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Under the weather: corticosterone levels in wild nestlings are associated with ambient temperature and wind

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25 **Abstract**

26 Animals time reproductive events to overlap with periods of favorable
27 environmental conditions. However, weather conditions can be unpredictable. Young
28 animals may be particularly susceptible to extreme weather during sensitive
29 developmental periods. Here, we investigated the effects of adverse weather conditions
30 on corticosterone levels (a hormone linked to the avian stress response) and body
31 condition of wild nestling zebra finches (*Taeniopygia guttata*). We sought to tease apart
32 the direct versus indirect (i.e. parental) effects of weather on nestling physiology and
33 condition by increasing parental work load with a clutch manipulation experiment. We
34 found that high temperatures were associated with lower levels of restraint-induced
35 corticosterone and high wind speeds were associated with higher levels of baseline
36 corticosterone. We found no associations between weather and nestling body condition.
37 However, clutch manipulation did affect body condition, with nestlings from
38 experimentally enlarged clutches in worse condition compared to nestlings from
39 experimentally reduced clutches. Our findings suggest that weather can directly affect
40 wild nestlings via changes in corticosterone levels. Further research is needed to
41 understand how changes in corticosterone levels affect phenotype and survival in wild
42 nestlings. Understanding how developing animals respond to changes in environmental
43 predictability and extreme weather is vital for understanding the potential for rapid
44 adaptation in the face of changing climatic conditions.

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47

48 **1. Introduction**

49 Animals are under selection to breed when environmental conditions are optimal
50 (Visser and Both, 2005). However, weather can be unpredictable and have significant
51 consequences on reproductive outcomes (e.g. Breuner and Hahn, 2003; Martin and
52 Wiebe, 2004). In birds, rainfall, wind, and high or low temperatures can affect nestling
53 development, morphology, body condition, and survival (Conrey et al., 2016; Oberg et
54 al., 2015). Developing animals can be particularly sensitive to perturbations in their
55 environment and developmental effects can have sustained effects on phenotype and
56 fitness across life-history stages and even generations (reviewed in Crino and Breuner,
57 2015; Monaghan and Haussmann, 2015; Schoech et al., 2011). Consequently, exposure to
58 extreme weather conditions during development could have profound and potentially
59 long-lasting effects on nestlings via direct and/or indirect mechanisms (i.e. parental
60 effects). Understanding how developing birds respond to extreme weather conditions is
61 of relevance for predicting how they will cope with rapidly changing global conditions.

62 Although the effects of weather on nestling condition and survival have been well
63 described (e.g. Christensen-Dalsgaard et al., 2018; Geiser et al., 2008; Sicurella et al.,
64 2015), the physiological mechanisms that modulate such changes in wild birds are less
65 well-known. The glucocorticoid hormone corticosterone (CORT) is an important
66 modulator of the physiological stress response (Romero, 2004) and is thought to be an
67 important mechanism that promotes adaptive responses during inclement weather
68 (reviewed in de Bruijn and Romero, 2018). CORT promotes physiological and behavioral
69 changes that allows birds to cope with environmental perturbations (Breuner et al., 2008;
70 Sapolsky et al., 2000; Wingfield and Kitaysky, 2002). Studies from poultry science have

71 established a well-supported link between high temperatures and elevated CORT levels
72 in developing and adult chickens (e.g. Najafi et al., 2015; Star et al., 2008). Additionally,
73 numerous studies have linked exposure to cold ambient temperatures to elevated CORT
74 levels in nestlings (Bize et al., 2010; Lopez-Jimenez et al., 2016; Lynn and Kern, 2014).
75 In nestlings, prolonged elevation of CORT levels can have negative effects on body size
76 and condition (e.g. Crino et al., 2014; Kraft et al., 2019) and can cause life-long changes
77 to the hypothalamic-pituitary-adrenal (HPA) axis (the neuroendocrine pathway that
78 modulates the release of CORT; Spencer et al., 2009).

