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Local adaptation or dispersal? How pied flycatchers cope with climate change

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Chapter 4

The role of conditional dispersal as possible adaptation to climate change in a migratory passerine, the pied flycatcher

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Abstract

1. Climate change alters the seasonal timing of organisms differentially and this can lead to mismatches between trophic levels. For mobile species, conditional dispersal could be an important mechanism to overcome mismatches and to adapt to environmental changes. Correlations between potential indicators of maladaptation and dispersal have been found, but experimental work, which manipulates environmental parameters, is needed to identify causal relationships.
2. We investigated in a migratory passerine, the pied flycatcher (*Ficedula hypoleuca*), if reproductive success, or environmental parameters such as habitat type are related to dispersal distances within a large study area. Furthermore, we experimentally tested, if food availability or timing of reproduction affected dispersal distance.
3. Neither breeding dispersal nor natal dispersal was higher for individuals that were breeding or were born late in the season. This result was corroborated by a lack of an experimental effect of manipulated hatch date on dispersal distances. Experimental food addition during the nestling phase also did not affect dispersal distance, suggesting that variation in matching the peak in food availability did not result in differential dispersal.
4. We found, that dispersal did not relate to prior breeding success but that birds, mainly females, which bred in oak habitat, dispersed further away in the next year. We also found that far-dispersing birds produced more fledglings later on, compared to philopatric birds, although dispersers did not preferentially switch to a habitat without oak trees.
5. During the years of the study, selection for early breeding was weak and this might explain the lack of strong correlations with dispersal. We however cannot rule out that dispersal is used as a solution to overcome increased local mismatches, as a result of climate change. We suggest, that varying competition between habitats plays an important role in affecting dispersal decisions. For many species, dispersal is likely to be important for adapting to climate change, but local adaptation through switching food sources or evolutionary responses might occur as well.

Introduction

Choosing a suitable breeding location is an important decision in an animals' life-history because it will have major consequences for reproductive success and survival of the individual. Dispersal is the movement of organisms between place of birth (natal dispersal) or place of last reproduction (breeding dispersal) and a new breeding location (Clobert et al. 2001). Dispersal could be beneficial because it reduces inbreeding avoidance and competition, and it may also be an active way of improving the match between the individual phenotype and environmental factors (Clobert et al. 2012). For instance, when rapid climate change occurs, dispersal could assist in speeding up micro-evolution or facilitate colonisation of new areas (Le Galliard et al. 2012).

Heterogeneous environments offer possibilities to disperse to locations that match the own phenotype better ("matching habitat choice", Edelaar, Siepielski & Clobert 2008). For an adaptive response in such a temporally and spatially heterogeneous environment, variation in dispersal propensity and distance must depend on environmental or fitness parameters that animals experience. Conditional dispersal has been investigated in many bird species (Clobert et al. 2012; Paradis et al. 1998), e.g. showing various relationships between dispersal and breeding success, habitat quality or hatch date (Examples for passerine birds: Nilsson 1989; Pärt & Gustafsson 1989; Verhulst et al. 1997; Winkler et al. 2005; Eeva et al. 2008; Schaub & von Hirschheydt 2009). In a spatially heterogeneous habitat, conditional dispersal has been found to result in rapid, small-scale evolutionary differentiation (Garant et al. 2005). Conditional dispersal might therefore be an important adaptive response for bird species which struggle to adjust locally to on-going climate change. Especially migratory species became maladapted to their current environment, because they failed to adjust their timing of breeding to the advancing phenology of their prey (Both et al. 2006). Dispersal would allow those species to adapt, without the need to change their rigid annual cycles.

The propensity of individuals to disperse might be flexible between breeding attempts, but could also be determined during early development, by natal environmental conditions (Benard & McCauley 2008). Studies investigating responses to conditions during early environment found, for example, that heavier male fledglings of great tit dispersed further away to their first breeding site (Tilgar et al. 2010), or that natal dispersal was affected by first-year overwintering conditions in American redstarts (*Setophaga ruticilla*) and did not change again later on (Studds et al. 2008). Alternatively, individuals might differ consistently in how far they disperse between breeding attempts, which may depend on syndromes of behavioural traits (Dingemanse et al. 2003; Duckworth & Badyaev 2007). In collared flycatchers (*Ficedula albicollis*), also a heritable component of dispersal behaviour was found (Doligez et al. 2009, but see Potti & Montalvo 1991). This might limit flexibility in responding to mismatches between phenotype and environment (Doligez & Pärt 2008).

