models that included winter temperatures (Figure 3, Table 1). Maps of average
235 | beak sizes across Australasia showed a similar pattern: species of each family
236 | tended to exhibit relatively larger beaks in northern Australia and New Guinea,
237 | and smaller beaks in central and southern Australia (Figure 4).
238 |
239 | ~~Our results show a prominent role for winter thermoregulation in driving beak~~
240 | ~~size variation among species.~~ We observed ~~this~~ the greatest effect ~~most strongly of~~

241 winter temperatures on beak length in Meliphagidae and Maluridae, and on beak
242 width in Acanthizidae (Figure 2C). ~~The effect on~~The relationship between winter
243 temperature and beak surface area, the most important beak characteristic in
244 terms of thermoregulation, was consistent across all families for univariate
245 analyses. Furthermore, measurements of beak area and scale accounting for
246 curvature in Meliphagids showed similar results (Figure 5). These results
247 provide ~~strong~~ support for the evolutionary relationship between climate and
248 extremity length, particularly beak size. ~~(see also Campbell-Tennant et al. 2015;~~
249 Gardner et al. 2016). Furthermore, our results show support for winter and not
250 summer temperatures driving beak size evolution across several clades adapting
251 to a broad range of climates. This pattern is not predicted by proximate
252 explanations ~~for Allen's rule that rely on a direct effect of temperature on skeletal~~
253 development (Serrat et al. 2008; Burness et al. 2013) ~~for Allen's rule,~~ as
254 developing songbirds grow exceptionally fast ~~(Starck and Ricklefs 1998)~~ and thus
255 reach their adult size prior to the onset of winter temperatures. ~~(Starck and~~
256 Ricklefs 1998). ~~However, birds can exhibit seasonal variation in size of the~~
257 keratin-based rhamphotheca, resulting in a slight increase in beak length during
258 the breeding season (Morton and Morton 1987; Greenberg et al. 2012). In our
259 study we measured specimens in breeding condition, thus we can to some extent
260 control for – but cannot describe – seasonal variation of the rhamphotheca.
261
262 ~~These findings suggest that selection in winter is the dominant~~Among seasons,
263 we found that winter temperatures were often significantly correlated with beak
264 size, while summer temperatures and summer heat stress were never correlated

265 | ~~with beak size. This suggests that selection in winter produces the most~~
266 | ~~detectable~~ effect at a broad phylogenetic scale, not that summer temperature has
267 | no impact on beak size. The evidence from North American sparrows clearly
268 | supports a gradient in beak size driven by summer heat stress (Greenberg et al.
269 | 2012b). However, this summer effect ~~is was~~ observed ~~only most prominently~~ in
270 | ~~coastal~~ regions where winters are ~~universally relatively~~ mild (Danner and
271 | Greenberg 2015). Similarly, we observed large beak sizes for species in coastal
272 | northern Australia, where summers are hot and winters tend to be mild (Figure
273 | 4). However, we observed small beak sizes for species in inland Australia, where
274 | summers are still hot but winter temperatures can be harsh as well. While
275 | selection on beak size in winter and summer appears to interact negatively across
276 | Australia's broad aridity gradient, these effects may interact positively along
277 | steep altitudinal gradients, where regions tend to be either hot or cool year-
278 | round. This could explain the drastic contrasts in beak size we observed between
279 | the central highlands and coastal lowlands of New Guinea in Meliphagidae and
280 | Acanthizidae (Figure 4), as well as those observed in Hawaiian elepaio
281 | (VanderWerf 2012). Path analysis studies (Hardenberg and Gonzalez-Voyer
282 | 2013) are needed to describe the effects of complex interactions between seasonal
283 | climates and elevation on morphological evolution.

