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Natal dispersal based on past and present environmental phenology in the pied flycatcher (*Ficedula hypoleuca*)

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31   Natal dispersal allows individuals to reach suitable breeding sites. The effect of present plant

32   phenology as a cue for dispersal into areas with favourable stages of development has been

33   well established across avian and mammalian taxa. However, the effect of past experience is

34   less understood. We studied the effect of past and present phenology of the environment on

35   the direction and distance of natal dispersal in a passerine bird, the pied flycatcher (*Ficedula*

36   *hypoleuca*). We monitored spring settlement of local recruits in six nest box plots along a 10

37   km stretch of a south-north gradient in the plant and caterpillar food development. We found

38   that males used both past experience of caterpillar phenology from early life and actual plant

39   phenology during the recruitment season as independent cues for breeding settlement. Males

40   that had experienced a mismatch with the caterpillar food peak as a nestling, and/or those that

41   arrived late in the spring in the recruitment year, moved north of their natal site, whereas

42   males that had experienced a better match with the caterpillars as a nestling, and/or those that

43   migrated earlier in the spring, settled at a similar site or more to the south. In females, no such

44   effects were found, suggesting that the usage of phenological cues is sex specific. In

45   summary, tracking environmental phenology by natal dispersal may represent an effective

46   mechanism for settling in new favourable areas, and may thus potentially cause rapid change

47   of a species´ geographical breeding range in response to climate change.

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52   *Keywords: breeding range, forest, habitat selection, synchrony, trophic interactions*

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Introduction

The recent world is characterized by rapid environmental dynamics, including unprecedented climatic change, which influences biological processes remarkably (Rosenzweig et al. 2008). Global warming associates with shifts in phenology, species interactions, ecosystem dynamics, extinction risks, and changes in geographical distributions across taxa (Walther et al. 2002; Parmesan 2006; Rosenzweig et al. 2008). In the Northern Hemisphere, northward shifts in the distributional ranges of birds typically result from milder climate allowing for improved feeding and physiological conditions (Parmesan et al. 2000; Crick 2004; Leech and Crick 2007). These effects may depend on the diet composition, with herbivorous species responding stronger than insectivores (Brommer 2008), presumably because insect development requires higher temperatures than that of plants (Schwartz 2003). Poleward range shifts in the Northern Hemisphere has been hypothesized to be primarily driven by increased survival and reproduction in the north, and/or decreased survival and reproduction in the south (Parmesan et al. 2000; Leech and Crick 2007).

Understanding movement decisions of dispersing individuals is an important prerequisite for studies on complex metapopulation dynamics (Hanski 2001) and gene flow in diversification/speciation (Garant et al. 2005; Tonnis et al. 2005; see also review in Ronce 2007). Traditionally, the focus has been devoted to explain why some individuals stay at their natal site while others disperse to a new place, and why some individuals settle at longer distances from their natal site than do others. Another line of research has focused on explaining habitat choice, often as a single phenomenon independent of dispersal. Decisions on whether to disperse, how far and where to settle, are however closely entangled (Benard and McCauley 2008; Studds et al. 2008; Piper 2011).

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79   Ultimate explanations for why dispersal happens include avoidance of inbreeding,

80   competition, parasitism and predation and bet-hedging against the environmental variability.

81   Allee effect (i.e. reduction in settlement and habitat search costs with increased conspecific

82   density) and habitat training/cueing have been invoked as additional explanations for adaptive

83   habitat choice (Hildén 1965; Cody 1985; Clobert et al. 2001; Benard and McCauley 2008).

84   Finally, parent–offspring conflict has been suggested to account for variability in dispersal

85   distance (Starrfelt and Kokko 2010).

86   Proximate cues are necessary for an individual to make a proper decision. Importance

87   of a given cue likely varies with the spatial scale of the movement decision (Orians and

88   Wittenberger 1991). Numerous studies have provided information on cues used by animals

89   for dispersal and habitat choice at the spatial scale of a territory or habitat. These include

90   innate preferences (Partridge 1974; Partridge 1976), habitat learning and/or body condition

91   (Stamps and Krishnan 1999; Ims and Hjermann 2001), and availability of food, suitable

92   breeding sites and presence of con- and heterospecific individuals (Alatalo et al. 1982;

93   Seppänen et al. 2011), including predators (Hildén 1965). Phenological stages of plant

94   growth serve as a cue for large scale movements in many ungulates (Skogland 1980; van der

95   Wal et al. 2000), and may also do so on small, local spatial scales in birds (Slagsvold et al.

96   2013). Less evidence is available on what cues are utilized for dispersal decisions at larger

97   spatial scales (landscape, latitude) in birds, likely because of technical limitations in tracking

98   the individuals.

99   By using an isotope analysis, Studds et al. (2008) indirectly demonstrated that redstarts

100   (*Setophaga ruticila*) that migrated later to their breeding grounds in North America dispersed

101   to more northern latitudes than did early birds, presumably to synchronize breeding with food

102   availability (van Noordwijk et al. 1995). Classical theory by Fretwell and Lucas (1969)

103   proposes that lower quality individuals or individuals from low quality habitats should

104   disperse to low quality habitats, while the opposite should hold for high quality individuals or

105   individuals from high quality habitats. Empirical evidence on the ideal free and ideal despotic

106   distribution is ample (Garant et al. 2005; Piper 2011). Yet, it is unclear whether some of the

107   cues involved in dispersal decisions at smaller spatial scales such as body condition apply also

108   for decisions at large spatial and longer temporal scales.

