

1 **Advancement of spring arrival in a long-term study of a passerine bird: sex, age**  
2 **and environmental effects**

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14 Running head: Environmental effects on phenology

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16 **Abstract**

17 In migratory birds, mistimed arrival might have negative consequences for individual fitness,  
18 causing population declines. This may happen if arrival time is not synchronized with  
19 breeding time, especially when earlier springs favour earlier reproduction. We studied spring  
20 arrival time to the breeding areas in a pied flycatcher *Ficedula hypoleuca* population in  
21 southern Norway during a 30-year period (1985–2014). We investigated trends in arrival both  
22 for the entire population and for different population fractions (e.g., early vs. late arrivals).  
23 We also studied sex and age class differences, along with repeatability of arrival. Finally, we  
24 explored how arrival is influenced by environmental conditions at the areas birds use  
25 throughout the year, using mixed-effects models and quantile regressions with individual-  
26 based data. Spring arrival advanced over five days, at a similar rate through the entire  
27 population. Males and adult birds arrived earlier than females and yearlings. Arrival was  
28 significantly repeatable for males and females. Birds arrived earlier in years with high  
29 temperature and rainfall at the breeding grounds, and low NDVI both on the Iberian  
30 Peninsula and in central Europe. Later fractions of the population showed a steeper response  
31 to these environmental variables. This intra-population heterogeneity in the responses to the  
32 environment probably stems from a combination between the different selection pressures  
33 individuals are subject to and their age-related experience. Our results highlight the  
34 importance of studying how migration phenology is affected by the environment not only on  
35 the breeding grounds but also on the other areas birds use throughout the year.

36

37 **Key-words:** mixed-effects models, NAO, NDVI, phenology, protandry, quantile regression,  
38 rainfall, repeatability, temperature.

39

## 40 **Introduction**

41 The timing of recurring life-history events, or phenology, has important consequences for  
42 natural populations (Knudsen et al. 2011; Gienapp and Bregnballe 2012). One key life-  
43 history event is the arrival at the breeding grounds after migration. In birds, early arrival  
44 facilitates selection of higher quality territories and mates, in addition to opportunities for  
45 replacement broods and extra matings (Newton 2008). However, arriving too early can be  
46 detrimental owing to poor weather conditions during the migratory journey and upon arrival  
47 (Newton 2007). Arrival time becomes particularly relevant in the case of long-distance  
48 migrants, because they often depart from a different climate zone (Newton 2008).

49       Migratory birds show a strong phenological response to climate change (Knudsen et al.  
50 2011), which has been related to a general advancement in spring phenology (Menzel et al.  
51 2006). This advancement has favoured an earlier peak of food availability for many species,  
52 and thereby also advancements in their breeding times (Dunn and Winkler 2010). For  
53 migratory birds, earlier reproduction can be constrained by the timing of arrival to the  
54 breeding grounds in spring (Both and Visser 2001). If arrival is not adjusted, the resulting  
55 mistiming might have negative consequences for individual fitness and cause population  
56 declines in the long term (Both et al. 2006a; Møller et al. 2008; Saino et al. 2011).

57       Birds cover vast distances between their wintering and breeding grounds (Newton  
58 2008), and the rate, direction and variability of climatic and other environmental changes in  
59 these regions may differ considerably (IPCC 2013). This may disrupt the links between the  
60 successive stages of migratory birds' annual cycle, uncoupling the timing of arrival and the  
61 availability of food, territories or mates (Knudsen et al. 2011). Some studies show that  
62 European short-distance migrants advance their phenology more than long-distance species  
63 that cross the Sahara Desert (e.g., Møller et al. 2008; Saino et al. 2011), suggesting that at  
64 short distances it may be possible to better track the conditions at the breeding areas.

65 However, other studies report the reverse situation (e.g., Jonzén et al. 2006). Long-distance  
66 migrants have evolved endogenous mechanisms to time their migration following cues  
67 related to photoperiod (Gwinner and Helm 2003). Some evidence suggests that these  
68 mechanisms can be fine-tuned by environmental cues (Studds and Marra 2011), but it is  
69 disputed whether these will be sufficient to induce birds to initiate migration in time to reach  
70 the peak of resource availability on their breeding grounds (Both and Visser 2001; Both et al.  
71 2006a).

72 Here we investigate the response to environmental variation of a Norwegian population  
73 of the pied flycatcher *Ficedula hypoleuca*, an insectivorous, long-distance migrant that breeds  
74 in temperate forests across large parts of Europe and Western Asia and winters in sub-  
75 Saharan, tropical West Africa (Lundberg and Alatalo 1992). Previous studies found that the  
76 timing of breeding has advanced over the last decades in many, but not all populations across  
77 Western Europe (Both et al. 2004). The timing of spring migration has also advanced in some  
78 populations, but not in others (Both 2010). Here, we use individual-based phenological data  
79 to provide a comprehensive analysis of (1) the entire arrival distribution of the population  
80 over a period of 30 years, (2) differences between different fractions of the population (e.g.,  
81 early vs. late arrivals), particularly with regard to sex and age, (3) how consistent individuals  
82 are in arriving early or late, i.e., the repeatability of arrival, and (4) how the environment in  
83 the areas where the birds range throughout the year influences arrival date. In this study,  
84 ‘environment’ refers to climatic parameters (e.g., temperature, rainfall) and indices reflecting  
85 ecological conditions, especially those related to food abundance (e.g., NDVI). We  
86 investigated the relationships between spring arrival and the environmental conditions on the  
87 African wintering quarters, along the migratory route, and on the Norwegian breeding  
88 grounds. Because of its relevance for breeding, we expected the environment on the breeding  
89 grounds to be most important for arrival.

90

## 91 **Materials and Methods**

### 92 **Pied flycatcher data**

93 Our study area (Sinober in Sørkedalen; 59°59'N, 10°38'E) is located near Oslo, in SE  
94 Norway. Wooden nest boxes have been available in the area since 1985 and this study covers  
95 the period 1985–2014 (see Supplement S1 for details on the study area and ringing  
96 procedures). The area was visited daily from late April (normally around a week before the  
97 first arrivals) to early July. For males, arrival date was defined as the first day a male was  
98 observed in the area. Males occupy a nest site and the immediate surroundings and start  
99 singing soon after arrival, to attract a female. If not previously ringed, the identity of a male  
100 can be judged from which nest box he is singing at, his dorsal plumage colour and the size of  
101 his white forehead patch (Lundberg and Alatalo 1992). During this stage males are readily  
102 attracted to nest boxes and trapped using song playback. Instances of male pied flycatchers  
103 helping with nest building have been reported (Martínez-de la Puente et al. 2009), but most  
104 nest construction is undertaken by females shortly after their arrival (Dale et al. 1992; Both et  
105 al. 2016). Thus, the start of nest construction was used to define female arrival dates (see  
106 Supplement S1 for a detailed explanation). Arrival data for females were not available or  
107 were of low quality for five years (1989, 2001, 2002, 2004 and 2005). Age (yearling or adult)  
108 was estimated according to Svensson (1992). All dates were transformed into Julian days  
109 (January 1<sup>st</sup> = 1) and, after taking leap years into account, used in subsequent analyses.