79 Weather could affect nestling physiology and condition through both direct and
80 indirect mechanisms. Extreme temperatures can directly affect nestlings through
81 increased energetic costs required to maintain body temperature within an optimal zone
82 (Angilletta et al., 2010). Weather could also affect nestlings indirectly by reducing the
83 ability of parents to feed and incubate their nestlings. In zebra finches (*Taeniopygia*
84 *guttata*), the level of foraging activity by adults is reduced by half during hot conditions
85 (between 35 and 40 °C) and spatially restricted to areas closest to water (Funghi et al.,
86 2019). Windy conditions affect reproductive outcomes in birds by adversely affecting
87 foraging ability in situations where extremely high winds increase the costs of foraging
88 (e.g. Evans, 1976). Adult birds may also face increased costs of incubation and brooding
89 in windy conditions (Hilde et al., 2016), likely due to the rate of water loss and
90 thermostatic costs in hot or cool environments respectively (Wolf and Walsberg, 1996).
91 Low levels of parental provisioning and nest attendance have been associated with
92 elevated levels of CORT in nestlings suggesting that parental behavior contributes to
93 nestling stress physiology (Rensel et al., 2010).

94 The effects of weather on nestling physiology and survival have been well
95 described in temperate bird species. However, no study has examined the effects of
96 ambient temperature on nestling physiology in arid environments that are prone to
97 unpredictable elevations in temperature. A recent comparative study of over 300
98 Australian birds found that the peak of reproduction in the arid zone occurs earlier than in
99 other biomes and the breeding of desert birds appears to be constrained by extreme
100 weather in the late spring and summer (Duursma et al., 2019). The arid zones in Australia
101 are predicted to be some of the most vulnerable in the world to global climate change
102 (Loarie et al., 2009; Williams et al., 2007). To our knowledge, no study to date has
103 examined how weather conditions affect nestling physiology in arid environments, and
104 yet such information is important in developing an understanding of species resilience to
105 a changing climate (Urban et al., 2016).

106 Here, we examined associations between weather, CORT levels, and body
107 condition in wild zebra finch nestlings in the arid Australian outback. Zebra finch nests in
108 the arid zone of Australia regularly reach temperatures exceeding 40°C, and sometimes
109 50°C for short periods of time (Griffith et al., 2016). Wild and captive-bred zebra finches
110 attain a smaller adult body size when reared during hot ambient conditions (Andrew et
111 al., 2017; Mariette and Buchanan, 2016). The arid Australian outback is also regularly
112 exposed to winds that peak during the hotter months of the year, with daily wind runs
113 between an average low of 250km in May and a peak of 393km in January (average data
114 for Fowlers Gap (AWS 046128, between 2004-2019: Bureau of Meteorology).

115 We predicted that nestlings would exhibit elevated baseline and restraint-induced
116 levels of CORT in high temperatures and windy conditions. Furthermore, we predicted

117 negative relationships between CORT levels and weather variables with body size. We
118 also sought to tease apart the direct versus indirect (i.e. parental) effects of weather
119 conditions on nestlings by experimentally altering parental effort with a clutch size
120 manipulation. We predicted that nestlings from enlarged clutches would be smaller and
121 have higher CORT levels compared to nestlings from control or reduced clutches and that
122 these effects would be greater during hotter and windier weather. Consistent with the
123 results from previous studies in this species (Naguib et al., 2004), we predicted that
124 nestlings from experimentally enlarged clutches would have higher levels of CORT and
125 lower body condition compared to nestlings from smaller clutches.

126

127 **2. Material and methods**

128 *2.1 Study site and clutch size manipulation*

129 This study was conducted on a population of zebra finches breeding in nest boxes
130 at Fowlers Gap, New South Wales, Australia (31° 05' S, 142° 42' E) from 9th October –
131 12th December, 2015 (Griffith et al., 2008). Throughout the experiment, we provided
132 zebra finches with supplementary seed via feeders in order to ensure that natural food
133 availability did not limit parental provisioning. The feeders were located in the center of
134 each breeding area and were checked daily and filled when necessary. A previous study
135 on this population showed that food availability did not determine nest site choice on
136 small scales (in areas 1-2 km wide; Mariette and Griffith, 2012).

