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

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Natal dispersal allows individuals to reach suitable breeding sites. The effect of present plant phenology as a cue for dispersal into areas with favourable stages of development has been well established across avian and mammalian taxa. However, the effect of past experience is less understood. We studied the effect of past and present phenology of the environment on the direction and distance of natal dispersal in a passerine bird, the pied flycatcher (*Ficedula hypoleuca*). We monitored spring settlement of local recruits in six nest box plots along a 10 km stretch of a south-north gradient in the plant and caterpillar food development. We found that males used both past experience of caterpillar phenology from early life and actual plant phenology during the recruitment season as independent cues for breeding settlement. Males that had experienced a mismatch with the caterpillar food peak as a nestling, and/or those that arrived late in the spring in the recruitment year, moved north of their natal site, whereas males that had experienced a better match with the caterpillars as a nestling, and/or those that migrated earlier in the spring, settled at a similar site or more to the south. In females, no such effects were found, suggesting that the usage of phenological cues is sex specific. In summary, tracking environmental phenology by natal dispersal may represent an effective mechanism for settling in new favourable areas, and may thus potentially cause rapid change of a species´ geographical breeding range in response to climate change.

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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Ultimate explanations for why dispersal happens include avoidance of inbreeding, competition, parasitism and predation and bet-hedging against the environmental variability. Allee effect (i.e. reduction in settlement and habitat search costs with increased conspecific density) and habitat training/cueing have been invoked as additional explanations for adaptive habitat choice (Hildén 1965; Cody 1985; Clobert et al. 2001; Benard and McCauley 2008). Finally, parent–offspring conflict has been suggested to account for variability in dispersal distance (Starrfelt and Kokko 2010).

Proximate cues are necessary for an individual to make a proper decision. Importance of a given cue likely varies with the spatial scale of the movement decision (Orians and Wittenberger 1991). Numerous studies have provided information on cues used by animals for dispersal and habitat choice at the spatial scale of a territory or habitat. These include innate preferences (Partridge 1974; Partridge 1976), habitat learning and/or body condition (Stamps and Krishnan 1999; Ims and Hjermann 2001), and availability of food, suitable breeding sites and presence of con- and heterospecific individuals (Alatalo et al. 1982; Seppänen et al. 2011), including predators (Hildén 1965). Phenological stages of plant growth serve as a cue for large scale movements in many ungulates (Skogland 1980; van der Wal et al. 2000), and may also do so on small, local spatial scales in birds (Slagsvold et al. 2013). Less evidence is available on what cues are utilized for dispersal decisions at larger spatial scales (landscape, latitude) in birds, likely because of technical limitations in tracking the individuals.

By using an isotope analysis, Studds et al. (2008) indirectly demonstrated that redstarts (*Setophaga ruticila*) that migrated later to their breeding grounds in North America dispersed to more northern latitudes than did early birds, presumably to synchronize breeding with food availability (van Noordwijk et al. 1995). Classical theory by Fretwell and Lucas (1969) proposes that lower quality individuals or individuals from low quality habitats should

disperse to low quality habitats, while the opposite should hold for high quality individuals or individuals from high quality habitats. Empirical evidence on the ideal free and ideal despotic distribution is ample (Garant et al. 2005; Piper 2011). Yet, it is unclear whether some of the cues involved in dispersal decisions at smaller spatial scales such as body condition apply also for decisions at large spatial and longer temporal scales.