110

### 111 **Climate and NDVI data**

112 To explore how between-year variability in environmental conditions influenced migration  
113 phenology, we considered eight variables representative of the wintering and breeding  
114 grounds, and along the migratory route (Fig. 1). For the wintering areas and the migration

115 route we used the Normalised Difference Vegetation Index (NDVI; Pettorelli et al. 2005),  
116 which has been used as a proxy for insect abundance in a number of bird migration studies  
117 (e.g., Both et al. 2006b; Gordo and Sanz 2008). To obtain a NDVI time series covering the  
118 whole period we needed to combine data from the NOAA AVHRR-based data from the  
119 GIMMS data set before 2006, and MODIS data afterwards. To define the areas and periods  
120 relevant for flycatcher migration we used averaged NDVI data and exploratory correlations  
121 with arrival dates (see Supplement S2 for details). Flycatchers breeding in Norway are not  
122 likely to depart from Africa before early April, and little is known on when they start  
123 preparing for migration (Ouwehand and Both 2016, Ouwehand et al. 2016). Therefore,  
124 March NDVI values for West Africa and along the migratory route in North Africa, and April  
125 values for the Iberian Peninsula and central Europe were considered in our models.

126 We studied the influence of weather conditions when crossing from Africa to Europe  
127 by using average rainfall along the northern African coast (April), roughly covering the  
128 coasts of Morocco, Algeria and Tunisia (Taylor and Christie 2015). Rainfall was aggregated  
129 from daily gridded weather data from the NCEP-DOE Reanalysis 2 (Kanamitsu et al. 2002).  
130 Data were provided by the Physical Sciences Division, NOAA Earth System Research  
131 Laboratory, and downloaded via ftp (<ftp://ftp.cdc.noaa.gov/>). We also used the North Atlantic  
132 Oscillation (NAO; December – March) index (Hurrell 1995), as a general proxy for  
133 conditions along the migratory route (Supplement S3).

134 We used data from the Norwegian Meteorological Institute, Blindern, Oslo station  
135 ([eklima.met.no](http://eklima.met.no)) to quantify temperature and rainfall at the breeding grounds. To determine  
136 the period most relevant for arrival, we calculated correlations between annual median arrival  
137 dates and imbricate 3-week periods (moving in 3-day steps from 1-March until 30-June) for  
138 mean temperature and rainfall (Ahola et al. 2004). As a result, the time windows selected

139 were 9-April – 17-May (5.4 weeks) for temperature and 9-May – 4-June (3.9 weeks) for  
140 rainfall (Supplement S3).

141

## 142 **Statistical analyses**

143 Analyses were carried out using the statistical programming environment R, version 3.2.2 (R  
144 Core Team 2015). In general, we performed regression analyses with linear mixed-effects  
145 models (LMM) with Gaussian error structures to study both the change in spring arrival and  
146 the factors affecting it. All models included a random intercept effect for individual identity,  
147 to account for the fact that the same birds were caught in subsequent years, and a random  
148 intercept for year, to account for the year-specific environmental conditions that all  
149 individuals experienced. LMM were run with the R package ‘lme4’ (Bates et al. 2013). To  
150 describe the proportion of variance explained by the models we used  $R^2$  as implemented on  
151 the R package ‘MuMIn’ (Bartoń 2015), based on Nakagawa and Schielzeth (2013) and  
152 Johnson (2014). In LMM,  $R^2$  is categorized into marginal  $R^2$  (variance explained by fixed  
153 effects only), and conditional  $R^2$  (variance explained by both fixed and random effects, i.e.,  
154 the entire model). Our analyses were based on 2485 arrivals registered for 1722 individuals.

155

## 156 **Temporal changes in arrival dates**

157 No evidence of temporal autocorrelation was found in any time series of arrival dates. We  
158 also tested for and found no influence of a few late arriving birds on our results (Supplement  
159 S4). The presence of a temporal trend in migration phenology was tested by regressing arrival  
160 date on year and comparing this model with another model fitted with the intercept only (null  
161 model), using a likelihood ratio test. In addition, trends in arrival of different fractions of the  
162 population were analysed by quantile regression (Cade and Noon 2003; Gordo et al. 2013),  
163 with year as explanatory variable, using the ‘quantreg’ package in R (Koenker 2015). We

164 calculated rates of change (slopes) at 5%-interval percentiles. We also analysed temporal  
165 trends in the width of the distribution of arrival dates by regressing the annual standard  
166 deviation of arrivals against year (Gordo et al. 2013).

167 We calculated the difference between the mean annual arrival date in males and  
168 females and explored its temporal trend with linear regression to investigate changes in the  
169 degree of protandry (i.e., the earlier arrival of males relative to females). The same procedure  
170 was used to examine differences in mean annual arrival between adults and yearlings.  
171 Further, we evaluated the influence of sex and age on migration phenology by including these  
172 variables together with year in models fitted using maximum likelihood and ranked according  
173 to the Akaike's Information Criterion (AIC).

174 We estimated repeatability using a LMM approach implemented in the 'rtpR' package  
175 in R (Nakagawa & Schielzeth 2010), using restricted maximum likelihood (REML).  
176 Repeatability describes the relative partitioning of phenotypic variance into within-individual  
177 and between-individual sources, and it describes, in this case, how consistent individuals  
178 were in their arrival phenology throughout time. Therefore, for this analysis we considered  
179 only the individuals for which we had multiple observations ( $n = 480$ ). We built models with  
180 arrival date as the dependent variable and individual identity as the random effect. We also  
181 included a fixed effect for age to account for differences between age classes. We analysed  
182 repeatability for absolute arrival dates and for arrival dates relative to the annual mean (i.e.,  
183 standardized). Analyses were first run with all the individuals and then separated by sex. To  
184 evaluate the uncertainty of the repeatability estimates we used a bootstrapping approach as  
185 implemented in 'rptR'.

186

187 **Climate and NDVI influence on arrival dates**



188 All the NDVI variables presented high between-year autocorrelation. To solve this problem  
189 and capture their year-to-year dynamics, NDVI data were modelled using time-series analysis  
190 with autoregressive integrated moving average (ARIMA) models. The model that best fit the  
191 data was an ARIMA(0,1,1) with an intervention variable coded as '0' prior to the (northern  
192 hemisphere) winter 2006–2007 and '1' thereafter. This was necessary to correct for the  
193 incomplete alignment between the AVHRR (1985-2006) and the MODIS (after 2006) data  
194 series (Supplement S2). The ARIMA models were fitted using the 'arimax' function in the R  
195 package 'TSA' (Chan and Ripley 2012). The residuals of the ARIMA(0,1,1) models were  
196 used as predictors in the subsequent analyses.

197       There was a temporal trend in temperature at the breeding grounds (Fig. 1). To avoid  
198 spurious significant relationships with arrival date, which also showed a temporal trend (see  
199 Results), we detrended temperature by regressing it on year and used the residuals as  
200 predictors in further analyses. Both temperature and the remaining environmental variables  
201 were standardized to mean = 0 and SD = 1 before use in subsequent analyses.

