Reduced compensatory growth capacity in mistimed broods of a migratory passerine

Gergely Hegyi · Gergely Nagy · János Török

Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University, Pázmány Péter sétány 1/C, H-1117 Budapest, Hungary

Correspondence: Gergely Hegyi. Tel: +36-13812193. Fax: +36-13812194. E-mail: everest@ludens.elte.hu

Author Contributions: GH and JT collected long-term data. GH, GN and JT compiled the long-term dataset. GH and JT conceived and designed the experiment. GH, GN and JT performed the experiment. GH analyzed the data. GH and JT wrote the paper.

15 **Abstract** Phenotypic plasticity has recently been proposed to increase population viability

16 when rapid anthropogenic environmental changes cannot be tracked by means of evolution.

17 This assumes that environmental changes do not constrain phenotypic plasticity itself, which

18 has rarely been examined in natural populations. In areas of climate warming, many long-

19 distance migratory birds breed increasingly late relative to the period of peak food supply, and

20 the temporal mismatch may constrain plastic life-history traits such as nestling growth. We

21 combined 23 years of food availability and breeding data with a three-year experimental

22 manipulation of nestling growth trajectories in a Central-European population of collared

23 flycatchers to examine the potential impact of climate-related mistimed breeding on nestling

24 developmental plasticity. Timing of the food peak was predicted by winter climate, and the

25 median hatching date of broods was earlier in springs with earlier food peaks. However, the

26 adjustment of hatching date was incomplete and the population largely missed the food peak

27 in years with very early food peaks. After imposing a temporary, experimental food shortage

28 on nestlings, the extent of compensatory growth in body mass differed among years, and this

29 difference was apparently related to the distance of hatching dates from the yearly food peak.

30 Growth compensation declined with distance from the peak. These results suggest that

31 mistimed phenology may not only create permanently adverse conditions for migratory

32 species, but it may also constrain the plastic responses of individuals to temporary

33 disturbances. Therefore, climate change may not only favour but also restrict phenotypic

34 plasticity.

35

36 **Keywords** body mass gain · breeding date · global warming · insect phenology · long-distance

37 migrant

Introduction

Phenotypic plasticity implies environmentally induced variation in the phenotype expressed

by a given genotype. Much of this environmentally induced variation is non-adaptive and

often arises from environmental constraints on trait expression (Ghalambor et al. 2007).

Climate warming has pervasive effects on wild populations in temperate latitudes, and the

apparent impacts have increased in the last few decades (Parmesan 2006). Population studies

of the impacts of climate change classically focus on micro-evolution (Palumbi 2001). In

these studies, phenotypic plasticity is generally mentioned as an alternative to micro-

evolutionary change (e.g. Brommer et al. 2008; Husby et al. 2010) or as an individual-

specific, evolvable character (e.g. Nussey et al. 2005). On the other hand, recent reviews and

theoretical treatments highlight the importance of plastic responses especially when evolution

is insufficient to keep track of environmental change (Chevin et al. 2010; Hoffmann and Sgró

2011). These approaches to phenotypic plasticity all assume the same degree of plasticity

across different environments. However, plasticity in life history traits may itself change with

environmental conditions, and this may limit the role plastic responses can play in mitigating

fitness costs due to environmental change. In other words, it is now well known that

evolutionary responses to global changes can be strongly constrained (Etterson and Shaw

2001; Wilson et al. 2006), while the extent to which phenotypic plasticity is environmentally

constrained has seldom been examined in the context of climate change (Both 2010; Chevin

et al. 2010).

In birds, the most widely known effect of global warming has been the dissociation of

food supply and demand due to the earlier phenology of vegetation and therefore insect food

relative to the breeding season (Visser et al. 1998; Thomas et al. 2001). Comparative analyses

have also highlighted certain groups that are most vulnerable to such mismatches, such as

long-distance migrants, species with narrow habitat requirements and seasonal habitats, and

63   food specialists (Rubolini et al. 2007; Both et al. 2010; Végvári et al. 2010; Moussus et al.

64   2011; Saino et al. 2011). Populations exhibiting weaker breeding date adjustments to the

65   shifting phenology seem to have declined relatively more strongly (Both et al. 2006, 2010;

66   Møller et al. 2008). In long-distance migrants, adjustment of migration times is hampered by

67   relatively independent and often conflicting climatic effects at the wintering, migratory and

68   breeding latitudes (e.g. Tottrup et al. 2008; Balbontin et al. 2009; Both 2010) that may often

69   cause changes in the distribution rather than the mean of arrival and breeding dates with time

70   (Laaksonen et al. 2006; Buskirk et al. 2009), i.e. no overall adjustment. Observed responses to

71   the temporal mismatch include reductions of breeding season length (Møller et al. 2010), the

72   probability of second broods (Husby et al. 2009), the length of the breeding bout (Matthysen

73   et al. 2011), and migration distance (Smallegange et al. 2010). Details of the breeding bout

74   other than timing-related issues are rarely examined (but see Husby et al. 2010 for analyses of

75   clutch size).

76   The growth of nestlings is a rapid and flexible process that usually strongly depends

77   on actual food supply (Starck and Ricklefs 1998). Nestling growth may therefore be an ideal

78   trait on which to examine the effects of climate-related temporal mismatch on the degree of

79   phenotypic plasticity. Most studies of nestling growth focused on the determinants of the

80   growth target or the whole growth trajectory (for a review see Hegyi et al. 2011). However,

81   birds of various diet groups (Emlen et al. 1991; Schleucher 2004) and particularly

82   insectivorous species (Lindstrom et al. 2005; Garcia-Navas and Sanz 2011) regularly

83   experience rapid temporal changes in food supply, e.g. due to weather fluctuations (Avery and

84   Krebs 1984; Siikamäki 1996; Arlettaz et al. 2010). Given that there is often strong directional

85   selection on the target of growth (Gebhardt-Henrich and Noordwijk 1991; McCarty 2001;

86   Moreno et al. 2008), compensatory growth after temporary food shortage may be selected for

87   (Metcalfe and Monaghan 2001). It is clear that more field experiments are needed, but several

88   studies suggest that growth compensation may be more widespread among birds than we

89   currently know (e.g. Bize et al. 2003; Brzek and Konarzewski 2004; Hegyi and Török 2007;

90   Honarmand et al. 2010).

91   Here we combine 23 years of breeding and food availability data with a three-year

92   experimental manipulation of nestling growth trajectories in a Central-European population of

93   collared flycatchers (*Ficedula albicollis*) to examine whether climate-related delays of

94   breeding time relative to peak food availability may limit the compensatory growth capacity

95   of nestlings in mismatched seasons and mismatched broods. Such a limitation would indicate

96   that reduced phenotypic plasticity may exacerbate the adverse consequences of climate

97   change for species that also experience short term environmental fluctuations (Chevin et al.

98   2010). Our main questions are the following. First, do large-scale climatic conditions

99   influence caterpillar peak date in our study area? Second, do birds breed earlier in years with

100   earlier food peaks? Third, is the mismatch between peak food time and median breeding time

101   larger in years with earlier food peaks? Fourth, does compensatory growth capacity differ

102   between years? Finally, is this year difference related to year-specific timing relative to the

103   food peak?

