

1 Running head: *Paradoxical trends in wing length*

2

3 **Dynamics of phenotypic change: declining wing length despite survival**
4 **advantage of longer wings in a resident farmland passerine**

5

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13

14 Environmental changes, such as climate change and land use change that alter
15 resource availability and energetics, are associated with changes in body size in
16 many taxa. Here, we use wing length as a proxy for overall structural body size to
17 examine a paradoxical trend of declining wing length within a Yellowhammer
18 *Emberiza citrinella caliginosa* population sampled over 21 years, where it has
19 been previously shown that longer wings improve survival. Higher temperatures
20 during the previous winter (prior to the moult determining current wing length)
21 explained 23% of wing length decrease within our population but may also be
22 correlated with non-climatic environmental variation such as changes in farming
23 mechanisms linked to food availability. We found no evidence for within-
24 individual wing lengths shrinking with age, but analysis suggested a progressive
25 decline in the sizes of immature birds recruiting to the population. This trend

26 was weaker, although not significantly, among adults, suggesting that the decline
27 in the sizes of recruits was offset by higher subsequent survival of larger birds
28 post-recruitment. These data support the notion that ecological processes can
29 contribute more than selection to observed phenotypic trends and highlight the
30 importance of long-term studies for providing longitudinal insights into
31 population processes.

32

33 **Keywords:** body size, climate change, longitudinal data, population dynamics

34

35

36 Environmental change, such as changes in temperature, food availability and
37 parasite prevalence, can cause rapid phenotypic responses within populations
38 over relatively few years (Poulin & Thomas, 1999; Ozgul *et al.*, 2009; Yom-Tov &
39 Geffen, 2011). As climate change causes temperatures to rise, individuals within
40 populations across multiple taxa have exhibited decreases in body size
41 (Teplitsky & Millien, 2014). Despite numerous studies demonstrating this, only
42 three have investigated whether body size decreases are adaptive, in terms of
43 positively influencing fitness of individuals within a population monitored
44 through time (Teplitsky & Millien, 2014). A 40-year study of Red-Billed Gulls
45 *Larus scopulinus* found no selection on body mass (Teplitsky *et al.*, 2008), and
46 studies of Great Tits *Parus major* and Soay Sheep *Ovis aries* found positive
47 selection for body size, suggesting that changes in response to climate change
48 may have reduced fitness (Ozgul *et al.*, 2009; Husby *et al.*, 2011). All things being
49 equal we would expect increases in survival to be favoured, and so it poses a
50 paradox if traits linked to survival or fitness, more generally, decrease. However,
51 the Soay Sheep population is growing (Ozgul *et al.*, 2009), and Great Tit
52 populations are generally stable or growing (PECBMS, 2015).

53

54 Environmental change, such as climate change, can drive phenotypic change
55 through selection changing gene frequencies (Rausher & Delph, 2015), through
56 the changing environment changing the expression of plastic traits (including
57 epigenetically through parental effects) (Ozgul *et al.*, 2009) or a combination
58 (Pelletier *et al.*, 2007). In order to mitigate the effects of environmental change
59 (e.g. Walther *et al.* 2002; Vasseur *et al.* 2014), we need to understand better how

60 environmental change impacts resource availability and requirements and how
61 this leads to phenotypic change.

62

63 Here, we explore data from a long-term (21 year) morphological dataset of a
64 declining, resident farmland bird, the Yellowhammer *Emberiza citrinella*
65 *caliginosa* (Linnaeus), using wing length as a proxy for body size. Wing length is
66 the best predictor of overall body size within our population (as represented by
67 a composite measure of morphometrics from a subset of our population; see
68 Appendix 1 for a full justification for this rationale) as well as the one for which
69 we have most data. We do not attempt to distinguish between genetic or plastic
70 drivers of phenotypic change, but rather explore a long-term morphological
71 dataset and test associations with potential ecological drivers of change. First, we
72 explore trends in Yellowhammer body size (wing length) at our study site.
73 Finding a long term significant trend towards shorter wings and knowing that
74 longer wings provide a survival advantage in our population (Dunn *et al.*, 2013),
75 we propose three (non-mutually exclusive) hypotheses to explain trends in wing
76 length:

77 1) Individuals show directional plasticity in wing length, with wing length
78 decreasing over time consistently across individuals;

79 2) Temporal trends in wing length differ between age classes, and demographic
80 change is driving the overall trend.