284

285 | ~~Surprisingly, we found no evidence of a significant relationship between beak size~~
286 | ~~and an approximation of diet; this observation was consistent across all clades we~~
287 | ~~examined, using both bivariate and multivariate analyses (Figure S1, Table 1).~~
288 | ~~Support for a relationship between beak size and diet was only observed for 2~~

289 ~~comparisons out of 24 (both beak characters were also related to climate; Table~~
290 ~~1). However, In this study we cannot rule out a strong major role for diet in the~~
291 evolution of beak size and shape in Meliphagoidea. ~~While the dietary categories~~
292 ~~used in this study may be expected to reflect some broad changes in diet, they are~~
293 ~~not capable of describing many of the dietary~~ While preferences ~~and foraging~~
294 ~~behavior that make up the key components of species' foraging niche. In~~
295 ~~particular, a preference~~ for seeds, insects, or the nectar in flowers are available in
296 most species descriptions, these dietary categories may be less important than
297 the size of ~~those objects~~ preferred items in driving the evolution of divergent beak
298 sizes (Grant et al. 1976). The manner in which these items are procured (e.g.,
299 pursuit and hawking vs. probing and gleaning) and the substrate they occupy
300 likely also influence adaptive beak evolution. ~~(Miller et al. 2017)~~. Such detailed
301 descriptions are typically unavailable for taxa in remote regions like central
302 Australia and New Guinea, making comparative studies difficult. Lastly,
303 particular food sources may increase or decrease in availability due to climate,
304 making it difficult to rule out diet in explaining differences in beak size between
305 regions. Thus, our results highlight the importance and need for thorough
306 descriptions of foraging niche at a broad taxonomic scale to better tease out the
307 relative roles of diet and thermoregulation in driving beak evolution.

308

309 It has long been clear that bird species employ a diverse range of specialized beak
310 shapes that are a close fit to their diets (Beecher 1951; Wooller and Richardson
311 1988). However, our results from a phylogenetic comparative study of
312 Australasian songbirds suggest that such structures likely also scale with the

313 demands of climate. Shorebirds provide an excellent example, where bill size has
314 dramatically increased with probing behavior (Barbosa and Moreno 1999). But
315 such species can be observed with their bills tucked into insulating plumage when
316 not in use, likely mitigating their thermoregulatory costs (Midtgård 1978).

317

318 For decades, the evolution of beak size in Galapagos finches has been an
319 instructive model system for the study of adaptation, and findings using this
320 system have largely highlighted the importance of trophic processes in the
321 evolution of beak size (Grant et al. 1976; Grant and Grant 2002). However as
322 island endemics, these species are only subject to the climates present in a
323 narrow (if dynamic) geographic range (Grant and Boag 1980). We predict that if
324 our study were repeated in that clade it would be difficult to find a similar effect
325 of climate on beak size evolution; this contrast underscores the importance of
326 broad comparative studies in evolutionary research. In contrast, our study of
327 honeyeaters and allies across Australasia spans both tropical and temperate
328 zones as well as including a continental gradient in precipitation and an extended
329 range of elevations up to above 4.5 km of elevation (Figure 4). ~~Our~~ We interpret
330 our findings to suggest that at greater spatial or temporal scales, (Meliphagoidea
331 originated 25-30 Mya in early Oligocene; Moyle et al. 2016, Marki et al. 2017), the
332 beak's thermoregulatory role explains may explain a more considerable amount of
333 evolutionary change (Figure 2) than previously thought. The relative importance
334 of this mechanism versus foraging niche divergence in explaining beak evolution
335 will be an exciting avenue of future research. Ultimately this finding highlights
336 the diversity of selective pressures acting on species morphological traits

337 (Schluter et al. 1991) and the contrasting patterns they may produce at different
 338 spatial and temporal scales (Carroll et al. 2007).