104   Potential for nestling growth plasticity under food limitation is jointly set by nestling

105   developmental and assimilatory constraints (Lepczyk and Karasov 2000), unequal nestling

106   competition for care (Szöllősi et al. 2007) and parental feeding limitations and decisions

107   reflecting a combination of environment and individual quality (Tinbergen and Verhulst

108   2000; Garamszegi et al. 2004). If growth potential was overwhelmingly set by parental care

109   decisions depending on food supply or parental quality, using the term "nestling phenotypic

110   plasticity" would be misdirected. We therefore repeated the analyses of food limitation (i.e.

111   year or relative timing) in all stages of the experimental growth manipulation at the levels of

112   both nestlings and broods, and compared the proportions of growth variance explained by

113   year/timing, treatment and their interaction in the nestling- versus brood-level analyses. If

114   nestling-level processes were important in determining growth responses, we predicted

115   systematically larger explained variances for these terms at the nestling than at the brood

116   level.

117

118

119   **Materials and methods**

120   Long-term data

121   This study was conducted in the Pilis Mountains, near Szentendre, Hungary (47°43'N,

122   19°01'E), where nestbox plots with a total number of approximately 800 boxes have been

123   maintained since the early 1980s in parts of a continuous, oak-dominated forest with scattered

124   clearings and different intensities of management. The present dataset comes from the years

125   1987 to 2009. The first collared flycatchers arrive at the plots in early April, and peak egg

126   laying is usually at the turn of April and May. Nestboxes were checked frequently (usually

127   every third or fourth day) to record first-egg dates. These could be back-calculated for nests

128   with incomplete clutches because laying gaps are very rare in this species while brood

129   parasitism has never been observed.

130   We used the time of the caterpillar peak as a proxy of yearly peak food time.

131   Caterpillars constitute an important part of the collared flycatcher diet (Török 1986). In our

132   population, the height of the yearly caterpillar peak very strongly determines the fitness

133   consequences of natural and manipulated brood sizes, and it also alters the direction of

134   selection on clutch size (Török et al. 2004). The timing of the caterpillar peak represents

135   another limiting factor. Flycatchers are long-distance migrants, and their nestling rearing

136   period is nearly always late relative to the yearly caterpillar peak. This contributes to the

137   generally observed directional selection for earlier breeding (Sheldon et al. 2003, Török et al.

138 2004). However, the adjustment to the very early food peaks of some years is hindered by the

139 apparent inability of birds to advance their migration, so we expected that years of early food

140 availability would represent a limiting environment for nestling rearing (Both and Visser

141 2001). We collected caterpillar frass every 4 days from 0.5 x 0.5m trays (4 or 5 trays in each

142 individual nestbox plot) placed randomly under the canopy of oak trees, and estimated

143 caterpillar supply from the mean daily mass of the fallen amount (Perrins 1991; Blondel et al.

144 1998). Finally, macroclimatic conditions were here represented by the winter North Atlantic

145 Oscillation (NAO) index (averaged from December to March; Jones et al. 1997). Analyses

146 using NAO were aimed to show that food peak timing in our population was related to yearly

147 climatic variation, and therefore potentially to climate change. Fluctuations of the NAO index

148 are related to global warming (Hurrell and Deser 2010), and the index itself strongly predicts

149 late winter and early spring temperature regimes in Europe (including our study area, our

150 unpublished data) that may directly influence both caterpillar phenology (van Asch and Visser

151 2007) and the life history of insectivorous long-term migrants (Hüppop and Hüppop 2011).

152 Data on the NAO index were taken from http://www.cru.uea.ac.uk/cru/data/nao/ and

153 http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm.

154

155 Experimental data

156 In three years we conducted a temporary food deprivation experiment to induce compensatory

157 growth during and following the time of maximum nestling growth (see Rosivall et al. 2005;

158 Hegyi et al. 2006). The first year of this experiment (2005) confirmed the presence of

159 compensatory growth (Hegyi and Török 2007). Here we add two more years (2006 and 2009)

160 and focus on the year- and date-dependence of compensatory growth in relation to caterpillar

161 phenology. The experimental protocol was the following. We looked for trios of nests with

162 the same hatching date and clutch size and a maximum brood size difference of one nestling,

163 where all males were older than one year (i.e. "adult" males; see Hegyi et al. 2006). At 2 days

164 of nestling age we partially cross-fostered two nests in each trio by reciprocally transferring

165 approximately half of both broods (3 nestlings in a brood of 6, or 3 or 4 nestlings in a brood

166 of 7). At 4d of age, we induced food shortage in one of the cross-fostered broods by capturing

167 the male and keeping it in a cage for three days with ad libitum food and water. Females

168 rearing the brood alone or with little male help are commonplace in this species due to male

169 polygyny, and these broods are less successful than those raised by two parents (Garamszegi

170 et al. 2004).

171   At 7d of age, the male was released and whole broods were moved between the three

172 nests of each trio in the direction deprived – control fostered – control unfostered. Thereafter,

173 nestlings from the deprived brood were reared by parents at the control fostered nest, and

174 control fostered nestlings were reared by parents at the control unfostered nest. Parents at the

175 male removal nest received control unfostered nestlings and these parents and nestlings were

176 not considered any further. This swap was done to ensure that both of the partially cross-

177 fostered broods were reared by non-manipulated parents from this point of nestling growth.

178 Nestlings of the deprived brood therefore had an opportunity to catch up in growth, while

179 their performance could be meaningfully compared to the partially fostered control brood of

180 the same trio. The nestlings in the two partially fostered broods were individually marked

181 from 2d of age and their body mass was measured at 2, 4, 7, 10, 12 and 14d of age by spring

182 balance. We also measured tarsus length from 7d of age onwards, but we do not report these

183 data here because we had no tarsus measurement before the deprivation and because, in line

184 with the literature, tarsus length showed no sign of compensatory growth even in the year in

185 which body mass did (Hegyi and Török 2007). We took blood samples from the nestlings at

186 10d of age and they were subsequently sexed using the PCR technique described in Rosivall

187 et al. (2004). This was necessary because growth trajectories had been shown to differ

188 between the sexes in this population (Rosivall et al. 2009). Individual nestling mortality in the

189 overall surviving broods was low in this experiment and nearly always concerned late-hatched

190 runts. Mortality events were evenly distributed between the experimental groups (deprived

191 versus control: 1 and 0 in 2005, 3 and 2 in 2006, 3 and 3 in 2009). Mortality was therefore not

192 considered further. Nestlings that died before 10d of age (see below) were removed from all

193 analyses.

194   The temporary food deprivation experiment was done in a total of 33 trios with 99

195 nests and 66 measured broods (12, 13 and 8 trios in 2005, 2006 and 2009, respectively).

196 Predation and brood desertion events in two years reduced this number to 24 trios with 72

197 nests and 48 measured broods (12, 7 and 5 trios in 2005, 2006 and 2009, respectively). Brood

198 predation occurred in 2009 only (two control fostered broods), while brood desertion (in 2006

199 only) mainly concerned females in the deprived group that abandoned their brood after male

200 removal (4 of 5 deserting females). The nest building and laying period was stressful due to

201 adverse weather in this year, and this stress may have caused the otherwise unusual

202 intolerance to experimental manipulation in these females. Importantly, the hatching date

203 distribution of the remaining trios closely matched that of the whole central study area in the

204 respective years (Fig. S1 in the Online Resource). Median hatching dates of the population

205 and the experimental units, respectively, were 23 and 21.5 May in 2005, 19 and 17 May in

206 2006, and 16 and 16 May in 2009. Moreover, 22 of the 24 trios (except for one late trio each

207 in 2006 and 2009) were within the interquartile range (i.e. middle 50%) of hatching dates in

208 the respective years.