109   In passerine birds, nestling survival and fledgling body mass may decrease as a result

110   of a mismatch between timing of breeding and the availability of food (van Balen 1973; Dias

111   and Blondel 1996; Siikamäki 1998; Naef-Daenzer and Keller 1999; Verboven et al. 2001;

112   Visser et al. 2006; Reed et al. 2013; for a review of the mismatch hypothesis see Durant et al.

113   2007). Caterpillars are major food items for nestlings of many species. Nestling body

114   condition is positively related to the proportion of caterpillars in the diet at least until a

115   threshold is reached (García-Navas and Sanz 2011; Burger et al. 2012). In a Dutch population

116   of great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*), seasonal peaks in the

117   abundance of caterpillars advanced more during warmer years than the timing of breeding of

118   these birds (Visser et al. 1998; Both et al. 2009). On the contrary, synchrony between birds

119   and caterpillars was maintained in British and Belgian populations of the same species

120   (Cresswell and McCleery 2003; Charmantier et al. 2008; Matthysen et al. 2011), and even

121   improved over the years in a Finnish population of willow tits (*Poecile montanus*) (Vatka et

122   al. 2011). A learning based model has attempted to explain habitat learning and selection

123   already from the time juveniles start encountering their environment by means of positive and

124   negative experiences (Stamps and Krishnan 1999). The critical assumption is that dispersal

125   propensity increases with higher frequency of negative experiences. A candidate is food

126   shortage caused by a mistimed reproduction. Contrary, the breeding habitat is chosen based

127   on positive experiences like favourable food conditions that have resulted in good body

128   condition (Piper 2011). Variation may often occur among individuals of a population of how

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129   they experience the availability of food during upbringing, causing differences in the amounts

130   of positive and negative habitat experiences, which in turn may cause variation in the

131   dispersal decisions.

132   In this study we build on traditional analysis of natal dispersal, i.e. whether and/or how

133   far animals disperse, by analysing direction of natal dispersal. As a model system, we study

134   natal dispersal of pied flycatchers between six woodland plots. Our focus is on explaining the

135   largest variation in dispersal movements, which comes from movements along the main

136   ecological gradient dictated by latitude. Distance between the southern- and northernmost plot

137   amounts to about ten kilometres while variation in movements along longitudinal and

138   altitudinal axis is comparably smaller. We first analyse (1) whether and how much hatching

139   dates and plant phenology in the recruitment year delay from south to north, and (2) whether

140   and how much body mass of nestlings and recruitment rate increase from south to north.

141   Given existence of such ecological gradients as potential foundation for behavioural

142   decisions, we (3) test the effect of two proximate cues of tracking latitudinal ecological

143   gradients by natal dispersal. Namely, we test the effect of past nestling experience measured

144   as a degree of mismatching with the caterpillar food peak at the natal site, and the plant

145   phenology at the time of settlement of the birds in the recruitment season. We test the

146   predictions that flycatchers that had hatched late relative to the caterpillar peak will settle to

147   breed to the north of their natal site, which would also be the case for flycatchers arriving and

148   nesting late in the recruitment season, with opposite prediction for birds that had hatched

149   relative early, and that arrived and settled relatively early. We hypothesized birds to disperse

150   to the north when the plant development at the natal site was too progressed during spring

151   arrival. We were particularly interested in determining whether the effect of past experience

152   (hatching mismatch) serves as a cue independent of the phenological conditions (plant

153   development upon arrival) in the recruitment year.

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Material and methods

Study area

The study was conducted in a larger valley area composed of mixed woodlands and
interspersed with farmland and settlements near Oslo, Norway, during 2009–2012. The
southern study plots were located on a south facing, warmer slope, whereas the northern study
plots were located in a valley with cold air coming down from the surrounding hills with
altitudes up to 600 m above sea level causing much later snow melt and lower temperatures.
This caused a stronger gradient in environmental phenology across the study plots (6–15 days,
see below) than would otherwise be expected (Lauscher et al. 1955). Nest boxes (n = 1234)
were provided in suitable breeding habitats for hole nesting passerines at six plots at an
altitude of about 100–250 m a.s.l. (see Online Resource, Table A1, for details on the study
plots). The boxes had similar inner depths of 13–16 cm from base of entrance hole to bottom,
and had an entrance hole of 32 mm in diameter. Pied flycatchers occupied about 155–175 nest
boxes annually. UTM geographic coordinates (± 5–10 m) of nest boxes were measured with a
GPS (Garmin GPSmap 60CSx). Nest box plots that were located at about the same latitude
were grouped and considered as three principal study locations ("SOUTH", "CENTRAL" and
"NORTH"; Fig. 1, Online Resource Table A1).

The forest vegetation in the SOUTH is dominated by deciduous trees (most commonly
ash *Fraxinus excelsior*, hazel *Corylus avellana*, maple *Acer platanoides*, elm *Ulmus glabra*,
birch *Betula* spp., grey alder *Alnus incana*, and willow *Salix caprea*). Vegetation in the
CENTRAL and NORTH is characterized by a mixture of spruce (*Picea abies*) and deciduous
trees (birch, willow and grey alder) with a scattered admixture of pine (*Pinus silvestris*),

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177　maple, elm, ash, hazel, oak (*Quercus rubur*), beech (*Fagus sylvatica*) and bird cherry (*Prunus*

178　*padus*). Dominance of coniferous trees increases with altitude at all locations.

