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**Article**

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1   Do British birds conform to Bergmann's and Allen's rules? An analysis of

2   body size variation with latitude for four species

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9

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12

13  Short title: Bergmann's and Allen's rules applied to four British birds

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26

27    Summary

28    Capsule

29    An analysis of body mass and wing length for four bird species shows

30    trends broadly in line with predictions from Bergmann's and Allen's rules

31    but with species- and sex-specific trends in terms of body size variation

32    with latitude in Britain.

33

34    Aims

35    To analyse body size characteristics for bird species with latitude in Britain

36    to test Bergmann's and Allen's rules (over a range of *c.* 740 km).

37

38    Methods

39    Body mass and wing length for four bird species (Blackbird *Turdus merula*,

40    House Sparrow *Passer domesticus*, Robin *Erithacus rubecula*, Song Thrush

41    *T. philomelos*) were analysed using Principal Components Regression

42    Analysis to investigate trends with latitude, longitude, or by sex and Julian

43    day.

44

45    Results

46    Evidence was found for latitudinal gradients in body mass for male

47    Blackbird, female House Sparrow (both increasing in size northwards),

48    and female Robin (decreasing in size northwards) and in wing length for

49    female Robin and male Song Thrush (decreasing and increasing

50    northwards, respectively).

51

52    Conclusion

53    Trends were broadly in line with predictions from Bergmann's and Allen's

54    rules except for Robin which had trends opposite to those expected.

55    Differences in trends between sexes suggest a role for an interplay

56    between natural and sexual selection with latitude that deserves further

57    consideration.

58

59    Introduction

60    Individuals in colder climates tend to have larger body sizes than

61    individuals of the same species in warmer climates. This well-known

62    biogeographic principle proposed by Bergmann (1847) relates body size

63    variation within species to the prevailing climate over large scales via

64    latitude. The mechanism for this rule is proposed to act via metabolism

65    and heat conservation because a larger body size optimises the surface

66    area to mass ratio so that a larger body size will tend to be at a selective

67    advantage at lower mean ambient temperatures (Mayr, 1963; Kendeigh,

68    1969; Lomolino et al., 2006).  One criticism of Bergmann's rule is whether

69    differences in size due to latitude would be too small to provide significant

70    heat conservation for homeotherms (Scholander, 1955; Irving, 1957)

71    compared to other factors. These might include maintaining a heat

72    balance by having a higher metabolic rate (Kendeigh, 1969), dropping the

73    core temperature (Reinertsen and Haftorn, 1986) or other factors such as

74    greater fat deposits, increasing heat production (e.g., by shivering), or by

75    behavioural adjustment, *viz*. by lowering the gradient (e.g., seeking

76    shelter), by decreasing heat dissipation (e.g., by raising feathers (or fur in

77    mammals)), and by decreasing the surface area by rolling up into a ball,

78    or by huddling (Schmidt-Nielsen, 1997). However, reviews have found

79    that Bergmann's rule holds for the majority (i.e., > 50%) of mammal and

80    bird species tested with statistically significant body size trends for most

81    species with latitude and temperature. Ashton et al. (2000) found that 78

82    of 110 mammal species showed significant correlations between size and

83    latitude, and 48 of 64 mammal species showed significant negative

84    correlations with temperature. Ashton (2002) found that 76 of 100 bird

85 species were significantly larger at higher latitudes; and Meiri and Dayan

86 (2003) 72% of 149 bird species and 65% of 149 mammal species followed

87 Bergmann's rule).

88

89 Body size in birds represents a problem in terms of finding a consistent

90 measure because the mass of birds can vary with age, sex, breeding

91 condition, migratory status, and time of year (Connell et al., 1960; Niles,

92 1973; Bairlein et al., 1983; Gosler, 1994; Gosler et al., 1998).  Therefore,

93 less variable measures tend to be used as a proxy for body size such as

94 wing, tail, or tarsus length. Wing length is a widely used proxy for bird

95 body size and is often highly correlated with body mass (e.g., Gosler et

96 al., 1998). However, wing length is not universally a good proxy for body

97 size since its association with body size tends to be species-specific

98 (Rising and Somers 1989, Gosler et al., 1998; Hogstad, 2011) and in

99 relation to latitude, wing length may show opposite trends to those

100 expected from Bergmann's rule because the lengths of the extremities of

101 endotherms may be inversely related to temperature, another classic

102 biogeographic pattern known as Allen's rule (Allen, 1877).

