CHAPTER SEVENTEEN

Insufficient adaptation to climate change alters avian habitat quality and thereby changes habitat selection

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Before approaching the main theme of this chapter I want to start with some intriguing field observations that, by accident, set me on the track of investigating the effects of climate change on avian ecology. Checking nest-boxes is like having a birthday party: opening boxes is always a surprise. While tramping from box to box, my mind works in overdrive to find patterns. One such pattern that started to fascinate me was that pied flycatchers *Ficedula hypoleuca* seem to prefer nest-boxes occupied by tits. Flycatchers are long-distance migrants that normally arrive when the tits already have started nest-building, and often have started egg-laying as well. Upon the flycatcher's arrival, many boxes are still empty, whereas others are occupied by various tit species. Still, flycatchers consistently prefer the boxes containing nest material of tits. I have recorded this pattern over many years and in several areas (unpublished data), so I truly believe this pattern is real. This is not just a minor fact of life, but a potentially deadly adventure for a pied flycatcher. Each year we find – mostly male – flycatchers killed in nest-boxes, and often these nest-boxes had been occupied by great tits *Parus major* (Slagsvold, 1975; Ahola *et al.*, 2007). It occasionally happens that great tits are incubating on extremely smelly nests, because a decomposing pied flycatcher had been included in the nest material. A closer look at the killed flycatchers further reveals that – more often than not – the brain has been eaten, a high-energy meal for an egg-laying bird early in the season. The attraction of already occupied nest-boxes for arriving pied flycatchers must have an enormous advantage, given its frequency and potentially lethal outcome.

Habitat selection is likely to be the answer as to why pied flycatchers prefer nest-boxes already occupied by tits (Forsman *et al.*, 2002; Seppanen and Forsman, 2007). Pied flycatchers are in a hurry and have little time upon arrival to figure out what the best breeding sites are. Spring develops quickly, and flycatchers have to race the clock to be able to profit from the narrow peak in caterpillar numbers in early spring. Gathering information on habitat quality, however, takes time, and a short-cut could be to rely on information provided by other species with near-similar ecological requirements. The

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reason why flycatchers prefer occupied nest-boxes thus may be – via information indirectly provided by tits – related to food availability, safety from predators or other important habitat features. The associated benefits clearly outweigh the chance of being killed. In the year 2000 I set out to test this idea with a simple experiment. Just before the flycatchers arrived in spring, I put moss (tit nesting material) in random nest-boxes, and kept others empty. It was an exceptionally warm April, and I did not want to start the experiment too early in order not to interfere with the tits' breeding behaviour. Therefore I waited for the first male pied flycatchers to arrive. Despite the high local temperatures, pied flycatchers arrived exceptionally late: I observed the first male on 20 April (normally 10 April), and set out to do the experiment on April 23. To my surprise, the first pied flycatcher had already an almost completely built nest! Three days after arrival of the first male, he got paired, his female immediately had built a nest and the first egg was laid on April 26! This high-speed start of the season came as a surprise, and was unlike anything I had experienced in previous years. Late arrival and early start of breeding have kept me busy ever since, whilst examining how climate change has affected the annual cycle of long-distance migrants. Interestingly, April layings of pied flycatchers in the Netherlands are no longer out of the ordinary.