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180　**Environmental phenology**

181　We monitored seasonal variation in caterpillar biomass from the time of flycatchers' arrival

182　(end of April) until the end of the breeding season (middle of July) at three plots during 2009–

183　2011 (See red crosses in Fig. 1 for locations). Faecal pellets were collected using traps placed

184　beneath a tree (frass nets hereafter) (Fischbacher 1998, Visser et al. 2006). Frass nets

185　consisted of a piece of cloth fixed to a 0.25 m^2 metal frame. Nets were placed about 0.5–2 m

186　from the trunk of a tree and at least 10 m apart. Five frass nets were placed at each two frass

187　fall sampling sites in 2009, and three sampling sites in 2010 and 2011 at SOUTH, 8 nets at

188　one sampling site at CENTRAL, and 8 nets at one sampling site at NORTH (see Online

189　Resource, Table A1, for tree species sampled). Composition of trees under which the nets

190　were placed was chosen to be approximately proportional to the abundance of tree species at

191　the respective study sites. Nets were emptied every 4th day (or later when raining heavily) and

192　were covered during heavy rains to prevent frass disintegration. After collection, frass was

193　dried at 60°C for 1 hour, separated from litter using Retsch test sieves (1200 µm and 600 µm)

194　and weighed (to nearest 0.1 mg). We calculated a proxy for the relative caterpillar biomass by

195　correcting mass of frass for the effect of ambient temperature during the sampling period,

196　following Tinbergen and Dietz (1994), and for the number of collection hours. Mean daily

197　temperatures for the closest meteorological station (Blindern, see black cross in Fig. 1) were

198　obtained from the Norwegian Meteorological Institute.

199　　　　Every 5 (4–6) days from the beginning of May until beginning of June we measured

200　length of the same three stretched leaves per tree (same individual trees were measured over

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201 the years) across five plots. Grey alders, birches and hazels were considered as the

202 representative species across locations. Sample trees were scattered evenly across the nest box

203 plots and were marked with a piece of waterproof tape for identification (see Online Resource

204 Table A1 for details). We calculated average daily values for each tree individual, from which

205 we calculated site-specific average values for each species. Species specific daily growth rates

206 were expressed as percentages of the lengths on the last day of measurement.

207   A generalized additive model (GAM) was fitted to smooth the effect of seasonal date

208 on caterpillar biomass and leaf growth following guidelines provided by Wood (2006). GAM

209 is a generalized linear model where the linear predictor of explanatory variables of the form $\sum$

210 $\beta_j(X_j)$ is replaced by a sum of smooth functions with estimated degrees of freedom ("edf"

211 hereafter) of explanatory variables $\sum s_j(X_j)$ (Wood 2006). The basis of the smooth functions is

212 represented by thin plate regression splines (or similar) and is estimated as a part of fitting

213 process. Effect of date (i.e. mid-date of the respective sampling period) on caterpillar biomass

214 was analysed separately for deciduous and coniferous trees because biomass showed a peak

215 for the deciduous trees but not for the coniferous trees (Online Resource, Figure A1). Peak

216 date of caterpillar mass was defined as the date of estimated maximum caterpillar biomass.

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218 **Bird observations**

219   After arrival pied flycatcher males choose a nesting hole, inspect it and engage in

220 courtship displays while protecting a very small territory around the nest box (von Haartman

221 1956). From the beginning of the breeding season we checked each nest box every five days

222 at all plots, except one where they were checked more frequently (a centrally located plot in

223 the gradient, Z in Fig. 1), in order to verify identity of males, check signs of nest building and

224 determine egg laying dates. Male identity was assigned based on a unique combination of

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225   colour rings. If necessary we used supplemental characteristics such as feather colour and

226   shape and size of head front patch to distinguish males banded with only metal ring. We

227   assigned the date of the first observation of a male as his arrival date. Arrival dates were

228   mostly unknown for females, except in study plot Z (Fig. 1). In four cases when no direct

229   observation was available before the nest building took place we assumed that a male arrived

230   shortly before first signs of nesting material; we assumed arrival on the previous day if little

231   material was present, and two days before if the nest box floor was covered by nesting

232   material. In the pied flycatcher, only females build nests, and they start very soon upon

233   arrival, often only after a few hours (Dale and Slagsvold 1995, 1996). We assumed one egg

234   laid per day in back calculations of first egg laying date if more than one egg was found in a

235   nest (Lundberg and Alatalo 1992). In study plot Z, with daily observations, a strong positive

236   correlation ($r = 0.8$–0.9 for each year of study) existed between arrival date of a female and

237   the date of her first egg laid. Hence, we used the latter measure as a proxy for female arrival

238   time in all sites. The correlation between arrival date of a male and the date of onset of laying

239   by his mate was much weaker ($r = 0.5$–0.6).

240   Plant phenology upon arrival date of males, and egg laying date of females, in the

241   recruitment year was characterized as a percentage of leaf growth at the respective natal

242   location on a given day. High values indicate late arrival and egg laying relative to the plant

243   development at the respective natal site if birds choose to settle there. Low values indicate

244   early arrival and egg laying at the respective natal site if birds choose to settle there.

245   Nest boxes were inspected every 1–2(3) days around hatching time. Hatching dates

246   (day 0) were based on nestling growth (Lundberg & Alatalo 1992; Thingstad 2001). Hatching

247   mismatch of each bird was measured as the difference (in days) between the respective

248   hatching date and the peak date of caterpillar biomass on deciduous trees. Peak on coniferous

249   trees was not considered because for such trees there is often a gradual increase in caterpillar

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250 biomass over the whole breeding season without a clear maximum (Veen et al. 2010; see also

251 Online Resource, Figure A1). On day 13 (or 12 in a few cases) we weighed nestlings to

252 nearest 0.25 g using a spring balance (Pesola) and ringed them with a uniquely coded metal

253 band. In 2010–2012 we also measured length of the left tarsus of all nestlings (from the bent

254 digits and including tibia) to nearest 0.1 mm using callipers at all sites. If some of the hatched

255 nestlings were not found in the nest at the time of weighing (i.e. before earliest possible

256 fledging date), we considered those as depredated or starved to death shortly after hatching.

257   In subsequent years, all adult birds with metal bands were caught for identification.

258 Females were caught during incubation and males when entering a nest box by means of a

259 trap door preventing them from leaving once they had entered. Two birds (one male and one

260 female) that were found breeding in natural holes just outside the study plots were caught

261 using mistnet. Males were further provided with 1–3 plastic bands of different colours for

262 ease of identification and length of the left tarsus was taken in the same way as in nestlings.