209

210 Statistical methods

211 Based on long-term breeding data, the median hatching date of each year was calculated for

212 the central plot system in which our experimental manipulations were done. We estimated

213   caterpillar peak time as the midpoint of the collection period with the highest daily frass fall

214   in a given year. Due to the unavoidable, accidental loss of a proportion of individual samples,

215   peak time had to be determined by pooling data from all trees, but this does not cause bias as

216   medians of tree-level peak dates are nearly always the same as the pooled-data peak for the

217   given plot (our unpublished data; only one plot was used in this experiment). The height of

218   the peak was highly variable (see Török et al. 2004) but it showed little correlation with peak

219   timing (log transformed peak height, $N = 23$ years, $r = -0.075$, $p = 0.735$), and there was little

220   difference in peak height between the three experimental years (data not shown), so we did

221   not consider peak height in our analyses. Frass collection was done at several distinct

222   locations over our greater study area. For this study, we used frass data from the central area

223   where our experimental nestling growth manipulations took place.

224   We first calculated the relationship between the NAO index and caterpillar peak time,

225   expecting a negative correlation (van Asch and Visser 2007). We then looked at the

226   adjustment of yearly median breeding time to food peak time. We expected a positive

227   correlation with earlier breeding in earlier food years. To see whether the adjustment was less

228   accurate in early-food years, we also correlated peak food time with the time lag from the

229   food peak to median hatching date. Constraints on adjustment may lead to a negative

230   correlation with the time lag increasing as the food peak becomes earlier.

231   In the experimental data, we focused on the environment-dependence of compensatory

232   growth capacity. Most of the mass growth is already over by 10d of age (Rosivall et al. 2005;

233   Hegyi and Török 2007). Moreover, our data indicated that treatment differences established

234   by 10d of age did not change afterwards, i.e. there was no noticeable compensation after 10d

235   of age (results not shown). Accordingly, we focused on the period up to 10d of age in the

236   present analyses since reporting the data for later ages would have increased the amount of

237   results without contributing to the understanding of compensatory growth patterns. We first

238 analysed the interactive effect of treatment and year on growth. Due to the multi-stage

239 experimental procedure, we processed our data separately for each stage (post-hatching and

240 pre-treatment masses, mass after deprivation, mass after potential compensation, raw and

241 residual mass changes during and after deprivation). We used general linear mixed models

242 (Satterthwaite correction, MIXED procedure of SAS 9.1) with one growth measure as

243 dependent variable, trio and nest of origin nested in trio as random factors, and year, nestling

244 sex and treatment as fixed factors. Residual mass changes were analysed by including mass

245 before the stage as a covariate. We also assessed all two- and three-way interactions between

246 the fixed factors.

247   In the second step, we replaced year by a continuous variable that described the timing

248 of experimental broods relative to the yearly food peak (Fig. S1). The right-tailed distribution

249 of relative timing is unlikely to reflect replacement broods in the late part of the season

250 because replacements seem to be more frequent early in the season, are largely restricted to

251 pre-hatching failures, and are initiated very shortly after clutch or nest failure in our

252 population (our unpublished data). In 2005, the food peak was relatively late and the breeding

253 season was compressed which implied that most birds bred in good food conditions. In 2006,

254 the food peak was earlier, but most of the population followed this change, with a tail of

255 broods lagging behind and probably experiencing caterpillar scarcity. In 2009, in contrast, the

256 food peak was extremely early, and the population as a whole largely missed it. (We note here

257 that population density in the central study area was smallest in the year with the most serious

258 timing delay (225 pairs in 2005, 204 in 2006 and 186 in 2009), so density effects likely made

259 our results regarding timing effects conservative.) Due to the distribution of relative hatching

260 times in the respective years, our experimental data exhibited a peak of early trios and a tail of

261 late ones (Fig. S1), so timing relative to the peak could not be transformed to fit a normal

262 distribution. Therefore, we ranked the trios based on their timing relative to the yearly food

263   peak and used these ranks as a covariate in the analysis (hereafter, timing). This is analogous

264   to a rank correlation analysis extended to multiple independent variables and their

265   interactions. We first entered timing as a replacement for year and retained all other aspects of

266   the above described model structure. We then statistically compared the proportions of

267   variance explained by year and relative timing for all growth variables. Finally, we also ran

268   models including both year and year-standardized timing. The results of these year-and-

269   timing models are reported in the Online Resource, but their principal findings are discussed

270   in the main text. If timing underlay some of the year effect on compensatory growth, we

271   expected that timing would explain similar or higher amounts of variance in growth than year

272   when the two are analysed separately. We also expected that timing would remain a

273   significant determinant of growth even after its variance associated with year is removed

274   (year-and-timing analysis). The rationale of the two different analyses of timing was that

275   standardization for the year-and-timing analysis drastically reduced the variance of timing

276   compared to the original distribution. Therefore, although estimates using this variable show

277   whether timing is important irrespective of year, it is informative to also look at the

278   relationship of timing in its full variance and compensatory growth and compare these

279   relationships to those with year.

280   To see whether the patterns we obtained could indeed be interpreted as nestling

281   growth plasticity (see Introduction), we repeated the analyses of year and timing at the level

282   of the rearing nest, using averages for all nestling parameters. We then computed the

283   differences in the mean variances explained by time, treatment and time x treatment in the

284   year versus the timing analyses. Explained variances were first standardized by bringing the

285   variance explained in the nest-level analysis to unity. We finally compared the overall mean

286   of these standardized differences to zero (one sample t test with $N = 6$ data points). Explained

287   variance was always computed as described by McNeil et al. (1996). We used backward

288   stepwise model simplification with reintroduction in all linear models (Hegyi and Garamszegi

289   2011).

290

291

292   **Results**

293   Long-term data

294   The temporal trends of food peak time and median hatching time were negative (Pearson

295   correlations; food peak time $N = 23$, $r = -0.312$, $p = 0.147$; median hatching time $N = 23$, $r = -$

296   0.616, $p = 0.002$) and statistically similar (Fisher $z = 1.25$, $p = 0.211$). Time lag from food

297   peak time to median hatching time did not systematically change across years, but it showed

298   great variation among years (Fig. 1a; temporal change $N = 23$, $r = 0.032$, $p = 0.886$). Food

299   peak time was negatively related to the NAO index in the preceding winter (Fig. 1b; $N = 23$, r

300    $= -0.446$, $p = 0.033$). Median hatching time was significantly positively related to food peak

301   time (Fig. 1c; $N = 23$, $r = 0.616$, $p = 0.002$), but the time lag between the food peak and

302   hatching time was very strongly negatively related to food peak time (Fig. 1d; $N = 23$, $r = -$

303   0.896, $p < 0.001$). This indicates that the adjustment of birds to earlier food phenology was

304   limited, with the greatest mismatch in the extremely early food years of 2007 and 2009 (Fig.

305   1c). Arrows in Fig. 1c show the position of the experimental years in this dataset.

306

307   Experimental data: year and timing in separate models

308   Results for body mass growth in relation to year and timing in the experimental data are

309   shown in Tables 1 and 2, respectively. The effects and interactions of year and timing were

310   extremely similar when considering that 2005, 2006 and 2009 correspond to small, medium

311   and large delays of breeding with respect to the food peak. The effect of year on body mass

312   was significant already at 4d of age, with higher masses in 2005 than in 2006 or 2009 (post

313   hoc contrasts 2005 vs. 2006: $F_{1,18.7} = 3.47$, $p = 0.078$; 2005 vs. 2009: $F_{1,23.8} = 5.80$, $p = 0.024$;

314   2006 vs. 2009: $F_{1,22.9} = 0.64$, $p = 0.432$). Timing had a marginally non-significant negative

315   effect on 4d mass ($p = 0.063$).