81 3) Temporal trends in wing length are associated with climatic trends at our
82 study site.

83

84 **Methods**

85 We analysed wing length data collected from 928 Yellowhammers captured
86 during 17 winters (November - April) over 21 years between 1986/7 and
87 2008/9 (mean \pm SE: 54.61 \pm 13.88 captures per winter); details of our study
88 population and capture methods are provided elsewhere (Dunn *et al.*, 2013).
89 Birds were ringed using British Trust for Ornithology individually numbered
90 metal leg rings, aged as either first-winter (immature) or older (adult) and sexed
91 using plumage characteristics as described by Svensson (1992) and updated by
92 Dunn and Wright (2009). Maximum wing chord was measured using a stopped
93 metal rule (\pm 0.5 mm). Any birds not sexed or aged at the time of capture were
94 removed from analysis and any birds recaptured in subsequent years were aged,
95 sexed and measured blind to previous capture data.

96
97 First, we determined whether a trend existed in wing length over time within
98 our study population. We constructed a general linear model (GLM) with
99 Gaussian error distributions, and designated wing length as the response
100 variable with age, sex (both as two-level factors), and year (as a continuous
101 variable) as predictor variables, along with all two-way interactions. We also
102 included month of sampling (where October = 1) as a fixed covariate to allow for
103 the possibility of wear reducing wing length over the winter. As we had only a
104 small number of between-year recaptures ($n = 41$), we excluded all but the first
105 measure from each individual from this analysis to ensure independence of data.
106 For all models, we used the 'dredge' function in the MuMIn library (Barton,
107 2012) in R (R Core Team, 2013) to identify the top set of models by comparing
108 all possible models using AIC comparisons, subsequently averaging all models

109 with $\Delta AIC < 2$ ($n = 6$) to create the final model. Age, sex and month were held
110 constant in the model (i.e. they could not be removed from models tested during
111 the dredge process). We determined significance throughout by establishing
112 whether 95% confidence intervals (CIs) in the final averaged model overlapped
113 zero, interpreting a term as influencing the response variable only when there
114 was no overlap. To determine whether any trend might be driven by
115 temperature, we re-ran our model including temperature (defined as the average
116 lowest maximum daily temperature during the winter of capture, for each bird
117 prior to its capture) as a fixed term.

118

119 Upon finding a significant decline in wing length over time, we further examined
120 our data to test potential mechanisms. To test hypothesis 1, whether this trend
121 was driven by within-individual decreases in wing length, we examined whether
122 trends in wing lengths of individual birds captured during more than one winter
123 ($n = 41$) declined between captures. We used a linear mixed-effects model with
124 Bird ID as a random effect and Measurement (first or second) as a fixed factor.
125 We also included Month of capture (with October = 1) to allow for any effects of
126 wear reducing wing length within winters. To test hypothesis 2, whether the
127 trend was more marked in first year birds than in adults, and therefore whether
128 there were differences in effect sizes within each age group, we examined
129 whether immatures or adults were driving this trend by re-running our original
130 model with immature ($n = 563$) and adult ($n = 267$) data separately. To test
131 hypothesis 3, whether temporal trends in wing length might be driven by
132 climatic variation at our study site, we first tested our assumption that winter
133 temperature increased at our study site over time. We used a linear model with

134 temperature as the response variable and winter (year, from November – April)
135 as a fixed term. We obtained temperature data (as described in Dunn *et al.*, 2013)
136 and used the average lowest maximum daily temperature prior to capture of
137 each bird, both because this gives a measure of energy intake requirements and
138 because ground that remains frozen during the day locks in seed, thus limiting
139 food availability for granivorous birds (e.g. Alonso *et al.* 1994). Statistics are
140 presented as Estimate \pm 1 SE; 95% CIs throughout unless stated otherwise.