103

104 To our knowledge there has only been one direct published test of

105 Bergmann's hypothesis applied to birds in Britain. Wyllie and Newton

106 (1994) used wing-length as a proxy for body size and determined a

107 latitudinal trend for Sparrowhawk, *Accipiter nisus*, finding an increase by

108 an average of 0.86 mm and 0.75 mm in adult males and females,

109 respectively, for each successive degree of latitude (c. 110 km).

110

111    Yom-Tov et al. (2006) undertook a test of body size changes with

112    temperature over time for 14 species over a period of 30-35 years from

113    two sites in Britain and found decreases in body size through time

114    consistent with temperature-related trends that could be attributed to

115    global warming (Gardner et al. 2009). Although such changes in body

116    mass are consistent with Bergmann's rule, Rising and Somers (1989)

117    suggested body mass tends to be a better measure of body size for males

118    rather than females due to gender-dependent variation in reproductive

119    condition. Yom-Tov et al. (2006) also found increases in wing length in

120    their study and ascribed these changes to Allen's rule. Accordingly, we

121    consider body mass and wing length separately in analyses and, whilst

122    both may be useful measures of body size, changes in relation to latitude

123    are expected where body mass is predicted to increase and wing length

124    predicted to decrease in line with Bergmann's and Allen's rules,

125    respectively.

126

127    The aims of this paper were to test whether Bergmann's and Allen's rules

128    hold for a small sample of bird species in the UK.  Accordingly, we

129    hypothesise that a latitude-related temperature gradient in the UK would

130    result in both increasing body size and decreasing wing length from south

131    to north. Trends that do not conform to these predictions may arise due to

132    latitudinal gradients that act via sexual rather than natural selection.

133

134    Materials and Methods

135    Body size variables and species selection

136 The data used here are derived from volunteer (or 'citizen-science')

137 collected sampling of birds using standard ringing methods. For inclusion

138 here, selected species had to be relatively common and widespread: they

139 had to be sufficiently common to be reflected by an adequate sample size;

140 and they had to be widespread in order to test for the geographic gradient

141 implicit in Bergmann's rule.

142

143 Sedentary rather than migratory species were selected because they are

144 most likely to be present in winter when conditions are more likely to be

145 limiting. Furthermore, being present all year round, sedentary species will

146 tend to have lower natal and breeding dispersal distances so that records

147 from ringing are more likely to reflect species resident in a particular

148 locality compared to those that might be on passage or that undergo

149 annual migratory movements (Paradis et al., 1998). Birds which

150 undertake long migrations will tend to have exhausted fat reserves on

151 arrival in spring and will have to build them up again before departing in

152 autumn (Newton, 2008). Although the species selected here are

153 considered to be native and sedentary we cannot rule out that either they

154 undertake regional movements within Britain or that populations in the UK

155 are not augmented by individuals from continental Europe (Wernham et

156 al., 2002). However, the mean breeding and natal dispersal distances of

157 the four selected species are typical of native species and are

158 proportionally smaller than migratory species (Ranges of geometric means

159 for natal dispersal distances are 0.21–0.59 km; and breeding dispersal

160 distances 0.15-0.36 km (Paradis et al., 1998)). To control for any

161  seasonal body mass and age-related variation, records were restricted to

162  the period 1st June – 31st July (all 2010) and to birds aged 4 – 6 years old.

163

164  The choice of species was also influenced by studies elsewhere. For

165  example, the House Sparrow *Passer domesticus* is a species that fits

166  Bergmann's rule in the USA (Johnston and Selander, 1971) and Finland

167  (Brommer et al., 2014). The Robin *Erithacus rubecula* is a sedentary

168  native species and in contrast to House Sparrow, is commonly considered

169  to exhibit only limited sexual dimorphism (e.g., Jovani et al., 2001). Two

170  further species, Blackbird *Turdus merula* and Song Thrush *T. philomelos*,

171  both members of the same family (Turdidae) were chosen. Attributes of

172  the sample used in these analyses are given in Table 1.