In passerine birds, nestling survival and fledgling body mass may decrease as a result of a mismatch between timing of breeding and the availability of food (van Balen 1973; Dias and Blondel 1996; Siikamäki 1998; Naef-Daenzer and Keller 1999; Verboven et al. 2001; Visser et al. 2006; Reed et al. 2013; for a review of the mismatch hypothesis see Durant et al. 2007). Caterpillars are major food items for nestlings of many species. Nestling body condition is positively related to the proportion of caterpillars in the diet at least until a threshold is reached (García-Navas and Sanz 2011; Burger et al. 2012). In a Dutch population of great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*), seasonal peaks in the abundance of caterpillars advanced more during warmer years than the timing of breeding of these birds (Visser et al. 1998; Both et al. 2009). On the contrary, synchrony between birds and caterpillars was maintained in British and Belgian populations of the same species (Cresswell and McCleery 2003; Charmantier et al. 2008; Matthysen et al. 2011), and even improved over the years in a Finnish population of willow tits (*Poecile montanus*) (Vatka et al. 2011). A learning based model has attempted to explain habitat learning and selection already from the time juveniles start encountering their environment by means of positive and negative experiences (Stamps and Krishnan 1999). The critical assumption is that dispersal propensity increases with higher frequency of negative experiences. A candidate is food shortage caused by a mistimed reproduction. Contrary, the breeding habitat is chosen based on positive experiences like favourable food conditions that have resulted in good body 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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maple, elm, ash, hazel, oak (*Quercus rubur*), beech (*Fagus sylvatica*) and bird cherry (*Prunus padus*). Dominance of coniferous trees increases with altitude at all locations.

Environmental phenology

We monitored seasonal variation in caterpillar biomass from the time of flycatchers' arrival (end of April) until the end of the breeding season (middle of July) at three plots during 2009–2011 (See red crosses in Fig. 1 for locations). Faecal pellets were collected using traps placed beneath a tree (frass nets hereafter) (Fischbacher 1998, Visser et al. 2006). Frass nets consisted of a piece of cloth fixed to a 0.25 m^2 metal frame. Nets were placed about 0.5–2 m from the trunk of a tree and at least 10 m apart. Five frass nets were placed at each two frass fall sampling sites in 2009, and three sampling sites in 2010 and 2011 at SOUTH, 8 nets at one sampling site at CENTRAL, and 8 nets at one sampling site at NORTH (see Online Resource, Table A1, for tree species sampled). Composition of trees under which the nets were placed was chosen to be approximately proportional to the abundance of tree species at the respective study sites. Nets were emptied every 4^{th} day (or later when raining heavily) and were covered during heavy rains to prevent frass disintegration. After collection, frass was dried at 60°C for 1 hour, separated from litter using Retsch test sieves (1200 µm and 600 µm) and weighed (to nearest 0.1 mg). We calculated a proxy for the relative caterpillar biomass by correcting mass of frass for the effect of ambient temperature during the sampling period, following Tinbergen and Dietz (1994), and for the number of collection hours. Mean daily temperatures for the closest meteorological station (Blindern, see black cross in Fig. 1) were obtained from the Norwegian Meteorological Institute.

Every 5 (4–6) days from the beginning of May until beginning of June we measured length of the same three stretched leaves per tree (same individual trees were measured over

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the years) across five plots. Grey alders, birches and hazels were considered as the representative species across locations. Sample trees were scattered evenly across the nest box plots and were marked with a piece of waterproof tape for identification (see Online Resource Table A1 for details). We calculated average daily values for each tree individual, from which we calculated site-specific average values for each species. Species specific daily growth rates were expressed as percentages of the lengths on the last day of measurement.

A generalized additive model (GAM) was fitted to smooth the effect of seasonal date on caterpillar biomass and leaf growth following guidelines provided by Wood (2006). GAM is a generalized linear model where the linear predictor of explanatory variables of the form $\sum \beta_j(X_j)$ is replaced by a sum of smooth functions with estimated degrees of freedom ("edf" hereafter) of explanatory variables $\sum s_j(X_j)$ (Wood 2006). The basis of the smooth functions is represented by thin plate regression splines (or similar) and is estimated as a part of fitting process. Effect of date (i.e. mid-date of the respective sampling period) on caterpillar biomass was analysed separately for deciduous and coniferous trees because biomass showed a peak for the deciduous trees but not for the coniferous trees (Online Resource, Figure A1). Peak date of caterpillar mass was defined as the date of estimated maximum caterpillar biomass.