141

142 **Results**

143 We found a significant decline in wing length (Table 1; Figure 1), with the
144 predicted decline from the final model of 1.88 mm, or 2.12%, over 21 years.
145 Forty-one individuals for which wing length was measured in multiple years
146 showed an increase in wing length between captures (Table 2; predicted mean
147 wing lengths during first and second captures: 1st = 88.99 mm; 2nd = 91.35 mm).

148

149 The Year \times Age interaction term in the original GLM was not statistically
150 significant (Table 1). However, within immatures, wing length declined over
151 time, with CIs not overlapping zero ($z = 4.753$, $p < 0.001$; -0.106 ± 0.022 ; $-0.15 - -$
152 0.06 mm per year). The trend within the adult data was slightly weaker but also
153 significant ($z = 1.95$, $p = 0.05$; -0.064 ± 0.025 ; $-0.114 - -0.014$ mm per year)..

154

155 Temperature increased significantly over the 21-year study period ($F_{1,15} = 6.67$, p
156 $= 0.02$; 0.098 ± 0.038 ; $0.017 - 0.178^\circ\text{C}$ per year). Further supporting this
157 finding, we also found a significant negative relationship between temperature
158 during the previous winter and wing length ($z_{8,822} = 2.69$, $p = 0.007$; -0.22 ± 0.08 ;

159 -0.38 - -0.06 mm per °C) with a corresponding decrease in AIC (model with
160 temperature: AIC = 3503.5; model without temperature AIC = 3510.1).

161

162 **Discussion**

163 Wing length within our population declined by 2.07% over a 21-year period.

164 When examining data from 321 birds sampled over four years, we found longer
165 wings confer a survival advantage within our population (Dunn *et al.*, 2013),
166 possibly due to an increased ability of larger birds to withstand cold winters.

167 Whilst we are unaware of data on heritability of wing length within our study
168 species, there is evidence from other species that wing length can be heritable
169 and is likely influenced by a combination of genetic and environmental factors
170 (e.g. Lessells & Ovenden, 1989). Therefore, this trend of decreasing wing length
171 presents an apparent paradox, with three possible (non-mutually exclusive)
172 explanations, all of them leading from the observation that ecological processes
173 can contribute more than selection to phenotypic trends (Ozgul *et al.* 2009).

174 These are: 1) Wing lengths of individual birds have decreased between years; 2)
175 Immature recruits to the population are getting ever smaller, leading to a larger
176 effect size in immatures than in adults and; 3) Body size changes are driven by
177 climatic or environmental impacts resulting from changing resources during
178 development. Additionally, the relationship between wing length and survival is
179 likely not constant. For example, smaller individuals may survive as food
180 becomes less limiting on survival (but not growth and size) (Ozgul *et al.*, 2009)
181 but then they may be more prone to the impacts of extreme weather. Thus, a
182 declining body size may be selected against only periodically although we do not
183 have sufficient data to test this within our population.

184

185 Recapture data show that within-individual wing lengths within our population
186 increase over time, suggesting that within-individual variation is not responsible
187 for the observed decline in wing length at the population level, and so failing to
188 support Hypothesis 1. We found weak support for Hypothesis 2: there was a
189 progressive decline in the wing lengths of immature birds recruiting into the
190 population, but the effect size among immatures was larger, although not
191 significantly, than that among adults (effect sizes -0.106 in immatures vs. 0.064
192 in adults), suggesting that the decline in the wing lengths of immature birds
193 recruiting into the population may have been offset by higher subsequent
194 survival of larger birds post-recruitment. It is possible this population-level
195 decline in size may result from genetic changes, even if selection is in the
196 opposite direction: for example, wing length may be genetically linked to another
197 trait under selection (Merilä *et al.*, 2001; Merila, 2012). This decline in the wing
198 length of immature birds may have been driven by adverse environmental
199 conditions such as low food availability during the nestling period (Hart *et al.*,
200 2006): our population is known to be resident year-round, with no ringing
201 evidence for a winter influx of birds from other populations (Robinson *et al.*
202 2015a) and immature birds do not moult flight feathers in their first winter.