Experimental studies, which manipulate parameters to create different degrees of mismatches, are necessary to test if mismatched birds respond by dispersing further away. Such experimental studies are rare, but immigration rates of juvenile great tits (*Parus major*) were affected by manipulated local sex ratios. Tinbergen (2005) and Nicolaus et al. (2012) found, in the same population, that natal dispersal distance increased for juveniles raised in experimentally enlarged broods. For two migratory passerine species, Haas (1998) found, that experimentally reduced breeding success caused the parent birds to disperse. Also, for migratory collared flycatchers, there is experimental evidence that birds use public information on densities and reproductive success, as they adjusted their immigration rate to manipulated local offspring quantities (Doligez, Danchin & Clobert 2002).

Our study species, the migratory pied flycatcher (*Ficedula hypoleuca*) breeds in both coniferous and deciduous forest habitats (Lundberg & Alatalo 1992) which differ in seasonality, especially regarding the timing and availability of caterpillars, which are important for nestling growth (Burger et al. 2012). While relatively early-breeding (well-timed) birds in oak forest can profit from abundant food due to a short, but steep peak in caterpillar availability, late breeders miss this peak. This resulted in an increased selection for early breeding (Both & Visser 2001) and in a decline in the number of breeding birds in habitats with an early food phenology (Both et al. 2006). Also, late-breeding females or late-born young return less often locally in the next year (Drent et al. 2003). It is however unclear, whether the decline in numbers is caused by increased mortality or by dispersal of mistimed or unsuccessful individuals, perhaps into alternative habitats with a later phenology.

Here we investigate, whether pied flycatchers might adapt to climate change by dispersing to habitats with a later phenology. In a descriptive analysis, we tested whether dispersal distances are related to reproductive success, and whether we find correlations with environmental parameters such as relative timing (breeding early or late relative to the mean), or habitat type. We expected that birds with low reproductive success would disperse further away. Furthermore, we assumed that birds breeding late in oak habitat are more mismatched and therefore disperse further away for their next year's breeding attempt. Also, we expected those birds to move more into non-oak habitat, because that habitat has a later phenology with more constant food availability (Burger et al. 2012). Studies often suggest, that food shortage is the cause of reduced fitness in late breeders, but experimental evidence is limited (Verhulst et al. 1997; Siikamäki 1998; Burger et al., in prep.). We experimentally delayed hatching of clutches and food-supplemented part of those broods to test whether birds respond to food availability and timing of breeding *per se*. We expected that experimentally delayed birds experienced lower food abundance and therefore would disperse more, unless the food availability was experimentally restored by food supplementation. We discuss, whether the observed patterns can be interpreted as an adaptive response to environmental change.

Methods

Study species

The pied flycatcher is a long-distance migratory passerine, wintering in Sub-Saharan Western Africa. It breeds in temperate forests across Europe and is often found in oak or oak-mixed habitat types but also uses coniferous habitats. It is single-brooded, shows bi-parental brood care and females lay between 4 and 8 eggs (Lundberg & Alatalo 1992). Nestlings fledge at an age of around 15 days. Nestling diet of pied flycatchers contains a large range of insect prey, with caterpillars being the most common food type in oak habitat, but less so in coniferous habitats (Sanz 1998, Burger et al. 2012).

Study site and data collection

The study was conducted during 6 consecutive breeding seasons (2007–2012), resulting in 5 years of data on dispersal (2008–2012). The study site consists of 12 plots with 50 or 100 nest boxes each (around 1050 boxes in total), spread over a large area in Drenthe, The Netherlands, and ranging from the “Drents-Friese-Wold” in the North across Dwingelderveld National Park to Boswachterij Ruinen as the most southern plot, roughly 25 km from North to South, and about 15 km from East to West. The size of the study area allowed us to also detect movements across longer distances. The plots consisted of either oak, coniferous (pine), or mixed forest patches. Because the main differences in food phenology (caterpillars) exist between oak/oak-mixed and other types of forests, we used two categories in our analyses: oak (including oak-mixed) and non-oak habitat. Habitat type was assigned per nest box, depending on the trees in a radius of about 100 m around the nest box, the area in which most foraging of pied flycatchers occurs (Von Haartman 1954). Distances between boxes were calculated using GPS-coordinates.

At nestling age of 7 days (day 7), parents were caught, ringed and measured (weight, tarsus) and nestlings were ringed and weighed. At day 12, nestlings were measured again (weight and tarsus measures from that age was used in analyses). Recruits were only used in the analysis, if they returned one or two years after birth. Pied flycatchers (especially males) frequently skip breeding in their second calendar year. Recruits born in 2011 were excluded from the analysis (only one year of recruitment data). The recapture rate of adult breeders was similarly high in all plots (>90%, unpublished data), for males and females, and we therefore did not apply any correction in the analyses (see Eeva et al. 2008).