Bird observations

After arrival pied flycatcher males choose a nesting hole, inspect it and engage in courtship displays while protecting a very small territory around the nest box (von Haartman 1956). From the beginning of the breeding season we checked each nest box every five days at all plots, except one where they were checked more frequently (a centrally located plot in the gradient, Z in Fig. 1), in order to verify identity of males, check signs of nest building and determine egg laying dates. Male identity was assigned based on a unique combination of

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colour rings. If necessary we used supplemental characteristics such as feather colour and shape and size of head front patch to distinguish males banded with only metal ring. We assigned the date of the first observation of a male as his arrival date. Arrival dates were mostly unknown for females, except in study plot Z (Fig. 1). In four cases when no direct observation was available before the nest building took place we assumed that a male arrived shortly before first signs of nesting material; we assumed arrival on the previous day if little material was present, and two days before if the nest box floor was covered by nesting material. In the pied flycatcher, only females build nests, and they start very soon upon arrival, often only after a few hours (Dale and Slagsvold 1995, 1996). We assumed one egg laid per day in back calculations of first egg laying date if more than one egg was found in a nest (Lundberg and Alatalo 1992). In study plot Z, with daily observations, a strong positive correlation ($r = 0.8–0.9$ for each year of study) existed between arrival date of a female and the date of her first egg laid. Hence, we used the latter measure as a proxy for female arrival time in all sites. The correlation between arrival date of a male and the date of onset of laying by his mate was much weaker ($r = 0.5–0.6$).

Plant phenology upon arrival date of males, and egg laying date of females, in the recruitment year was characterized as a percentage of leaf growth at the respective natal location on a given day. High values indicate late arrival and egg laying relative to the plant development at the respective natal site if birds choose to settle there. Low values indicate early arrival and egg laying at the respective natal site if birds choose to settle there.

Nest boxes were inspected every 1–2(3) days around hatching time. Hatching dates (day 0) were based on nestling growth (Lundberg & Alatalo 1992; Thingstad 2001). Hatching mismatch of each bird was measured as the difference (in days) between the respective hatching date and the peak date of caterpillar biomass on deciduous trees. Peak on coniferous trees was not considered because for such trees there is often a gradual increase in caterpillar
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biomass over the whole breeding season without a clear maximum (Veen et al. 2010*;* see also Online Resource, Figure A1). On day 13 (or 12 in a few cases) we weighed nestlings to nearest 0.25 g using a spring balance (Pesola) and ringed them with a uniquely coded metal band. In 2010–2012 we also measured length of the left tarsus of all nestlings (from the bent digits and including tibia) to nearest 0.1 mm using callipers at all sites. If some of the hatched nestlings were not found in the nest at the time of weighing (i.e. before earliest possible fledging date), we considered those as depredated or starved to death shortly after hatching.

In subsequent years, all adult birds with metal bands were caught for identification. Females were caught during incubation and males when entering a nest box by means of a trap door preventing them from leaving once they had entered. Two birds (one male and one female) that were found breeding in natural holes just outside the study plots were caught using mistnet. Males were further provided with 1–3 plastic bands of different colours for ease of identification and length of the left tarsus was taken in the same way as in nestlings. Length of the left tarsus measured in the first year of life correlated strongly with measures taken at age 13 days ($r = 0.86$, $p < 0.001$, $n = 69$). Body condition of birds when 13 days old was calculated as residuals from a linear regression of log transformed body mass when 13 days old on log transformed length of left tarsus. Euclidean distance between the nest box of first breeding and the natal nest box was used to characterize direction of natal dispersal ("change in latitude" hereafter). Positive and negative values indicate natal dispersal to the north and south, respectively. During 2010–2012 we recovered 99 natal dispersers (47 females, 52 males), i.e. individuals that had fledged from one of our nest boxes and that had settled at one of our study plots during the first year of life. Seven local recruit males that were repeatedly observed at their dispersal site trying to attract a female to a nest box but were unsuccessful were also included in the analysis. We did not include birds that we first found breeding during their second ($n = 10$) or third ($n = 4$) year of life because we focus on

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natal dispersal and the latter birds may have tried breeding somewhere else in their first year (applies to one third of local recruits; Lundberg & Alatalo 1992).