316   During the food deprivation (4-7d), raw and residual mass changes indicated an

317   experimental effect that was independent of year, with deprived broods gaining less mass and

318   also growing slower relative to mass before the stage than controls (Fig. 2a-f). After the food

319   deprivation (7d of age), the year effect on mass was accompanied by an experimental effect

320   with deprived broods being lighter than controls (Fig. 2g-i). Timing had significant main

321   effects during and after the food deprivation phase, with better growth when closer to the food

322   peak. The experimental effects were the same as in the year analysis.

323   During potential compensation (7-10d), uncorrected mass change showed an

324   interaction between year and treatment, and between timing and treatment. The year

325   difference in treatment effects was significant between all pairs of years, although the greatest

326   difference was between 2005 and the other two years (2005 vs. 2006, $F_{1,193} = 11.36$, $p <$

327   0.001; 2005 vs. 2009, $F_{1,166} = 19.40$, $p < 0.001$; 2006 vs. 2009, $F_{1,108} = 4.23$, $p = 0.042$).

328   Deprived chicks gained more mass than controls in 2005 (Fig. 2j; $F_{1,133} = 68.22$, $p < 0.001$).

329   The difference was in the same direction but weaker in 2006 (Fig. 2k; $F_{1,69.1} = 5.22$, $p =$

330   0.025), while it was non-significant in 2009 (Fig. 2l; $F_{1,31.5} = 0.75$, $p = 0.392$). In the timing

331   analysis, the uncorrected mass increment of deprived broods was greater than that of control

332   broods when they were close to the food peak, but the two groups exhibited a similar, large

333   mass increase when away from the peak (Fig. 3a-b).

334   When expressing mass change during potential compensation relative to mass before

335   the stage, we again found an interaction between year or timing and treatment. In the year

336   analysis, 2006 and 2009 significantly differed in the treatment effect from 2005, but only

337   marginally so from each other (year x treatment interactions; 2005 vs. 2006, $F_{1,193} = 17.77$, p

14

338 < 0.001; 2005 vs. 2009, $F_{1,163} = 22.86$, $p < 0.001$; 2006 vs. 2009, $F_{1,108} = 3.29$, $p = 0.073$). In

339 2005, deprived broods grew faster relative to mass before the stage than controls (Fig. 2m;

340 $F_{1,133} = 27.38$, $p < 0.001$), i.e. there was true compensatory growth acceleration. In 2006,

341 deprived chicks did not improve their growth over the level expected from their lower mass

342 before the stage (Fig. 2n; $F_{1,76.6} = 0.04$, $p = 0.833$), i.e. there was no compensatory growth

343 acceleration. In 2009, deprived chicks grew significantly slower relative to their mass before

344 the stage than controls (Fig. 2o; $F_{1,29.3} = 4.93$, $p = 0.034$), which further aggravated their

345 situation. In the timing analysis, residual mass growth was faster in deprived broods than in

346 controls when close to the food peak, but the situation was the reverse, indicating an

347 advantage to controls, when far from the food peak (Fig. 3c-d).

348   Finally, body mass after the potential compensation period (10d of age) also showed a

349 significant interaction between year or timing and treatment. In the year analysis, the

350 treatment effects were similar in 2006 and 2009 (year x treatment interaction 2006 vs. 2009,

351 $F_{1,96.1} = 0.09$, $p = 0.763$), but both differed from 2005 (2005 vs. 2006, $F_{1,192} = 13.29$, $p <$

352 0.001; 2005 vs. 2009, $F_{1,152} = 6.91$, $p = 0.010$). Deprived broods no longer differed from

353 controls in 2005 (Fig. 2p; $F_{1,122} = 1.44$, $p = 0.232$), but they were still lighter than controls in

354 2006 and 2009 pooled (Fig. 2q-r; $F_{1,96.7} = 38.24$, $p < 0.001$). In the timing analysis, deprived

355 broods were similar in mass to controls when close to the food peak, but lagged behind

356 controls when away from the food peak (Fig. 3e-f).

357

358 Does timing contribute to the year effect?

359 The effect sizes of year and timing and their confidence intervals are shown in Table S1 in the

360 Online Resource. The compared effect sizes refer to 1) the main effects of year/timing if these

361 showed no interaction with treatment or 2) the separate effects of year/timing in the two

362 treatment groups if the interaction was significant. For all growth variables in all experimental

363 stages and treatments, the effect sizes of year and timing were statistically and often also

364 numerically similar. On average (excluding zero effects) timing explained 1.28 times more

365 variance than year. Analysing year and year-standardized timing in the same model brought

366 significant interactions between year and standardized timing in all four measures of growth

367 and residual growth, although there was little timing effect or interaction in uncorrected

368 masses (see Table S2 in the Online Resource). The year-specific effects of timing on growth

369 and residual growth were predominately negative (significantly negative in 7 cases, non-

370 significant in 4 cases, positive in only 1 case, details not shown). Note that in the latter

371 analysis most of the variance of timing had been removed by the year-standardization. Given

372 the similar effect sizes and the very similar patterns obtained for year and timing when alone

373 in the model (compare Figs. 3a-b, c-d and e-f with Figs. 2j-l, m-o and p-r, respectively), and

374 the often significant patterns of year-standardized timing when included together with year

375 (Table S2), we conclude that, in our case, timing relative to the caterpillar peak may play an

376 important part in the observed differences among years in nestling growth trajectories.

377

378 Plasticity of parents or nestlings?

379 Unsigned effect sizes for time (year or timing), treatment and their interaction at the brood

380 and the nestling levels are listed in Table S3 in the Online Resource. There was a very high

381 correlation between the two levels (with year: $N = 24$, $r = 0.904$, $p < 0.001$; with timing: $N =$

382 24, $r = 0.884$, $p < 0.001$). However, the mean effect sizes of the six terms at the nestling level

383 systematically exceeded those at the brood level (one-sample t test of standardized

384 differences, see Methods for details; $t_5 = 2.76$, $p = 0.020$). This suggests that individual

385 differences among nestlings played a significant additional role, over the role of parents, in

386 determining growth responses to natural and experimental environmental conditions in our

387 experiment, so referring to nestling growth plasticity is justified.

390   **Discussion**

391   In our insectivorous, long-distance migratory study species, delayed breeding relative to the

392   food peak was most likely in years with early food peaks, which corresponds to the situation

393   experienced in areas of intense climate warming. Nestling growth compensation after an

394   experimental food shortage was reduced or absent in years when the timing of the breeding

395   season was delayed relative to peak food time. Moreover, timing of breeding relative to the

396   food peak seemed to contribute to the year effect on the compensatory growth response of the

397   experimental broods. These results suggest a link between climate, timing of breeding and

398   phenotypic plasticity, with implications to the role of phenotypic plasticity in mitigating the

399   adverse effects of environmental change.

400   The last decade has seen a shift of focus towards phenotypic plasticity in the study of

401   climate change (and also in other fields; McGuigan et al. 2008; Beldade et al. 2011; Reed et

402   al. 2011). When studying the effects of recent environmental change on wild populations,

403   evolutionary ecologists traditionally tended to focus on evolutionary responses (Umina et al.

404   2005; Karell et al. 2011) and their constraints (Etterson and Shaw 2001; Husby et al. 2011).