173

174  Data Analysis

175  Data for the four species was supplied by the BTO and were derived from

176  710 separate sites and from 654 registered ringers (n = 1407). Data

177  came from as far south as Lancing in Sussex (50°50'N 0°19'W) and as far

178  north as Rowansgarth Greens (57°30'N 2°18'W) (Grampian Region,

179  Scotland), a straight line distance of 752km, or 741km due north

180  (calculated using http://www.movable-type.co.uk/scripts/latlong.html)

181  (i.e., 7°20' difference).  The mean minimum and maximum January

182  temperatures for these locations ranged from -3.7 to 2.0 and 4.7 to 8.4

183  °C, respectively, from north to south, and by taking the mid-points the

184  representative difference is 7.4 °C at the harshest time of year,

185  approximately 1 °C per degree of latitude (data for the years 1971–2000

186  http://www.metoffice. gov.uk/climate/uk/averages/19712000/). In order

187     to control for potential topographic variation the data were restricted to

188     samples from lowland sites <span style="color:red">south of the Moray Firth and east of a line</span>

189     <span style="color:red">joining Inverness, Scotland, and Chichester, England thus excluding all</span>

190     <span style="color:red">significant upland areas.</span>

191

192     Analyses in relation to latitude were done by calculating relative weights

193     using Principal Components Regression Analysis (PCRA)(Johnson, 2000).

194     <span style="color:red">Regressing against principal components yields regression weights which</span>

195     <span style="color:red">are free of any (linear) dependences present in the original data, because</span>

196     <span style="color:red">the principal components are orthogonal. These weights can be projected</span>

197     <span style="color:red">back onto the original data to provide estimates of regression weights for</span>

198     <span style="color:red">the data, free of any dependences amongst the independent variables.</span>

199     Although data were carefully selected on the basis of controlling for

200     potentially confounding factors (e.g., seasonal and age-related change)

201     there remained a complex set of cross correlations that had to be

202     controlled for since, for example, not only does <span style="color:red">body mass</span> vary by time of

203     day (Rands et al., 2006) but also varies over the breeding period meaning

204     there may be phenological-related delays due to latitude. Further, after

205     taking into account sex, <span style="color:red">wing</span> length can vary with age of bird and

206     migratory distance (at least in Blackcap *Sylvia atricapilla* Pérez-Tris and

207     Tellería, 2003), and stage of moult (in Great Tit *Parus major*: Dhondt,

208     1981). PCRA was chosen because this method addresses cross

209     correlations between predictor variables (Schielzeth, 2010).

210

211     Separate models were constructed for <span style="color:red">wing length</span> and <span style="color:red">body mass</span>. Both

212     models included latitude, longitude, Julian day and sex, and in addition,

213 the model for body mass included wing length because its inclusion

214 controls the mass analysis for the effects of body size to allow inferences

215 about variation in mass with latitude independently of size.

216

217 The data selected were restricted to the period 1st June – 31st July

218 encompassing the breeding season and for Blackbirds the end of the

219 breeding season. Body mass is particularly sensitive to breeding – most

220 birds show an interrupted foraging response and add mass while breeding

221 (MacLeod et al., 2005). This is lost at the end of the breeding season;

222 therefore Julian Day was included to take into account any seasonal

223 effects on body mass.  As moult follows after breeding, Julian Day was

224 also included in the analysis of wing length. PCRA was done in R version

225 3.1 (no date) and tests of differences between males and females using

226 Analysis of Variance (ANOVA) were done in Minitab (2010).

227

228 Results

229 For all species, females had a statistically significantly greater body mass

230 compared to males, whereas wing length was longer for males compared

231 to females (Table 2). Tables 3 and 4 present the results of the PCRA

232 analyses. All but one of the analyses of regression weights for body mass

233 were statistically significant with total percentage variance explained

234 varying from 6.95% to 25.6%. However, latitude accounted for the

235 greater part of the variance in only three models: male Blackbird (5.4%),

236 female House Sparrow (6.8%), and female Robin (12.8%)(Table 3, Figure

237 1). Longitude explained the greatest amount of variance for one species,

238 male Song Thrush; Julian day explained the greatest amount of variance

239    for female Song Thrush; and wing length explained the greatest amount

240    of variance for male and female Blackbird, female House Sparrow, male

241    Robin, and male Song Thrush (Table 3). The percentage variance

242    explained in all cases were low with no model exceeding 25.6% overall

243    and with latitude explaining no more than 12.8% in any single model.

244

245    For wing length there were statistically significant models for female

246    Blackbird and female Robin (with that for male Song Thrush being

247    marginally non-significant) although for Blackbird the overall $R^2$ was very

248    small at 3.5%. The total $R^2$ values for female Robin and male Song Thrush

249    were 11.9% and 8.8% respectively with latitude accounting the majority

250    of the variation in both cases (Table 4). Except for Blackbird, these

251    relationships are shown in Figure 2 where the data are presented along

252    with those for the opposite sex (which were not statistically significant) for

253    comparison. Wing length for male Song Thrush increased whilst that for

254    female Robin decreased with latitude, respectively.