In this chapter my aim is to explore how climate change affects habitats and, by inference, habitat selection of birds. Of special interest is the timing of breeding in birds relative to the timing of other trophic levels. How individuals gather information about where to settle in anticipation of climate change is an exciting new line of research, which falls outside the scope of the present study. I do acknowledge that the view presented in this chapter is highly biased towards phenology and how birds match their own breeding time with the seasonality of their environment. Other effects of climate change on avian habitat quality and use could be (at least as) important in many systems, depending on features of both the habitat and the bird species involved. One such process is the interaction between birds and their parasites, which may alter habitat suitability through changes in parasite prevalence and phenology, or range changes of parasites and/or birds as a result of climate change (see review in Merino and Møller, 2010). Also the structure of communities may change, through a differential effect of climatic variables on different (groups of) species and hence shifting the competitive balance and thereby affecting habitat suitability (Brotons and Jiguet, 2010). This could be through a change in migratory behaviour (Lehikoinen and Sparks, 2010), or due to an increase in winter survival for resident species (Robinson *et al.*, 2007), leading to a shifting balance between resident and migrant species competing for the same resources (Böhning-Gaese and Lemoine, 2004; Ahola *et al.*, 2007). With all processes involved we need to address the question of whether the observed adjustments are sufficient given the plethora of (possible) changes in the habitat and, if not, how birds could either adjust their phenotypes or their habitat selection to maintain population size. The examples given in this chapter all relate to these major questions.

Seasonally varying habitats: a matter of timing

Almost all habitats change through time, seasonally as well as over the years. This change is epitomised by vegetation structure, with its associated cycles of leafing, flowering and fruiting and, in the long run, changes in composition and density. Profound transformations of the environment, impact every living creature from bottom to top and vice versa. My research is mainly focused on the effect of seasonal variations in food availability on birds. Species that rely on seasonally fluctuating food sources have to change their diet, or switch habitat in order to find sufficient food to survive. Seasonal changes in diet have been observed in a wide range of birds, and often require profound changes in the digestive system. Bearded tits *Panurus biarmicus*, for example, switch from an insectivorous diet in summer to a granivorous diet in winter (seeds), only possible by changing their digestive tract (Spitzer, 1972). Other species do not change their diet, and have to migrate to a different habitat to survive periods of food shortage. Many, mainly insectivorous, long-distance migrants migrate from their temperate breeding habitats to tropical winter habitats.

The seasonality in habitats weighs heavily on important life-history decisions. To a large extent, the timing of life-history decisions determines fitness of individual birds, especially if habitats are strongly seasonal. Important decisions include the timing of breeding, whether birds should breed more than once in a season, how long they care for their offspring, when they moult, whether and when to migrate to distant wintering areas, and when to return to the breeding grounds (Perrins, 1970; Drent, 2006). Each decision is intricately linked with others, and has fitness consequences determined by the phenology of the habitat. Raising chicks before, during or after the food peak clearly resonates in number and condition of offspring. The timing of the annual cycle of birds thus should be adapted to the seasonality of the habitats they use. Changes in seasonality are expected to pose problems if birds cannot adjust to novel circumstances.

Climate change affects the timing of different components within the ecosystem. This effect is not always synchronous across different species, and therefore birds can get out of sync with vital resources such as food. The best examples come from long-term nest-box studies on forest-dwelling insectivorous passerines, mainly tits (*Paridae*) and *Ficedula* flycatchers. To a large extent, both groups of species feed their nestlings on caterpillars, and hence are dependent on the narrow but high peak in caterpillar abundance in forest ecosystems. The long-term studies showed that since about 1980 laying dates in many populations have advanced (Winkel and Hudde, 1997; Visser *et al.*, 1998; McCleery and Perrins, 1998; Slater, 1999), although responses differed between populations across Europe (Visser *et al.*, 2003; Both *et al.*, 2004). For collared *Ficedula albicollis* and pied flycatchers, the rate of advance was strongly correlated with the rate of local spring warming. The larger advancements were recorded in areas where it became warmer, suggesting that climate change indeed played an important role (Both *et al.*, 2004). Data on the timing of the caterpillar peak in a Dutch habitat showed that caterpillars advanced much more than annual median hatching dates of tit species and flycatchers (Fig. 17.1; Both *et al.*, 2009). Probably as a consequence, the fitness penalty of late breeding increased over the years, as late nests became progressively more mismatched with the food peak (Visser *et al.*, 1998; Both and Visser, 2001; Visser *et al.*, 2006). The breeding habitat for these species thus became less suitable over time. In contrast, the great tit population of Wytham Woods (near Oxford, UK) showed the opposite: the laying date of the birds advanced