405   These authors discussed phenotypic plasticity only as an alternative of micro-evolution (Réale

406   et al. 2003; Teplitsky et al. 2008). More recently, it has been noted that demonstrating actual

407   micro-evolutionary change is difficult both in general and in conjunction with climate change

408   (Postma 2006; Gienapp et al. 2008). Recent analyses of long-term data indeed often tend to

409   suggest plastic changes rather than micro-evolution in response to climate warming

410   (Charmantier et al. 2008; Ozgul et al. 2009).

411   Compensatory growth is a very special form of phenotypic plasticity in at least three

412   respects. First, phenotypic plasticity is generally advantageous only if reliable cues are

413   available regarding the preferred phenotype (Beldade et al. 2011). In the case of retarded

414   nestlings, however, the preferred phenotype virtually always requires growth compensation

415   (Both et al. 1999; Cleasby et al. 2010), so availability of information may not generally limit

416   the spread of compensatory growth. Second, compensatory growth is also special because it

417   does not represent environment-dependent phenotypic divergence, but rather the reduction of

418   deviation from a genetically set developmental target (Smith and Wettermark 1995), which

419   brings it close to canalization (Braendle and Felix 2009). Third, compensatory growth is often

420   governed by the actual resource shortage that may have caused the deviation from the

421   developmental target in the first place (Ghalambor et al. 2007; Szöllősi et al. 2007).

422   All of these special attributes of compensatory growth can be detected in our study

423   population. First, in contrast to other nestling categories, late-hatched and therefore

424   handicapped young experience uniformly positive recruitment selection on nestling growth

425   rate across years of very different food conditions (Hegyi et al. 2011; it must be noted here

426   that the fitness consequences of compensation itself will have to be explored in future

427   studies). With the very small and treatment-independent mass growth after 10d of age (see

428   Materials and Methods), the lack of observed compensation likely compromised the fledging

429   body mass of young, with possible long-term consequences. Second, in the good year of 2005

430   and after the end of the deprivation, simulations indicate that deprived nestlings accelerated

431   their growth relative to that expected from the control growth curve, thereby getting closer to

432   the expected growth trajectory of their age (Hegyi and Török 2007). Third, food supply is

433   clearly limiting in our population. Long-term experiments confirmed the decisive role of peak

434   caterpillar availability for fitness (Török et al. 2004), although the timing of peak food

435   availability, an attribute independent of the peak amount (see Materials and methods), has

436   received less attention. When looking at food peak timing in our present experiment, 2005

437   was the best year due to its compressed breeding season and late food peak, while 2009 was

438   the worst due to an extremely early food peak that left the whole breeding population in a

439   situation of reduced food availability during nestling rearing. A corresponding growth

440   difference could be detected already before the experimental deprivation as 4d nestling

441   masses were higher in 2005 than in the other two years.

442   Importantly, however, response to the temporary food deprivation was nevertheless

443   similar in the three years, thereby ensuring the comparability of growth trajectories among

444   years in the period of potential compensation. Uncorrected mass change, residual mass

445   change and post-fasting mass were all reduced in deprived broods relative to controls to a

446   similar extent in the three years. This indicates that the experimental removal of the male

447   parent represented a strong effect that swamped the relatively smaller influence of other

448   environmental conditions in the deprivation phase. After the return of original food supply, on

449   the other hand, deprived nestlings gained more mass than controls in 2005 and to a lesser

450   extent also in 2006, but not in 2009. Interestingly, the year-dependence of the treatment effect

451   was largely due to the control groups which grew much less in 2005 than in the other two

452   years, while the mass gain of the deprived groups was similarly high in the three years. This

453   suggests that mass growth in the poorly timed years was already close to its maximum and

454   could not be substantially elevated to compensate for an additional, temporary food shortage.

455   As a result, the period of potential compensation did not improve the position of deprived

456   nestlings in 2006, and it actually worsened their situation in 2009.

457   Our results therefore suggested constraints on developmental plasticity in years of

458   mistimed reproduction (2006 and especially 2009). To see whether these year-specific

459   constraints were indeed related to the mistiming, we introduced a continuous, rank-

460   transformed variable, timing, representing the temporal position of the given experimental

461   unit relative to the food peak. In all growth variables before, during or after the deprivation,

462   timing showed similar patterns and explained similar amounts of variation as year. Well timed

463   broods exhibited rapid early growth before the deprivation and true compensatory growth

464   after the deprivation, while mistimed broods grew less before the deprivation and did not

465   compensate for their handicap after the deprivation. Moreover, timing had an overall negative

466   effect on growth (although not on uncorrected masses) even when we standardized it for year,

467   thereby removing most of its variance. These results suggest that some of the observed year-

468   dependent compensatory growth capacity can be traced back to timing relative the food peak.

469   Experimental manipulations of timing would be necessary to confirm the causal link.

470   Micro-evolution in response to climate change may be constrained by the specific lack

471   of genetic variation for the trait under selection (Kellermann et al. 2009) or by the

472   disagreement between the multivariate genetic correlation structure of traits and the

473   predominant direction of multivariate selection (Walsh and Blows 2009). When facing such

474   genetic constraints under the strong directional selection pressure imposed by climate change,

475   theoretical analyses indicate that low-cost phenotypic plasticity may reduce the risk of

476   extinction (Chevin et al. 2010). However, our results suggest that phenotypic plasticity may

477   have its own, environmental constraints under certain conditions (see also Both 2010).

478   Moreover, in our case, these certain conditions are apparently those when the population is far

479   from its optimum set by climate-related food phenology. Since the expression of genetic

480   variation may be low specifically in situations of adverse environment and strong selection

481   (Wilson et al. 2006), the need for phenotypic plasticity may be the greatest in exactly those

482   conditions when it is suppressed. The reason for this suppression may be food limitation due

483   to the mistiming that acts through both parental feeding and nestling competition. Comparing

484   our results at the nest and the brood levels suggests that variation among individual nestlings

485   is important in shaping the picture we observed, so it is valid to interpret the patterns as

486   nestling plasticity, although this plasticity is clearly linked to the environment through the

487   interface of parental behaviour.

488   *Ficedula* flycatchers are favourite subjects of studies of climate-related phenology.

489   The pied flycatcher (*F. hypoleuca*) has experienced reduced breeding success due to the

490   advancing phenology of food apparently because its arrival from migration could not track the

491   advancement (Both and Visser 2001; Sanz et al. 2003; Both 2010). A population comparison

492   in the Netherlands indicated that populations better adjusting their breeding dates to yearly

493   food peak timing declined less seriously (Both et al. 2006). Finally, a continent-wide analysis

494   of collared and pied flycatchers showed that laying date advanced more strongly in

495   populations experiencing stronger climate warming (Both et al. 2004). In Central Europe

496   including our study area, there has been only relatively mild warming in the last decades

497   (Both et al. 2004). Accordingly, breeding dates in our population have apparently successfully

498   followed the weak phenological trend of food in the sense that the mean magnitude of

499   mismatch has not increased with time. However, our population can be seriously mistimed in

500   years when the food peak is early. This apparently leads not only to impaired nestling growth

501   from shortly after hatching, but also a reduced capacity to buffer the effects of temporary food

502   shortages on the growth trajectory.

503   Therefore, in populations where the mismatch from food supply increases over time

504   due to climate change, we expect that the negative impact of unpredictable events on

505   reproductive success will also increase. Climate change is accompanied by a general increase

506   not only in temperature but also in the occurrence of extreme weather events (Easterling et al.