202       To test for multicollinearity we calculated variance inflation factors for our predictors,  
203 using the 'vif' function in the R package 'car' (Fox and Weisberg 2011). Values of these  
204 were in all cases < 5, which is commonly interpreted as absence of multicollinearity. For  
205 model selection, we started with a model that included all the climatic and NDVI variables,  
206 along with year, sex and age, and ran all possible candidate models that could be built (2560),  
207 using the 'MuMIn' package in R (Bartoń 2015). Models were fitted using maximum  
208 likelihood and ranked according to both the Akaike's (AIC) and the Bayesian Information  
209 Criteria (BIC). AIC favours models with a higher number of parameters whereas BIC is more  
210 restrictive because it penalizes model complexity more heavily (Burnham and Anderson  
211 2002). By referring to both we aimed at getting a clearer picture of which environmental  
212 variables were most important to explain variability in arrival phenology. Top models were

213 selected based on  $\Delta AIC < 2$  and  $\Delta BIC < 2$ , and the proportion of variance explained by each  
214 one of them ( $R^2$ ) computed. We calculated Akaike weights for each candidate model. We  
215 also calculated the relative importance (RI) for each predictor variable included in the set of  
216 top models as the sum of the Akaike weights for all models in which the variable appeared  
217 (Burnham and Anderson 2002).

218 We built partial regression plots to visualize the effects of the environmental variables  
219 retained in the set of top models (hereafter these variables are denoted ‘top predictors’) on  
220 arrival date, using the function 'avPlots' from the 'car' package (Fox and Weisberg 2011).  
221 Partial regression plots show the effect of the predictor variable of interest on the response  
222 variable, while removing the effect of all the other predictor variables in the model. First, the  
223 residuals of regressing the response variable on all the predictors except the one of interest  
224 are computed; then, the residuals of regressing the predictor variable of interest on the  
225 remaining predictors are computed; finally, the residuals from the first regression are plotted  
226 against the residuals of the second regression, obtaining a relationship between the two after  
227 having removed the effects of the other predictor variables on both. The models used to build  
228 these graphs were LMM combining all the effects described, both regarding sex and age,  
229 along with the environmental effects given by the top predictors.

230 We built LMM to investigate possible interactions between the top predictors and sex  
231 and age, respectively, using the ‘MuMIn’ package in R (Bartoń 2015). Finally, we tested for  
232 within-population differences in the relationship between these top predictors and arrival date  
233 using the above-mentioned quantile regression method.

234

## 235 **Results**

### 236 **Temporal changes in arrival**

237 Flycatchers arrived on average on 16-May (SD: 9.06 days; range: 24-April to 19-June; n =  
238 2485 arrivals). Spring migration phenology advanced over the study period (likelihood ratio  
239 test:  $\chi^2 = 5.42$ , d.f. = 1,  $P = 0.02$ ) and birds arrived on average  $0.18 \pm 0.07$  (SE) days year<sup>-1</sup>  
240 earlier, resulting in an advancement of 5.4 days over the study period. For the model with the  
241 trend, the marginal  $R^2$  was 0.026 and the conditional  $R^2$  was 0.426, i.e., the amount of  
242 variation explained by year was 2.6% and by the entire model (including the random effects)  
243 was 42.6%. When analysing arrivals with quantile regression, all the fractions of the  
244 population showed a similar significant trend towards arriving earlier. The width of the  
245 arrival distribution did not present any temporal trend ( $F_{1,28} = 0.007$ ,  $P = 0.93$ ).

246 Males arrived on average on 14-May (SD: 9.33 days; n = 1611 arrivals), and females  
247 on 19-May (SD: 7.67 days; n = 874 arrivals). Adults arrived on average on 14-May (SD: 8.72  
248 days; n = 1557 arrivals), and yearlings on 19-May (SD: 8.46 days; n = 928 arrivals). Thus,  
249 both the degree of protandry and the difference in arrival between age classes were on  
250 average five days. This average difference did not change throughout the study period,  
251 neither with regards to sex ( $F_{1,23} = 0.134$ ,  $P = 0.71$ ) nor age ( $F_{1,28} = 1.291$ ,  $P = 0.27$ ). Across  
252 the years, mean values for male and female arrival were closely correlated (Pearson's  $r =$   
253  $0.56$ ,  $P = 0.003$ ), as were those for adult and yearling arrival (Pearson's  $r = 0.73$ ,  $P < 0.001$ ).

254 Sex and age contributed to explain variation in arrival date, since both were included in  
255 the set of top models (n = 4). The interactions between year, and sex and age, respectively,  
256 were not significant, indicating that the advancement in arrival was similar for sex and age  
257 classes. However, a significant interaction between sex and age was retained in the set of top  
258 models. The different sex and age classes arrived at significantly different times ( $F_{3,2485} =$   
259  $120.7$ ,  $P < 0.001$ ; Fig. 2 and Supplement S5). Yearling males (n = 556 arrivals) and adult  
260 females (n = 502 arrivals) arrived, on average, at a similar time (17-May,  $t = -0.377$ ,  $P =$   
261  $0.71$ ), whereas adult males (n = 1055 arrivals) arrived significantly earlier (11-May,  $t = -$

262 12.64,  $P < 0.001$ ), and yearling females ( $n = 372$  arrivals) significantly later (19-May,  $t =$   
263 4.021,  $P < 0.001$ ).

264 Spring arrival dates were significantly repeatable. Repeatability in arrivals relative to  
265 the annual mean was slightly higher ( $R = 0.234$ ,  $CI = 0.175-0.306$ ;  $n = 1243$  arrivals in 480  
266 individuals) than in absolute arrival dates ( $R = 0.212$ ,  $CI = 0.145-0.277$ ), but the highly  
267 overlapping confidence intervals indicate that the estimates are not different. The same  
268 applies when studying repeatabilities separated by sex. In males, repeatability in relative  
269 arrivals was  $R = 0.195$  ( $CI = 0.119-0.265$ ;  $n = 975$  arrivals in 364 males), and in absolute  
270 arrivals it was  $R = 0.167$  ( $CI = 0.095-0.239$ ). For females, only the repeatability estimate for  
271 relative arrival dates was significantly different from zero ( $R = 0.173$ ,  $CI = 0.032-0.309$ ;  
272 absolute arrival dates  $R = 0.078$ ,  $CI = 0.000-0.216$ ;  $n = 268$  arrivals in 116 females).

273

#### 274 **Climate and NDVI influence on arrival dates**

275 All eight environmental variables contributed to explain variability in arrival dates when  
276 considering the set of models with  $\Delta AIC < 2$  ( $n = 14$ ; Table 1). However, only three were  
277 present in all the models ( $RI = 1.00$ ): temperature and rainfall at the breeding grounds, and  
278 the NDVI in central Europe. The same three variables were retained on the set of top models  
279 when considering  $\Delta BIC < 2$  ( $n = 4$ ; Table 1), along with the NDVI at the Iberian Peninsula.  
280 The relative importance ( $RI$ ) of the NDVI in central Europe was higher than on the Iberian  
281 Peninsula when considering  $AIC$  (1.00 vs. 0.70), but lower when considering  $BIC$  (0.15 vs.  
282 0.59). Because of this, we considered both NDVI variables, along with temperature and  
283 rainfall at the breeding grounds, to be the top environmental predictors. Figure 3 shows the  
284 relationships between these variables and arrival date. Birds arrived earlier in warmer and  
285 rainier springs, and later in years with high NDVI both at the Iberian Peninsula and in central  
286 Europe. Year was not included in any of the models with  $\Delta BIC < 2$ , and in many but not all

287 the models with  $\Delta AIC < 2$  (RI = 0.95), probably because its effect was captured by the  
288 environmental variables.