Every year, a portion of complete clutches (ca. 20 %) was subjected to experimental cross-fostering as a part of another study (see Online Resource, Appendix 1). However, experimental treatment included as explanatory covariate in our analysis on change in latitude was not significant ($p > 0.05$) and is therefore not considered further.

Statistical analysis

The differences in mean hatching date and nestling body mass between locations was tested by ANOVA. Post hoc Tukey's HSD test was used for pairwise comparisons. Results were similar for index of body condition and we therefore do not present them.

Local natal recruitment rate was defined as the proportion of yearling birds arriving at their respective natal location (SOUTH, CENTRAL, or NORTH) in year x+1 from all nestlings ringed at the respective location in year x. Chi square test was used to test for differences in natal recruitment rate between locations (Sokal and Rohlf 1995). We used Box-Cox transformation to remedy violations from normality.

A linear mixed model implemented in nlme library (Pinheiroet al. 2013) was fitted by restricted maximum likelihood (REML) to test the effect of ecological factors on change in latitude separately for males and females. Explanatory variables included were hatching mismatch and length of the left tarsus as a proxy for body size. Julian hatching date and hatching date centred by annual local mean were included as alternative explanatory variables to hatching mismatch. Plant phenology upon arrival date at the respective natal site in the recruitment year was used as third explanatory variable in the model on males, while plant 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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change in latitude in males observed in our study is therefore very unlikely to be caused by chance.

Phenology and natal dispersal in females

In females, there was no effect of hatching mismatch, or plant phenology in the recruitment year, on change in latitude during natal dispersal (fixed factors: $b_{\text{hatching mismatch}} \pm SE = -28.8 \pm 76$, $t = -0.38$, $p = 0.71$; $b_{\text{recruitment year phenology}} \pm SE = -597 \pm 2523$, $t = -0.23$, $p = 0.81$; $df = 36$; random effects: $SD_{\text{location}} = 1541.3$, $SD_{\text{year}} = 1917.7.8$, $SD_{\text{residual}} = 2175.5$; $n = 47$, Fig. 2c-d).

Discussion

Decision theory predicts that breeding dispersal and habitat choice are primarily based on the breeding experience (Schmidt and Whelan 2010; Piper 2011). Here we show that natal dispersal in pied flycatcher males was driven by both the experience from the nestling period (Fig. 2a), and by phenological conditions prevailing during territory settlement in the breeding season of the recruitment year (Fig. 2b). The interaction between the two factors was not significant so these effects turned out to be independent of each other. Effect size indicated similar importance of hatching mismatch and plant phenology in the recruitment year for the direction of natal dispersal in males (Fig. 2). Our data support the hypothesis that experience gained already during the nestling stage drives natal dispersal behaviour in the subsequent season. Ultimately, this may be because temporal matching of breeding with caterpillar phenology can improve when previously mismatched males disperse to the north where the caterpillars develop later. In females, however, none of the factors were significant (Fig. 2c,d).

Time perspective in cues of natal dispersal direction

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When natal dispersal takes place, individuals do not yet have their own breeding experience. To make a settlement decision, they have to count on the past experience from the periods preceding first breeding, such as from the nestling or fledgling stage in birds, and from the prevailing phenology during the recruitment season.

Mammals and birds seem able to track current plant phenology to reach favourable feeding and breeding conditions (Skogland 1980; van der Wal et al. 2000; Studds et al. 2008; Slagsvold et al. 2013). Such movements might, at least partly, be caused by body condition or past experience, although this has rarely been explored (Potti and Montalvo 1991; Verhulst et al. 1997; Studds et al. 2008; Tilgar et al. 2010).