263 Length of the left tarsus measured in the first year of life correlated strongly with measures

264 taken at age 13 days (r = 0.86, p < 0.001, n = 69). Body condition of birds when 13 days old

265 was calculated as residuals from a linear regression of log transformed body mass when 13

266 days old on log transformed length of left tarsus. Euclidean distance between the nest box of

267 first breeding and the natal nest box was used to characterize direction of natal dispersal

268 ("change in latitude" hereafter). Positive and negative values indicate natal dispersal to the

269 north and south, respectively. During 2010–2012 we recovered 99 natal dispersers (47

270 females, 52 males), i.e. individuals that had fledged from one of our nest boxes and that had

271 settled at one of our study plots during the first year of life. Seven local recruit males that

272 were repeatedly observed at their dispersal site trying to attract a female to a nest box but

273 were unsuccessful were also included in the analysis. We did not include birds that we first

274 found breeding during their second (n = 10) or third (n = 4) year of life because we focus on

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275   natal dispersal and the latter birds may have tried breeding somewhere else in their first year

276   (applies to one third of local recruits; Lundberg & Alatalo 1992).

277   Every year, a portion of complete clutches (ca. 20 %) was subjected to experimental

278   cross-fostering as a part of another study (see Online Resource, Appendix 1). However,

279   experimental treatment included as explanatory covariate in our analysis on change in latitude

280   was not significant (p > 0.05) and is therefore not considered further.

281

282   **Statistical analysis**

283   The differences in mean hatching date and nestling body mass between locations was

284   tested by ANOVA. Post hoc Tukey's HSD test was used for pairwise comparisons. Results

285   were similar for index of body condition and we therefore do not present them.

286   Local natal recruitment rate was defined as the proportion of yearling birds arriving at

287   their respective natal location (SOUTH, CENTRAL, or NORTH) in year x+1 from all

288   nestlings ringed at the respective location in year x. Chi square test was used to test for

289   differences in natal recruitment rate between locations (Sokal and Rohlf 1995). We used Box-

290   Cox transformation to remedy violations from normality.

291   A linear mixed model implemented in nlme library (Pinheiroet al. 2013) was fitted by

292   restricted maximum likelihood (REML) to test the effect of ecological factors on change in

293   latitude separately for males and females. Explanatory variables included were hatching

294   mismatch and length of the left tarsus as a proxy for body size. Julian hatching date and

295   hatching date centred by annual local mean were included as alternative explanatory variables

296   to hatching mismatch. Plant phenology upon arrival date at the respective natal site in the

297   recruitment year was used as third explanatory variable in the model on males, while plant

298   phenology at egg laying at the respective natal site in the recruitment year was used in the

299   model on females. Explanatory variables were not correlated (r = -0.002– -0.18, all p > 0.2).

300   The effects of fixed explanatory factors were evaluated against the null hypothesis by means

301   of t-values. Corresponding degrees of freedom were calculated as a minimum number of

302   random effects that affected the tested terms (Pinheiro et al. 2013). We first built models

303   including main effects of hatching mismatch, length of the left tarsus and plant phenology in

304   the recruitment year and their interactions. Non-significant terms were then eliminated. Study

305   location and year nested within study location were used as random effects to account for

306   non-independence of observations in all models. From five nests and different years, two

307   nests of males and three nests of females, we recovered two natal recruits of the same sex.

308   From another five nests and different years we recovered two natal recruits of different sex.

309   We did however not include a random effect for nest because of low sample size.

310   Finally, we used a randomization test to analyse whether the observed effect of

311   hatching mismatch and plant phenology in the recruitment year on change in latitude in males

312   could have been caused by the study design (i.e. males hatched in the SOUTH and hence

313   experiencing pronounced hatching mismatch could only be observed further north). We did

314   the randomization tests for males only because for females there was no effect of the

315   explanatory variables (see below).To test whether our observation of the slope of the effect of

316   hatching mismatch on change in latitude yielded by the final fixed effect model could have

317   been obtained by chance (and was thus without biological foundation) we compared it with

318   the distribution of 5000 simulations. We simulated the final fixed effect model of hatching

319   mismatch and plant phenology in the recruitment year on change in latitude by for each male

320   randomly drawing a potential dispersal site based on the set of all potential breeding sites

321   occupied by flycatchers in a given breeding season (See Online Resource, Appendix 2 for R

322   code of the simulation).

323   All statistical analyses were performed in R 2.15.2 (R Core Team 2012).
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Results

Latitudinal gradients

From SOUTH to NORTH, the peak date of caterpillar biomass on deciduous trees was
delayed with a magnitude of 6–15 days (Online Resource, Figure A1) and the day when the
leaf length reached 50 % of the total length was delayed with a similar magnitude of 6–9 days
(Online Resource, Figure A2). The difference in mean egg laying date of all established nests
between SOUTH and NORTH amounted to 2–3 days during 2009–2011. Similarly, mean
hatching dates of broods surviving until ringing differed among locations and years with the
difference between at least two locations differing among at least two years (ANOVA;
location: $F_{2,508} = 15.32$, p < 0.001; year: $F_{2,508} = 39.98$, p < 0.001; location*year interaction:
$F_{4,508} = 2.51$, p = 0.04). Generally, hatching dates were earlier in the SOUTH than in the
CENTRAL location (post-hoc Tukey's HSD tests, p < 0.001) and NORTH (p < 0.001), but
did not differ between CENTRAL and NORTH (p = 0.99; Table 1, Online Resource, Figure
A1). Temporal match between hatching dates and caterpillar peak dates improved from the
SOUTH to the NORTH (Table 1, Online Resource, Figure A1). Body mass of ringed
nestlings differed among locations when accounting for the effect of year (ANOVA; location:
$F_{2,512} = 14.69$, p < 0.001, year: $F_{2,512} = 12.55$, p < 0.001) being lower in the SOUTH than in the
CENTRAL (post-hoc Tukey's HSD tests, p < 0.001) and NORTH (p < 0.001), but not
differing between CENTRAL and NORTH (p = 0.99). From SOUTH to NORTH mean body
mass increased by 0.45–1.09 g during 2009–2011. Local recruitment rate averaged across all
years depended on location ($\chi_2^2 = 27.9$, N = 2665, p < 0.001) and increased from the SOUTH
to the NORTH (see Table 1 for year specific local recruitment rates).