507   2000; Mitchell et al. 2006), and the effects of these must be mitigated via phenotypic

508   plasticity in life-history traits including growth compensation (Robinson et al. 1992).

509   Therefore, the reduced growth plasticity of mistimed broods we demonstrated here may

510   contribute to the fitness reduction observed in species and populations experiencing climate-

511   caused phenological shifts (Leech and Crick 2007; Carey 2009). We conclude that the role of

512   phenotypic plasticity in dampening the negative impact of strong selection imposed by

21

513   climate change (Chevin et al. 2010; Hoffmann and Sgró 2011) needs further study along the

514   line of environmental constraints.

515

516

525

526

527   **Conflict of interest**

528   The authors declare that they have no conflict of interest.

529

530

531   **References**

532   Arlettaz R, Schaad M, Reichlin TS, Schaub M (2010) Impact of weather and climate variation

533   on hoopoe reproductive ecology and population growth. J Ornithol 151:889-899

534   Avery MI, Krebs JR (1984) Temperature and foraging success of great tits *Parus major*

535   hunting for spiders. Ibis 126:33-38

536   Balbontin J, Møller AP, Hermosell IG, Marzal A, Reviriego M, de Lope F (2009) Individual

537   responses in spring arrival date to ecological conditions during winter and migration in a

538   migratory bird. J Anim Ecol 78:981-989

539   Beldade P, Mateus ARA, Keller RA (2011) Evolution and molecular mechanisms of adaptive

540   developmental plasticity. Mol Ecol 20:1347-1363

541   Bize P, Roulin A, Bersier LF, Pflüger D, Richner H (2003) Parasitism and developmental

542   plasticity in Alpine swift nestlings. J Anim Ecol 72:633-639

543   Blondel J, Maistre M, Perret P, Hurtrez-Boussés S, Lambrechts MM (1998) Is the small

544   clutch size of a Corsican blue tit population optimal? Oecologia 117:80-89

545   Both C (2010) Flexibility of timing of avian migration to climate change masked by

546   environmental constraints en route. Curr Biol 20:243-248

547   Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a

548   long-distance migrant bird. Nature 411:296-298

549   Both C, Visser ME, Verboven N (1999) Density-dependent recruitment rates in great tits: the

550   importance of being heavier. Proc R Soc B 266:465-469

551   Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, Eeva T, Enemar A, Gustafsson

552   L, Ivankina EV, Järvinen A, Metcalfe NB, Nyholm NEI, Potti J, Ravussin PA, Sanz JJ,

553   Silverin B, Slater FM, Sokolov LV, Török J, Winkel W, Wright J, Zang H, Visser ME

554   (2004) Large-scale geographical variation confirms that climate change causes birds to

555   lay earlier. Proc R Soc B 271:1657-1662

556   Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines

557   in a long-distance migratory bird. Nature 441:81-83

558   Both C, van Turnhout CAM, Bijlsma RG, Siepel H, van Strien AJ, Foppen RPB (2010) Avian

559   population consequences of climate change are most severe for long-distance migrants

560   in seasonal habitats. Proc R Soc B 277:1259-1266

561   Braendle C, Felix MA (2009) The other side of phenotypic plasticity: a developmental system

562   that generates an invariant phenotype despite environmental variation. J Biosci 34:543-

563   551

564   Brommer JE, Rattiste K, Wilson AJ (2008) Exploring plasticity in the wild: laying date-

565   temperature reaction norms in the common gull *Larus canus*. Proc R Soc B 275:687-693

566   Brzek P, Konarzewski M (2004) Effect of refeeding on growth, development and behavior of

567   undernourished Bank Swallow (*Riparia riparia*) nestlings. Auk 121:1187-1198

568   Buskirk J van, Mulvihill RS, Leberman RC (2009) Variable shifts in spring and autumn

569   migration phenology in North American songbirds associated with climate change.

570   Global Change Biol 15:760-771

571   Carey C (2009) The impacts of climate change on the annual cycles of birds. Phil Trans R Soc

572   B 364:3321-3330

573   Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC (2008) Adaptive

574   phenotypic plasticity in response to climate change in a wild bird population. Science

575   320:800-803

576   Chevin L-M, Lande R, Mace GM (2010) Adaptation, plasticity, and extinction in a changing

577   environment: towards a predictive theory. PLOS Biol 8:e1000357

578   Cleasby IR, Nakagawa S, Gillespie DOS, Burke T (2010) The influence of sex and body size

579   on nestling survival and recruitment in the house sparrow. Biol J Linn Soc 101:680-688

580   Easterling DR, Meehl GA, Parmesan C, Changnon AS, Karl TR, Mearns LO (2000) Climate

581   extremes: observations, modelling and impacts. Science 289:2068-2074

582   Emlen ST, Wrege PH, Demong NJ, Hegner RE (1991) Flexible growth rates in nestling

583   white-fronted bee-eaters: a possible adaptation to short-term food shortage. Condor

584   93:591-597

585   Etterson JR, Shaw RG (2001) Constraint to adaptive evolution in response to global warming.

586   Science 294:151-154

587   Garamszegi LZ, Török J, Michl G, Møller AP (2004) Female survival, lifetime reproductive

588   success and mating status in a passerine bird. Oecologia 138:48-56

589   García-Navas V, Sanz JJ (2011) The importance of a main dish: nestling diet and foraging

590   behaviour in Mediterranean blue tits in relation to prey phenology. Oecologia 165:639-

591   649

592   Gebhardt-Henrich SG, van Noordwijk AJ (1991) Nestling growth in the great tit I.

593   Heritability estimates under different environmental conditions. Journal of Evolutionary

594   Biology 4:341-362

595   Ghalambor CK, McKay JK, Carroll S, Reznick DN (2007) Adaptive versus non-adaptive

596   phenotypic plasticity and the potential for contemporary adaptation to new

597   environments. Funct Ecol 21:394-407

598   Gienapp P, Teplitsky C, Alho JS, Mills JA, Merilä J (2008) Climate change and evolution:

599   disentangling environmental and genetic responses. Mol Ecol 17:167-178

600   Hegyi G, Garamszegi LZ (2011) Using information theory as a substitute for stepwise

601   regression in ecology and behavior. Behav Ecol Sociobiol 65:69-76

602   Hegyi G, Török J (2007) Developmental plasticity in a passerine bird: an experiment with

603   collared flycatchers *Ficedula albicollis*. J Avian Biol 38:327-334

604   Hegyi G, Rosivall B, Török J (2006) Paternal age and offspring growth: separating the

605   intrinsic quality of young from rearing effects. Behav Ecol Sociobiol 60:672-682

606   Hegyi G, Rosivall B, Szöllősi E, Eens M, Török J (2011) Context-dependent effects of

607   nestling growth trajectories on recruitment probability in the collared flycatcher. Behav

608   Ecol Sociobiol 65:1647-1658

609   Hoffmann AA, Sgró CM (2011) Climate change and evolutionary adaptation. Nature

610   470:479-485

611   Honarmand M, Goymann W, Naguib M (2010) Stressful dieting: nutritional conditions but

612   not compensatory growth elevate corticosterone levels in zebra finch nestlings and

613   fledglings. PLoS ONE 5:e12930

614   Hüppop O, Hüppop K (2011) Bird migration on Helgoland: the yield from 100 years of

615   research. J Ornithol 152:S25-S40

616   Hurrell JW, Deser C (2010) North Atlantic climate variability: the role of the North Atlantic

617   Oscillation. J Marine Syst 79:231-244

618   Husby A, Kruuk LEB, Visser ME (2009) Decline in the frequency and benefits of multiple

619   brooding in great tits as a consequence of a changing environment. Proc R Soc B

620   276:845-1854

621   Husby A, Nussey DH, Wilson AJ, Visser ME, Sheldon BC, Kruuk LEB (2010) Contrasting

622   patterns of phenotypic plasticity in reproductive traits in two great tit (*Parus major*)

623   populations. Evolution 64:2221-2237

624   Husby A, Visser ME, Kruuk LEB (2011) Speeding up microevolution: the effects of

625   increasing temperature on selection and genetic variance in a wild bird population.