255

256    Discussion

257    Overall there were several statistically significant relationships for body

258    mass and wing length with latitude but overall explanatory power was

259    low.  Increases in body size with latitude may be attributed to Bergmann's

260    rule if they act on both males and females simultaneously. In the PCRA

261    analyses only Blackbird and Song Thrush had statistically significant

262    results for both males and females as predicted by Bergmann's rule but

263    the percentage variance explained by latitude was greater than 5% for

264    just male Blackbird and less than 2% for female Blackbird and both sexes

265 of Song Thrush (Table 3). For House Sparrow and Robin the percentage

266 variance explained by latitude was greater than 5% for just female House

267 Sparrow and female Robin but, in contrast to the other species, body

268 mass for both male and female Robin decreased with latitude (Figure 1).

269 The expected change in body mass for those three species with the

270 highest percentage variation explained by latitude, male Blackbird, female

271 House Sparrow, and female Robin from the most southern to the most

272 northern stations were 6.2 g (equivalent to 6.5% of their mean mass), 1.8

273 g (6.5%), and -2.4 g (-13.4%), respectively (Table 3). Thus, with the

274 exception of Robin, the results are broadly in agreement with Bergmann's

275 rule. For female House Sparrow this result is consistent with published

276 trends for USA and Finland but unfortunately body mass was not used in

277 these studies to enable a specific comparison of variation with latitude to

278 be made (Johnston and Selander 1971, Brommer et al., 2014).

279

280 Results for wing length were statistically significant for only single sexes of

281 two species and, although statistically significant, female Blackbird had a

282 very low percentage variance explained by latitude so can be disregarded

283 (Table 4). Female Robin had a percentage variance explained of 9.9% and

284 the trend was consistent with Allen's rule (Figure 2); male Song Thrush

285 was marginally non-significant but showed an increasing trend counter to

286 that expected from Allen's rule (Figure 2, Table 4).

287

288 Hence only female Blackbird showed any consistency between the

289 analyses for both body mass and wing length in line with predictions from

290 Bergmann's and Allen's rules simultaneously but the percentage variance

291 explained was very small (1.6% and 1.3%, respectively). Female Robin

292 also showed statistically significant results in both sets of analyses but

293 whereas the results for wing length were consistent with Allen's rule (in

294 that wing length was shorter with increasing latitude), they ran counter to

295 predictions from Bergmann's rule as body mass declined with latitude

296 (Figures 1 and 2).

297

298 The reasons why these results do not all conform to the expected patterns

299 from Bergmann's and Allen's rules may be due to sex-related allometric

300 scaling relationships, resulting from an interplay between sexual and

301 natural selection with latitude (Blanckenhorn et al., 2006).  Thus, any

302 body size clines will depend upon the strength of selection of the opposing

303 pressures. If, for example, a warmer climate in the south leads to better

304 survival rates (e.g., of nestlings), or in greater food supply (e.g., of

305 invertebrates), this could lead to higher populations and thus greater

306 competition for territory resulting in higher selection pressure on mate

307 choice. Shine (1989) suggested such a process could result in greater

308 sexual dimorphism in warmer climates and, conversely, less sexual size

309 differentiation when conditions are limiting. Tobias (1997), for example,

310 suggested that temperature affects territoriality in Robin *Erithacus*

311 *rubecula* and that social behaviour may be disrupted by food supply and

312 environmental conditions (as could be the case in the north). Further

313 evidence for sexual selection-related effects with latitude come from a

314 study by Badyaev (1997) who proposed a hypothesis related to elevation

315 that could easily be transferred to latitude. Badyaev examined 126 species

316 of cardueline finches and found that interspecific variation in sexual

317  dimorphism was more strongly associated with changes in elevation than

318  with other potential factors such as habitat, nest dispersion and

319  placement, and migratory status. He attributed this pattern to colder

320  temperatures at higher elevations and the need for biparental care for

321  successful breeding in birds under such conditions.

322

323  As previously noted, the only previous direct analysis of Bergmann's rule

324  in Britain found that wing length increased with latitude for Sparrowhawk

325  (Wyllie and Newton 1994) – a finding at variance with Allen's rule but

326  consistent with Bergmann's. Sparrowhawks are also sexually dimorphic –

327  more so in terms of body size than any of the four species considered

328  here. Thus, explanations as to whether wing length conforms to Allen's or

329  Bergmann's rule deserve further consideration but may also lie in the

330  degree of sexual dimorphism with latitude.