137 Nest boxes were monitored regularly to determine nesting activity and hatch date
138 of each nestling. We manipulated clutch size with one of three treatments: enlarged
139 (n=25), reduced (n=38), or no change (n=22). We manipulated clutch size six days after

140 clutch completion (± 2 days) by reducing (minus 3 eggs) or enlarging (plus 3 eggs)
141 clutches. We matched nests with eggs at the same developmental stage and transferred
142 eggs from reduced clutches to nests with enlarged clutches (methods as per Brandl et al.,
143 2018). We were unable to use nestlings from all manipulated nests in this study because
144 of logistical constraints of another study. Nestlings were individually marked by cutting
145 down feathers in a unique combination when clutches were manipulated and then ringed
146 with a numbered aluminum ring at 11 days post-hatching. We collected blood samples to
147 measure CORT when nestlings were 11 days post-hatching (see below). The mean brood
148 sizes for each treatment at the time of sampling were: enlarged clutches (mean= 4.84, s.d.
149 = 1.17), control clutches (mean = 3.79, s.d. = 1.37), and reduced clutches (2.64, s.d. =
150 1.17).

151

152 *2.2 Blood collection and morphological measurements*

153 We sampled 169 nestlings from 85 nests for hormone analyses and body size
154 measurements. We collected blood from the first two nestlings that hatched in each nest
155 box at 11 days post-hatching between the hours of 6:30 and 12:00. A baseline sample was
156 collected within three minutes of first disturbing the nest box (mean=125.8 \pm 51.0
157 seconds). The nestling was then held in a cloth bag out of direct sun exposure for 15
158 minutes, at which time a second blood sample was collected to quantify restraint-induced
159 CORT (mean=985.0 \pm 54.9 seconds) (as per Crino et al., 2017). To collect blood, we
160 punctured the alar vein with a 27-gauge needle and collected 25-50 μ l of blood with
161 heparinized microcapillary tubes. We stored the blood on ice until it could be centrifuged
162 to separate plasma from red blood cells (7000 rpm for ten minutes) within three hours of

163 collection. After separation, the plasma was isolated and stored at -20°C until the samples
164 were transported to Deakin University on dry ice and stored at -80°C until assayed. After
165 collecting blood samples, we weighed nestlings and measured tarsal length. We
166 calculated nestling body condition using the scaled mass index derived from mass and
167 tarsal length (Peig and Green, 2009).

168 This research was conducted under approval of Macquarie University Ethics
169 Committee.

170

171 *2.3 Corticosterone assays*

172 We quantified CORT levels from extracted plasma using Enzyme Immunoassay
173 (EIA) kits (Cat No. ADI 900-097, Enzo Life Sciences, USA). Samples were spiked with
174 one pg of tritiated CORT (1,2,6,7-³H; Perkin Elmer, Australia) prior to steroid extraction
175 to determine recovery percentage. We extracted CORT from raw plasma using a double
176 wash of dichloromethane. Samples were then dried under nitrogen gas and reconstituted
177 in buffer solution (1:20 ratio). We adjusted hormone values for the average sample
178 recovery (70.7%). We used an adjusted protocol to assay the reconstituted samples using
179 half the volume of all the reagents supplied with the EIA kits (Crino et al. 2016). An
180 external standard of 500 pg/ml was run on every plate and used to calculate inter-plate
181 variation. All samples and standards were run in triplicate. Plates were read on a
182 VarioskanLUX microplate reader (Cat. No. N16046, Finland) at 405 nm corrected at 580
183 nm. Levels of CORT were determined from a six point standard curve ranging from
184 20,000 to 15.53 pg/ml. Intra- and inter-plate variation was 5.9 and 17.8% respectively.
185 The detection limit of the assay was 0.02 ng/ml.