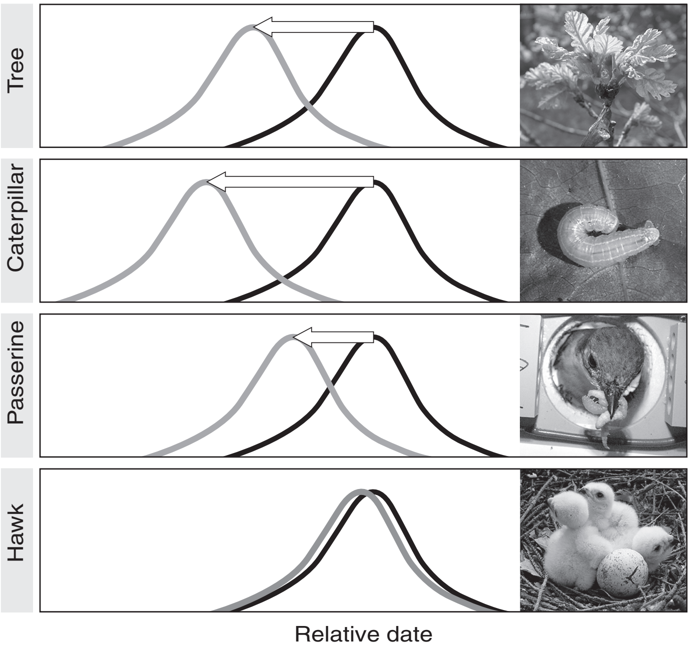

Figure 17.1 Relative changes in timing of four trophic levels in a Dutch forest shown from top to bottom: oak budburst, caterpillar availability, passerine hatching dates, sparrowhawk hatching dates. Dark curves represent the relative timing of the trophic levels around 1985, and the grey curves at about 2005. Caterpillars changed more than budburst, passerines changed less than their caterpillar prey and sparrowhawks did not change, whereas their passerine prey did change phenology. After Both *et al.* (2009). Photos: C. Both, M.E. Visser and R.G. Bijlsma.

more than the caterpillar peak, and the average bird became better timed with the food peak (Cresswell and McCleery, 2003; Charmantier *et al.*, 2008). In the Czech Republic, advancements of laying dates in collared flycatcher and great tit were very much in synchrony with the change in the timing of the caterpillar peak between 1961–2001 (Bauer *et al.*, 2010), again showing enormous variation between geographic areas. Why the mismatches between caterpillars and birds increased in the Dutch breeding habitat, improved in the English breeding habitat and remained unaffected in the Czech habitat is not well understood, and shows that effects of climate change differ depending on either subtle variation between habitats or changes in the temporal structure of temperature change within seasons.

An advancement of the food peak in spring could lower habitat quality for birds but, in contrast, other changes may be favourable. For example, Dutch tits and flycatchers may profit from a reduction in post-fledging predation, as the breeding phenology of one of their main predators was even less affected by increased spring temperatures (Both *et al.*, 2009). At present, most tits and flycatchers fledge well in advance of the peak food demand of sparrowhawks *Accipiter nisus* (Fig. 17.1). The process of unequal trophic responses may thus also be beneficial if birds escape to some extent the brunt of predation. Nest predation is another important determinant of reproductive success (Martin, 1995), but long-term data are scarce and correlations with climate change unexplored (Wesołowski and Maziarz, 2009; Wesołowski *et al.*, 2009). Changing conditions, climatic or otherwise, are likely to also affect the abundance of nest predators (either positively or negatively), with effects on habitat choice and abundance of prey species. In this respect, the interaction between mast-seeding trees, rodents (as seed- and nest-predators) and ground-breeding passerines springs to mind (Wesołowski *et al.*, 2009). Masting frequency of trees like beech (*Fagus sylvatica*) is related to summer temperatures, and has increased over the years (Overgaard *et al.*, 2007). Overwinter survival of rodents, in its turn, is positively affected by mast seeding (Schmidt and Ostfeld, 2008). As a result, birds breeding after high mast years are confronted with high numbers of rodents, which could reduce nest success and post-fledging survival via predation (Schmidt *et al.*, 2008), or even force birds into other habitats (Wesołowski *et al.*, 2009). Climate-induced changes in one component of the habitat (increased frequency of mast seeding) could thus have cascading effects via an increase in the frequency of nest predation by rodents, finally leading to more years with a lowered breeding success.