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Phenology and natal dispersal in males

There was a tendency for the negative effect of hatching mismatch on body weight when 13

days old, and also a negative effect of body weight at age 13 days on subsequent arrival date

as a recruit (Online Resource, Appendix 3). The final linear mixed model on males showed

that direction of natal dispersal was positively affected both by hatching mismatch and plant

phenology in the recruitment year (fixed effects: $b_{\text{hatching mismatch}} \pm SE = 195 \pm 90$, $t = 2.17$, $p = 0.04$; $b_{\text{recruitment year phenology}} \pm SE = 6055 \pm 2271$, $t = 2.66$, $p = 0.01$; $df = 41$; random effects:

$SD_{\text{location}} = 1446.8$, $SD_{\text{year}} = 0.3$, $SD_{\text{residual}} = 3390.8$; $n = 52$, Fig. 2a). The interaction between

the explanatory factors was not significant ($t = -1.23$, $p = 0.23$). Change in latitude predicted

by this model for the lowest and highest hatching mismatch at mean value of the plant

phenology in the recruitment year were -2310 m and 3790 m, respectively. Similarly

predicted values of change in latitude for the earliest and latest plant phenology in the

recruitment year at mean value of hatching mismatch were -1830 m and 3980 m, respectively

(Fig. 2a, b). Neither Julian hatching date ($b_{\text{date}} = -130.5 \pm 135.4$, $t = -0.96$, $p = 0.34$, $b_{\text{recruitment year phenology}} \pm SE = 5553 \pm 2418$, $t = 2.30$, $p = 0.03$; $df = 41$; random effects: $SD_{\text{location}} = 1982.2$, $SD_{\text{year}} = 1473.2$, $SD_{\text{residual}} = 3292.8$), nor relative hatching date ($b_{\text{date\_centr}} = -55.9 \pm 138.7$, $t = -0.40$, $p = 0.69$, $b_{\text{recruitment year phenology}} \pm SE = 5404 \pm 2443$, $t = 2.21$, $p = 0.03$; $df = 41$;

random effects: $SD_{\text{location}} = 2144.1$, $SD_{\text{year}} = 1524.8$, $SD_{\text{residual}} = 3304.6$), turned significant

predictors when used in the finale linear mixed model instead of hatching mismatch.

Slope estimates for the effect of hatching mismatch ($b_{\text{hatching mismatch}}$) on change in

latitude in males derived from simulations were greater than the observed value of 195 only

in 13 out of 5000 cases, yielding a two tailed p–value of 0.005 (Fig. 3). Similarly, slope

estimates for the effect of plant phenology in the recruitment year ($b_{\text{recruitment year phenology}}$) were

greater than the observation in only 3 out of 5000 simulations, yielding a two tailed p–value

of 0.001. Effect of hatching mismatch and plant phenology in the recruitment year on the

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373   change in latitude in males observed in our study is therefore very unlikely to be caused by

374   chance.

375   **Phenology and natal dispersal in females**

376   In females, there was no effect of hatching mismatch, or plant phenology in the recruitment

377   year, on change in latitude during natal dispersal (fixed factors: $b_{hatching\ mismatch} \pm SE = -28.8 \pm$

378   76, $t = -0.38$, $p = 0.71$; $b_{recruitment\ year\ phenology} \pm SE = -597 \pm 2523$, $t = -0.23$, $p = 0.81$; $df = 36$;

379   random effects: $SD_{location} = 1541.3$, $SD_{year} = 1917.7.8$, $SD_{residual} = 2175.5$; $n = 47$, Fig. 2c-d).

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381   **Discussion**

382   Decision theory predicts that breeding dispersal and habitat choice are primarily based on the

383   breeding experience (Schmidt and Whelan 2010; Piper 2011). Here we show that natal

384   dispersal in pied flycatcher males was driven by both the experience from the nestling period

385   (Fig. 2a), and by phenological conditions prevailing during territory settlement in the breeding

386   season of the recruitment year (Fig. 2b). The interaction between the two factors was not

387   significant so these effects turned out to be independent of each other. Effect size indicated

388   similar importance of hatching mismatch and plant phenology in the recruitment year for the

389   direction of natal dispersal in males (Fig. 2). Our data support the hypothesis that experience

390   gained already during the nestling stage drives natal dispersal behaviour in the subsequent

391   season. Ultimately, this may be because temporal matching of breeding with caterpillar

392   phenology can improve when previously mismatched males disperse to the north where the

393   caterpillars develop later. In females, however, none of the factors were significant (Fig.

394   2c,d).

395

396   **Time perspective in cues of natal dispersal direction**
.

397 When natal dispersal takes place, individuals do not yet have their own breeding experience.

398 To make a settlement decision, they have to count on the past experience from the periods

399 preceding first breeding, such as from the nestling or fledgling stage in birds, and from the

400 prevailing phenology during the recruitment season.

401   Mammals and birds seem able to track current plant phenology to reach favourable

402 feeding and breeding conditions (Skogland 1980; van der Wal et al. 2000; Studds et al. 2008;

403 Slagsvold et al. 2013). Such movements might, at least partly, be caused by body condition or

404 past experience, although this has rarely been explored (Potti and Montalvo 1991; Verhulst et

405 al. 1997; Studds et al. 2008; Tilgar et al. 2010).

