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

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Chapter 7

General discussion

Claudia Burger

Pied flycatchers are rather well-adapted to their breeding environment

A good understanding of how species cope with changes in their environment requires the study of their ecology (e.g. the trophic levels they depend on), and the mechanisms through which adaptation could occur. The work presented in this thesis, provides new insights about the importance of mismatches during reproduction. During the study period, I found surprisingly little support for food limitation and little fitness penalties of late breeding. Based on my findings in chapter 2, and relative to previous work, I suggest that, apparently, selection for early breeding has diminished again in recent years. This idea is supported by a study on pied flycatchers in the Hoge Veluwe, The Netherlands (Both et al., in preparation). There, long-term data on selection differentials shows that, after increasingly strong fitness penalties for late breeders from 1980-1996 (Both & Visser 2001), those penalties have declined again in the last 15 years. At present, pied flycatchers only seem to suffer mildly from breeding late relative to the caterpillar peak (Chapter 2, Figure 2.4), which is in clear contrast to earlier descriptive studies. Interestingly, their timing with the caterpillar peak date did not improve (during two out of our three experimental years, birds were breeding late relative to the caterpillar peak, Chapter 2, Figure 2.5). This apparent adaptation to current phenological circumstances needs to be explained.

Selection pressures commonly vary in strength and direction between years (Siepielski, DiBattista & Carlson 2009; Merilä, Kruuk & Sheldon 2001) and this variation can limit adaptive evolution. Causes for this variation are however difficult to identify (Siepielski, DiBattista & Carlson 2009) and more research is needed here. In the case of the pied flycatcher, I suggest that inter- and intraspecific competition could be important in explaining changes in fitness penalties of late breeders in seasonal habitats: reduced breeding densities of pied flycatchers and other late-breeding long-distance migrants in the most seasonal areas (see Both et al. 2006; Both et al. 2010) could have released competition for food, so that mismatched individuals still profit from abundant alternative food. Evidence for density-dependent selection for early breeding exists for a Finnish study on pied flycatchers (Ahola et al. 2012). Also long-term changes in predation rates (e.g. less predation on late broods) or in habitat richness could theoretically cause such patterns, but we have no evidence for that.

Selection differentials for laying dates have been frequently linked to mismatches, although a direct relationship was demonstrated only in one study population (Van Noordwijk, McCleery & Perrins 1995; Charmantier et al. 2008). In pied flycatchers, there is so far no evidence that selection for early breeding is directly correlated with the interval between brood rearing and the caterpillar peak. All these arguments on selection are based on fitness estimates that are rather incomplete, because only locally surviving offspring and parents can be counted. Selection differentials based on survival rates thus ignore the important between-population processes of emigration and immigration: late-born offspring might not survive less well but might instead

disperse further away from the place of birth and outside the study area, and thus more often remain undetected. If dispersal in late born young increases with increasing mismatches, this could have explained the change towards selection for early breeding individuals in former studies (Both & Visser 2001).

In this study, I found no indication for dispersal to be related to birth date, and this was also true when mistiming was experimentally induced (Chapter 4). It is therefore unlikely that conditional dispersal explained the increased selection for early breeding in earlier studies. The fieldwork for this thesis was conducted in a large study area, which improved the reliability of our survival estimates for adults, but the dispersal distances of recruits (mean distances for males and females: 3179 m) suggest that we still retrieved only a fraction of surviving offspring (recruitment rate was only around 6 % in our population, Chapter 4). While, on average, 65% of first-year breeders in great tits were locally born (Gienapp 2005), in our study population in 2009 only around 20% of first-time breeders (second calendar year birds) were locally born.

Incomplete fitness estimates have been recognized as a major problem in the study of adaptation (Sheldon, Kruuk & Merilä 2003; Doligez & Pärt 2008), but still few studies address this issue. I clearly demonstrated in Chapter 2, that different fitness parameters showed indeed rather different seasonal patterns: Seasonal declines in fledging weights (Chapter 2, Figure 2.1) were comparable to other studies (Veen et al. 2010), but adult survival declined only for females while it increased for males (Chapter 2, Figure 2.2), and recruitment rates showed hardly any seasonal decline. I argue that the different fitness parameters need to be integrated to draw reliable conclusions about the fitness penalties of breeding late and the need for adaptation, thus using estimates based on fecundity- as well as viability-selection. Especially for species with long natal dispersal distances, selection differentials based on recruitment rates should be treated with care and should be complemented with calculations of selection differentials based on additional fitness parameters (adult survival, number of fledglings). New technology, which allows large-scale tracking of small birds, could help to improve fitness estimates further, because dispersal can be separated from mortality.