203

204 We also found support for Hypothesis 3. Temperature increased over the 21
205 years of the study and was strongly linked to wing length. Despite 23% of
206 variation in wing length being explained by temperature variation in our study
207 population, this does not negate the influence of other factors. Loss of habitat,
208 loss of prime sources of food, higher temperatures leading to more parasites and

209 reduced weather-related mortality potentially all create grounds for more severe
210 competition and immune challenges (Yom-Tov & Geffen, 2011; Goodman *et al.*,
211 2012). Yellowhammer populations within the UK, including our study population
212 are declining (Robinson, *et al.* 2015b), due to removal of breeding habitat and a
213 reduction in the availability of both summer and winter food (e.g. Cornulier *et al.*
214 2011), likely leading to increased competition with both conspecifics and
215 heterospecific granivorous birds. Eglington and Pearce-Higgins (2012) found a
216 tighter link between Yellowhammer population trends and land use than with
217 climate. We recently found a high prevalence of haemoparasites within this same
218 Yellowhammer population during the non-breeding season: a time of year where
219 levels of circulating haemoparasites were previously thought to be negligible
220 (Dunn *et al.*, 2014): we also found associations between parasite infection and
221 wing length, where infected birds had shorter wings than uninfected birds
222 during one, mild, year (Dunn *et al.*, 2013). Parasite infection may potentially
223 contribute to wing length variation within our population, especially because
224 haemoparasite prevalence is predicted to increase with increasing temperatures
225 (Møller, 2010); however we currently have no longitudinal parasite prevalence
226 data to test this hypothesis directly.

227

228 Yellowhammer population declines have been linked to a reduction in over-
229 winter survival (Siriwardena *et al.*, 2008), but reduced reproductive success has
230 also been linked to a reduction in the availability of invertebrate food for chicks
231 during the breeding season (Hart *et al.*, 2006); thus a reduction in food
232 availability and/or habitat quality may be behind the wing length decline in
233 immature birds within our declining study population (Robinson *et al.* 2015b).

234 Either immature birds do not, on average, reach the same body size as they did
235 previously, or larger fledglings now have reduced survival; additional data from
236 young fledglings would be required to distinguish between these two
237 hypotheses. Elsewhere, we suggest that behavioural changes induced by
238 increased nest predation risk and reduced chick food availability may lead to a
239 reduction in fledgling body condition (Dunn *et al.*, 2010), potentially concurring
240 with our reduction in first-year wing length.

241

242

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250

251 **References**

- 252 Alonso, J., Alonso, J., Bautista, L., 1994. Carrying capacity of staging areas and
253 facultative migration extension in common cranes. *J. Appl. Ecol.* 31, 212–
254 222.
- 255 Barton, K., 2012. MuMIn: Multi-model inference. R package version 1.7.7.
256 <http://CRAN.R-project.org/package=MuMIn>.
- 257 Cornulier, T., Robinson, R.A.A., D.Elston, Lambin, X., Sutherland, W.J., Benton, T.G.,
258 2011. Bayesian reconstitution of environmental change from disparate
259 historical records: hedgerow loss and farmland bird declines. *Methods Ecol.*
260 *Evol.* 2, 86–94.
- 261 Dunn, J.C., Goodman, S., Benton, T., Hamer, K., 2014. Active blood parasite
262 infection is not limited to the breeding season in a declining farmland bird. *J.*
263 *Parasitol.* 100, 260–266.