331

332  The findings presented here represent a preliminary study with only a

333  limited number of species being analysed. It is recommended that

334  analyses should be extended to a greater range of species, plus

335  differences between sexes with latitude in relation to population density,

336  food supply and, the relative strengths of sexual versus natural selection.

337  Also, of particular interest would be a study of Robin and why it shows

338  trends opposite to those expected.

339

14

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483

484
485

486    Figures
487
488
489    Figure 1. Body mass versus latitude for male Blackbird (upper, blue),
490    female House Sparrow (middle, red), and female Robin (lower, black).
491    Only the first two of these are consistent with Bergmann's rule.
492
493    Figure 2. Wing length versus latitude for male and female Song Thrush
494    (upper pair, red, increase with latitude) and Robin (lower pair, black,
495    decrease with latitude), respectively. Significant relationships (male Song
496    Thrush, female Robin) are shown by solid lines, non-significant
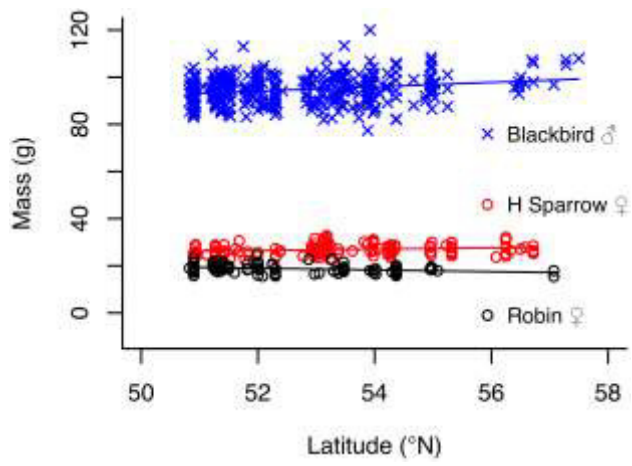497    relationships (female Song Thrush, male Robin) by dashed lines.
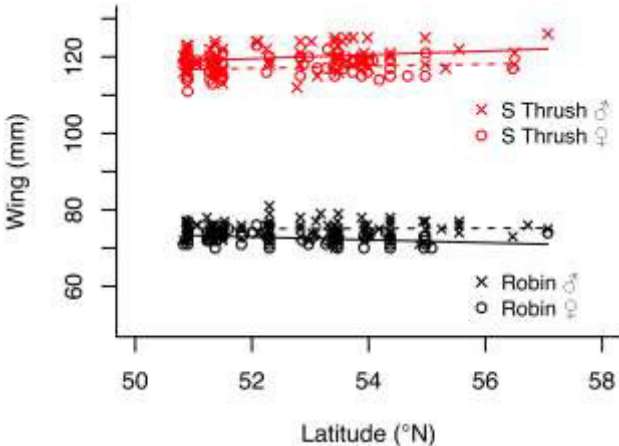498
499

Figure 1

Figure 2

Table 1. Summary statistics for the species chosen for this study by sex.

| Common name | Sex | Blackbird ♂ | Blackbird ♀ | Song Thrush ♂ | Song Thrush ♀ | House Sparrow ♂ | House Sparrow ♀ | Robin ♂ | Robin ♀ |
|---|---|---|---|---|---|---|---|---|---|
| Wing length (mm) | n | 383 | 282 | 85 | 59 | 160 | 148 | 116 | 78 |
| | Min | 121.0 | 118.0 | 112.0 | 111.0 | 72.0 | 68.0 | 70.0 | 70.0 |
| | Max | 141.0 | 138.0 | 126.0 | 123.0 | 82.0 | 79.0 | 81.0 | 77.0 |
| | Mean | 131.3 | 126.4 | 119.8 | 117.2 | 77.9 | 75.2 | 75.1 | 72.6 |
| | SD | 3.38 | 3.13 | 2.98 | 2.45 | 1.74 | 1.66 | 1.81 | 1.61 |
| Body mass (g) | n | 368 | 266 | 81 | 58 | 141 | 140 | 114 | 83 |
| | Min | 77.4 | 75.5 | 61.9 | 62.0 | 23.3 | 22.6 | 15.7 | 15.4 |
| | Max | 120.0 | 133.7 | 80.3 | 90.0 | 32.0 | 32.8 | 20.6 | 24.3 |
| | Mean | 94.8 | 95.9 | 69.3 | 75.9 | 26.9 | 26.9 | 18.1 | 18.7 |
| | SD | 5.96 | 7.86 | 3.73 | 6.74 | 1.49 | 2.2 | 1.04 | 1.86 |