To get an estimate of the caterpillar phenology, we sampled frass fall from caterpillars under oak trees throughout the season, for the years 2007 to 2011. Frass was collected using pieces of cheese cloth of 0.25 m² on a wire frame, which were placed under oak trees and emptied approximately every four days. The collected frass was dried and weighed and approximate caterpillar peaks were calculated (Tinbergen & Dietz 1994). We used data from one study plot (from four individual oak trees) which

had one of the highest breeding densities of pied flycatchers in our study area, and caterpillar peaks did not differ much between areas (C. Both, personal observation).

Experimental manipulation

During three consecutive breeding seasons (2009–2011), we conducted an experiment in our study site in which we manipulated hatch dates of clutches and food-supplemented parents during brood-rearing (see Burger et al., in prep.). We used four treatment categories: delayed nests, delayed nests that received food-supplementation, control nests and control nests with food-supplementation. Delayed nests hatched five (2010–2011) or six (2009) days later than control nests, because they were stored cold in the ground directly after laying, while females were incubating on dummy eggs, supplied by us. Food supplementation of the respective treatment groups started when the young were three days old (day 3). Daily, 30 g of mealworms were provided in a cup attached to the outside of the nest box. Parents could use the food for themselves or for their young. Daily food supplementation lasted from day 3 until the nestlings fledged. A small number of nests and individuals in our study site were manipulated for a different experiment (translocation experiment, Burger et al. in prep.), and those were excluded from the dataset.

Statistical Analyses

The spread in dispersal distances ranged between 0 m (same box) and 18 km. Therefore, log-transformation ($\log_{10}(x+1)$) was used. However, the distribution of these log-transformed values puts much influence on distances of 1 m. We therefore chose to add 50 m (instead of 1) to all distances, to make small values less influential. 50 m is the average distance between two neighbouring boxes in our study area and birds can be regarded site-faithful when returning within this distance, as their former nest box could be occupied upon return requiring the bird to move to a neighbouring box. This transformation of distances was used in all subsequent analyses. All analyses were done using R 2.15.1 (R DevelopmentCoreTeam 2008). Repeatability was calculated using the log-transformed values of dispersal distance and function *rpt.remLMM* from package *rptR* (R DevelopmentCoreTeam 2008). Calculations were done separate for males and females. We separately analysed correlations with dispersal distances, within seasons and between seasons, for adults and recruits, using mixed model analysis (package *lme4*) with normal (for distance or hatch date as dependent), poisson (for number of fledglings) or binomial (for habitat) error distributions. For each analysis, we built a number of biologically meaningful candidate models to test effects of parameters and their interactions of which we were interested in. Model selection was done using AIC to rank models. Models within a $\Delta AIC \leq 2$ were considered as “best models” and parameters were averaged across those models, if they occurred in more than one model (package *AICmodavg*). For the analyses of breeding dispersal, all candidate models were mixed models with ring number, year ($n = 5$) and area ($n = 12$) as random effects (random intercepts). Candidate models investi-

gating causes of dispersal in un-manipulated nests (occasions: $n = 495$, individuals: $n = 391$) included as parameters: habitat, offspring hatch date in year n , number of fledglings in year n , sex and interactions of sex and habitat and sex and birth date. For the analyses of natal dispersal, all candidate models were mixed models and contained year ($n = 5$) and area ($n = 12$) as random effects (random intercepts). Candidate models investigating correlations with dispersal included habitat, hatch date (of recruits), weight and tarsus at day 12 and sex, and the interaction of sex and habitat as well as sex and birth date ($n=266$ individuals).

Results

For the years 2007 to 2011, we calculated the interval between median hatch dates and caterpillar peaks as an indicator of mistiming. In all years, except 2010, median hatch dates occurred after the peak of caterpillars (between 8.3 and 19.3 days later), only in 2010 hatching occurred 4.1 days before the peak. Median hatch dates were very similar between years (between day 51 and 54 (days from 1st April)). Birds were therefore breeding relatively late in all years, except in 2010 when they were well-timed with regard to the caterpillar peak.

For birds caught first as adult breeders across all years (2007–2011), 25.3% of females and 36.3% of males were recaptured as breeders in one of the study areas ($n = 699$ returning individuals). Of those, the median dispersal distances were 119.1 m (0–17157 m) for males and 178.2 m (0–18218 m) for females. 77 out of 699 returning birds switched study plots, which were 11% (25 out of 392) of males and 17% (52 out of 307) of females. With our large study area, it seems likely that we were very well able to capture the range over which most adult birds disperse.

