

1 **Reduced compensatory growth capacity in mistimed**
2 **broods of a migratory passerine**

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14 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

38 **Introduction**

39 Phenotypic plasticity implies environmentally induced variation in the phenotype expressed
40 by a given genotype. Much of this environmentally induced variation is non-adaptive and
41 often arises from environmental constraints on trait expression (Ghalambor et al. 2007).
42 Climate warming has pervasive effects on wild populations in temperate latitudes, and the
43 apparent impacts have increased in the last few decades (Parmesan 2006). Population studies
44 of the impacts of climate change classically focus on micro-evolution (Palumbi 2001). In
45 these studies, phenotypic plasticity is generally mentioned as an alternative to micro-
46 evolutionary change (e.g. Brommer et al. 2008; Husby et al. 2010) or as an individual-
47 specific, evolvable character (e.g. Nussey et al. 2005). On the other hand, recent reviews and
48 theoretical treatments highlight the importance of plastic responses especially when evolution
49 is insufficient to keep track of environmental change (Chevin et al. 2010; Hoffmann and Sgró
50 2011). These approaches to phenotypic plasticity all assume the same degree of plasticity
51 across different environments. However, plasticity in life history traits may itself change with
52 environmental conditions, and this may limit the role plastic responses can play in mitigating
53 fitness costs due to environmental change. In other words, it is now well known that
54 evolutionary responses to global changes can be strongly constrained (Etterson and Shaw
55 2001; Wilson et al. 2006), while the extent to which phenotypic plasticity is environmentally
56 constrained has seldom been examined in the context of climate change (Both 2010; Chevin
57 et al. 2010).

58 In birds, the most widely known effect of global warming has been the dissociation of
59 food supply and demand due to the earlier phenology of vegetation and therefore insect food
60 relative to the breeding season (Visser et al. 1998; Thomas et al. 2001). Comparative analyses
61 have also highlighted certain groups that are most vulnerable to such mismatches, such as
62 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 (Metcalf 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 (Szöllösi 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 (Hegyí 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, $F_{1,193} = 17.77, p$

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.

388

389

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

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

515

516

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525

526

527 **Conflict of interest**

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

529

530

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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	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>
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	<i>F</i>	Df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>	df	<i>F</i>
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.