- 264 Dunn, J.C., Goodman, S.J., Benton, T.G., Hamer, K.C., 2013. Avian blood parasite
265 infection during the non-breeding season: an overlooked issue in declining
266 populations? *BMC Ecol.* 13, 30.
- 267 Dunn, J.C., Hamer, K.C., Benton, T.G., 2010. Fear for the family has negative
268 consequences: indirect effects of nest predators on chick growth in a
269 farmland bird. *J. Appl. Ecol.* 47, 994–1002.
- 270 Dunn, J.C., Wright, C., 2009. Ageing and sexing the Yellowhammer *Emberiza*
271 *citrinella caliginosa* during the non-breeding season. *Ring. Migr.* 24, 240–
272 252.
- 273 Eglinton, S.M., Pearce-Higgins, J.W., 2012. Disentangling the relative importance
274 of changes in climate and land-use intensity in driving recent bird
275 population trends. *PLoS One* 7, 1–8. doi:10.1371/journal.pone.0030407
- 276 Goodman, R.A.E.E., Lebuhn, G., Seavy, N.E., Gardali, T., Bluso-Demers, J., 2012.
277 Avian body size changes and climate change: warming or increasing
278 variability? *Glob. Chang. Biol.* 18, 63–73. doi:10.1111/j.1365-
279 2486.2011.02538.x
- 280 Hart, J.D., Milsom, T.P., Fisher, G., Wilkins, V., Moreby, S.J., Murray, A.W.A.,
281 Robertson, P.A., 2006. The relationship between yellowhammer breeding
282 performance, arthropod abundance and insecticide applications on arable
283 farmland. *J. Appl. Ecol.* 43, 81–91. doi:10.1111/j.1365-2664.2005.01103.x
- 284 Husby, A., Hille, S.M., Visser, M.E., 2011. Testing mechanisms of Bergmann's rule:
285 phenotypic decline but no genetic change in body size in three passerine
286 bird populations. *Am. Nat.* 178, 202–13. doi:10.1086/660834
- 287 Lessells, C., Ovenden, G., 1989. Heritability of Wing Length and Weight in
288 European Bee-Eaters (*Merops apiaster*). *Condor* 91, 210–214.
- 289 Merila, J., 2012. Evolution in response to climate change: In pursuit of the
290 missing evidence *BioEssays* 34, 811–818. doi:10.1002/bies.201200054
- 291 Merilä, J., Sheldon, B., Kruuk, L., 2001. Explaining stasis: microevolutionary
292 studies in natural populations. *Genetica* 112–113, 199–222.
- 293 Møller, A.P., 2010. Host–parasite interactions and vectors in the barn swallow in
294 relation to climate change. *Glob. Chang. Biol.* 16, 1158–1170.
- 295 Ozgul, A., Tuljapurkar, S., Benton, T.G., Pemberton, J.M., Clutton-Brock, T.H.,
296 Coulson, T., 2009. The dynamics of phenotypic change and the shrinking
297 sheep of St. Kilda. *Science* 325, 464–7. doi:10.1126/science.1173668
- 298 PECBMS, 2015. Population trends of common European breeding birds: 2015
299 update. Prague.
- 300 Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S., Coulson, T., 2007.
301 The Evolutional Demography of Ecological Change: Linking Trait Variation
302 and Population Growth. *Science* 315, 1571–1574.
- 303 Poulin, R., Thomas, F., 1999. Phenotypic variability induced by parasites: Extent
304 and evolutionary implications. *Parasitol. Today* 15, 28–32.
305 doi:10.1016/S0169-4758(98)01357-X
- 306 R Core Team, 2013. R: A language and environment for statistical computing.

307 Rausher, M.D., Delph, L.F., 2015. When does understanding phenotypic evolution
308 require identification of the underlying genes? *Evolution* 69, 1655–1664.
309 doi:10.1111/evo.12687

310 Redfern, C., Clark, J., 2001. *Ringers' Manual*. British Trust for Ornithology,
311 Thetford.

312 Robinson, R., Leech, D., Clark, J., 2015a. The Online Demography Report: Bird
313 ringing and nest recording in Britain & Ireland in 2014. BTO, Thetford
314 (<http://www.bto.org/ringing-report>, Creat. 11-December-2015).