Of ringed and measured nestlings (still alive at age 12 days), 5.96% (322 of 5401) returned as breeders in the two years after birth. Recruits showed a median dispersal distance of 1521 m (mean: 3179 m) between place of birth and place of first reproduction (including birds returning only in their second year). 42% (134 out of 322) of juveniles moved to a study plot other than where they were born. This however also suggests, that a large proportion of surviving offspring moved out of those areas and remained undetected.

We found, that breeding dispersal distance is repeatable among individuals ($n = 138$ with two to four dispersal events, $R = 0.34$). Males and females differed in repeatability estimates: males had a much higher repeatability of dispersal distance ($R = 0.49 \pm 0.076$ SE, CI = [0.325, 0.63], $p < 0.01$) than females ($R = 0.16 \pm 0.091$, CI = [0, 0.325], $p = 0.07$).

Analyses of adult pied flycatchers

We found no clear indication that birds based the decision to disperse on their past reproductive success: the number of fledglings produced in year n was at most weakly

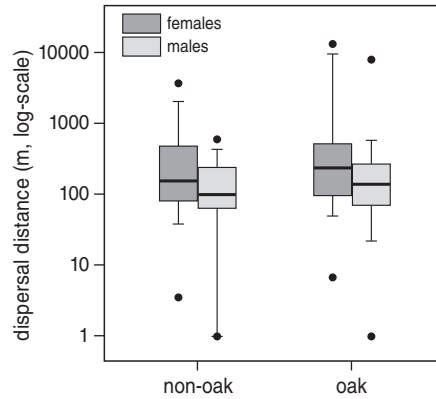


Figure 4.1 Differences in (median) dispersal distances (breeding dispersal in the next year) for adult birds breeding in different habitats, and between males and females. Medians are shown, with boxes for the 25% to 75% percentiles, whiskers for 10% to 90% of the data and crosses for 5% and 95% percentiles. Medians: females-oak: 235 m, females-other: 149 m; males-oak: 136 m, males-other: 120 m. (Averages: females-oak: 1910 m, females-other: 652 m; males-oak: 855 m, males-other: 440 m).

correlated with dispersal distance, as were the interactions with sex (Table 4.1). Moreover, we did not find that later breeders dispersed further away. The best models investigating causes of variation in dispersal distances showed a sex difference, an effect of habitat in year n , and weak effects of number of fledglings, and interactions with sex (Table 4.1): males dispersed significantly shorter distances than females, and birds breeding in oak dispersed further away in the next year, with mostly females from oak habitat dispersing further (interaction SC*hab1, Figure 4.1). Habitat specific averages were: females-oak: 1910 m, females-non-oak: 652 m; males-oak: 855 m, males-non-oak: 440 m.

The experimental effect of hatching delay was in line with the descriptive results: against our initial expectations, neither food supplementation nor hatching delay treatment showed strong correlations with dispersal distances (Adults, $n = 211$). In this subset of data, again females dispersed further away than males (significant difference, Figure 4.4). One of the best candidate models also showed a small positive effect of food supplementation on dispersal distance but this was not significant in the model (Table 4.4).

Individual birds that dispersed further produced a higher number of fledglings in the next year (Figure 4.3). This was mostly the case for females. The two best candidate models contained distance, sex and the interaction between distance and sex (Table 4.3). Clutch size was strongly positively related to the number of fledglings and was included in all candidate models (not shown in the table). Excluding clutch size from the candidate models still resulted in a significant positive relationship between the number of fledglings and dispersal distance in the two best models.

Dispersal distance showed a weak positive correlation with laying dates in year $n+1$ which was slightly stronger in males (not significant, Table 4.2). However, all candidate models were very similar in AIC values (Table 4.2), indicating that none of the parameters explained much of the variation in dispersal distances. There were also no strong correlations of dispersal distance with subsequent habitat choice, far dispersing birds did not preferentially settle in a certain habitat. The best model contained only the intercept, the second and third best model (within $2 \Delta AIC$) contained a small (not significant) positive effect of either sex or distance, respectively, on habitat choice (no table is shown because effects were marginal).

Table 4.1 Correlations with dispersal distance for adult dispersers ($n = 495$). For the sex difference, the estimate for males relative to females is shown. For Habitat, the estimate for oak relative to other habitat is shown. Coefficients of parameters with asterisks were significantly different from 0 ($p < 0.05$).