289 All the interactions between the four top predictors and sex and age were included in  
290 the set of top models with  $\Delta AIC < 2$  (n = 24), but none of them were present in all of the  
291 models (RI < 1.00). In addition, no interactions were retained when considering  $\Delta BIC < 2$  (n  
292 = 1). Because of this, we did not consider these interactions further.

293 When analysing the relationship between arrival and each of the four top predictors  
294 using quantile regression, we found a consistent pattern in almost all cases. The negative  
295 relationship between arrival and temperature got progressively more pronounced towards the  
296 end of the arrival distribution, implying that the later fraction of birds responded stronger to  
297 temperature (Fig. 4a). A similar pattern was observed with rainfall at the breeding grounds  
298 (Fig. 4b). The positive relationship between arrival date and NDVI was more pronounced  
299 towards the end of the arrival distribution (Fig. 4c), suggesting that late individuals arrived  
300 even later in years with high NDVI at the Iberian Peninsula. However, with the NDVI in  
301 central Europe no clear pattern could be recognised (Fig. 4d).

302 To integrate the results above, we built a model incorporating the main effects  
303 described, fitted it with restricted maximum likelihood (REML) and calculated its  $R^2$  (Table  
304 2). Its marginal  $R^2$  was 0.231 and its conditional  $R^2$  was 0.452, i.e., the fixed effects  
305 explained around 23% of the variability in arrival dates, whereas the entire model explained  
306 around 45%.

307

## 308 **Discussion**

### 309 **Temporal changes in arrival**

310 The population of pied flycatchers in southern Norway advanced its spring arrival by 5.4  
311 days over a period of 30 years. This is in agreement with previous studies that described

312 advancing phenology in this species (Hüppop and Hüppop 2003; Jonzén et al. 2006; Both  
313 2010). However, there are noticeable differences between populations; while some have  
314 shown advancing arrival or passage date (Germany: Hüppop and Hüppop 2003; Hüppop and  
315 Winkel 2006; Italy: Jonzén et al. 2006), others have shown either no change (central Europe:  
316 Hüppop and Winkel 2006) or changes within populations or areas, with only some  
317 individuals advancing arrival (Finland: Ahola et al. 2004; Fennoscandia: Jonzén et al. 2006).  
318 These population-specific responses may arise as a consequence of several factors, including:  
319 a) adaptation to local conditions (e.g., Sparks et al. 2007), b) different sensitivity to climatic  
320 changes (e.g., Gordo and Sanz 2010), or c) differences in population trends, especially when  
321 population declines may affect the detectability of the earliest individuals (e.g., Gordo and  
322 Doi 2012). In addition, heterogeneity in climatic trends across the planet (IPCC 2013) may  
323 cause birds to experience changes with different intensity and direction. This can be  
324 especially relevant when birds' life cycles comprise movements at continental scales  
325 (Newton 2008), as is the case for the pied flycatcher. Different climatic cues between  
326 wintering and breeding grounds may cause mismatches between arrival time and the peak of  
327 food availability, and this has been suggested as a possible mechanism causing population  
328 declines on migratory birds (Both et al. 2006a, Møller et al. 2008, Saino et al. 2011). In the  
329 pied flycatcher, different European populations winter in different areas in Africa (Ouwehand  
330 et al. 2016), and differences between these areas, both in climate or other environmental  
331 factors, may help explain the diversity of phenological responses found among populations.  
332 For example, Ouwehand and Both (2017) found that departure from the African wintering  
333 grounds, rather than migration speed, determines variation in spring arrival in Dutch pied  
334 flycatchers. Other examples may be extreme events that impact the birds during migration,  
335 affecting only some populations in specific instances, causing delays in arrival and lower  
336 survival (Briedis et al. 2017).

337 Changes in bird migration phenology have traditionally been studied using temporal  
338 trends in measures of central tendency (mean, median or mode) or in arrival dates of first  
339 individuals (Gordo 2007; Knudsen et al. 2007). In the pied flycatcher, the 5-10%, 50% and  
340 90-95% quantiles have often been investigated (e.g., Ahola et al. 2004; Jonzén et al. 2006),  
341 with studies finding that early individuals were advancing their arrival at faster rates than  
342 later ones. This is in contrast with our results, which show a consistent change in timing  
343 throughout the entire distribution of arrivals. Possible reasons for this difference include: a)  
344 population-specific responses; b) the different periods considered between our and other  
345 studies; our study includes more recent years than previous investigations, which might either  
346 better capture the warming trend (see Fig. 1) or simply reflect differences between sampled  
347 periods; or c) the fact that we sampled the entire distribution of arrivals at 5% intervals,  
348 which provides a more comprehensive approach than only considering the median, the very  
349 early or the very late individuals.

350 Annual variation in male and female arrival was closely correlated. Males arrived, on  
351 average, five days before females throughout the study period. Absence of temporal changes  
352 in protandry has been found previously for the pied flycatcher (Rainio et al. 2007; Tøttrup  
353 and Thorup 2008). In contrast, Harnos et al. (2015) found an increasing degree of protandry,  
354 with only males arriving earlier. In other species, previous studies observed both increases  
355 and decreases in protandry in response to global warming (e.g., Spottiswoode et al. 2006;  
356 Tøttrup and Thorup 2008; Bauböck et al. 2012). Direct comparisons with other studies are  
357 difficult because of differences in sample periods, regions sampled and in migration routes,  
358 however, the observed differences may also be attributed to population-specific responses.  
359 These population differences may explain the results by Harnos et al. (2015), who studied  
360 flycatchers from Hungary, which are likely to follow a more easterly route on their spring

361 migration, where they experience different environmental conditions than populations like  
362 ours that use more westerly routes (Ouwehand et al. 2016).

363         Adult birds arrived on the breeding ground, on average, five days before yearlings, and  
364 this difference did not change throughout the study. Earlier arrival of adult flycatchers with  
365 similar time lags for yearlings has been documented before (Potti 1998; Both et al. 2016), and  
366 it may arise from a number of factors: 1) less experience, e.g., lower foraging efficiency at  
367 the stopover sites (Lundberg and Alatalo 1992); 2) higher susceptibility to environmental  
368 variability *en route* (Saino et al. 2004; Sergio et al. 2014); 3) dominance of adults at the  
369 stopover sites; or 4) slower rates of progress due to wing shape where juveniles have shorter  
370 and less pointy wings (e.g., Potti 1998; de la Hera et al. 2014).