Differential changes among habitats

Habitats may differ in how they are affected by climate change and, depending on ecology, how birds respond. One of the few examples, showing habitat-related differences in population trends of pied flycatchers, comes from the

Netherlands. Nest-box monitoring showed that in deciduous (oak) stands on fertile soils the pied flycatcher population declined strongly from the late 1980s onwards, whereas flycatchers breeding in coniferous and mixed forests were still thriving (Fig. 17.2 and Visser *et al.*, 2004). In an attempt to explain the variable patterns among habitats, we measured the timing of the caterpillar peak in nine study plots, expecting populations to decline most strongly in areas with an early food peak as opposed to areas with a more extended food peak. This was precisely what we found: population trends were strongly negative in areas with an early food peak and no change occurred in areas with a late food peak (Both *et al.*, 2006). Furthermore, in areas with an early food peak, breeding dates of birds responded least to annual variations in temperature, probably because the birds in these areas were already

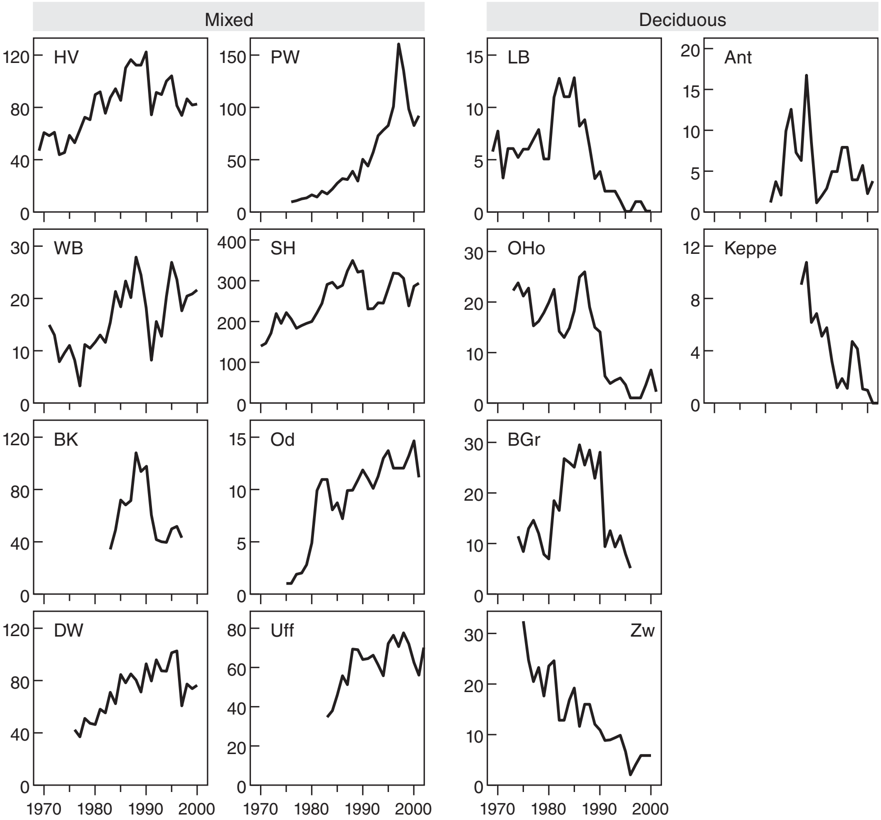

Figure 17.2 Population trends of nest-box populations of pied flycatchers across the Netherlands and northern Belgium in relation to forest habitat type. Until the late 1980s most populations grew as part of a general range expansion from east to west in the Netherlands. Thereafter, populations showed markedly different trends, depending on habitat type. Abbreviations refer to different study plots.