Parameter	Model average				Model rank (best models within $\Delta AIC = 2$)				
	β	SE	95% CI from	95% CI to	1	2	3	4	5
Sex*	-0.22	0.05	-0.32	-0.13	x	x	x	x	x
Habitat*	0.07	0.02	0.03	0.12	x	x	x	x	x
# Fledglings	-0.01	0.01	-0.03	0.01			x	x	x
Habitat:Sex	-0.06	0.05	-0.15	0.03		x		x	x
# Fledglings:Sex	-0.01	0.01	-0.02	0.01					x
ΔAIC					0	0.38	1.07	1.26	1.27
AIC_w					0.25	0.21	0.15	0.13	0.13
Random structure									
RingNr(intercept)									
Area(intercept)									
Year(intercept)									

Table 4.2 Correlations of dispersal distance with first egg date (dependent) in year $n+1$, for adult dispersers ($n = 483$). Distances are log-transformed. The coefficient for males relative to females is shown.

Parameter	Model average				Model rank (best models within $\Delta AIC = 2$)			
	β	SE	95% CI from	95% CI to	1	2 (intercept)	3	4
Distance	0.55	0.53	-0.49	1.59			x	x
Sex	1.06	0.61	-0.13	2.26	x		x	x
Distance:Sex	1.42	1.06	-0.66	3.5				x
ΔAIC						0.82	0.93	1.15
AIC_w					0.32	0.21	0.2	0.18
Random structure								
Identity (intercept)								
Area(intercept)								
Year(intercept)								

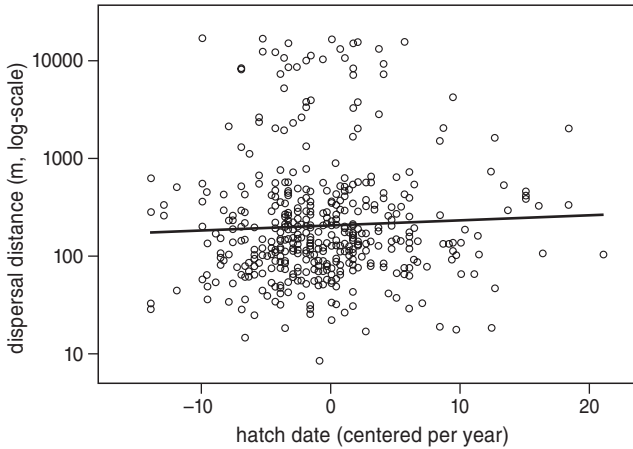


Figure 4.2 Effect of hatch date (centered per year) on dispersal distance (log-scale), for adult males and females. The regression line for this relationship was plotted.

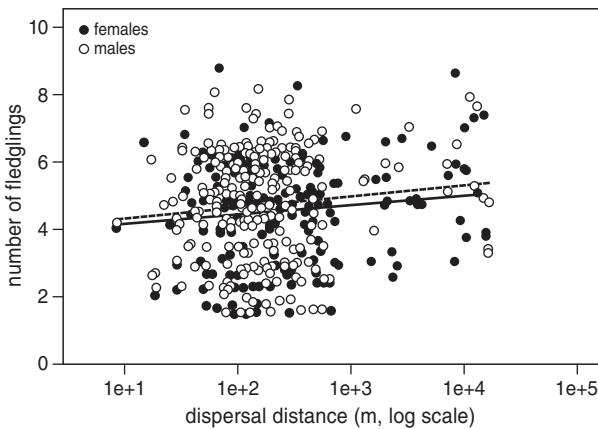


Figure 4.3 The relation between dispersal distance and the number of fledglings produced per nest, in year $n+1$, separate for males and females. Fitted values from the model (Table 4.3) for the number of fledglings are shown here, to better visualize the correlation (using raw values produces many overlapping datapoints). Regression lines are shown, for males (dashed) and females (solid).

Analyses of Recruits

There were no significant correlations of habitat, weight, tarsus or own birth date of the first brood with natal dispersal distances. The best models contained sex, hatch date and habitat but only the effect of sex was significant, showing that female recruits dispersed further away than male recruits, similar to the pattern found in adults (Medians: 1998 m in females vs. 857 m in males, Table 4.5). Hatch date and habitat

had coefficients around zero and are probably not very important in affecting dispersal distances. Again, the experimental results were in line with the descriptive results: recruits, which were experimentally delayed in their hatching dates or food supplemented during chick phase ($n = 70$), did not respond to the manipulations by dispersing differentially. This lack of effect is similar to what we found for adult breeders. Here, sample size was however rather small and models are therefore not presented in detail.