371         Repeatability is the fraction of total phenotypic variance that could be attributed to the  
372 individual, and thus it depends on how consistent individuals are and on the amount of  
373 phenotypic variance present (Conklin et al. 2013; Both et al. 2016). Even though the  
374 repeatability estimates for relative and for absolute arrival dates were not different, relative  
375 arrivals reflect better whether birds are consistent in arriving earlier or later than the average,  
376 regardless of the specific annual conditions that may advance or delay the general phenology  
377 of the entire population. In general, the repeatabilities we found are slightly lower than those  
378 from other studies, both for flycatchers and other migrant species (see Table 1 at Both et al.  
379 2016). Both et al. (2016) consider consistent individual variation in departure dates from the  
380 wintering grounds as the most likely cause of repeatability in arrival dates. This initial  
381 individual variation can be balanced out by environmental conditions during migration,  
382 which might synchronise the entire population's arrival in some years, leading to lower  
383 repeatability. Accordingly, this synchronisation effect might be higher in our study  
384 population than in other areas. The overlapping confidence intervals between the male and  
385 female repeatability estimates indicates no sex-related difference, which is in agreement with



386 other studies on the same species (Both et al. 2016). Repeatability shows how consistent a  
387 phenotypic trait is within individuals and may, thus, be a first pointer towards understanding  
388 its genetic basis (Both et al. 2016). The low repeatability values we found might suggest that  
389 the advancement in arrival dates we observed might be caused by phenotypic plasticity.  
390 Indeed, this would be in agreement with the results of Tarka et al. (2015), who find that  
391 phenotypic plasticity best explains advancement of arrival date in a great reed warbler  
392 *Acrocephalus arundinaceus* population.

393

#### 394 **Climate and NDVI influence on arrival dates**

395 Contrary to other studies (e.g., Saino et al. 2004; Both et al. 2006b; Ouweland and Both  
396 2017), conditions at the wintering grounds and departure from West Africa, along with those  
397 at potential stopovers in Northern Africa, contributed relatively little to variation in arrival  
398 phenology. The likelihood of targeting the right geographical areas, where flycatchers  
399 actually are or fly through, is lower on these wintering and passage regions than on the  
400 breeding grounds. This difference might be part of the reason of the results we found. In  
401 addition, recent studies have shown that flycatchers migrate relatively fast and with little  
402 variation in migration speed (Ouweland et al. 2016; Ouweland and Both 2017). If this is,  
403 indeed, a general pattern, it would mean that conditions *en route* may contribute relatively  
404 little to variation in arrival phenology.

405       Birds arrived earlier in years with warmer springs and more rainfall at the breeding  
406 grounds (Fig. 3). Advancement in arrival date with increasing temperature is probably the  
407 most reported effect of climate change on migratory birds (Knudsen et al. 2011; Saino et al.  
408 2011). Higher temperature can influence the progress of migration and arrival date directly  
409 by increasing migration speed through better weather conditions and more efficient use of  
410 migratory fuel (Ahola et al. 2004). Alternatively, temperature could influence migration

411 progress indirectly via propagation of phenological effects through the food chain (Knudsen  
412 et al. 2011). In this case, milder temperatures would favour an earlier development of  
413 vegetation and, hence, the availability of food (Hüppop and Hüppop 2003), thus facilitating  
414 arrival. Such an effect might be noticed by earlier arrival phenology following high NDVI  
415 values when passing through central Europe. However, this is the opposite of what we found  
416 in this study (Fig. 3), suggesting that temperature affects migration directly by enabling  
417 higher speed. We also found that flycatchers arrived earlier during rainy springs, which may  
418 be counterintuitive, since rain is expected to slow down progress and delay arrival (Newton  
419 2008). However, the low-pressure systems associated with rainfall and higher temperatures  
420 may explain early arrival in southern Norway. These systems bring southerly tailwinds that  
421 would speed up the last stage of the migratory journey while minimizing energy expenditure  
422 (e.g., Alerstam and Lindström 1990).

423 Flycatchers arrived later in years with higher greening (high NDVI), and, presumably,  
424 higher food abundance both at the Iberian Peninsula and in central Europe (Fig. 3). This is  
425 somewhat counterintuitive, because faster refueling rates would be expected under improved  
426 foraging conditions, facilitating earlier arrival. Previous research on the effects of NDVI on  
427 the timing of arrival and passage is mixed (Saino et al. 2004; Gordo and Sanz 2008; Tøttrup  
428 et al. 2008; Balbontín et al. 2009; Robson and Barriocanal 2011), and delayed arrival has  
429 been suggested as a response to improved foraging conditions *en route* (e.g, Møller and  
430 Merilä 2004). Several hypotheses may explain this pattern: 1) If NDVI and, hence, foraging  
431 conditions are good *en route*, birds would spend more time at stopover areas, but with low  
432 NDVI and poor conditions birds would skip those areas and arrive earlier. If this is true, birds  
433 would arrive in better condition on years with high NDVI than otherwise, which would be  
434 reflected by a positive correlation between body condition and NDVI values. We computed  
435 body condition by two different methods and performed *ad hoc* correlations with NDVI both

436 at the Iberian Peninsula and in central Europe, but we observed, contrary to expected,  
437 negative, very low, but significant correlations (see Supplement S6). This relationship, thus,  
438 deserves further investigation. 2) If ecological conditions during the winter have led to poorer  
439 body condition, migrants might spend more time at stopover sites increasing their condition  
440 (Gordo 2007; Gordo et al. 2013). However, we found no effects from the wintering grounds  
441 on phenology, and, in addition, whether and why this would correlate with NDVI in southern  
442 and central Europe remains unknown. 3) Some studies show that birds that either lose or  
443 increase fuel stores at a high rate would leave a stopover site quickly, whereas birds  
444 increasing fuel stores at intermediate rates would stay longer (Schaub et al. 2008); this would  
445 account for the observed pattern only if high NDVI entails intermediate refuelling rates. 4)  
446 Delayed arrival may also indicate difficult progress in the north if mild weather in southern  
447 Europe correlates with severe weather in Scandinavia as might occur in winters with positive  
448 NAO (Stenseth et al. 2003). However, none of the correlations performed *ad hoc* to test this,  
449 between the NDVI on the Iberian Peninsula and, respectively, the NDVI in central Europe,  
450 temperature and rainfall on the breeding grounds, were significant (see Supplement S6). 5) In  
451 many flycatcher populations, a large fraction of young individuals skips breeding the first  
452 year (Both et al. 2017), which could be because they arrive too late. It could be the case that  
453 profitable conditions during migration (high NDVI) allow more young individuals to arrive at  
454 the breeding grounds in time, but, since these individuals are later, this would result in a  
455 positive slope between NDVI and arrival. In conclusion, reasons for the positive arrival-  
456 NDVI relationships are still unclear and further research on this issue needs to be carried out.