186

187 *2.4 Weather data*

188 Weather data were downloaded from the Australian Bureau of Meteorology
189 automated weather station at Fowlers Gap (within 20km of the study site). Temperature
190 and wind speed were taken from the hourly reading closest to the time the first blood
191 sample was collected to examine short-term associations between weather conditions and
192 nestling physiology (hereafter: *immediate weather*). To examine sustained effects of
193 weather conditions on nestlings, we averaged the maximum daily temperature and wind
194 speed for the ten days prior to collecting blood from nestlings and used the means in
195 separate models (hereafter: *sustained weather*). We averaged across the ten days prior to
196 sampling (on nestling age 11 days), to account for the conditions experienced by the
197 nestling during the whole period since hatching.

198

199 *2.5 Statistical analyses*

200 We analyzed data using the lme4, MuMIn, and lsmeans packages in R 3.4.1
201 (Barton, 2009; Bates et al., 2015; Lenth, 2016). We used generalized linear mixed models
202 with gamma distributions and log link functions to examine the effects of immediate and
203 sustained weather on CORT levels. We used baseline CORT and restraint-induced CORT
204 as dependent variables and wind speed, temperature, and clutch manipulation treatment
205 as fixed factors, and nest identity as a random factor. We estimated p-values from Wald's
206 test statistic. The time to collect blood samples was correlated with baseline CORT levels
207 ($P < 0.001$). The time to collect blood samples was used as a covariate in all models that
208 utilized a gamma distribution with baseline CORT as a variable. For linear models, we

209 used the residuals obtained from regressing baseline CORT against collection time as an
210 explanatory variable. To examine associations between weather and body condition, we
211 used linear mixed models with condition as the dependent factor and baseline CORT
212 residuals, restraint-induced CORT, wind speed, temperature, and clutch manipulation as
213 fixed factors and nest identity as a random factor. We compared differences in body
214 condition between clutch manipulation treatments using post-hoc Tukey's HSD tests. We
215 estimated p-values using the normal approximation. Normality and homoscedasticity of
216 GLM models of best fit were tested and confirmed using Kolmogorov-Smirnoff tests, and
217 visual examination of residual plots and histograms.

218 For all models, we used backward stepwise regression to remove the greatest non-
219 significant term ($p > 0.10$) until arriving at models with the lowest AIC scores. We present
220 the results from the most parsimonious models for each factor; however, the significant
221 results for full and parsimonious models are identical. A small number of samples were
222 lost due to collection problems. Sample sizes are $n=156$ and 147 for baseline and restraint
223 induced CORT respectively and $n=169$ for scaled mass measurements.

224

225 **3. Results**

226 3.1 Weather and nestling CORT levels

227 Baseline CORT was positively associated with the immediate wind speed when
228 nestlings were sampled ($F_{1,155}=7.08$, $p=0.02$, Figure 1A), but not the sustained wind
229 speed for the ten days preceding sampling ($F_{1,155}=0.45$, $p=0.55$). Baseline CORT was not
230 associated with either immediate temperature ($F_{1,155}=1.05$, $p=0.10$) nor the sustained
231 temperature ($F_{1,155}=0.06$, $p=0.80$ respectively). CORT levels following restraint stress

232 were negatively associated with immediate temperature ($F_{1,146}=10.64$, $p=0.01$, Figure 1B,
233 but not the sustained temperature ($F_{1,146}=0.08$ $p=0.62$). There were no associations
234 between restraint-induced CORT levels and immediate nor sustained wind speed
235 ($F_{1,146}=0.53$, 0.45 , $p=0.58$, 0.46 respectively).

236 For models examining the effects of immediate weather condition on nestling
237 CORT levels there was no effect of clutch reduction or enlargement, compared to control
238 clutches, on baseline CORT levels ($p=0.73$, 0.70 , $d.f.=2$, 155) or restraint-induced CORT
239 levels ($p=0.57$, 0.98 , $d.f.=2$, 146). Likewise, models examining the effects of sustained
240 weather on nestlings CORT levels found no effect of clutch manipulation on baseline
241 ($p=0.79$, 0.86 , $d.f.=2$, 155) or restraint-induced CORT levels ($p=0.66$, 0.31 , $d.f.=2$, 146).
242 Including clutch manipulation in the statistical analyses resulted in models with lower
243 AIC scores and so the term was removed from all final models.