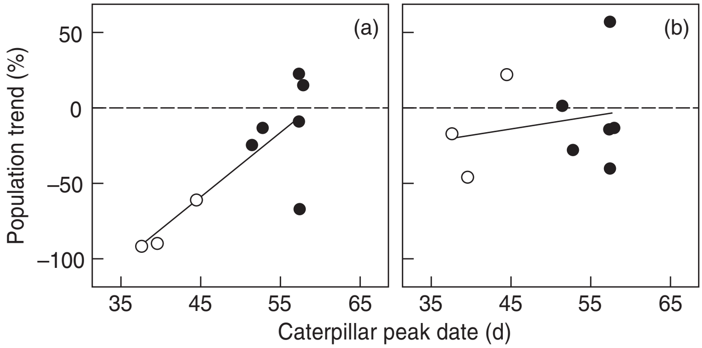

Figure 17.3 Population trends of Dutch nest-box populations of pied flycatchers (a) and great tits (b) in relation to the local date of the caterpillar peak in 2003. Population trends are expressed as the percentage change between 1983 and 2003. Open dots are deciduous habitats, filled dots mixed deciduous-coniferous habitats. Caterpillar peaks are in all cases measured under oak. After Both *et al.* (2006).

performing at the very limits of early breeding, but even so, missed the caterpillar peak and had to make do with the descending part of the food cycle. It is not likely that these areas with early food peaks had deteriorated in overall quality, because population trends of local great tits were unrelated to the date of the food peak (Fig. 17.3), and absolute peak densities of caterpillars were highest in areas with the earliest food peaks (Both *et al.*, 2006).

Interestingly, pied flycatchers are known to prefer deciduous forest over coniferous forest (Lundberg and Alatalo, 1992), and also normally reproduce better in deciduous forest (Siikamäki, 1995). We have no direct data showing that the decline in deciduous forests was caused by reduced reproductive success or by dispersal from purely deciduous to mixed and coniferous forests. In Spain, reproductive success of pied flycatchers in oak forests has declined strongly over the last decades, possibly due to an increased mismatch with the food (Sanz *et al.*, 2003). Flycatchers feed their chicks a rather diverse diet, depending on both habitat (Sanz, 1998), and timing of breeding. Early birds are known to feed their chicks mostly with caterpillars, and as caterpillar abundance drops with advancing season, so does the proportion of caterpillars in the diet. This change in diet is reflected in recruitment rates of chicks, which decline the later the chicks are born (Both, 2010b). The seasonal decline in reproductive success is typical for pied flycatchers, and for most other bird species (Smith and Moore, 2005; Verhulst and Nilsson, 2008), and indeed is caused by the seasonal decline in food abundance (Siikamäki, 1998). The reliance on caterpillars in oak forests was particularly pressed upon us when mass mortality of chicks occurred in the spring of 2009. In one of our study areas caterpillars were so abundant that they defoliated the trees just after budburst, and most caterpillars starved before the flycatcher eggs had hatched. The chicks in ten out of eleven nests all died shortly after hatching, despite the high food density earlier in the season. Tits that bred ten days earlier were hardly affected.