315 Robinson, R., Marchant, J., Leech, D., Massimino, D., Sullivan, M., Eglinton, S.,
316 Barimore, C., Dadem, D., Downie, I., Hammond, M., Harris, S., Noble, D.,
317 Walker, R., Baillie, S., 2015b. *BirdTrends 2015: trends in numbers, breeding
318 success and survival for UK breeding birds*. Thetford.

319 Siriwardena, G.M., Calbrade, N.A., Vickery, J.A., 2008. Farmland birds and late
320 winter food: does seed supply fail to meet demand? *Ibis* 150, 585–595.

321 Svensson, L., 1992. *Identification Guide to European Passerines*. British Trust for
322 Ornithology, Thetford.

323 Teplitsky, C., Millien, V., 2014. Climate warming and Bergmann's rule through
324 time: is there any evidence? *Evol. Appl.* 7, 156–68. doi:10.1111/eva.12129

325 Teplitsky, C., Mills, J.A., Alho, J.S., Yarrall, J.W., Merilä, J., 2008. Bergmann's rule
326 and climate change revisited: Disentangling environmental and genetic
327 responses in a wild bird population. *Proc. Natl. Acad. Sci.* 105, 13492–13496.

328 Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D.G., Mccann, K.S.,
329 Savage, V., Tunney, T.D., Connor, M.I.O., 2014. Increased temperature
330 variation poses a greater risk to species than climate warming. *Proc. R. Soc.
331 B* 281, 20132612

332 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.,
333 Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses
334 to recent climate change. *Nature* 416, 389–395.

335 Yom-Tov, Y., Geffen, E., 2011. Recent spatial and temporal changes in body size of
336 terrestrial vertebrates: probable causes and pitfalls. *Biol. Rev.* 86, 531–41.
337 doi:10.1111/j.1469-185X.2010.00168.x

338

339

340 Appendix 1. Rationale for using wing length as a surrogate for body size.

341

342 For a subset of our population ($n = 126$) we obtained a range of morphometric
343 measurements. These were wing length, measured as the maximum wing chord
344 using a stopped metal rule (± 0.5 mm); head and bill length, measured from the
345 tip of the bill to the centre of the back of the skull (Redfern and Clark, 2001);
346 mass (measured using a digital electronic balance ± 0.1 g; Satrue, Taiwan), tarsus
347 length, measured as the minimum tarsus length from the foot to the inside of the
348 tarso-metatarsal joint; tail length, measured from the tail base to the tip of the
349 longest outer rectrix; bill length, measured from the the feathering to the tip of
350 the bill; and bill depth, measured at the point of feathering (Svensson, 1992); as
351 detailed in Dunn & Wright (2009). All measurements apart from wing length
352 and mass were taken using Vernier digital callipers (± 0.1 mm; Draper Tools,
353 UK). Where we had duplicate measurements for the same bird ($n = 6$) we
354 removed the second measurement to avoid pseudoreplication.

355

356 We carried out a principal components analysis (PCA) based on a covariance
357 matrix using the *pcal* command in R. Factor loadings and the proportion of
358 variance explained by each PCA are given in Table A1.

359

360 Table A1. Factor loadings from the PCA analyses performed to identify the
361 strongest predictor of overall body size in Yellowhammers in West Yorkshire, UK

362

PCA1	PCA2	PCA3	PCA4	PCA5	PCA6	PCA7
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Head bill length		-0.140			-0.793	0.567	-0.151
Wing length	-0.719		0.688				
Mass	-0.147	-0.968	-0.147		0.128		
Bill length				-0.122	-0.572	-0.809	
Bill depth					-0.104	0.111	0.987
Tail length	-0.678	0.201	-0.704				
Tarsus length				0.991			
% variance explained	0.797	0.082	0.061	0.039	0.014	0.004	0.002

363

364

365

366 **Table 1.** Model estimates, adjusted standard errors and 95% CIs from the final
 367 averaged model predicting wing length of Yellowhammers in north-east England
 368 between 1986 and 2008 inclusive (prior to the addition of temperature to the
 369 model). The final averaged model predicted 64% of variation in wing length (R^2
 370 = 0.64). Terms in bold denote significant terms where 95% CIs do not overlap
 371 zero.