339

340

341 **References**

342

- 343 Adams, D. C., and E. Otárola-Castillo. 2013. *geomorph*: An R package for the
 344 collection and analysis of geometric morphometric shape data. *Methods*
 345 *Ecol. Evol.* 4:393–399.
- 346 Allen, J. A. 1877. The influence of physical conditions in the genesis of species.
 347 *Radic. Rev.* 1:108–140.
- 348 Baab, K. L., J. M. G. Perry, F. J. Rohlf, and W. L. Jungers. 2014. Phylogenetic,
 349 ecological, and allometric correlates of cranial shape in malagasy
 350 lemuriforms. *Evolution.* 68:1450–1468.
- 351 Barbosa, A., and E. Moreno. 1999. Evolution of foraging strategies in shorebirds:
 352 an ecomorphological approach. *Auk* 116:712–725.
- 353 Beecher, W. J. 1951. Adaptations for food-getting in the American Blackbirds.
 354 *Auk* 68:411–441.
- 355 Benson-Amram, S., B. Dantzer, G. Stricker, E. M. Swanson, and K. E. Holekamp.
 356 2015. Brain size predicts problem-solving abilities in mammalian
 357 carnivores. *Proc. Natl. Acad. Sci.* 133:2532–2537.
- 358 Birdlife International, and NatureServe. 2011. Bird species distribution maps of
 359 the world. Birdlife International and NatureServe, Cambridge.
- 360 Bried, J., P. Jouventin, S. C. Loughheed, and T. E. Dowling. 1997. Morphological
 361 and vocal variation among subspecies of the Black-faced Sheathbill.
 362 *Condor* 99:818–825.
- 363 Burness, G., J. R. Huard, E. Malcolm, and G. J. Tattersall. 2013. Post-hatch heat
 364 warms adult beaks: irreversible physiological plasticity in Japanese quail.
 365 *Proc. Biol. Sci.* 280:20131436.
- 366 [Campbell-Tennant, D. J. E., J. L. Gardner, M. R. Kearney, and M. R. E. Symonds.](#)
 367 [2015. Climate-related spatial and temporal variation in bill morphology](#)
 368 [over the past century in Australian parrots. *J. Biogeogr.* 42:1163-1175.](#)

- 369 Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on
370 ecological time-scales. *Funct. Ecol.* 21:387–393.
- 371 Cartar, R. V., and R. I. Guy Morrison. 2005. Metabolic correlates of leg length in
372 breeding arctic shorebirds: the cost of getting high. *J. Biogeogr.* 32:377–
373 382.
- 374 [Cooney, C. R., J. A. Bright, E. J. R. Capp, A. M. Chira, E. C. Hughes, C. J. A.](#)
375 [Moody, L. O. Nouri, Z. K. Varley, G. H. Thomas. 2017. Mega-evolutionary](#)
376 [dynamics of the adaptive radiation of birds. *Nature* 542:344–347.](#)
- 377 Cox, R. M., S. L. Skelly, and H. B. John-Alder. 2003. A comparative test of
378 adaptive hypotheses for sexual size dimorphism in lizards. *Evolution.*
379 57:1653–69.
- 380 Danner, R. M., and R. Greenberg. 2015. A critical season approach to Allen's
381 rule: bill size declines with winter temperature in a cold temperate
382 environment. *J. Biogeogr.* 42:114–120.
- 383 del Hoyo, J., A. Elliott, and D. A. Christie. 2007. *Handbook of the Birds of the*
384 *World. Volume 12: Picathartes to Tits and Chickadees.* Lynx Edicions,
385 Barcelona.
- 386 del Hoyo, J., A. Elliott, and D. A. Christie. 2008. *Handbook of the Birds of the*
387 *World. Volume 13: Penduline-Tits to Shrikes.* Lynx Edicions, Barcelona.
- 388 Ellers, J., and C. L. Boggs. 2003. The evolution of wing color: male mate choice
389 opposes adaptive wing color divergence in *Colias* butterflies. *Evolution.*
390 57:1100–6.
- 391 Freckleton, R. P. 2009. The seven deadly sins of comparative analysis. *J. Evol.*
392 *Biol.* 22:1367–1375.
- 393 Freckleton, R. P., and W. Jetz. 2009. Space versus phylogeny: disentangling
394 phylogenetic and spatial signals in comparative data. *Proc. R. Soc. B Biol.*
395 *Sci.* 276:21–30.
- 396 Friedman, N. R., and V. Remeš. 2016. Global geographic patterns of sexual size
397 dimorphism in birds: Support for a latitudinal trend? *Ecography.* 39:17–
398 25.
- 399 [Gardner, J. L., M. R. E. Symonds, L. Joseph, K. Ikin, J. Stein, and L. E. B. Kruuk.](#)
400 [2016. Spatial variation in avian bill size is associated with humidity in](#)