So far we have seen that a species like the pied flycatcher has not responded sufficiently to climate change, because its breeding phenology no longer matches the phenology of its main food. The reason why these birds got out of sync with their main food is pre-destined by their annual cycle. These birds are long-distance migrants, wintering in sub-Saharan West Africa. The evidence from western and central Europe shows that at least the males have not advanced their arrival time during the last three decades (Both *et al.*, 2005; Hüppop and Winkel, 2006). Also, for females there is some evidence that they have not advanced arrival either. The advance in breeding dates is therefore mostly due to a reduction in the interval between arrival and the start of breeding (Both and Visser, 2001). The inflexibility in arrival time has been explained by a rather rigid and photoperiodically controlled annual cycle (Gwinner, 1996; Both and Visser, 2001; Gwinner and Helm, 2003). New evidence shows, however, that pied flycatchers breeding in western and central Europe have advanced their spring migration passage through North Africa, but this advance has not led to earlier arrival at the breeding grounds because environmental constraints in southern Europe preclude uninterrupted continuation of migration (Both, 2010a). Pied flycatchers, and many other long-distance migrants that breed in more northerly regions have, however, advanced their arrival time (Ahola *et al.*, 2004; Lehikoinen *et al.*, 2004; Marra *et al.*, 2005; Jonzén *et al.*, 2006; Rubolini *et al.*, 2007), which is explained by their advanced timing of migration in response to warming temperatures in southern and central Europe during the migration window (Ahola *et al.*, 2004; Both and te Marvelde, 2007). Even so, long-distance migrants generally have responded less to warming with their arrival dates than short-distance migrants (Lehikoinen *et al.*, 2004; Rubolini *et al.*, 2007), and whether they show a response mostly depends on whether conditions en route at the time of travelling have improved.

The limited change in migration timing of long-distance migrants in comparison to the advanced phenology of their breeding habitats makes them more vulnerable to mismatches with food abundance than residents and short-distance migrants. Within migrants across Europe, species with the smallest advancement in spring arrival had declined most by the end of the twentieth century (Møller *et al.*, 2008). If a trophic mismatch with food availability for the offspring lies at the heart of the matter, we expect this to differ between habitats, depending on how food availability changes throughout the season. Fitness penalties associated with breeding at exactly the right time are most severe when the timing is out of sync. Indeed, we found evidence for habitat differences in long-term population trends of bird species that were consistent with the notion of increased trophic mismatches mainly affecting long-distance migrants in more seasonal habitats (Both *et al.*, 2010). Comparing Dutch forests and marshlands revealed narrow food peaks for insectivorous birds in the former, whereas marshland had an extended period of insect abundance over much of the spring and summer. All long-distance migrants in the forest declined; short-distance migrants and residents did not show systematic declines (Fig. 17.4a). In the less seasonal marshlands we found no systematic decline in long-distance migrants, nor any difference in trends between groups with different migration strategy. That timing relative to the food peak could be a reason for the decline in forest migrants was suggested by the strong correlation between arrival date and population trend: the later a species arrived in spring, the more it declined (Fig. 17.4c). The habitat differences in trends were also found in some generalist migratory species: they declined more in forest and increased in numbers in marshland (Fig. 17.4b). As with the habitat-related population trends of pied flycatchers, generalist species may have changed their habitat preference from forest to marsh. If so, this may have been triggered by marshland becoming better in comparison to forest, which could be due to forests deteriorating, marshlands improving, or both. Because the specialised forest species also declined, and often steeply so (up to 85% decline in the icterine warbler *Hippolais icterina*), there is reason to believe that for these species the forest habitat must have lost much of its attraction. In contrast, many resident and short-distance migrants, which generally breed earlier than long-distance migrants, have shown increases in the forest habitat, suggesting that the habitat per se did not decline in quality (Both *et al.*, 2010). It is unlikely that these effects were strongly mediated through habitat change in the winter: also within generalist species the decline was much stronger in the forest compared to the marsh. Changes in habitat suitability caused by differential phenological responses resulting from climate change are in general expected especially in habitats with strong seasonality, and for species that are least flexible in adjusting their phenology to changes at other trophic levels.