A major strength of the present study, compared to most previous work on mismatches, is our use of an experimental approach, while earlier studies were descriptive (Both et al. 2006, Goodenough, Hart & Stafford 2010). The manipulation of breeding dates for part of the population allowed me to disentangle effects of date *per se* from effects due to individual quality (Chapter 1, Figure 1.2). I found, that part of the variation in reproductive success over the season was indeed due to higher individual or territory quality of naturally early breeders (Chapter 2), and those quality effects contributed to the moderate seasonal declines in reproductive success. Studies which manipulated timing of breeding or food-supplemented broods were often conducted in single years, habitats and populations and, when repeated in another year, they often found strong year differences (Török et al. 2004; Verhulst, van Balen & Tinbergen 1995). Expanding such experimental manipulations to more years and

habitats will improve our understanding of the important links in an ecosystem, and how climate change affects them.

Manipulating the timing of breeding might also come with potential costs for the birds and this can result in biases on the outcome of such experiments, depending on the type of manipulation, e.g. prolonged incubation period in delayed birds (Verhulst & Nilsson 2008). In our study, we had no indication that prolonged incubation was related to high fitness costs, which would have biased our results towards stronger date effects (Chapter 2).

Trophic links differ between habitats

This thesis highlights the importance of habitat differences in trophic relationships and the need to study differences in resource use across habitats. In a comparative analysis (Chapter 3), I show that, in oak habitats, birds can increase the proportion of caterpillars in the nestling diet by breeding relatively early, while in other habitats there is no such relationship. Thus, mismatches with caterpillar peaks are mainly important in oak-dominated forests. Oak forests have a short and steep food peak, which varies strongly with spring temperature (Visser, Holleman & Gienapp 2006), while other forest types apparently exhibit lower, but more constant caterpillar supply, even in warm springs (Chapter 3). My findings show that birds breeding in oak habitats need higher phenotypic flexibility to match the food peak and are thus more susceptible to rapid increases in spring temperatures (Chapter 3, Figure 3.2). Especially in the experimental year 2009, we had clear support for this: the outbreak of geometrid caterpillars (most notably winter moth and mottled umber) resulted in early defoliation of the oaks in one of our pure oak stands. This happened so quickly that most caterpillars died from starvation before the flycatchers hatched. Although great tit broods were performing well, 10 out of 11 flycatcher nests died a few days after hatching, both in control and delay treatments, and food supplementation did not help. Apparently, no alternative prey was available that flycatchers could switch to.

Differences in seasonal patterns of caterpillar abundance, depending on tree species, have been described in single studies (Veen et al. 2010; Van Balen 1973; Southwood et al. 2005; Mägi et al. 2009). Those habitat differences regarding caterpillars are related to the different patterns of leaf-growth in tree species (Niemela & Haukioja 1982) and associated differences in life-cycles of caterpillar species: Oak trees produce fresh leaves only during a short period in spring, which leads to a steep peak of lepidopteran caterpillars ('chewing phytophages', Southwood et al. 2005) in spring. A typical caterpillar species which forages on fresh leaves of oak (and other deciduous) trees in spring, is the winter moth (*Operophtera brumata*/ssp., Visser & Holleman 2001). Other phytophages (e.g. miners, suckers or galls) on oak occur also later in the season, but those emerge in lower numbers and peak mostly in summer, after the breeding season of birds (Southwood et al. 2005). In comparison to oak