The distance moved between place of birth and place of first reproduction was not correlated with the number of fledglings produced. The best model contained only clutch size as parameter (significantly positively related to the number of fledglings,

Table 4.3 Correlations of dispersal distance with the number of fledglings (dependent) in year $n+1$, for adult dispersers. Distances are log-transformed. The coefficient for males relative to females is shown.

Parameter	Model average				Model rank (best models within $\Delta AIC = 2$)	
	β	SE	95% CI from	95% CI to	1	2
Distance (log)	0.11	0.04	0.03	0.19	x	x
Sex difference (males)	0.04	0.04	-0.05	0.13	x	x
Distance:Sex(male)	-0.09	0.08	-0.25	0.07		x
ΔAIC						0.75
$AIC w$					0.53	0.37
Random structure						
Identity (intercept)						
Area(intercept)						
Year(intercept)						

Table 4.4 Effects of experimental treatment on subsequent dispersal distances in adults ($n = 211$). For the sex difference, the effect for males relative to females is shown.

Parameter	Model average				Model rank (best models within $\Delta AIC = 2$)		
	β	SE	95% CI from	95% CI to	1	2	3
Sex difference (for males)	-0.31	0.07	-0.44	-0.17	x	x	x
Food	0.08	0.07	-0.05	0.21		x	
Delay treatment	0	0.07	-0.13	0.14			x
ΔAIC				0	0.67	2	
$AIC w$				0.33	0.23	0.12	
Random structure							
RingNr(intercept)							
Area(intercept)							
Year(intercept)							

Table 4.5 Correlations of natal conditions with dispersal distance in recruits ($n = 266$), for unmanipulated birds. The coefficient for males relative to females is shown. For habitat, the effect for oak relative to other habitat is shown.

Parameter	Model average				Model rank (best models within $\Delta AIC = 2$)		
	β	SE	95% CI from	95% CI to	1	2	3
Sex difference (for males)	-0.23	0.08	-0.39	-0.07	x	x	x
Birth date	0.01	0.01	-0.01	0.02		x	
Habitat	0.03	0.05	-0.06	0.12			x
ΔAIC					0	1.24	1.57
$AIC w$					0.32	0.17	0.15
Random structure							
Area(intercept)							
Year(intercept)							

Table 4.6 Effects of natal dispersal distances on laying dates in year $n+1$ (dependent), for unmanipulated recruits. Distances are log-transformed. The coefficient for males relative to females is shown.

Parameter	Model average				Model rank (best models within $\Delta AIC = 2$)		
	β	SE	95% CI from	95% CI to	1 (intercept)	2	3
Sex	-0.35	1	-2.3	1.61		x	
Distance	-0.65	0.79	-2.2	0.9			x
ΔAIC					0	1.36	1.88
$AIC w$					0.46	0.23	0.18
Random structure							
Area(intercept)							
Year(intercept)							

Table 4.7 Correlation of natal dispersal distance with habitat type (oak or other) in year $n+1$ (dependent). Distances are log-transformed. For the sex difference, the coefficient for males relative to females is shown.

Parameter	Model average				Model rank (best models within $\Delta AIC = 2$)		
	β	SE	95% CI from	95% CI to	1 (intercept)	2	3
Sex	0.09	0.3	-0.49	0.67			x
Distance	0.06	0.24	-0.42	0.53			x
ΔAIC						1.91	1.94
$AIC w$					0.5	0.19	0.19
Random structure							
Area(intercept)							
Year(intercept)							

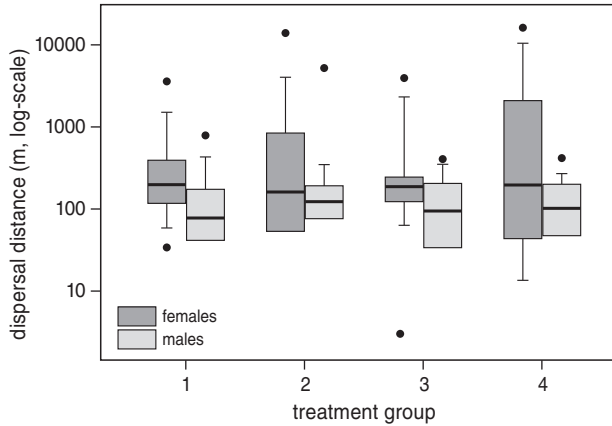


Figure 4.4 Effects of experimental treatment on dispersal distances in adult pied flycatchers ($n = 211$). Treatment categories: 1:control-no food; 2:control-food; 3:delay-no food; 4:delay-food. Medians are shown, with boxes for the 25% to 75% percentiles, whiskers for 10% to 90% of the data and crosses for 5% and 95% percentiles, for males and females.