406   We could not entirely disentangle whether the effects from the nestling period on

407 dispersal behaviour were due to just being early or late in the season, or due to experience.

408 However, neither calendar date, nor date centred by mean local hatching date turned

409 significant when included in the model on change in latitude instead of hatching mismatch.

410 An ecologically relevant yardstick has to be found in order to define what is early or late in

411 the season. In our study, caterpillar peak date on deciduous trees turned out to be much more

412 informative than calendar date. Our data therefore support the notion that the natal dispersal

413 decisions are affected by the experience associated with being early or late relative to the

414 caterpillar peak date, rather than calendar date *per se*.

415

416 Mechanisms behind directional dispersal

417   There are at least three adaptive and one non-adaptive mechanism for choosing a

418 breeding site based on ecological conditions experienced early in life.

.

419   (1) The juveniles may be sensitive to the quality of food provided by the parents. Pied

420   flycatchers prefer to bring caterpillars to the offspring. These may occur plentiful early in the

421   breeding season, but be less abundant later on, forcing parents to bring more flies, ants,

422   beetles etc. (Burger et al. 2012). The juveniles may judge the phenological matching from

423   whether the abundance of caterpillars is increasing, stable, or decreasing during the nestling

424   and post-fledging periods. A decreasing abundance of caterpillars already early in the life of

425   the juvenile may be used as reflecting an unsuitable location for future breeding. A simple

426   rule of thumb is that moving to higher altitudes and latitudes than the natal site would usually

427   mean finding a place with later phenological development of vegetation and insects.

428   (2) Juvenile birds may learn specific locations suitable for future breeding. The

429   learning of such sites may occur already during the post-fledging period (Berndt and Winkel

430   1979; Vallin and Qvarnström 2011). Little is known about the post-fledging behaviour in

431   passerines in general (Slagsvold et al. 2013), and in flycatchers in particular. However,

432   families of blue tits (*Cyanistes caeruleus*) and great tits seem able to track environmental

433   phenology and move post-fledging to areas with later development (Slagsvold et al. 2013).

434   After fledging, pied flycatcher families may stay a few days in the vicinity of their natal nest

435   site but then move quickly away (pers. obs.; van Balen 1979). We suggest that the families

436   may move to areas with later occurrence of caterpillars at higher latitudes or altitudes. Next

437   year the latter sites may become destinations for breeding.

438   (3) The birds may not learn specific locations but general features of a suitable habitat

439   and let such features guide later choice of nest site. One such cue may be the caterpillar

440   phenology of the rearing site, as mentioned above, and of sites visited together with the

441   parents post-fledging, and after independence. It has been hypothesized that in order to match

442   the phenology of caterpillars with nestling dietary demands, previously mismatched

443   flycatchers may disperse to coniferous habitats. This is because the proportion of caterpillars

.

444   in the diet generally decreases in deciduous but not in coniferous habitats over the season

445   (Burger et al. 2012). Ultimately, preference for coniferous habitat may result from habitat

446   cueing and habitat training (Stamps 2001) on the caterpillar food primarily available on

447   coniferous trees later in the season (Online Resource, Figure A1). In our study area,

448   mismatched birds that disperse to the north disperse at the same time to more coniferous

449   habitats.

450   (4) At the time of late arrival, prime territories may already be occupied by earlier

451   arriving, superior males, thereby forcing later arriving, inferior males to disperse elsewhere.

452   Indeed, mismatched males tended to be on average in poorer condition (Online Resource,

453   Appendix 3), which may explain their later arrival to the breeding grounds from their

454   wintering areas in Africa (Online Resource, Appendix 3). Two arguments exist against this

455   mechanism. First, there is no expectation of directionality in dispersal movements of inferior

456   males, although their behaviour may have been constrained by habitat configuration in our

457   study. Second, more empty nest boxes were available in the south than in the north in each

458   year of study, which does not support the idea that the flycatchers were forced to move north

459   simply from competition for a nest site. Presence of empty nest boxes may not necessarily

460   reflect availability of suitable nesting opportunities. However, it is difficult to estimate the

461   popularity of a specific nest box by the flycatchers because a number of confounding factors

462   are involved, like the use of nest boxes for nesting and roosting by other species, species that

463   usually occupy a nest box before the spring arrival of the flycatchers.

464   The fact that there were more empty nest boxes in the south than the north may have

465   biased the results from the randomization test. A way to deal with this may be to exclude from

466   the test all nest boxes that were never occupied. This is however problematic from the reasons

467   mentioned above. Even if the occupation rate did cause a bias, it may still be argued that the

468   reason why so many next boxes were empty in the southern plots could be that mismatched

469   individuals dispersed to the north. Clearly, experimental manipulation of availability of

470   suitable territories along the environmental gradient, and close tracking of individuals, are

471   necessary to test whether males are using the delayed phenological development of the

472   arthropods and of the vegetation, against the alternative that the males are forced to disperse

473   by intra- and interspecific competition for good breeding sites and habitats.

474

475   **Sex differences in the environmental drivers of natal dispersal**

476   Contrary to males, we did not find any effect of environmental phenology on dispersal

477   behaviour in females. Despite a strong positive correlation between arrival date and first egg

478   laying date, the latter may not have been as good measure for timing of migration in females.

479   Female pied flycatchers usually chose a mate and start nest building very soon after spring

480   arrival (Dale and Slagsvold 1995). However, the time elapsing from start of nest building to

481   egg laying may sometimes range from 5–6 days to 2(3) weeks, depending on prevailing

482   environmental conditions (per. obs.). Hence, we cannot exclude the possibility that weather

483   and phenological conditions upon arrival also affect settlement decisions in females, as

484   reported for other bird species (Studds et al. 2008). Apparently, the earlier breeding time in

485   the south (on average 2–3 days) was not enough to compensate for a gradient of 6–15 days in

486   the environmental phenology, nor a phenological mismatch experienced as a juvenile seemed

487   to affect dispersal direction in females. The latter result can hardly be explained by

488   methodological differences between the sexes.