trees, other tree species, e.g. birch *Betula* ssp., continue shoot-growth and therefore provide fresh leaves for caterpillar species throughout spring (Niemela & Haukioja 1982). Also, on pine trees (*Pinus* ssp), larvae of *Panolis flammea* have a different life-cycle than winter moth, emerging only later in spring and thus providing food for birds later in the breeding season and after fledging of the young (van Balen 1973). In addition to *Lepidoptera* larvae and other phytophages on trees, caterpillars of a range of other (*Lepidoptera*) species occur on shrubs or grasses. The sampling of nestling diets using photo-cameras shows a large variety of *Lepidoptera* and *Hymenoptera* larvae (personal observation). I found that the abundance of caterpillars in the diet does not always match frass-fall data, as this data only captures abundance of tree-dwelling caterpillars (Chapter 6, Figure 6.3), while, especially in southern Sweden, parents collected many caterpillars from shrubs or grasses. Using high-resolution cameras for sampling nestling diets, prey items can often be identified to family or genus level, so that the associated habitat layer or host plant can be identified. Using this information, the important habitat features can be assessed and a more fine-scale habitat classification could be made in future studies, when studying causal links between birds and their prey.

My findings in chapter 3 clearly suggest that the mismatch hypothesis is only applicable to environments with a steep food peak during the breeding season and thus not to marsh habitats or coniferous woodlands, or for species that forage mainly on insect groups which increase throughout the season, like flying insects (Lundberg et al. 1981; Dunn et al. 2011; Both et al. 2010). Habitat differences likely explain the lack of correlations between caterpillar peaks and seasonal declines in breeding success in some studies (Eeva, Ryömä & Riihimäki 2005; Veen et al. 2010). However, it is interesting to note that the other delay and food supplementation study in pied flycatchers (Siikamäki 1998) was carried out in a non-oak habitat (probably containing other deciduous tree species, no data given on habitat type), without a supposed narrow caterpillar peak as we see it in oak habitats, whereas a clear decline in reproductive success was found that was due to food limitation in later broods (Siikamäki 1998). There is a strong need to take those habitat differences into account when investigating mismatches and adaptations, within and between species.

Late breeders were not food limited across habitats

Habitat differences in resource (caterpillar) use across populations were striking, but, surprisingly, I found no evidence that the fitness penalties of breeding late differed between habitats, within our study area (Chapter 2). There, even in oak habitat, late breeders were performing relatively well. Only in one year (2009), average fledgling weights were lower in oak, relative to other habitats. Oak forests are described as the preferred habitat in pied flycatchers (Lundberg & Alatalo 1992), but also showed the strongest population declines (Both et al. 2006). One explanation for these declines

could be that, in pure oak habitats, high bird densities require a close match with the caterpillar peak to avoid food limitation and thus fitness penalties of mistiming are high. In our study area, most habitat patches contained oak trees mixed with other tree species. In some oak-mixed patches, nest box occupancy rate of all species combined was close to 100%, while coniferous habitats often had lower occupancy rates. I did not explore in detail, if breeding densities were related to fitness penalties of late breeding. A study on pied flycatchers in Finland found stronger selection for early breeding at high densities (Ahola et al. 2012), while this was not found in a second study in the Netherlands (using the decline in clutch sizes, Both 2000). Mixed habitats might however generally contain a greater diversity of prey types and provide abundant food throughout the season, even at high densities, so that we could not detect strong fitness consequences of mistiming. Detailed information on habitat types has not been consistently reported in previous studies (e.g. Both et al. 2006), which makes studies hard to compare.

In our study area, I found no indication for food limitation of late broods during a food-supplementation experiment (Chapter 2), while a previous study did, using a similar set-up (Siikamäki 1998). The finding of no or little food limitation was present for all three years of the experiment, although the years differed in spring temperatures and caterpillar phenologies: 2009 was a warm year with an early and high peak, 2010 was cold with a late and low peak, and 2011 was a warm spring with an early but low peak (see Chapter 2, Figure 2.5). One may argue that only in 2011 one would have expected an effect of food being limiting for late breeders because birds were highly mistimed and caterpillars were scarce. However, also in this year we found little evidence for this. In all years, any seasonal declines in fitness parameters were rather related to (unknown) date effects other than food, or to the higher individual or territory quality of early breeders.