We could not entirely disentangle whether the effects from the nestling period on dispersal behaviour were due to just being early or late in the season, or due to experience. However, neither calendar date, nor date centred by mean local hatching date turned significant when included in the model on change in latitude instead of hatching mismatch. An ecologically relevant yardstick has to be found in order to define what is early or late in the season. In our study, caterpillar peak date on deciduous trees turned out to be much more informative than calendar date. Our data therefore support the notion that the natal dispersal decisions are affected by the experience associated with being early or late relative to the caterpillar peak date, rather than calendar date *per se*.

Mechanisms behind directional dispersal

There are at least three adaptive and one non-adaptive mechanism for choosing a breeding site based on ecological conditions experienced early in life.

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(1) The juveniles may be sensitive to the quality of food provided by the parents. Pied flycatchers prefer to bring caterpillars to the offspring. These may occur plentiful early in the breeding season, but be less abundant later on, forcing parents to bring more flies, ants, beetles etc. (Burger et al. 2012). The juveniles may judge the phenological matching from whether the abundance of caterpillars is increasing, stable, or decreasing during the nestling and post-fledging periods. A decreasing abundance of caterpillars already early in the life of the juvenile may be used as reflecting an unsuitable location for future breeding. A simple rule of thumb is that moving to higher altitudes and latitudes than the natal site would usually mean finding a place with later phenological development of vegetation and insects.

(2) Juvenile birds may learn specific locations suitable for future breeding. The learning of such sites may occur already during the post-fledging period (Berndt and Winkel 1979; Vallin and Qvarnström 2011). Little is known about the post-fledging behaviour in passerines in general (Slagsvold et al. 2013), and in flycatchers in particular. However, families of blue tits (*Cyanistes caeruleus*) and great tits seem able to track environmental phenology and move post-fledging to areas with later development (Slagsvold et al. 2013). After fledging, pied flycatcher families may stay a few days in the vicinity of their natal nest site but then move quickly away (pers. obs.; van Balen 1979). We suggest that the families may move to areas with later occurrence of caterpillars at higher latitudes or altitudes. Next year the latter sites may become destinations for breeding.

(3) The birds may not learn specific locations but general features of a suitable habitat and let such features guide later choice of nest site. One such cue may be the caterpillar phenology of the rearing site, as mentioned above, and of sites visited together with the parents post-fledging, and after independence. It has been hypothesized that in order to match the phenology of caterpillars with nestling dietary demands, previously mismatched 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
.

individuals dispersed to the north. Clearly, experimental manipulation of availability of suitable territories along the environmental gradient, and close tracking of individuals, are necessary to test whether males are using the delayed phenological development of the arthropods and of the vegetation, against the alternative that the males are forced to disperse by intra- and interspecific competition for good breeding sites and habitats.

Sex differences in the environmental drivers of natal dispersal

Contrary to males, we did not find any effect of environmental phenology on dispersal behaviour in females. Despite a strong positive correlation between arrival date and first egg laying date, the latter may not have been as good measure for timing of migration in females. Female pied flycatchers usually chose a mate and start nest building very soon after spring arrival (Dale and Slagsvold 1995). However, the time elapsing from start of nest building to egg laying may sometimes range from 5–6 days to 2(3) weeks, depending on prevailing environmental conditions (per. obs.). Hence, we cannot exclude the possibility that weather and phenological conditions upon arrival also affect settlement decisions in females, as reported for other bird species (Studds et al. 2008). Apparently, the earlier breeding time in the south (on average 2–3 days) was not enough to compensate for a gradient of 6–15 days in the environmental phenology, nor a phenological mismatch experienced as a juvenile seemed to affect dispersal direction in females. The latter result can hardly be explained by methodological differences between the sexes.