- 401 | [summer among Australian passerines. *Climate Change Responses* 3:1-11.](#)
- 402 Gill, F. B. 2007. *Ornithology*. WH Freeman, New York, NY.
- 403 Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the
- 404 Panglossian paradigm: a critique of the adaptationist programme. *Proc. R.*
- 405 *Soc. B Biol. Sci.* 205:581–598.
- 406 Grant, P. R., and P. T. Boag. 1980. Rainfall on the Galápagos and the demography
- 407 of Darwin's finches. *Auk* 97:227–244.
- 408 Grant, P. R., and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of
- 409 Darwin's Finches. *Science*. 296:707–711.
- 410 Grant, P. R., B. R. Grant, J. N. Smith, I. J. Abbott, and L. K. Abbott. 1976.
- 411 Darwin's finches: population variation and natural selection. *Proc. Natl.*
- 412 *Acad. Sci.* 73:257–261.
- 413 Greenberg, R., V. Cadena, R. M. Danner, and G. J. Tattersall. 2012a. Heat loss
- 414 may explain bill size differences between birds occupying different
- 415 habitats. *PLoS One* 7:e40933.
- 416 Greenberg, R., R. Danner, B. Olsen, and D. Luther. 2012b. High summer
- 417 temperature explains bill size variation in salt marsh sparrows. *Ecography*.
- 418 35:146–152.
- 419 | Greenberg, R., [M. Etterson, and R. M. Danner. 2013. Seasonal dimorphism in the](#)
- 420 [horny bills of sparrows. *Ecology and Evolution*. 3:389-98.](#)
- 421 | [Greenberg, R.,](#) and R. M. Danner. 2012. The influence of the California marine
- 422 layer on bill size in a generalist songbird. *Evolution*. 66:3825–35.
- 423 Greenberg, R., and R. M. Danner. 2013. Climate, ecological release and bill
- 424 dimorphism in an island songbird. *Biol. Lett.* 9:20130118.
- 425 Greenberg, R., and S. Droege. 1990. Adaptations to tidal marshes in breeding
- 426 populations of the Swamp Sparrow. *Condor* 92:393–404.
- 427 Grenier, J. L., and R. Greenberg. 2005. A biogeographic pattern in sparrow bill
- 428 morphology: parallel adaptation to tidal marshes. *Evolution*. 59:1588.
- 429 Hagan, A. A., and J. E. Heath. 1980. Regulation of heat loss in the duck by
- 430 vasomotion in the bill. *J. Therm. Biol.* 5:95–101.
- 431 Hardenberg, A. von, and A. Gonzalez-Voyer. 2013. Disentangling evolutionary
- 432 cause-effect relationships with phylogenetic confirmatory path analysis.

- 433 Evolution. 67:378–387.
- 434 Hijmans, R. J. 2015. raster: Geographic Data Analysis and Modeling. R package
435 version 2.4-20.
- 436 Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very
437 high resolution interpolated climate surfaces for global land areas. Int. J.
438 Climatol. 25:1965–1978.
- 439 Joseph, L., A. Toon, A. S. Nyári, N. W. Longmore, K. M. C. Rowe, T. Haryoko, J.
440 Trueman, and J. L. Gardner. 2014. A new synthesis of the molecular
441 systematics and biogeography of honeyeaters (Passeriformes:
442 Meliphagidae) highlights biogeographical and ecological complexity of a
443 spectacular avian radiation. Zool. Scr. 43:235–248.
- 444 Lee, J. Y., L. Joseph, and S. V Edwards. 2012. A species tree for the Australo-
445 Papuan Fairy-wrens and allies (Aves: Maluridae). Syst. Biol. 61:253–71.
- 446 Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. Biogeography. 3rd Editio.
447 Sinauer Associates, Sunderland, MA.
- 448 Marki, P. Z., K. A. Jønsson, M. Irestedt, J. M. T. Nguyen, C. Rahbek, J. Fjeldså.
449 2017. Supermatrix phylogeny and biogeography of the Australasian
450 Meliphagides radiation (Aves: Passeriformes). Mol. Phylogenet. Evol.
451 107:516-529.
- 452 Mayr, E. 1956. Geographical character gradients and climatic adaptation.
453 Evolution. 10:105–108.
- 454 Midtgård, U. 1978. Resting ~~Postures~~postures of the Mallard *Anas platyrhynchos*.
455 Ornis Scand. 9:214–219.
- 456 Miller, E. T., A. E. Zanne, R. E. Ricklefs. 2013. Niche conservatism constrains
457 Australian honeyeater assemblages in stressful environments. Ecol. Lett.
458 16:1186–1194.
- 459 Miller, E. T., S. K. Wagner, L. J. Harmon, R. E. Ricklefs. 2017. Radiating despite a
460 lack of character: ecological divergence among closely related,
461 morphologically similar honeyeaters (Aves: Meliphagidae) co-occurring in
462 arid Australian environments. Am. Nat. 189:E14-E30.
- 463 Morton, M. L., and G. A. Morton. Seasonal changes in bill length in summering
464 mountain White-crowned Sparrows. Condor. 89:197-200.