457 We found intra-population heterogeneity in responses to environmental conditions with  
458 later arriving birds showing greater sensitivity to temperature, rainfall and NDVI (Fig.  
459 4a,b,c). Saino et al. (2004) and Tøttrup et al. (2008) also found intra-population differences in  
460 how migration phenology varied with environmental conditions in differing age classes and

461 during different phases of migration, respectively. The explanation for this diverse intra-  
462 population sensitivity to the environment may lie in a combination between different  
463 selective pressures and individual experience. In males, competition for suitable nest sites is  
464 severe, and they are, thus, under pressure to arrive early (Newton 2008), which provides  
465 greater opportunities for polygyny (“mate opportunity” hypothesis; Canal et al. 2012). This  
466 pressure affects both adult and yearling males, but the less experience of the latter may make  
467 them more dependent upon environmental conditions. Arriving early is a trade-off between  
468 costs and benefits, where the territory-holding males have more to gain than the females  
469 (Newton 2008), which are not subject to the same selective pressures. Females do compete  
470 for partners, but a male without a nest site would lose the opportunity to breed, while a late-  
471 arriving female could still mate with hitherto unpaired and/or polygynous males.

472 Here we showed advanced arrival date in the pied flycatcher in southern Norway  
473 following environmental conditions on the breeding grounds and *en route* in southern and  
474 central Europe. However, in contrast to other studies, we found little influence from the  
475 wintering quarters or other passage areas. We also showed that different population fractions  
476 vary in their response, highlighting the importance of studying the entire population to  
477 achieve a more realistic understanding of the responses to environmental variation.

478

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487

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657

658 **Table 1.** Top models ( $\Delta AIC < 2$  and  $\Delta BIC < 2$ ) relating age, sex and environmental conditions to spring arrival date in a pied flycatcher  
659 population in Norway during 1985–2014. Models are linear mixed-effects models with individual identity and year as crossed random effects. A:  
660 age; S: sex; T<sub>N</sub>: mean spring temperature at the breeding grounds; P<sub>N</sub>: mean spring rainfall at the breeding grounds; NAO: North Atlantic  
661 Oscillation index; Eur: average April NDVI in central Europe; IbP: average April NDVI at the Iberian Peninsula; NAf: average March NDVI in  
662 North Africa; P<sub>NAf</sub>: average April rainfall along the northwestern African coast; WAf: average March NDVI in West Africa; K: number of  
663 parameters; AIC: Akaike’s Information Criterion; BIC: Bayesian Information Criterion; Weights: Akaike weights; RI: relative importance. \*  
664 represents interactions.

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Id.	Model (AIC)													K	$\Delta$ AIC	Weights	Marginal R <sup>2</sup>	Conditional R <sup>2</sup>
1	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO	+IbP					13	0.00	0.13	0.248	0.447
2	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO	+IbP	+NAf				14	0.64	0.10	0.249	0.447
3	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO	+IbP	+NAf	+P <sub>NAf</sub>			15	0.95	0.08	0.252	0.447
4	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO	+IbP			+Waf		14	1.01	0.08	0.250	0.448
5	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y		+IbP	+NAf				13	1.07	0.08	0.244	0.446
6	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO						12	1.08	0.08	0.243	0.447
7	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO	+IbP		+P <sub>NAf</sub>			14	1.26	0.07	0.249	0.447
8	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO				+Waf		13	1.30	0.07	0.247	0.448
9	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO			+P <sub>NAf</sub>	+Waf		14	1.74	0.06	0.250	0.448
10	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO	+IbP		+P <sub>NAf</sub>	+Waf		15	1.88	0.05	0.252	0.448
11	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO		+NAf	+P <sub>NAf</sub>			14	1.91	0.05	0.248	0.446
12	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y		+IbP	+NAf	+P <sub>NAf</sub>			14	1.92	0.05	0.246	0.446
13	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur			+IbP	+NAf				12	1.92	0.05	0.240	0.446
14	A	+S	+A*S	+T <sub>N</sub>	+P <sub>N</sub>	+Eur	+Y	+NAO		+NAf				13	1.96	0.05	0.244	0.446
RI	1.00	1.00	1.00	1.00	1.00	1.00	0.95	0.82	0.70	0.46	0.36	0.26	-	-	-	-	-	-

Id.	Model (BIC)													$\Delta$ BIC				
1	A	+S	+A*S	+T <sub>N</sub>	+IbP	+P <sub>N</sub>								10	0.00	0.32	0.226	0.446
2	A	+S	+A*S	+T <sub>N</sub>	+IbP									9	0.27	0.28	0.199	0.441
3	A	+S	+A*S	+T <sub>N</sub>										8	0.44	0.25	0.176	0.444
4	A	+S	+A*S	+T <sub>N</sub>		+Eur								9	1.46	0.15	0.199	0.443
RI	1.00	1.00	1.00	1.00	0.59	0.32	0.15	-	-	-	-	-	-	-	-	-	-	-

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674 **Table 2.** Parameter estimates with standard error (SE) based on the top models (with  $\Delta AIC < 2$  and  $\Delta BIC < 2$ ) testing environmental influence  
675 on migration phenology in the pied flycatcher (see Table 1). \* represents interactions.

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	Estimate	SE	t-value
(Intercept)	138.26	0.54	257.42
Sex	-5.59	0.44	-12.60
Age	2.25	0.51	4.38
Spring mean temperature	-2.03	0.45	-4.56
Spring mean rainfall	-1.18	0.43	-2.72
Mean April NDVI Iberian Peninsula	1.18	0.46	2.56
Mean April NDVI central Europe	0.85	0.48	1.78
Sex*Age	2.75	0.64	4.28