626   PLOS Biol 9:e1000585

627   Jones PD, Jónsson T, Wheeler D (1997) Extension to the North Atlantic Oscillation using

628   early instrumental pressure observations from Gibraltar and South-West Iceland.

629   International J Climatol 17:1433-1450

630   Karell P, Ahola K, Karstinen T, Valkama J, Brommer JE (2011) Climate change drives

631   microevolution in a wild bird. Nature Comm 2:208

632   Kellermann V, van Heerwaarden B, Sgró CM, Hoffmann AA (2009) Fundamental

633   evolutionary limits in ecological traits drive *Drosophila* species distributions. Science

634   325:1244-1246

635   Laaksonen T, Ahola M, Eeva T, Väisänen RA, Lehikoinen E (2006) Climate change,

636   migratory connectivity and changes in laying date and clutch size of the pied flycatcher.

637   Oikos 114:277-290

638   Leech DI, Crick HQP (2007) Influence of climate change on the abundance, distribution and

639   phenology of woodland bird species in temperate regions. Ibis 149:S128-S145

640   Lindstrom A, Enemar A, Andersson G, von Proschwitz T, Nyholm NEI (2005) Density-

641   dependent reproductive output in relation to a drastically varying food supply: getting

642   the density measure right. Oikos 110:155-163

643   Matthysen E, Adriaensen F, Dhondt AA (2011) Multiple responses to increasing spring

644   temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus, Parus*

645   *major*). Global Change Biol 17:1-16

646   McCarty JP (2001) Variation in growth of nestling tree swallows across multiple temporal

647   and spatial scales. Auk 118:176-190

648   McGuigan K, Van Homrigh A, Blows MW (2008) Genetic analysis of female preference

649   functions as function-valued traits. Am Nat 172:194-202

650   McNeil K, Newman I, Kelly FJ (1996) Testing research hypotheses with the general linear

651   model. Southern Illinois University Press, Carbondale and Edwardsville

652   Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? Trends

653   Ecol Evol 16:254-260

654   Mitchell JFB, Lowe J, Wood RA, Vellinga M (2006) Extreme events due to human-induced

655   climate change. Phil Trans R Soc B 364:2117-2133

656 Møller AP, Rubolini D, Lehikoinen E (2008) Populations of migratory bird species that did

657   not show a phenological response to climate change are declining. Proc Natl Acad Sci

658   USA 105:16195-16200

659 Møller AP, Flensted-Jensen E, Klarborg K, Mardal W, Nielsen JT (2010) Climate change

660   affects the duration of the reproductive season in birds. J Anim Ecol 79:777-784

661 Moreno J, Lobato E, Morales J, Merino S, Martínez-De La Puente J, Tomás G (2008) Pre-

662   laying nutrition mediates maternal effects on offspring immune capacity and growth in

663   the pied flycatcher. Oecologia 156:727-735

664 Moussus J-P, Clavel J, Jiguet F, Julliard R (2011) Which are the phenologically flexible

665   species? A case study with common passerine birds. Oikos 120:991-998

666 Nussey DH, Postma E, Gienapp P, Visser ME (2005) Selection on heritable phenotypic

667   plasticity in a wild bird population. Science 310:304-306

668 Ozgul A, Tuljapurkar S, Benton TG, Pemberton JM, Clutton-Brock TH, Coulson T (2009)

669   The dynamics of phenotypic change and the shrinking sheep of St. Kilda. Science

670   325:464-467

671 Palumbi SR (2001) Humans as the world's greatest evolutionary force. Science 293:1786-

672   1790

673 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu

674   Rev Ecol Evol Syst 37:637-669

675 Perrins CM (1991) Tits and their caterpillar food supply. Ibis 133:S49-S54

676 Postma E (2006) Implications of the difference between true and predicted breeding values

677   for the study of natural selection and micro-evolution. J Evol Biol 19:309-320

678 Réale D, McAdam AG, Boutin S, Berteaux D (2003) Genetic and plastic responses of a

679   northern mammal to climate change. Proc R Soc B 270:591-596

680 Reed TE, Schindler DE, Waples RS (2011) Interacting effects of phenotypic plasticity and

681   evolution on population persistence in a changing climate. Cons Biol 25:56-63

682 Robinson JA, Hamer KC, Chivers LS (1992) Developmental plasticity in arctic terns *Sterna*

683   *paradisaea* and common terns *Sterna hirundo* in response to a period of extremely bad

684   weather. Ibis 144:344-346

685 Rosivall B, Török J, Hasselquist D, Bensch S (2004) Brood sex ratio adjustment in collared

686   flycatchers (*Ficedula albicollis*): results differ between populations. Behav Ecol

687   Sociobiol 56:346-351

688 Rosivall B, Szöllősi E, Török J (2005) Maternal compensation for hatching asynchrony in the

689   collared flycatcher. J Avian Biol 36:531-537

690 Rosivall B, Szöllősi E, Hasselquist D, Török J (2009) Effects of extra-pair paternity and sex

691   on nestling growth and condition in the collared flycatcher (*Ficedula albicollis*). Anim

692   Behav 77:611-617

693 Rubolini D, Møller AP, Rainio K, Lehikoinen E (2007) Intraspecific consistency and

694   geographic variability in temporal trends of spring migration phenology among

695   European bird species. Climate Res 35:135-146

696 Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Hüppop K, Hüppop O,

697   Lehikoinen A, Lehikoinen E, Rainio K, Romano M, Sokolov L (2011) Climate

698   warming, ecological mismatch at arrival and population decline in migratory birds. Proc

699   R Soc B 278:835-842

700 Sanz JJ, Potti J, Moreno J, Merino S, Frias O (2003) Climate change and fitness components

701   of a migratory bird breeding in the Mediterranean region. Global Change Biol 9:461-

702   472

703 Schleucher E (2004) Taxonomy, energetics, and ecology. Physiol Biochem Zool 77:942-949

704   Sheldon BC, Kruuk LEB, Merilä J (2003) Natural selection and inheritance of breeding time

705   and clutch size in the collared flycatcher. Evolution 57:406-420

706   Siikamäki P (1996) Nestling growth and mortality of pied flycatchers *Ficedula hypoleuca* in

707   relation to weather and breeding effort. Ibis 138:471-478

708   Smallegange E, Fiedler W, Köppen U, Geiter O, Bairlein F (2010) Tits on the move:

709   exploring the impact of environmental change on blue tit and great tit migration

710   distance. J Anim Ecol 79:350-357

711   Smith HG, Wettermark KJ (1995) Heritability of nestling growth in cross-fostered European

712   starlings. Genetics 141:657-665

713   Starck JM, Ricklefs RE (1998) Avian growth and development: evolution within the altricial-

714   precocial spectrum. Oxford University Press, Oxford.