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- 465 [Moyle, R. G., C. H. Oliveros, M. J. Andersen, P. A. Hosner, B. W. Benz, J. D.](#)
466 [Manthey, S. L. Travers, R. M. Brown, B. C. Faircloth. 2016. Tectonic](#)
467 [collision and uplift of Wallacea triggered the global songbird radiation.](#)
468 [Nat. Comm. 12709.](#)
- 469 Nudds, R. L., and S. A. Oswald. 2007. An interspecific test of Allen's Rule:
470 evolutionary implications for endothermic species. *Evolution*. 61:2839–
471 2848.
- 472 Nyári, Á. S., and L. Joseph. 2012. Evolution in Australasian mangrove forests:
473 multilocus phylogenetic analysis of the *Gerygone* warblers (Aves:
474 Acanthizidae). *PLoS One* 7:e31840.
- 475 Paradis, E. 2013. Molecular dating of phylogenies by likelihood methods: a
476 comparison of models and a new information criterion. *Mol. Phylogenet.*
477 *Evol.* 67:436–44.
- 478 Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of Phylogenetics
479 and Evolution in R language. *Bioinformatics* 20:289–290.
- 480 QGIS Development Team. 2015. QGIS Geographic Information System.
- 481 Rangel, T. F., J. A. F. Diniz-Filho, and L. M. Bini. 2010. SAM: a comprehensive
482 application for Spatial Analysis in Macroecology. *Ecography*. 33:46–50.
- 483 Revell, L. J. 2009. Size-correction and principal components for interspecific
484 comparative studies. *Evolution*. 63:3258–3268.
- 485 Rohlf, F. J. 2003. TpsDig. Department of Ecology and Evolution, State University
486 of New York, Stony Brook, NY.
- 487 Schluter, D., T. D. Price, and L. Rowe. 1991. Conflicting selection pressures and
488 life history trade-offs. *Proc. R. Soc. B Biol. Sci.* 246:11–17.
- 489 Schodde, R., and I. J. Mason. 1999. The Directory of Australian Birds: Passerines.
490 CSIRO, Melbourne.
- 491 Serrat, M. A., D. King, and C. O. Lovejoy. 2008. Temperature regulates limb
492 length in homeotherms by directly modulating cartilage growth. *Proc.*
493 *Natl. Acad. Sci.* 105:19348–19353.
- 494 Starck, J. M., and R. E. Ricklefs. 1998. Avian Growth and Development:
495 Evolution Within the Altricial-precocial Spectrum. Oxford University
496 Press, Oxford, UK.