We suggest that the lack of response in females was related to a general difference between the sexes in the focal species in how they locate nest sites and mates. Males may use experience gained already in the first summer of life to locate potential nest sites (Doligez et al. 2002). Females can only choose territories that are already occupied and advertised by

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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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immediate environmental phenology induced by climate change. The effect of such a natal dispersal – phenology driven mechanism may cause a species to alter its breeding range faster, and thus adapt more quickly to environmental change, given that there exist suitable breeding habitats at higher latitudes and altitudes. Analyses of spring phenology of plants in Norway have shown a general delay of 2–3 days per degree of increasing latitude, with a similar delay for each 100 m increase in altitude above sea level (Lauscher et al. 1955). Thus, a natal dispersal – phenology driven mechanism may be quite significant because the birds would have to move rather long distances to benefit from delays in seasonal peaks in the abundances of food resources.

Our finding on the significance of environmental phenology at the time of rearing, may also be important to resident species, because even in such species the natal dispersal may be quite extensive (Paradis et al. 1998). In migratory pied flycatchers, instances of natal dispersal over even hundreds of kilometres have been reported (Both et al. 2012). Response to environmental change by range shift may further be facilitated by breeding dispersal, but this is generally a less important source of movement in birds. Determining the ability of females in tracking environmental phenology when not constrained by male settlement behaviour (e.g. during migration, or on the wintering grounds) remains to be studied.

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Tables

Table 1. Mismatch between mean hatching dates of the local populations of pied flycatchers and peak dates of the caterpillar biomass on deciduous trees, and natal recruitment rates (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

Figure 1. Map of three study locations ("SOUTH", "CENTRAL", "NORTH") near Oslo, Norway. Black dots denote all provided nest boxes in the six plots. Letters denote plot names (D = Dæli, H = Haga, Z = Zinober, T = Tangen, B = Brenna, S = Skolen, see Online Resource, Table A1). Thin and thick brown lines denote contour lines of 200 and 400 m a.s.l., respectively, blue line denotes sea coast at the northern tip of the Oslo fjord, red crosses denote caterpillar frass fall sampling sites and the black cross denotes position of Blindern meteorological station. Complete UTM coordinates are: grid zone 32 V, north grid position 6643000–6655000, east grid position 0584000–0596000.

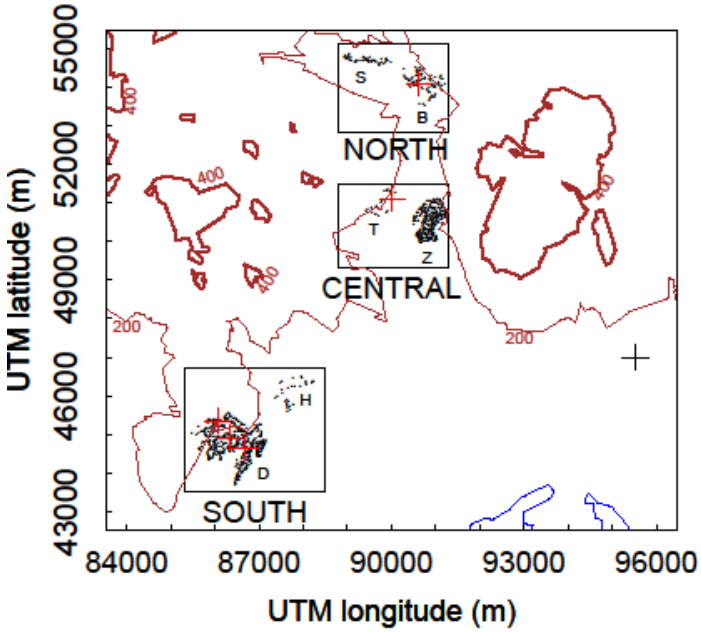

Figure 2. The effect of hatching mismatch, and plant phenology in the recruitment year, on change in latitude during natal dispersal in male (a, b; open circles) and female (c, d; full circles) pied flycatchers. Hatching mismatch in year *x* is the difference in days between hatching date and peak date of caterpillar biomass on deciduous trees. Plant phenology in 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.