Table 2. Results of ANOVA for differences between male and female body mass and wing length giving number of cases, n, the F-statistic, and level of significance, p. All tests were statistically significant.

| | Statistic | Body mass | Wing length |
|---|---|---|---|
| Blackbird | n (♂:♀) | 352:257 | 367:273 |
| | F | 4.2 | 183.0 |
| | p | 0.04 | <0.001 |
| Song Thrush | n (♂:♀) | 78:52 | 82:53 |
| | F | 21.3 | 13.7 |
| | p | <0.001 | <0.001 |
| House Sparrow | n (♂:♀) | 141:140 | 160:148 |
| | F | 3.4 | 99.3 |
| | p | 0.04 | <0.001 |
| Robin | n (♂:♀) | 110:81 | 112:76 |
| | F | 5.3 | 37.3 |
| | p | 0.006 | <0.001 |

Table 3. PCRA regression weights of body mass against latitude, longitude, Julian day, and wing length. Statistically significant p-values indicated in bold. Variation provides estimates of body mass from the southern-most to the northern-most stations.

| Species | Sex | % variance explained by | | | | Total % $R^2$ | p-value | Variation south to north (g) |
|---|---|---|---|---|---|---|---|---|
| | | Latitude | Longitude | Day | Wing | | | |
| Blackbird | ♂ | 5.4 | 0.3 | 0.8 | 6.9 | 13.5 | **<<0.001** | 93.0 - 99.2 |
| | ♀ | 1.6 | 0.1 | 2.6 | 2.7 | 7.0 | **<0.001** | 94.3 – 99.9 |
| Song Thrush | ♂ | 0.8 | 6.6 | 1.4 | 16.8 | 25.6 | **<0.001** | 68.2 – 72.9 |
| | ♀ | 0.2 | 0.0 | 12.0 | 11.5 | 23.7 | **0.013** | 75.8 – 76.5 |
| House Sparrow | ♂ | 0.4 | 0.2 | 0.4 | 2.1 | 2.9 | 0.34 | |
| | ♀ | 6.8 | 1.4 | 0.0 | 4.8 | 13.0 | **<0.001** | 26.2 – 28.0 |
| Robin | ♂ | 1.5 | 0.0 | 0.6 | 9.4 | 11.5 | **0.02** | 18.2 – 17.7 |
| | ♀ | 12.8 | 0.2 | 3.0 | 4.8 | 20.8 | **0.013** | 19.4 – 17.0 |

Footnote. Regression of body mass against latitude for each species, both sexes combined but with sex as a categorical variable, indicates that only Robin has a significant difference between the sexes in terms of body mass variation with latitude ($p<0.05$).

Table 4. PCRA regression weights of wing length against latitude, longitude, and Julian day. Statistically significant p-values indicated in bold.

| Species | Sex | % variance explained | | | Total % $R^2$ | p-value | Variation south to north (mm) |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | Latitude | Longitude | Day | | | |
| Blackbird | ♂ | 0.3 | 0.1 | 0.0 | 0.5 | 0.61 | |
| | ♀ | 1.3 | 0.9 | 1.3 | 3.5 | **0.019** | 125.8 – 127.8 |
| Song Thrush | ♂ | 6.8 | 0.3 | 1.7 | 8.8 | 0.058 | |
| | ♀ | 2.7 | 0.1 | 0.6 | 3.4 | 0.59 | |
| House Sparrow | ♂ | 1.2 | 0.2 | 0.5 | 1.9 | 0.39 | |
| | ♀ | 0.1 | 0.2 | 0.6 | 0.9 | 0.74 | |
| Robin | ♂ | 1.0 | 3.3 | 0.0 | 4.4 | 0.17 | |
| | ♀ | 9.9 | 2.0 | 0.0 | 11.9 | **0.024** | 73.4 – 70.8 |

Footnote. Regression of wing length against latitude for each species, both sexes combined but with sex as a categorical variable, indicates that only Robin has a significant difference between the sexes in terms of wing length variation with latitude ($p<0.05$).