An apparent change from food limitation for late breeders in previous years, towards sufficient food abundance throughout the season, as the present results suggest, could have several explanations: food phenology changed locally, or birds have become more flexible in their prey choice, or birds shifted locally to breed in less seasonal habitat patches. There is no evidence that caterpillar peaks have become wider during previous warm years (between 1985-2004, Visser, Holleman & Gienapp 2006). Furthermore, little is known about long-term changes in the phenology of other prey types and whether overall food abundance increased. Rather, habitat quality generally deteriorated during recent climate change (Jiguet et al. 2007). Also more research is needed to investigate the birds' ability of using alternative prey types when caterpillars are scarce. It has to be recognized that pied flycatchers are rather flexible in their choice of nestling diets (Sanz 1998) and cope rather well with food limitations (Qvarnström et al. 2005), compared to other species like collared flycatchers (*Ficedula albicollis*), great tits or blue tits (Garcia-Navas & Sanz 2011).

Pied flycatchers can thus also profit from foraging on alternative arthropod groups like *Diptera*, *Coleoptera*, *Hymenoptera* or *Arachnida*. The phenology and abundance of

those groups differs from that of caterpillars. I showed, for example, that the abundance of flying insects increased throughout the season (Appendix Chapter 6, see also Lundberg 1981). Future work should include the study of resource use across prey taxa, related to prey abundance (Naef-Danzer et al. 2000) and prey quality, to identify potential limitations for birds.

Limited evidence for adaptive conditional dispersal and habitat shifts

Dispersal could become an increasingly important mechanism to facilitate adaptation of species to climate change, and the ability to disperse could reduce extinction risks (Le Galliard et al. 2012) and promote colonization of new environments (Benton & Bowler 2012). Using descriptive and experimental approaches, I studied dispersal on two scales: the frequent local movements of pied flycatchers within and between study plots (distances from 0 to 18 km), and the less frequent, but potentially influential movements of individuals into a distant population (550 km to the Northeast).

In chapter 4, I showed that, within our study area, pied flycatchers, tended to move away from oak habitat. This effect was mainly driven by females which also, on average, dispersed further away from the previous breeding locations in oak, compared to more philopatric males (Lundberg & Alatalo 1992). Conditional dispersal could thus result in habitat shifts, as a response to climate change, and this is corroborated by the finding of Both et al. (2006), that populations in early oak habitats declined. Such asymmetric dispersal into suitable habitat could facilitate adaptation to environmental changes (Kawecki & Holt 2002). In chapter 4, I did not find that dispersers preferentially moved into the less seasonal habitat. However, I also showed before (chapter 2), that fitness penalties did not differ between habitats. Thus, I suggest that birds did not respond directly to habitat type *per se* for their dispersal decision, but to other correlated parameters like breeding densities (Matthysen 2005). Females which dispersed further away, slightly improved their reproductive output, indicating an adaptive response (Chapter 4). Similar correlations of reproductive success with dispersal distances have been found before (e.g. Schaub & von Hirschheydt 2009; Eeva et al. 2008), but, across studies, there is little empirical evidence that environmental mismatches (e.g. with food peaks) affect dispersal behaviour (some evidence in a soil mite, Bowler & Benton 2009).

For short-lived species, conditional dispersal might be most beneficial if performed by first-year breeders (Greenwood 1980). I however did not find correlations of dispersal distance with birth habitat or birth date for recruiting offspring. Furthermore, recruits which dispersed further away did not advance their timing of breeding or move into alternative habitat (Chapter 4). Correlations of dispersal distances with potentially important parameters like timing or reproductive success were weak, although overall sample sizes in our study were high. This could be explained if individuals had already chosen the best breeding location for their

breeding phenotype (Edelaar, Siepielski & Clobert 2008). However, experimentally induced mismatches corroborated the previous findings: delayed breeding and food supplementation had no effect on dispersal distances. Fitness penalties of breeding late have been rather low during the years of this study (chapter 2), which might explain the weak responses: apparently, our induced mismatches did not increase fitness penalties enough, and thus, conditional dispersal as adaptive response is not expected.