Dispersal as adaptation to climate change

If habitats become less suitable because birds increasingly miss the local food peak, then dispersal to areas where the food peak matches their breeding phenology is an option. This might take place on a small spatial scale, as was discussed for pied flycatchers that *could* choose between nearby areas differing in food peak dates. But dispersal on larger spatial scales is equally possible: if Dutch pied flycatchers arrive too late on their former breeding grounds, why then not continue migration to more northerly sites? Their migration speed is much higher than the ‘speed’ with which spring moves northwards, and by

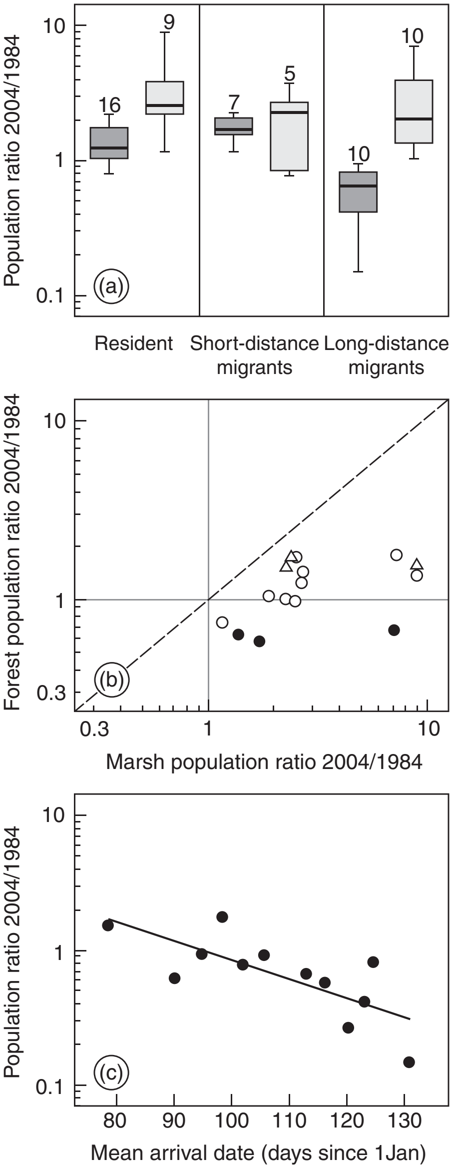

Figure 17.4 (a) Population trends of passerines in Dutch forests and marshlands between 1984 and 2004 for species with different migration behaviour. Results GLM: interaction habitat*migration status: $F_{2,51} = 6.16$, $p = 0.004$ (dark boxes: forest, pale boxes: marsh; numbers refer to number of species). (b) Within-species comparison of population trends in forests and marshes, showing that within species long-distance migrants decline stronger in forests than in marshes (open triangles: residents, open circles: short-distance migrants, filled circles: long-distance migrants). GLM: dependent variable – forest growth rate, explanatory variables: marsh growth rate: $F_{1,11} = 7.08$, $p = 0.022$, migration status: $F_{2,11} = 18.49$, $p < 0.001$, interaction: $F_{2,9} = 0.82$, $p = 0.47$. (c) Population trends of migratory passerines living in forests and their spring arrival date at the breeding grounds. Later arriving species declined most (GLM: mean arrival date: $F_{1,10} = 12.41$, $p = 0.006$). Population trends are expressed as the ratio of the densities present in 2004 relative to 1984, which is based on the annual population growth rates (1 = stable, 0.1 is a 90% decline, 10 is a tenfold increase). Population trends are from the Dutch Breeding Bird Monitoring Programme. Arrival data are based on the first three males arriving annually at a study site in Drenthe (northern Netherlands). After Both *et al.* (2010).

selecting a more northerly located breeding site they should be able to restore the match between their own phenology and the phenology of chick food (Fig. 17.5). Evidence for directional dispersal in response to phenological mismatches is non-existent, and data on long-distance dispersal are generally mostly anecdotal. Using stable isotope ratios from feathers moulted in the