715   Szöllősi E, Rosivall B, Török J (2007) Is hatching asynchrony beneficial for the brood? Behav

716   Ecol 18:420-426

717   Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J (2008) Bergmann's rule and climate

718   change revisited: Disentangling environmental and genetic responses in a wild bird

719   population. Proc Natl Acad Sci USA 105:13492-13496

720   Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR (2001) Energetic and

721   fitness costs of mismatching resource supply and demand in seasonally breeding birds.

722   Science 291:2598-2600

723   Tinbergen JM, Verhulst S (2000) A fixed energetic ceiling to parental effort in the great tit? J

724   Anim Ecol 69:323-334

725   Török J (1986) Food segregation in three hole-nesting bird species during the breeding

726   season. Ardea 74:129-136

727   Török J, Hegyi G, Tóth L, Könczey R (2004) Unpredictable food supply modifies costs of

728   reproduction and hampers individual optimization. Oecologia 141:432-443

729   Tøttrup AP, Thorup K, Rainio K, Yosef R, Lehikoinen E, Rahbek C (2008) Avian migrants

730   adjust migration in response to environmental conditions en route. Biol Lett 4:685-688

731   Umina PA, Weeks AR, Kearney MR, McKechnie SW, Hoffmann AA (2005) A rapid shift in

732   a classical clinal pattern in *Drosophila* reflecting climate change. Science 308:691-693

733   Van Asch M, Visser ME (2007) Phenology of forest caterpillars and their host trees: the

734   importance of synchrony. Annu Rev Entomol 52:37-55

735   Végvári Z, Bókony V, Barta Z, Kovács G (2010) Life history predicts advancement of avian

736   spring migration in response to climate change. Global Change Biol 16:1-11

737   Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to

738   mistimed reproduction in great tits (*Parus major*). Proc R Soc B 265:1867-1870

739   Walsh B, Blows MW (2009) Abundant genetic variation plus strong selection = multivariate

740   genetic constraints: a geometric view of adaptation. Annu Rev Ecol Evol Syst 40:41-59

741   Wilson AJ, Pemberton JM, Pilkington JG, Coltman DW, Mifsud DV, Clutton-Brock TH,

742   Kruuk LEB (2006) Environmental coupling of selection and heritability limits

743   evolution. PLOS Biol 4:1270-1275

Table 1 The main and interactive effects of year, nestling sex and temporary food deprivation treatment on various aspects of nestling growth

	Year		Sex		Treatment		Year x sex		Year x treatment		Sex x treatment		Year x sex x treatment	
	df	F	df	F	df	F	df	F	df	F	df	F	df	F
M2	2, 22.7	2.34	1, 239	3.06	1, 221	0.01	2, 238	0.22	2, 221	0.83	2, 236	0.20	7, 229	0.51
M4	2, 21.1	3.60*	1, 240	0.81	1, 219	1.17	2, 238	0.14	2, 220	0.76	1, 236	0.64	7, 229	0.55
DM4-7	2, 22.2	1.49	1, 246	5.44*	1, 241	191.41***	2, 247	0.17	2, 240	2.08	1, 245	0.47	7, 241	1.11
RDM4-7[a]	2, 22.4	0.96	1, 245	5.20*	1, 240	197.84***	2, 246	0.11	2, 239	2.19	1, 244	0.75	7, 240	1.32
M7	2, 22	3.65*	1, 238	3.01	1, 219	88.20	2, 236	0.19	2, 220	1.24	1, 235	0.00	7, 227	0.43
DM7-10	2, 21.6	1.50	1, 244	3.24	1, 243	6.86**	2, 246	1.38	2, 241	12.54***	1, 243	0.93	6, 241	1.16
RDM7-10[a]	2, 21.3	0.59	1, 242	8.08**	1, 244	0.19	2, 241	1.06	2, 238	16.36***	1, 242	1.06	5, 230	0.63
M10	2, 21.1	1.12	1, 237	9.86**	1, 222	33.21***	2, 235	0 24	2, 220	7.99***	1, 234	0 35	5, 232	0.17

General linear mixed models with stepwise backward selection and reintroduction. M, mass; DM, mass change; RDM, residual mass change. [a], the covariate of mass before the stage is not described ($p < 0.001$ in each case); *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Table 2 The main and interactive effects of ranked timing relative to the yearly food peak ("timing"), nestling sex and temporary food deprivation treatment on various aspects of nestling growth

	Timing		Sex		Treatment		Timing x sex		Timing x treatment		Sex x treatment		Timing x sex x treatment	
	df	F	Df	F	df	F	df	F	df	F	df	F	df	F
M2	1, 24.9	1.61	1, 239	3.06	1, 221	0.01	1, 239	0.57	1, 222	0.72	1, 236	0.20	3, 236	0.45
M4	1, 24.1	3.81	1, 239	0.82	1, 221	1.43	1, 240	0.02	1, 222	1.86	1, 235	0.46	3, 237	0.87
DM4-7	1, 23.7	4.41*	1, 247	5.41*	1, 241	189.63***	1, 251	1.82	1, 242	0.12	1, 246	0.42	3, 247	0.84
RDM4-7[a]	1, 23.9	3.21	1, 245	5.20*	1, 240	197.84***	1, 250	1.82	1, 241	0.00	1, 244	0.75	3, 245	0.88
M7	1, 23.6	7.42*	1, 239	3.26	1, 220	87.77***	1, 238	0.58	1, 221	1.54	1, 235	0.00	3, 236	0.65
DM7-10	1, 23.1	1.58	1, 246	3.16	1, 240	47.28***	1, 251	2.28	1, 243	17.06***	1, 245	1.18	2, 251	1.39
RDM7-10[a]	1, 23.2	0.14	1, 244	7.47**	1, 231	23.93***	1, 243	1.38	1, 222	17.94***	1, 243	1.52	2, 250	1.01
M10	1, 22.2	3.02	1, 240	9.40**	1, 220	0.72	1, 239	0.00	1, 222	4.28*	1, 236	0.70	2, 247	0.12

General linear mixed models with stepwise backward selection and reintroduction. M, mass; DM, mass change; RDM, residual mass change. [a], the covariate of mass before the stage is not described ($p < 0.001$ in each case); *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Fig. 1 The temporal pattern of the time lag from the caterpillar peak to median hatching date in collared flycatchers during the study period (**a**) and its potential determinants: (**b**) food peak time in relation to preceding winter NAO, (**c**) median hatching time in relation to food peak time and (**d**) the time lag itself in relation to food peak time. In **c**, the central line corresponds to the exact coincidence of peak date and median hatching date, while the arrows indicate the position of our three experimental years.

Fig. 2 Nestling growth in the deprived and the control groups during the periods of deprivation and potential growth compensation: (**a, b, c**) 4-7d mass change, (**d, e, f**) 4-7d residual mass change, (**g, h, i**) 7d mass, (**j, k, l**) 7-10d mass change, (**m, n, o**) 7-10d residual mass change, and (**p, q, r**) 10d mass. The data are (**a, d, g, j, m, p**) from 2005, (**b, e, h, k, n, q**) 2006 and (**c, f, i, l, o, r**) 2009. Note that the treatment effect is statistically similar across years in the deprivation period (**a-i**) but significantly different among years in the compensation period (**j-r**).

Fig. 3 Nestling growth during the period of potential growth compensation, in relation to ranked timing relative to the food peak ("timing"): (**a-b**) 7-10d mass change, (**c-d**) 7-10d residual mass change and (**e-f**) 10d mass. Different symbols refer to different years: circles, 2005; squares, 2006; triangles, 2009. Brood-level averages are shown for greater transparency.