Usually, oak/deciduous forests have been described as the preferred breeding habitat of pied flycatchers (Alatalo & Lundberg 1992). Only in hybrid zones of pied and collared flycatchers, pied flycatchers preferred coniferous over deciduous habitats (Saetre et al. 1999; Adamik & Bures 2007) and birds were coping well with those coniferous habitats (Veen et al. 2010). Our finding of greater dispersal distances in females, following reproduction in oak habitats (Chapter 4, Figure 4.1), might indicate that, on the long term, pied flycatchers might shift to occur mainly in the less seasonal, coniferous and other forest habitats. If this is an adaptive response to environmental conditions, climate change could change species distributions, and consequently ecosystem composition, because (key) species disappear, while new species might establish (Benton & Bowler 2012).

Garant et al. (2005) found in great tits, that differences in habitat quality affected settlement decisions of individuals depending on body mass, and that this lead to the evolutionary differentiation of body mass on small spatial scales. Thus, differential dispersal depending on habitat type could theoretically result in directional gene flow and thus in the evolution of certain traits, e.g. via selection for an earlier laying date. However, life-history traits like laying dates have generally low heritabilities (Sheldon, Kruuk & Merilä 2003), in contrast to a morphological trait like body size. It is therefore unclear if adaptation through directional gene flow could operate on such life-history traits and there is to date little empirical evidence in birds. For great tits, Postma & van Noordwijk (2005) found indeed that fine-scale differentiation in clutch size was mainly maintained by non-random dispersal, and Coltman (2005) suggested that differentiation through dispersal may be rather common, but difficult to detect.

New insights into the consequences of long-distance dispersal

Long-distance dispersal is notoriously difficult to study, but very interesting from the point of adaptation to large-scale environmental change. To avoid problems of non-random dispersal (Doligez & Pärt 2008), we developed a new set-up for translocating birds to a chosen breeding location, independent of the choice of the individual bird (Chapter 5). This method is therefore a very useful new tool for studying the fitness consequences of habitat choice in the wild. The set-up can be used to move birds across different spatial scales, between habitats, but also to simulate long-distance dispersal. This tool enabled us, for the first time, to study fitness consequences of long-

distance dispersal in pied flycatchers and thus evaluate the importance of this mechanism for adapting to climate change (Chapter 6). The expectation was that, if birds arrive too late at their former breeding site, they could profit from moving further to the North and reproducing at a location, where prey phenology is later. Although this seems to be an easy way of adapting to advancing phenologies, there may be a cost in terms of other traits becoming locally maladaptive at the new breeding location.

Our translocation experiment (Chapter 6) suggests that translocated females introduced their early breeding phenotype into the northern population and that maladaptation to other environmental parameters plays a minor role. The experiment can be considered as evidence that long-distance dispersers can successfully reproduce at a distant location. Such insights into the fitness consequences of long-distance dispersal are crucial, because they form the basis for predictions on the adaptive value of such a mechanism for coping with climate change. Our experiment also has implications for conservation efforts: For species which cannot adapt or disperse fast enough to keep up with climatic changes, assisted colonization has been suggested as a tool (Hoegh-Guldberg et al. 2008). One shortcoming of our experiment was, that spring temperatures in that year were below average values, while direct benefits of breeding early were only expected in a relatively warm year. Repeated translocations could capture the year-variation, but this was beyond the scope of this thesis. Furthermore, settlement success of our long-distance translocated birds was rather low, which hints at a potentially large cost of settling at a distant breeding location.

Large-scale movements to new breeding locations will only be a valid option for certain species: I propose that pied flycatchers are exceptionally suitable in this respect: as long-distance migrants, they have strong flight abilities, they are flexible in their choice of insect diets, and they seem to cope well with novel environments (Chapter 6). For a number of other species, like great tits, Marr, Keller & Arcese (2002) report disadvantages of immigrants relative to residents and emphasize the importance of site experience. More information on the properties of immigrants is thus needed and we show that this can be achieved by using new methods for tracking birds and novel set-ups for moving birds to new locations. We still do not know whether Southern birds breed earlier compared to Northern birds because they possess genes for breeding early, or whether this is a consequence of Southern birds being born earlier in spring (carry-over effect). Estimates of heritabilities and selection pressures of relevant traits will advance our understanding of this type of adaptations in the context of climate change.