244

245 *3.2 Body condition*

246 The final model examining variation in body condition in relation to immediate
247 weather conditions included an effect of clutch manipulation ($F_{2,146}=3.30$, $p=0.04$, Figure
248 2) and non-significant effects of restraint-induced CORT levels ($F_{1,146}=3.04$, $p=0.08$) and
249 temperature ($F_{1,146}=1.75$, $p=0.19$). Nestlings from reduced clutches were in better body
250 condition than nestlings from enlarged clutches ($p=0.03$). However, there were no
251 differences in body condition between nestlings from reduced and control clutches
252 ($p=0.72$) nor control and enlarged clutches ($p=0.35$). Body condition was not associated
253 with immediate wind speed ($F_{1,146}=1.04$, $p=0.31$) or baseline CORT levels ($F_{1,142}=0.10$,
254 $p=0.74$).

255 The final model examining variation in body condition in relation to sustained
256 weather conditions included an effect of clutch manipulation ($F_{1,146}=3.29$, $p=0.04$) and a
257 non-significant effect of restraint-induced CORT ($F_{1,146}=2.16$, $p=0.14$). There were no
258 association between body condition and temperature and wind speed in the ten days
259 preceding sampling ($F_{1,146}=1.88$, 0.01 , $p=0.17$, 0.93 respectively). There was no
260 association between body condition and baseline CORT levels in models examining the
261 effects of immediate ($F_{1,142}=0.12$, $p=0.72$) or sustained weather conditions ($F_{1,142}=0.03$,
262 $p=0.86$). Results from all models are presented in Table 1.

263

264 **4. Discussion**

265 Our study found that nestling CORT levels reflected current weather conditions.
266 Specifically, baseline CORT levels were positively associated with wind speeds and
267 restraint-induced CORT levels were negatively associated with temperatures when
268 nestlings were sampled. We found no association between weather conditions and body
269 condition, or CORT levels and body condition. However, nestlings from experimentally
270 enlarged clutches were in lower body condition compared to nestlings from
271 experimentally reduced clutches. We found no effects of clutch manipulation on nestling
272 CORT levels, suggesting that the effects of immediate weather conditions on nestling
273 physiology are not indirectly modulated through changes in parental behavior.

274 We found a negative association between the temperature nestlings experienced at
275 the time of sampling and restraint-induced CORT levels. In birds, prolonged exposure to
276 acute stress is linked to decreased expression of glucocorticoid receptors in regions of the
277 brain associated with negative feedback (Banerjee et al., 2012). In our study, high

278 ambient temperatures may have shortened the amount of time needed for nestlings to
279 reach peak CORT secretion. In this scenario, nestlings would have low levels of CORT
280 after 15 minutes of restraint stress, because negative feedback mechanisms reduce CORT
281 levels back to baseline levels (Banerjee et al., 2012).

282 In contrast to negative association between temperature and restraint-induced
283 CORT levels, we found a positive association between wind speed and baseline CORT.
284 Wind speed could affect nestling CORT levels by disrupting feeding behavior and nest
285 attendance (Rensel et al., 2010). However, we found that weather was not associated with
286 nestling body condition, suggesting that windy conditions did not affect the ability of
287 parents to feed nestlings. It is possible that high wind speeds influence the microclimate
288 in nest boxes by decreasing the relative humidity in the surrounding area. It is also
289 possible that high winds create an artificially noisy environment in nest boxes that
290 contributes to changes in CORT physiology (Crino et al., 2013; Injaian et al., 2018).
291 Future experiments could address these hypotheses by measuring noise in nest boxes and
292 nest microclimate.