372

	Estimate	SE	Lower CI	Upper CI
Intercept	87.01	0.68	85.68	88.34
Age	-2.26	0.62	-3.48	-1.04
(Immature)				
Sex (Male)	4.56	0.60	3.39	5.72
Year	-0.08	0.03	-0.14	-0.02
Month	-0.07	0.05	-0.17	0.02
Age × Sex	-0.63	0.30	-1.22	-0.04
Age × Year	-0.02	0.03	-0.11	0.02
Sex × Year	0.02	0.03	-0.01	0.10

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376

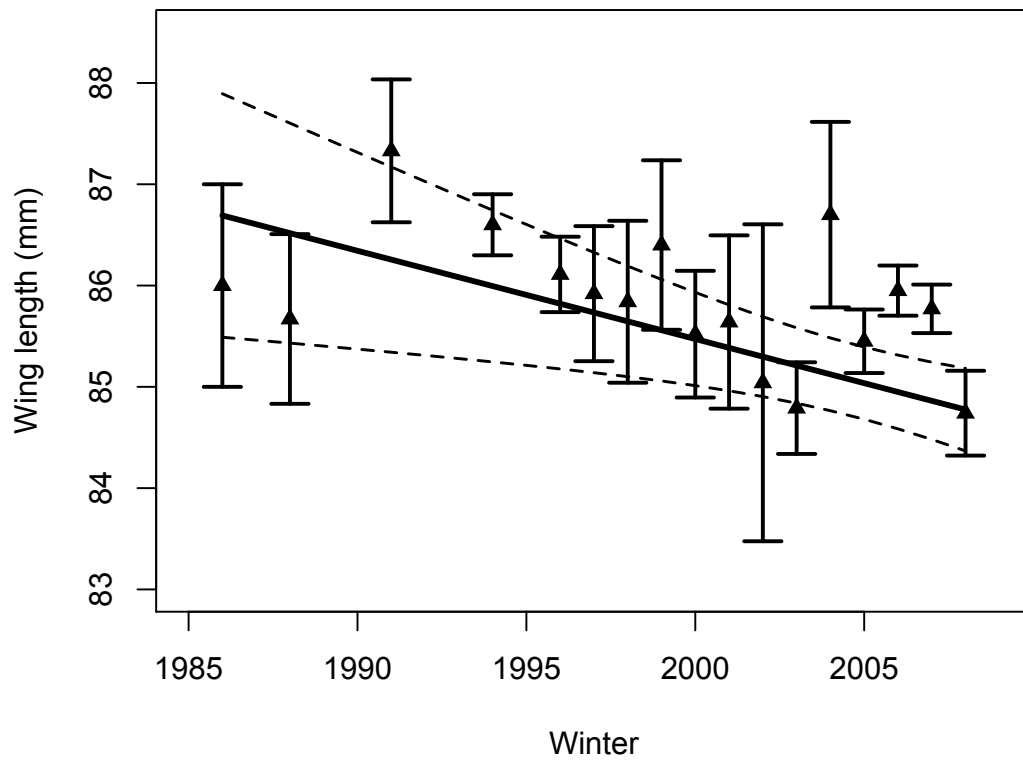
377 Table 2. Model estimates, adjusted standard errors and 95% CIs from the linear
378 mixed-effects model determining whether individual Yellowhammer wing
379 lengths decrease over time from birds caught in more than one winter. Terms in
380 bold denote significant terms where 95% CIs do not overlap zero.
381

	Estimate	SE	Lower CI	Upper CI
Intercept	82.98	1.04	80.95	85.02
Measurement	2.36	0.30	1.77	2.94
Month	0.11	0.14	-0.18	0.39

382

383

384 Figure 1: Declining mean wing length (± 1 SE) over time in a population of
385 Yellowhammers. Lines are predicted mean $\pm 95\%$ CI from the averaged model
386 (Table 1) for adult females.
387



388

389