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679 **Figure legends**

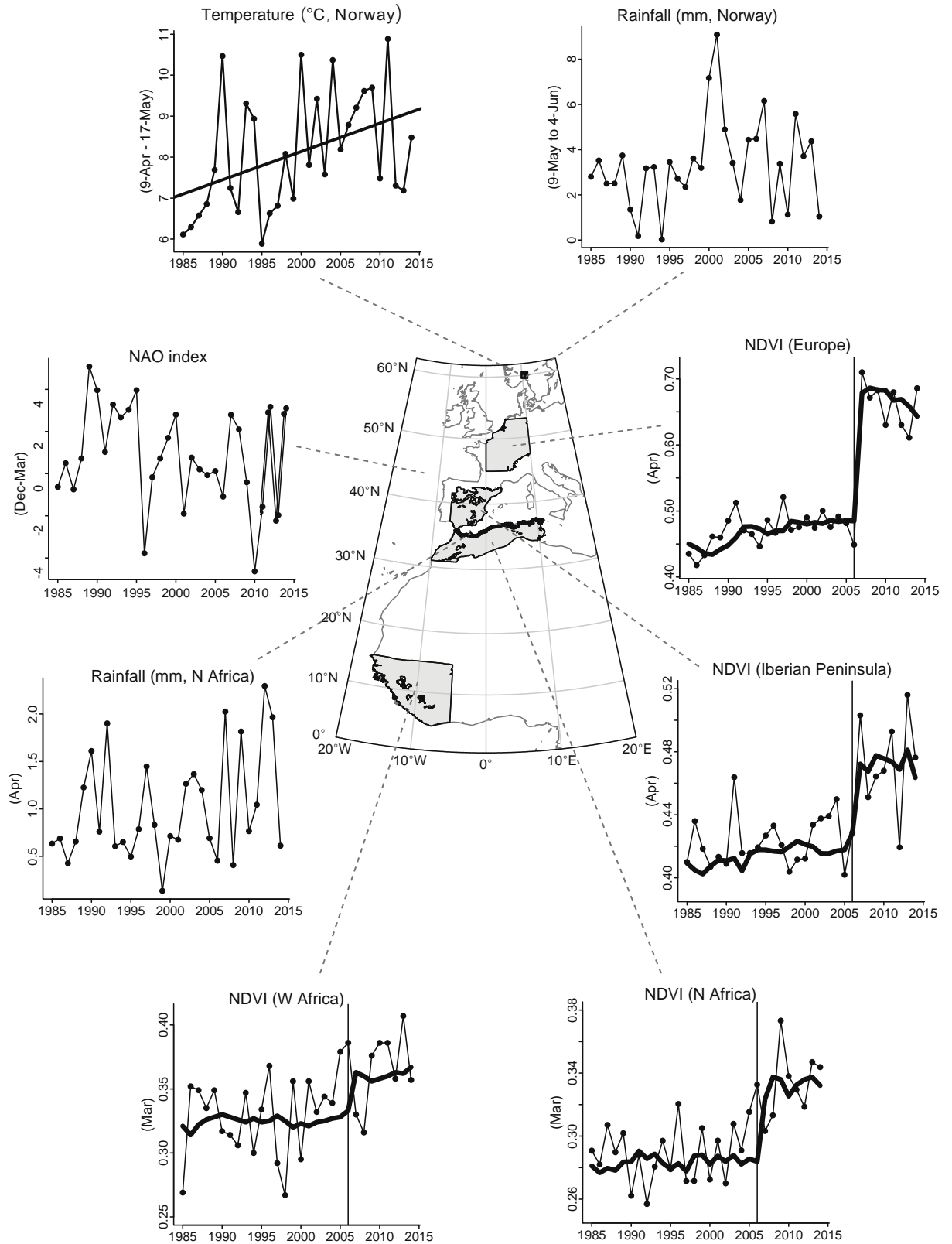
680 **Fig. 1.** Variables used to study the influence of environmental variation on spring  
681 arrival phenology of a pied flycatcher population in southern Norway (1985–2014).  
682 X-axes represent time in years; y-axes show the period for which each variable was  
683 used. The straight regression line represents a significant temporal trend. The NDVI  
684 time-series were composites of AVHRR data before 2006 (vertical line) and MODIS  
685 data afterwards, and were smoothed with an ARIMA(0,1,1) model (thick lines). The  
686 black square shows the study area in Norway.

687 **Fig. 2.** Sex- and age-related distribution of arrival dates to the breeding grounds in a  
688 Norwegian pied flycatcher population during the period 1985–2014. Numbers above  
689 the boxes indicate number of arrivals in each category. Numbers in brackets on the x-  
690 axis correspond to the unique individuals in each category. Note that individuals were  
691 caught several times as adults.

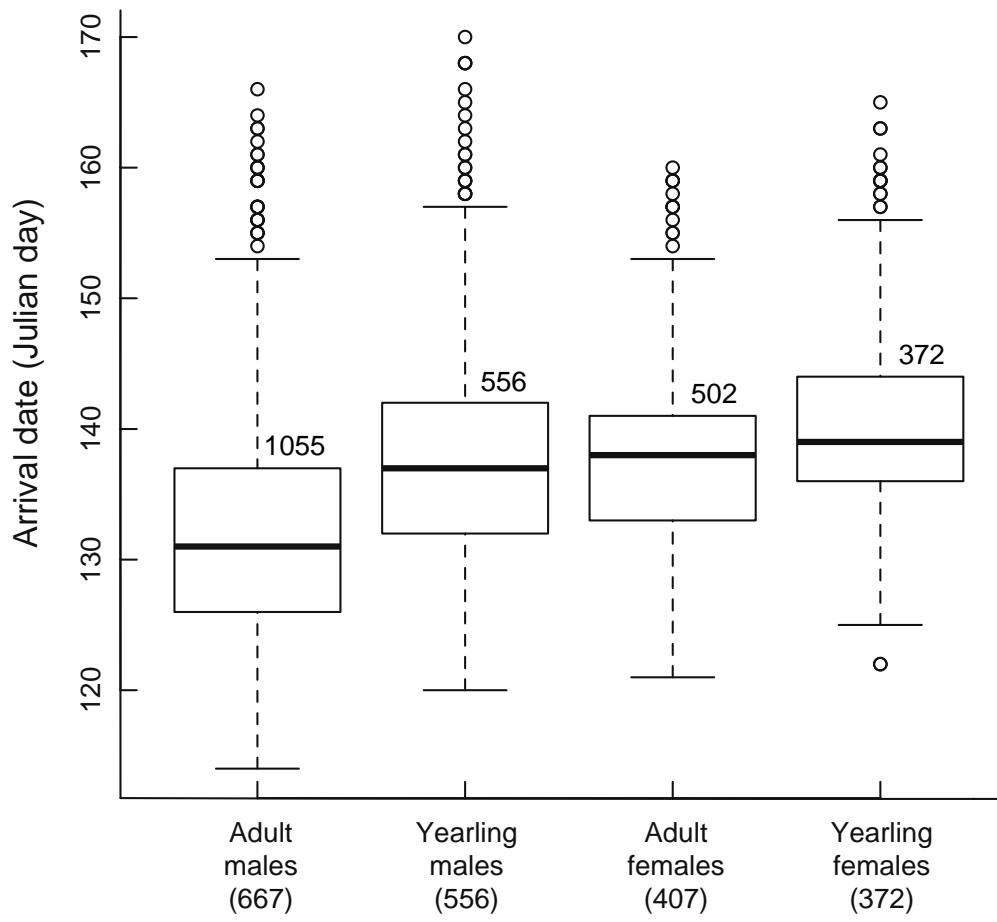
692 **Fig. 3.** Partial regression plots showing the effects of environmental variables from  
693 the breeding grounds, the Iberian Peninsula and central Europe on arrival date (2485  
694 arrivals) in a Norwegian pied flycatcher population during 1985–2014.

695 **Fig. 4.** Intra-population heterogeneity in the responses to the environment in a  
696 Norwegian pied flycatcher population during 1985–2014. Relationships between the  
697 top environmental predictors and arrival date at the different fractions of the  
698 population: a) temperature and b) rainfall at the breeding grounds, c) NDVI at the  
699 Iberian Peninsula and d) in central Europe. Dots on the line show the slope values of  
700 specific regressions of arrival on the corresponding variable carried out at 5%  
701 intervals of the arrival distribution (quantile regressions); grey fields indicate 95%  
702 confidence intervals; the straight lines show the population's mean slope.