293 In our study, nestlings from experimentally enlarged clutches were in poorer body
294 condition compared to nestlings from smaller clutches. However, we found no
295 associations between nestling CORT levels and body condition, suggesting there may be
296 no immediate effects of short-term elevation of CORT levels on nestling survival.
297 However, even a single exposure to an acute stressor can have detectable effects on wild
298 nestlings up to \approx 50 days post-fledging (Lynn et al., 2010). Future studies could more
299 comprehensively evaluate nestling stress physiology by examining changes in negative
300 feedback in response to weather. Additionally, future studies should track the effects of

301 exposure to extreme weather over multiple life-history stages to determine the long-term
302 fitness consequences for nestlings.

303 Although we found effects of both temperature and wind speed on CORT, in both
304 cases, this was for the measure taken on the day of sampling rather than the average of
305 these parameters over the ten-day nestling period. These results demonstrate the
306 importance of acute effects of weather on nestling physiology. However, we caution that
307 the apparent lack of chronic effects may be partly due to limitations in our sampling. For
308 logistical reasons, we sampled the nestlings over a total period of 65 days, which
309 represents a relatively small range of the climatic extremes in which zebra finches
310 reproduce. The averaged climate across the ten day developmental period will be less
311 variable than the immediate values taken on just a single day (given the daily variability
312 in climate). From our study, the coefficient of variance for the sustained measures (CV =
313 0.03, 0.05; temperature, wind) was much lower than that for the immediate measures
314 (CV= 0.27, 0.49; temperature, wind) in our sample. An earlier study from the same
315 location, found that nestlings were smaller when they developed during hotter periods,
316 and this analysis focused on a larger number of nestlings ($n \approx 900$) reared over a seven
317 month period, that included both cooler and hotter periods, than the current study
318 (Andrew et al., 2017). These earlier findings, on overall body size (but not body
319 condition) are consistent with the idea that nestling growth is limited in sub-optimal
320 weather conditions.

321 Global climate change has led to an increased incidence of extreme and
322 unpredictable weather both generally and during periods when animals might not
323 normally expect to encounter such conditions (McKechnie et al., 2012). The ecoregions

324 of Australia are considered to be some of the most vulnerable to global climate change
325 (Loarie et al., 2009; Williams et al., 2007). Past studies have focused on the effects of
326 elevated temperature on nestlings in temperate areas (Bize et al., 2010; Dawson et al.,
327 2005; Fairhurst et al., 2012), but no study to date has examined how weather conditions
328 affect nestling physiology in arid environments, and yet such information is important in
329 building a picture of resilience to a changing climate (Urban et al., 2016). Understanding
330 how developing birds respond to extreme weather conditions is of great relevance for
331 predicting how they will cope with rapidly changing global conditions.

332

333 **5. Conclusions**

334 Our data suggest that nestlings are susceptible to extreme weather conditions via
335 changes in CORT secretion. In a world with rapidly changing climatic conditions, it is
336 imperative to assess the effects of weather on developing animals. Future studies should
337 investigate the sustained effects of weather conditions on developing animals and
338 whether or not or not such effects are adaptations to the forecasted environment or
339 developmental constraints.

340

341 **Authors' contributions**

342 O.C, S.D., and S.G designed this study. S.D. and H.B. conducted the field research. O.C.
343 conducted the hormone assays and wrote the manuscript with S.G. and K.B. All authors
344 agree to be held accountable for the content of this paper and approve the final version of
345 the manuscript.

346

347 **Competing interests**

348 The authors declare no competing interests.

349

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358

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512 **Figure Legends**

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514 **Figure 1.** Nestling CORT levels were associated with weather during the time of
515 sampling: A) baseline CORT levels were higher when sampled under conditions with
516 higher wind speeds, and B) restraint-induced CORT levels were lower when sampled
517 under conditions with high ambient temperatures.