- 497 Symonds, M. R. E., and G. J. Tattersall. 2010. Geographical variation in bill size
498 across bird species provides evidence for Allen's rule. *Am. Nat.* 176:188–
499 97.
- 500 Tattersall, G. J., D. V Andrade, and A. S. Abe. 2009. Heat exchange from the
501 toucan bill reveals a controllable vascular thermal radiator. *Science*.
502 325:468–470.
- 503 Tello, J. S., and R. D. Stevens. 2012. Can stochastic geographical evolution re-
504 create macroecological richness-environment correlations? *Glob. Ecol.*
505 *Biogeogr.* 21:212–223.
- 506 VanderWerf, E. A. 2012. Ecogeographic ~~Patterns~~patterns of ~~Morphological~~
507 ~~Variation~~morphological variation in ~~Elepaio~~elepaio (*Chasiempis* spp.):
508 Bergmann's, Allen's, and Gloger's Rules in a ~~Microcosm~~microcosm.
509 *Ornithol. Monogr.* 73:1–34.
- 510 Wainwright, P. C. 2007. Functional ~~Versus Morphological Diversity~~versus
511 morphological diversity in ~~Macroevolution~~macroevolution. *Annu. Rev.*
512 *Ecol. Evol. Syst.* 38:381–401.
- 513 Warren, D. L., M. Cardillo, D. F. Rosauer, and D. I. Bolnick. 2014. Mistaking
514 geography for biology: inferring processes from species distributions.
515 *Trends Ecol. Evol.* 29:572–580.
- 516 Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W.
517 Jetz. 2014. EltonTraits 1.0: Species-level foraging attributes of the world's
518 birds and mammals. *Ecology* 95:2027.
- 519 Willson, M. F., J. R. Karr, and R. R. Roth. 1975. Ecological aspects of avian bill-
520 size variation. *Wilson Bull.* 87:32–44.
- 521 Wooller, R. D., and K. C. Richardson. 1988. Morphological relationships of
522 passerine birds from Australia and New Guinea in relation to their diets.
523 *Zool. J. Linn. Soc.* 94:193–201.
- 524 Yom-Tov, Y., and H. Nix. 1986. Climatological correlates for body size of five
525 species of Australian mammals. *Biol. J. Linn. Soc.* 29:245–262.
- 526
- 527

528 Figure Titles

529

530 | Figure 1: Allometric plot of \log_{10} beak surface area against \log_{10} body sizemass,
531 | with body sizemass raised to the $2/3$ power to account for the dimensional
532 | difference between area and volume. Minimum winter temperatures, averaged
533 | across species ranges, are shown as the color of the points in the scatterplot,
534 | while taxonomic families are depicted with different symbols. Ordinary least
535 | squares linear models are shown to aid visualization of climate patterns relative
536 | to allometry relationships, with lines colored by family. Most species in regions
537 | with warm winters have large beaks for their body mass, whereas most species in
538 | regions with cold winters have small beaks for their body mass.

539

540 | Figure 2: (A-B) Comparisons of beak surface area, as residuals of the relationship
541 | shown in Figure 1, to climate averages and diet. (C-D) Effects of climate averages
542 | on four measures of beak size, shown as effect sizes (standardized β) with 95%
543 | confidence intervals. These effect sizes describe bivariate spatial PGLS models
544 | comparing trait values across species and including body sizemass as a covariate
545 | to account for allometry. Taxonomic families are represented by the symbols
546 | shown in the legend in the upper right.

547

548 | Figure 3: Comparison of model support across spatial PGLS analyses. Bar plots
549 | show Akaike weights for models including combinations of predictor variables
550 | that reflect a priori hypotheses. Models that include minimum temperature have
551 | majority support in all analyses explaining beak surface area. Summer heat stress

552 | (MaxTemp:~~MinPrecip~~Precip) models are a better fit as explanations of beak
553 | depth in Acanthizidae and Maluridae. However, these associations with summer
554 | heat stress were not statistically significant when winter minimum temperature
555 | was included in multivariate analyses (Table 1).

556

557 | Figure 4: Geographic distribution of minimum winter temperature (a) and
558 | maximum summer temperature (b) from the Bioclim dataset (Hijmans et al.
559 | 2005). Beak surface area averaged across species present in 0.5° grid cells (as
560 | residuals of regression with body mass) for Meliphagidae (c), Acanthizidae (d)
561 | and Maluridae (e). Larger beaks are shown in red and smaller beaks are shown in
562 | blue. Cells with less than two species present were excluded (white).

563

564 | Figure 5: At left, landmark (red) and sliding semi-landmark (magenta) positions
565 | used in scoring beak area and size. Semi-landmarks were set at equal intervals
566 | between landmarks. At right, effect sizes (standardized β) of spatial PGLS models
567 | comparing climate predictor variables to landmark-based measures of beak area
568 | and size; lines represent 95% confidence intervals.

569