Conclusions

Based on my findings in this thesis, I conclude that, currently, pied flycatchers cope relatively well with climate change, although they did not restore synchrony with the caterpillar peak. It is important to note that fitness penalties for late breeding varied

for the different fitness parameters, but were weak overall. As expected, I show that trophic links between birds and caterpillars consistently differ between habitat types. The most surprising result was, however, that late breeders in our study area were not food-limited and that this was independent of the type of breeding habitat. Apparently, pied flycatchers are able to rely on alternative prey, if caterpillars on trees are scarce. Currently, there is no fully convincing explanation why fitness penalties for late breeding have diminished again in recent years. Some of the previous population declines in oak habitats (Both et al. 2006; and increases in coniferous habitats, unpublished data) could however be explained by emigration from those habitats, which suggests that local mismatches affect both dispersal behaviour and population dynamics. The flexibility of pied flycatchers regarding diet choice and the ability to cope well with new breeding environments indicates that few limitations for conditional dispersal and habitat shifts exist, but conditional dispersal might be unnecessary because birds were rather well-adapted locally.

Other bird species, which are more specialized on breeding in habitats with a short food peak, which are inflexible in resource use, and which are constrained by their migratory schedules, will be more affected by trophic mismatches due to climate change. Even the closely related collared flycatcher could be affected much more, because that species is more specialized regarding its diet and habitat choice (Veen et al. 2010). Thus, although pied flycatchers seem to adapt at present, this may not be the case for many other long-distance migrants that are currently under great decline (Sanderson et al. 2006, Both et al. 2010).

Here, I point out three areas, to which future research efforts should be directed to:

1. We need to identify the cause of diminishing selection for early laying during the last years, despite on-going climate change, in pied flycatchers. For this aim, it is important to understand why the strength of selection for early laying often differs, depending on the fitness parameters it is calculated on (e.g. adult survival or recruitment rates). First, we need to explore temporal correlations of selection differentials with a range of ecological parameters. This should be followed up by manipulating correlated ecological parameters in the field, to pinpoint the responsible parameter(s). The use of animal models to estimate within-population genetic variance could reveal, if any micro-evolution in laying dates has been going on, which resulted in adaptation.
2. The resource use of (alternative) prey types should be investigated further, and across habitats, so that the importance of matching breeding with certain food sources can be estimated. Efforts should be made to quantify food abundance in the environment and how birds utilize those resources. Breeding densities might be important in this respect, because they might affect resource availability and competition for food.
3. More insight is needed into meta-population dynamics. Heterogeneous dispersal could be a key process for adaptation to climate change (Coltman 2005). The input of new genetic variation into populations, which could speed up micro-evolution,

depends on natural immigration rates, the origin of immigrants and the success of those immigrants (Benton & Bowler 2012). There is a need to develop new methods (e.g. stable isotope analysis, Hansson, Bensch & Hasselquist 2004) and conduct experiments which provide crucial information on those immigrants. This, together with the use of genomics, could improve our insight into gene flows and meta-population dynamics.

Currently, the major threat for pied flycatchers might not be mistiming due to climate warming, but the rapid habitat loss which is happening at their African wintering grounds (Sanderson et al. 2006, Pimm 2008). In general, interpreting the recent population declines in many long-distance migrants (Saino et al. 2011) needs to be done with care: declines likely not just result from reduced survival due to mistiming, but could also be related to other factors, like climatic conditions during wintering (Saether et al. 2003), wintering habitat quality (Norris et al. 2004), or emigration from former breeding areas. Some species currently seem well-adapted to their environments, but adaptations are not yet understood. Moreover, predicted rates of climate change until the end of this century are severe (IPCC 2007) and this will affect ecosystems dramatically (Thomas et al. 2004). It is totally unclear how birds will be coping with the forecasted rise in spring temperatures of around 4°C by the end of this century (Difffenbaugh & Field 2013). What research should do is to identify the important ecological links and life-history factors throughout the annual cycle of species and across the distribution range. This is needed in order to make predictions about the future persistence of species, habitat or range shifts, and extinction risks. The ability of species to disperse will be crucial for allowing those shifts and thus for reducing extinction risks (Kokko & Lopez-Sepulcre 2006, Travis & Dytham 2012).