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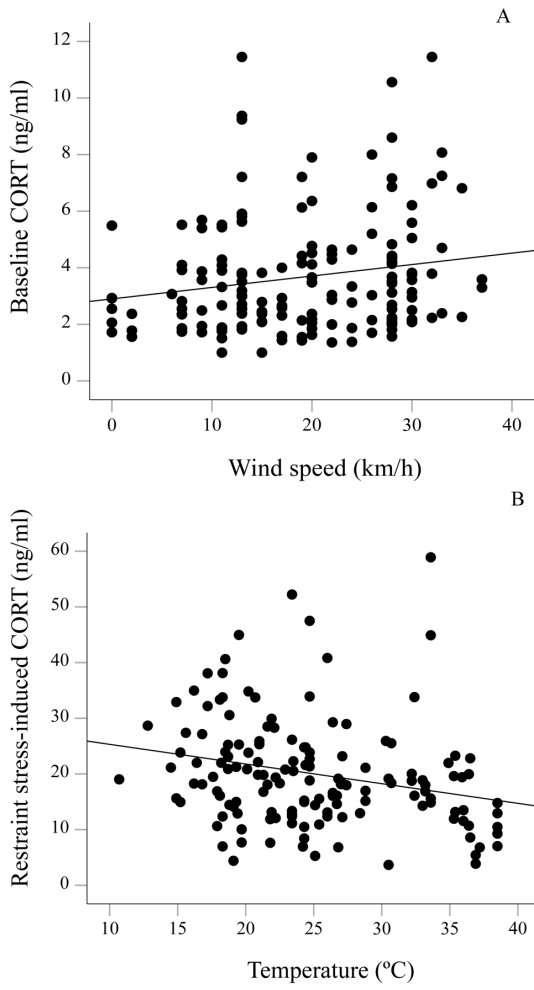
519 **Figure 2.** Average nestling body condition as determined by the scaled mass index from
520 experimentally reduced, control, and experimentally enlarged clutches.

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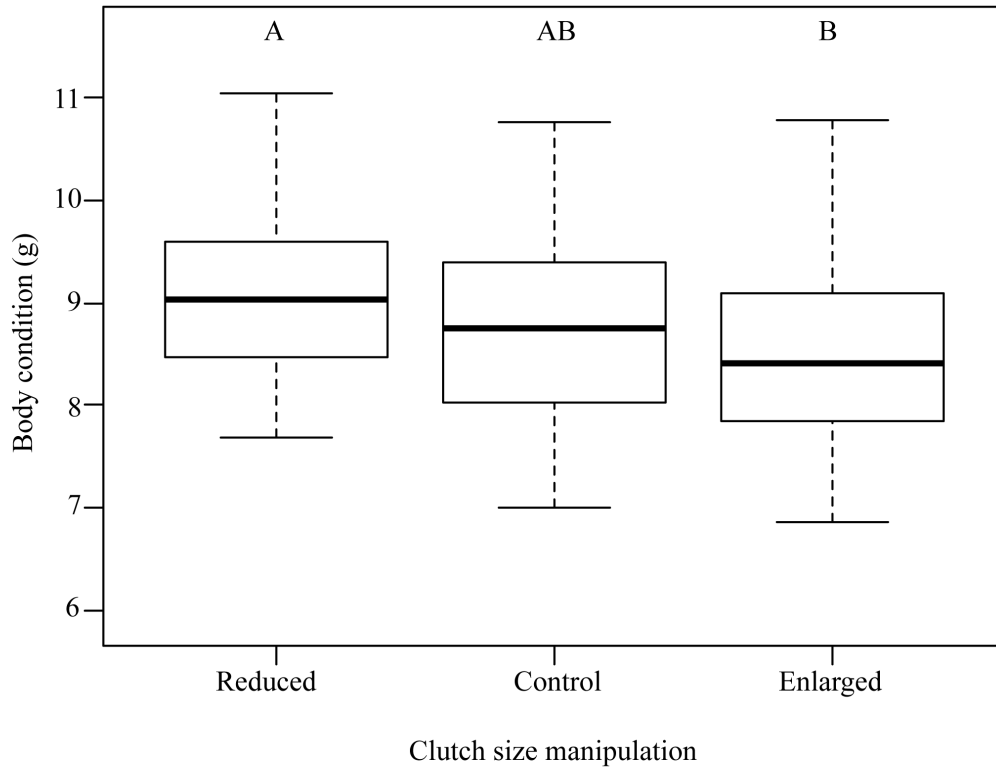
524 Fig 1



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527 Fig 2



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