489   We suggest that the lack of response in females was related to a general difference

490   between the sexes in the focal species in how they locate nest sites and mates. Males may use

491   experience gained already in the first summer of life to locate potential nest sites (Doligez et

492   al. 2002). Females can only choose territories that are already occupied and advertised by

.

493   males (Alatalo et al. 1986; Slagsvold 1986; Lampe and Espmark 2003). Competition for

494   males and territories is strong among flycatcher females, and many may not breed at all. Most

495   females arrive during a short period in spring and settle very quickly, only after a few hours or

496   days (Dale et al. 1992, Dale and Slagsvold 1996). Females with more extensive prospecting

497   may risk that a suitable nest site and mate is occupied by another female on return; the new

498   female will be dominant already after a few hours of settlement as shown by removal

499   experiments in the study area (Dale and Slagsvold 1995),

500

501   **Changes in geographical range**

502   Many factors may affect dispersal distance or dispersal propensity, such as personality (Fraser

503   et al. 2001; Duckworth and Badyaev 2007), social status (Dhondt 1979; Arcese 1989),

504   territory isolation (Pasinelli et al. 2004), and population density (Nilsson 1989), and maternal

505   effects (Bitume et al. 2011). Whether these factors act in concert or opposition with the effect

506   of present and past environmental phenology in determining direction of natal dispersal

507   remains to be tested. The main question also remains whether overall distribution of animals

508   might be random (e.g. Campbell et al.2010), despite the determinism of dispersal and habitat

509   choice demonstrated here and in other studies (Pärt 1990; Orians and Wittenberger 1991; Potti

510   and Montalvo 1991; Garant et al. 2005).

511   We show that birds may be able to track environmental phenology at scales much

512   finer than continent-wide geographical gradients and longer than one or two seasons (Studds

513   et al. 2008). This provides some insights on how quickly bird populations may respond to

514   environmental change. Geographical range of breeding populations may not only move

515   towards the north because of reduced reproductive success and increased mortality in

516   southern parts of the range, but because of dispersal of juveniles being able to track

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517   immediate environmental phenology induced by climate change. The effect of such a natal

518   dispersal – phenology driven mechanism may cause a species to alter its breeding range

519   faster, and thus adapt more quickly to environmental change, given that there exist suitable

520   breeding habitats at higher latitudes and altitudes. Analyses of spring phenology of plants in

521   Norway have shown a general delay of 2–3 days per degree of increasing latitude, with a

522   similar delay for each 100 m increase in altitude above sea level (Lauscher et al. 1955). Thus,

523   a natal dispersal – phenology driven mechanism may be quite significant because the birds

524   would have to move rather long distances to benefit from delays in seasonal peaks in the

525   abundances of food resources.

526   Our finding on the significance of environmental phenology at the time of rearing,

527   may also be important to resident species, because even in such species the natal dispersal

528   may be quite extensive (Paradis et al. 1998). In migratory pied flycatchers, instances of natal

529   dispersal over even hundreds of kilometres have been reported (Both et al. 2012). Response to

530   environmental change by range shift may further be facilitated by breeding dispersal, but this

531   is generally a less important source of movement in birds. Determining the ability of females

532   in tracking environmental phenology when not constrained by male settlement behaviour (e.g.

533   during migration, or on the wintering grounds) remains to be studied.

534

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729 **Tables**

730 **Table 1.** Mismatch between mean hatching dates of the local populations of pied flycatchers

731 and peak dates of the caterpillar biomass on deciduous trees, and natal recruitment rates

732 (number of arrived yearlings from ringed nestlings the previous year) across three locations.

location	year	Hatching mismatch in days	number of hatched broods	Local recruitment in year+1
NORTH	2009	9	50	4.9%
	2010	1	56	4.9%
	2011	8	78	3.7%
	mean	**5.7**	-	**4.5%**
CENTRAL	2009	13	39	0.9%
	2010	6	48	1.4%
	2011	8	53	0.7%
	mean	**9.0**	-	**1.0%**
SOUTH	2009	20	67	2.6%
	2010	5	70	1.1%
	2011	13	72	0.0%
	mean	**12.7**	-	**1.2%**

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Figure legends

749 **Figure 1**. Map of three study locations ("SOUTH", "CENTRAL", "NORTH") near Oslo,

750 Norway. Black dots denote all provided nest boxes in the six plots. Letters denote plot names

751 (D = Dæli, H = Haga, Z = Zinober, T = Tangen, B = Brenna, S = Skolen, see Online

752 Resource, Table A1). Thin and thick brown lines denote contour lines of 200 and 400 m a.s.l.,

753 respectively, blue line denotes sea coast at the northern tip of the Oslo fjord, red crosses

754 denote caterpillar frass fall sampling sites and the black cross denotes position of Blindern

755 meteorological station. Complete UTM coordinates are: grid zone 32 V, north grid position