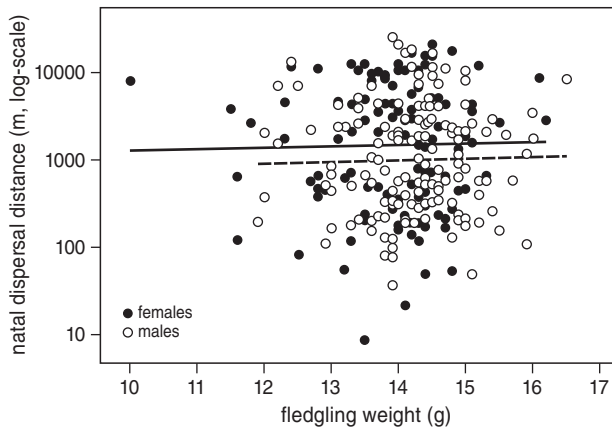


Figure 4.5 Correlation of fledgling weights (average per nest) with dispersal distance (log-scale) in recruits ($n = 266$), for males and females. Regression lines are plotted separate for males (dashed) and females (solid), showing the sex difference in dispersal distances.

Table 4.6). Thus, in contrast to adult birds, variation in natal dispersal distance was not related to differential reproductive success. When removing clutch size from candidate models, the best model is one containing the intercept only. Natal dispersal distance was not (significantly) related to offspring laying date at first reproduction. The best models contained just the intercept, or sex and/or distance. There were only very weak positive correlations of males choosing more often for oak habitat than females (Table 4.7), and of further dispersing birds choosing more often for oak habitat

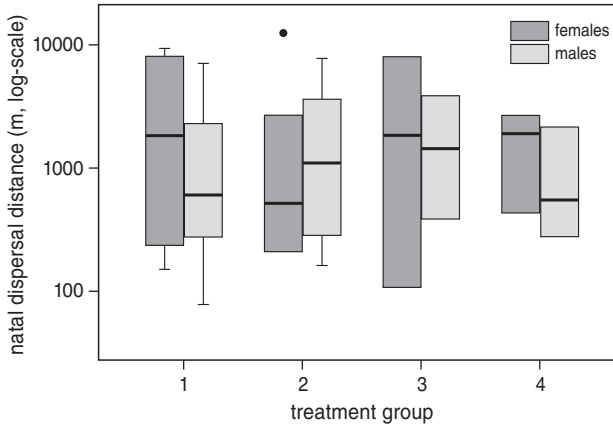


Figure 4.6 Effect of experimental treatment on dispersal distances in recruits ($n = 70$). Treatment categories: 1:control-no food; 2:control-food; 3:delay-no food; 4:delay-food. Boxplot shows median distances with 10% (whiskers), 25%, 75% and 90% (whiskers) percentiles, for males and females.

than for other habitat. Coefficients were however rather close to zero. The best candidate models here contained just the intercept, the sex difference or dispersal distance, respectively, showing little relations of dispersal and subsequent habitat selection.

Discussion

Based on previous work on the effects of climate change in forest-breeding passerines, we expected that a large part of the population of pied flycatchers is breeding too late, relative to the food peak. We assumed, that matching the food (caterpillar) peak is crucial for a birds' fitness (Both et al. 2006; Visser, Holleman & Gienapp 2006) and birds should therefore respond to mistiming, either by advancing their timing of breeding or, if unable to do so, by dispersing to areas with a late phenology. In our descriptive analysis, we did not find that individuals with low breeding success or which were breeding late, dispersed more or moved into another habitat. However, if birds had chosen the best habitat already for their individual phenotype (Edelaar, Siepielski & Clobert 2008), this could explain why individuals did not move to another location in the next year.

To investigate conditional dispersal experimentally, we manipulated hatch dates and food abundance, but again we neither found that birds with a delayed brood dispersed more often, nor that individuals with abundant food were more site faithful. This was the case for both adult birds and for recruits from experimental nests. The results suggest that individual birds do not adjust to an individual mismatch by seeking a better breeding habitat in the next year. We could not measure overall food

availability in the environment, but the lack of experimental effects of delay and food supplementation on survival and reproductive success indicates that date effects were rather weak during the three years of the experiment (Burger et al. in prep). Therefore, the lack of experimental effects of mismatches between food peaks and individual timing should be taken with caution, as in circumstances with clear asynchrony conditional dispersal may play a more important role.