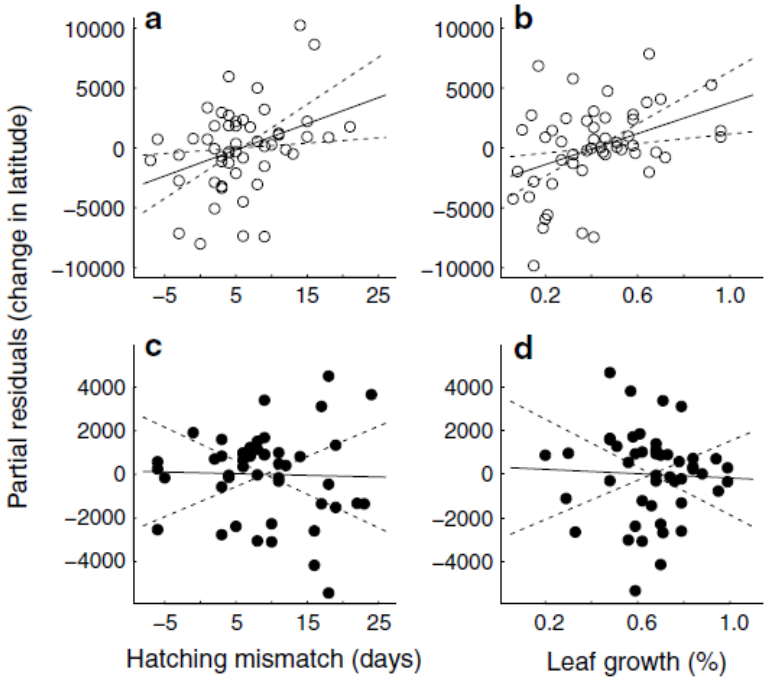

Figure 3. Distribution of slopes of the effect of hatching mismatch on change in latitude in male pied flycatchers from 5000 simulated linear mixed effect models. Mixed effect models were fitted to randomized change in latitude and included hatching mismatch and phenology in the recruitment year as fixed 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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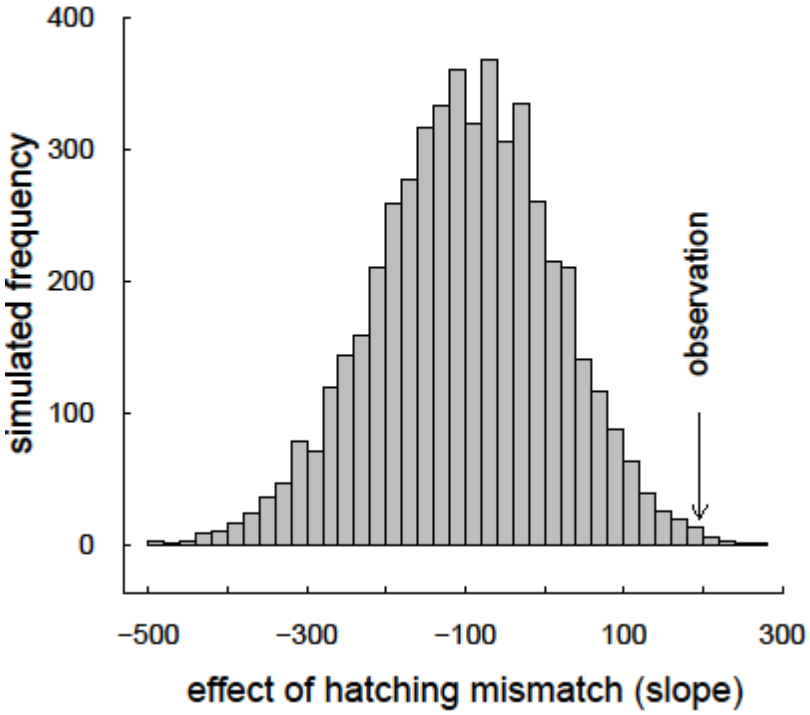
400
300
200
100
0
simulated frequency
observation
−500
−300
−100
100
300
effect of hatching mismatch (slope)

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