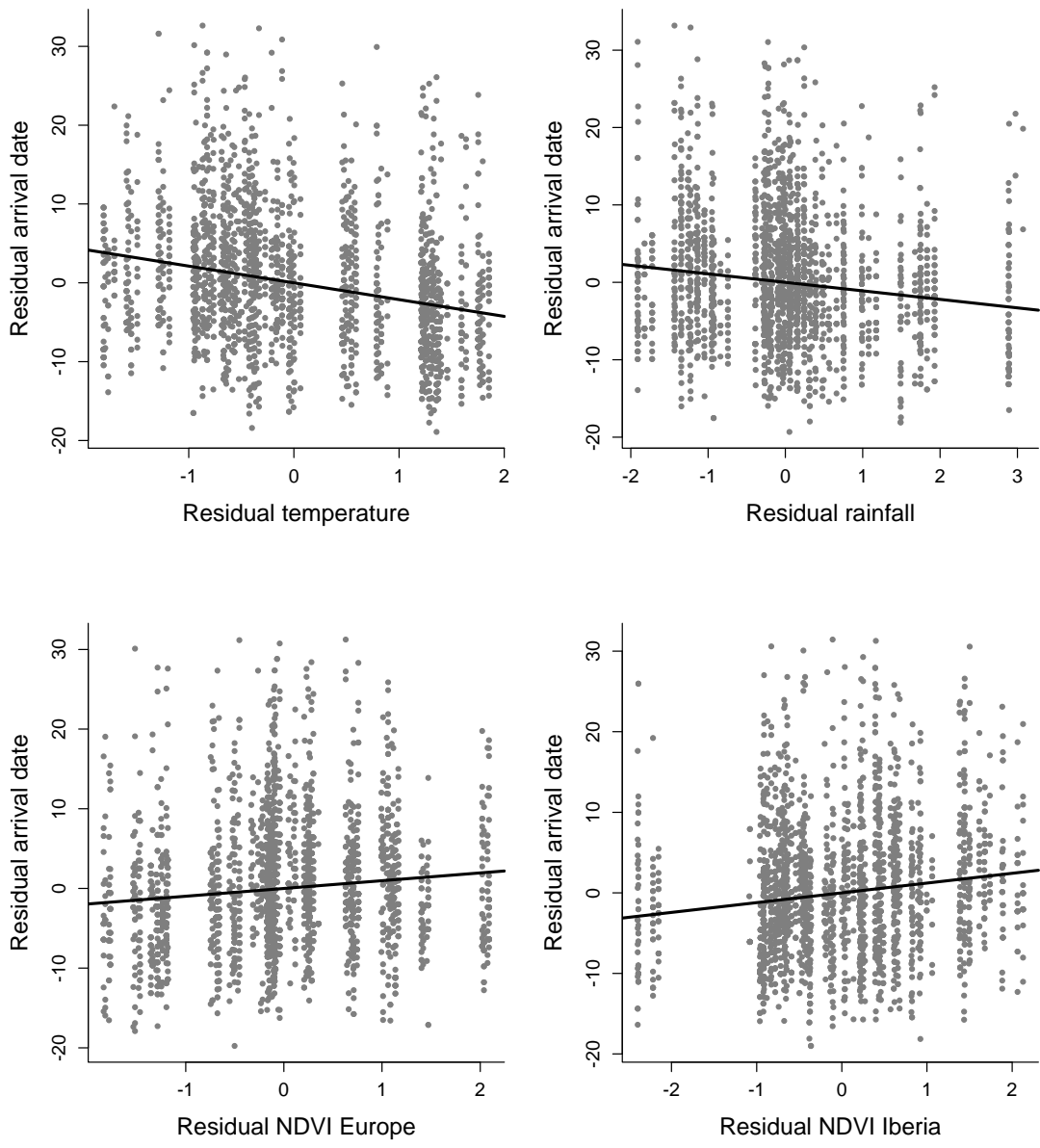




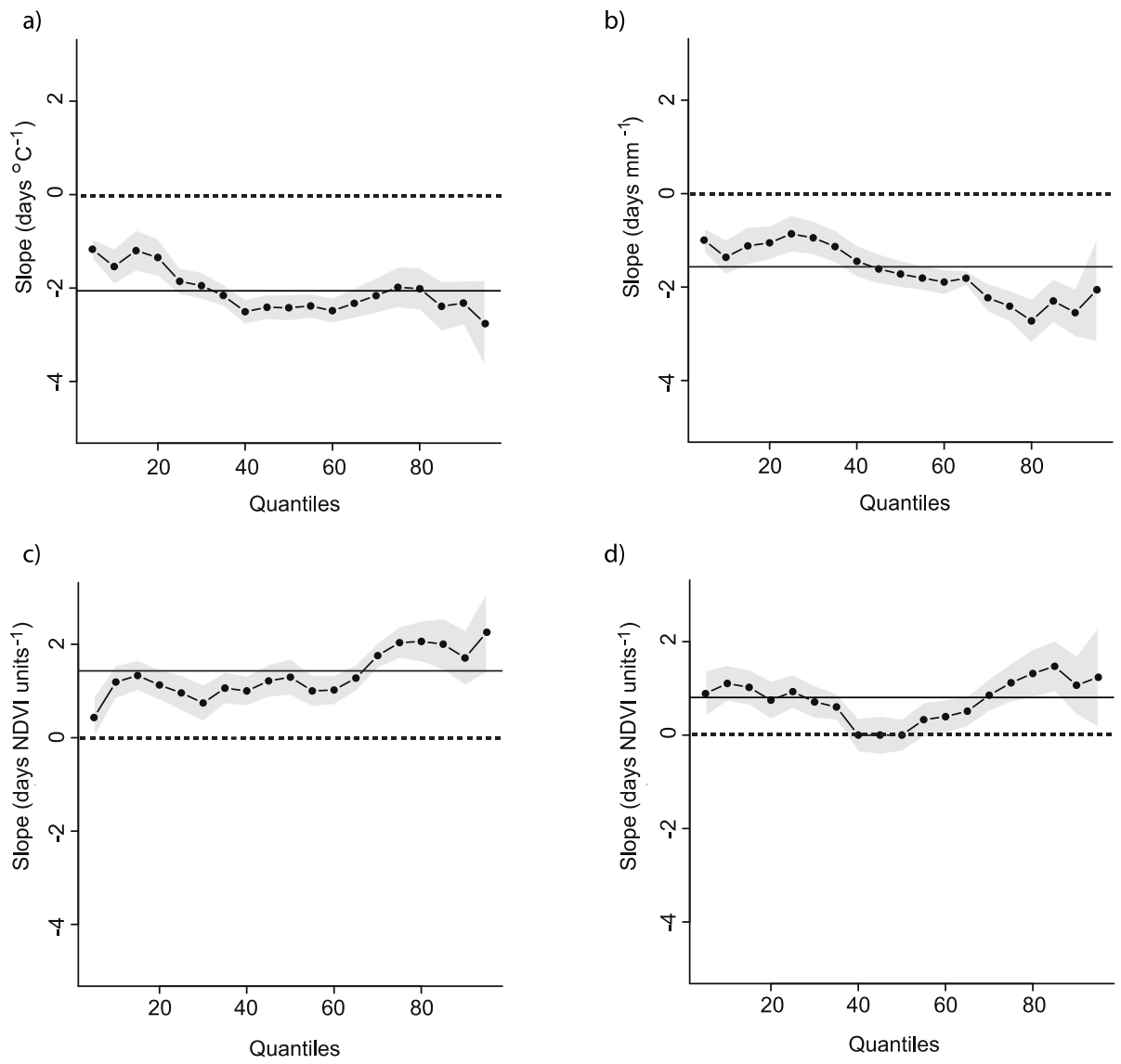
**Figure 1**



**Figure 2**



**Figure 3**



**Figure 4**