In our descriptive analysis, we found that breeding dispersal was habitat dependent, with birds from oak habitat dispersing further away in the next year. The pattern existed for both males and females, but was stronger in females. This finding might suggest that the decline of pied flycatcher densities in oak forests in the Netherlands (Both et al. 2006) is not just related to reduced survival of late breeders but also to emigration. We did not see that birds which dispersed far away switched habitat type, which suggests that the cue to disperse is not habitat type *per se* but possibly another parameter that we did not measure but which is correlated with habitat. Differential dispersal distances between habitats could be explained with differences in breeding densities which are often higher in oak vs. other habitat (Lundberg & Alatalo 1992), and which could force birds to move further away in order to avoid competition and find a vacant nest box (see Matthysen 2012, on density dependence). Dispersal behaviour might therefore not be directly related to (changing) environmental parameters but rather be a response to varying competition between habitat types. The finding, that females actually showed a stronger response than males might be explained with the generally higher propensity of females to disperse while males often benefit more from familiarity with an area (see Greenwood 1980) and engage more in competition (e.g. males try to take over nest boxes from interspecific competitors like great tits, Both et al., personal observation). The analysis of male arrival dates in relation to dispersal could also give better insight into intraspecific competition, because brood hatch dates of males are hardly related to arrival dates (C. Both, unpublished data). The observed pattern seemed unrelated to the distribution of available habitat, and we controlled for the variation between plots and between years in the random effects of our models.

We also found, mainly in females, that dispersing individuals improved their reproductive success. This was not the result of an earlier start of reproduction, as hatch dates of offspring did not advance but were rather delayed after birds dispersed further away. Despite this small delay in hatching dates, dispersing further away seemed to be an adaptive response within our study area. However, we could not measure whether dispersal is compromised by e.g. reduced survival of those individuals, as fitness costs are difficult to quantify for dispersing versus non-dispersing individuals (Doligez & Pärt 2008).

The same pattern was also found for female pied flycatchers in a Finnish study (Eeva et al. 2008), where researchers suggested that females, which disperse far away, might acquire better territories or higher-quality mates. Because of the patchy structure of our study area, it is unlikely that nest-site quality varies with absolute dispersal

distance, but far-dispersing females might be of higher individual quality (Verhulst et al. 1997) which could result in high reproductive success. We therefore found no indication that dispersal within our study area is costly in terms of reproductive success, due to e.g. un-familiarity with the habitat. Pied flycatchers are occasionally found to disperse over much greater distances (Both et al. 2012), and experimental work suggests that even moving over hundreds of kilometres to the north does not involve high reproductive costs (Burger et al., submitted).

If the propensity to disperse is determined during the developmental phase (Balbontin et al. 2009), this might result in some individuals consistently dispersing far away between subsequent breeding attempts while others returned close-by. We found, that male dispersal behaviour between subsequent breeding attempts had a high repeatability. Especially if habitats are neither spatially nor temporally predictable, it is imaginable that such a polymorphism can be maintained, because on average, both the dispersers and the non-dispersers can have equal fitness. Our results of higher reproductive success of the more dispersing individuals must then be offset against a presumably lower survival, although the higher breeding success was mostly found for females which have much lower repeatabilities of dispersal distance.

For dispersal to be an adaptive strategy, birds should cue on indicators of maladaptation such as low food abundance and respond accordingly. On the scale of this study, we did not find that unsuccessful birds dispersed further away or into the less seasonal habitat (coniferous woodlands). Conditional dispersal might only occur in certain seasons when birds experience severe negative consequences of breeding too late, which was not the case during the years of this study (Burger et al., in prep). Moreover, birds might use other indicators of maladaptation, like temperature (Pärn & Saether 2012).

For certain species, local adaptation to changing environments might not just occur through tracking a certain food source (caterpillars), but through a switch in diet. Pied flycatchers have been reported to have a much more diverse nestling diet compared to great tits or blue tits (Eeva, Ryömä & Riihimäki 2005) and they were found to cope rather well with limitations in food availability or quality (Qvarnström et al. 2005). Flycatchers therefore likely use a combination of strategies in order to adapt to environmental changes and dispersal is only one possible mechanism (Le Galliard et al. 2012). Demographic effects (see Matthysen 2005; Bowler & Benton 2005) often play an important role in affecting inter- and intraspecific competition and subsequent dispersal behaviour. Negative fitness consequences of breeding late (resulting in strong selection for early laying) were for example only found when breeding densities and therefore competition was high (Ahola et al. 2012). Ecological differences between species and year variation in environmental parameters will thus greatly affect the outcome of studies on the adaptiveness of dispersal behaviour. More experimental work, especially manipulations which induce environmental mismatches, is needed in order to study how species respond to climate change and how this affects population dynamics.

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