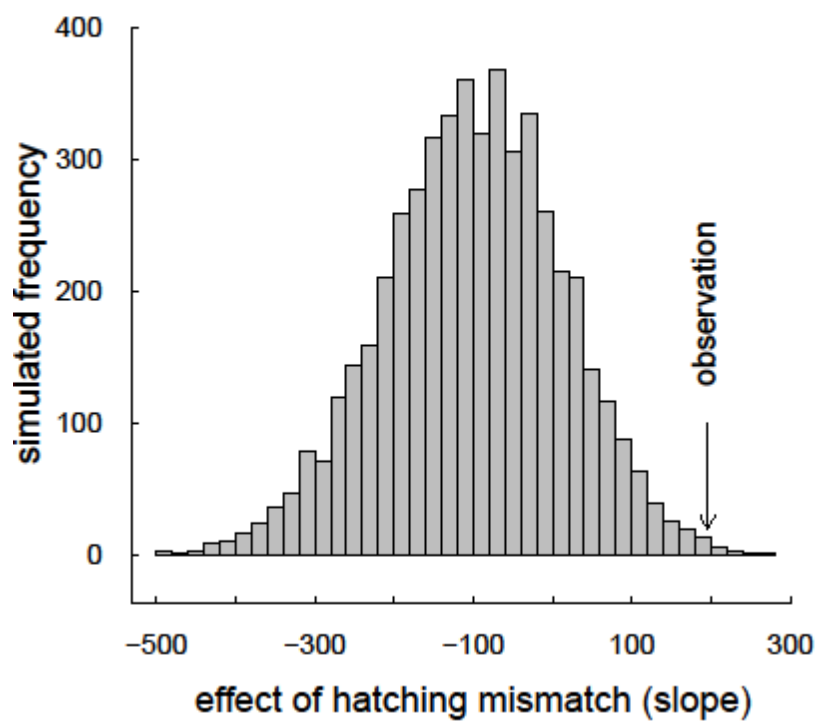756 6643000–6655000, east grid position 0584000–0596000.
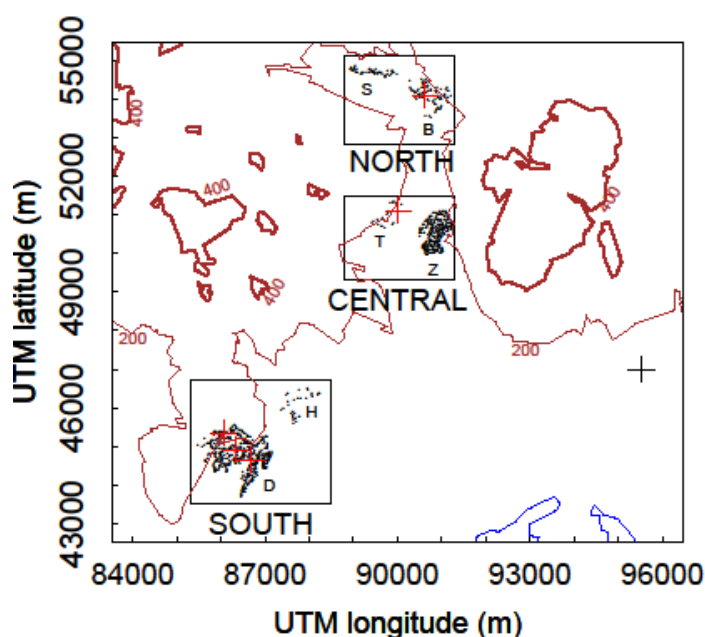
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758 **Figure 2.** The effect of hatching mismatch, and plant phenology in the recruitment year, on

759 change in latitude during natal dispersal in male (a, b; open circles) and female (c, d; full

760 circles) pied flycatchers. Hatching mismatch in year x is the difference in days between

761 hatching date and peak date of caterpillar biomass on deciduous trees. Plant phenology in

762 recruitment year $x+1$, when natal dispersal happens, is a percentage of leaf length referring to

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natal site at arrival date in males, and first egg laying date in females. The lines and their 95%

confidence intervals are fits of the two generalized linear mixed models on the effects of

nestling mismatch and phenology in the recruitment year on change in latitude in males and

females. Shown are the partial residuals of change in latitude for smooth functions of the two

explanatory factors with estimated degrees of freedom $edf = 1$. These are obtained by varying

the factor of interest while keeping the other factor fixed at mean value. Site and year nested

within site were included as random effects.
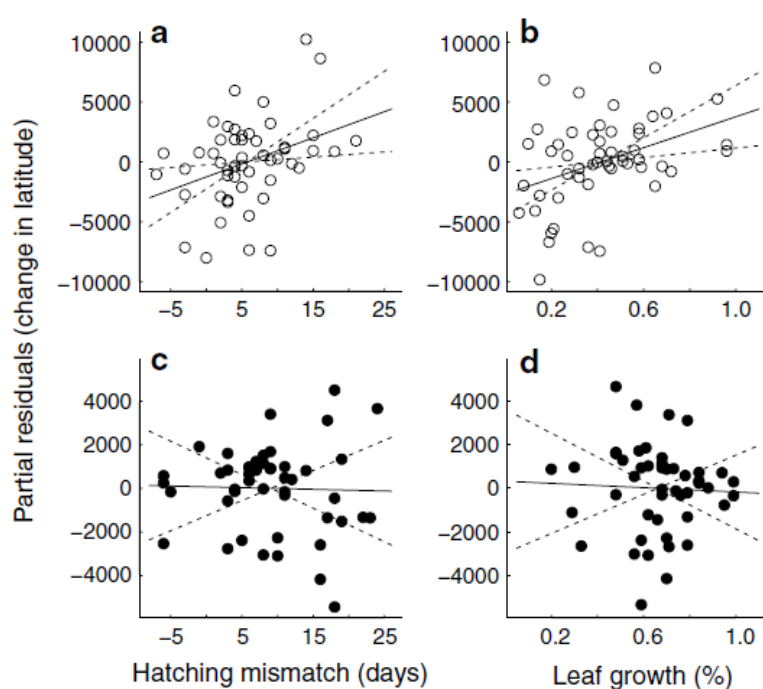
Figure 3. Distribution of slopes of the effect of hatching mismatch on change in latitude in

male pied flycatchers from 5000 simulated linear mixed effect models. Mixed effect models

were fitted to randomized change in latitude and included hatching mismatch and phenology

in the recruitment year as fixed effects. Year nested within site were included as random

effects. Estimate from the mixed effect model with the same structure fitted to original

observations is denoted by arrow.

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effect of hatching mismatch (slope)

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