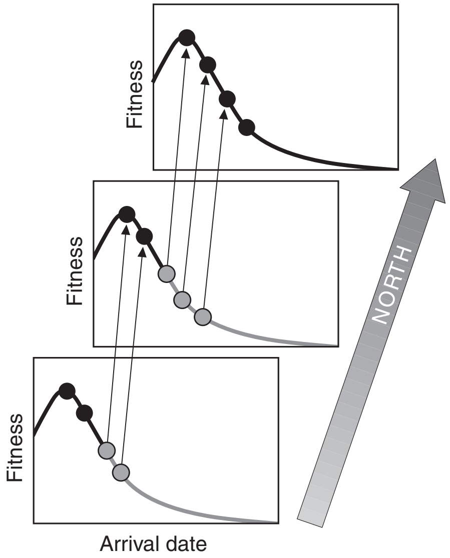

Figure 17.5 Hypothetical changes in fitness consequences of breeding date at different latitudes, and how birds may move depending on their timing of arrival. Within each area, the curve gives the hypothetical change in fitness over the date. The black part could be the realised curve, because late birds may prefer to move northwards (arrows from grey to black symbols), rather than breed too late relative to the phenology in a southern area. If birds had complete freedom to move without costs, one would expect within areas only a narrow peak of arrival and laying dates, and no decline in fitness with date.

previous breeding season could allow such long-distance dispersal to be detected (Hobson *et al.*, 2004; Hobson, 2005; Studds *et al.*, 2008). The hydrogen/deuterium ratio, in particular, changes with latitude, and therefore could be used to pinpoint the breeding/natal origin of immigrant birds. The expectation would be that in warmer years, individuals disperse more often to higher latitudes, and that these immigrants also breed earlier than the philopatric individuals at these places.

It is an alluring idea that birds could disperse to areas with a better phenological match, but in practice this may have attendant difficulties. It is important to make a distinction between the importance for individuals to improve their reproductive success by dispersing, and the importance it could have for the evolutionary dynamics of local adaptation. To begin with the second point, the movement of a rather small number of individuals to other populations may introduce new genetic material on which selection can act, allowing evolutionary change. Migratory birds that do breed more to the north not only breed later in spring, but also migrate later from their wintering sites (Bell, 1996; Studds *et al.*, 2008; Langin *et al.*, 2009; Both, 2010a). If this latitudinal variation in migration time between breeding populations has a genetic background (Pulido *et al.*, 2001; Pulido and Berthold, 2004; Pulido, 2007), individuals dispersing to more northern breeding populations could introduce genes for earlier migration. This could have a selective advantage, as climate change advances the phenology of other parts of the ecosystem. Thus, if the population in which these new genes are introduced, is also mismatched with the phenology of main food sources, the immigrants bring genes for earlier arrival and earlier breeding, and therefore have a selective premium.

Any advantage, however, depends on how well these immigrants perform relative to the original population. In other words, how important local adaptation is with respect to other heritable traits and local knowledge of the area for successful breeding. In general, local residents perform better than immigrants (Bensch *et al.*, 1998; reviewed in Marr *et al.*, 2002), although in inbred populations immigrants may entail a fitness advantage (Marr *et al.*, 2002). Interestingly, in the example of the song sparrows *Melospiza melodia* of Mandarte Island, immigrants had higher fitness in this inbred population, but their descendants had much lower fitness, which was attributed to their lack of locally adapted gene-complexes (Marr *et al.*, 2002). Philopatric individuals could have higher fitness because they have the residents' advantage of familiarity with the area, and they have lower costs in searching for important resources like nest sites (Parn *et al.*, 2009). Several studies found that immigrant males performed worse than philopatric males, whereas no difference was found among females (Bensch *et al.*, 1998; Parn *et al.*, 2009). This suggests that local experience may have a larger effect on immigrant fitness than local genetic adaptation.

As far as I know there are no studies examining fitness consequences of long-distance dispersers, because the origin of most dispersers is unknown, and most likely the majority originates from nearby sites. In contrast to short-distance dispersal, long-distance dispersers may in fact perform more poorly because they lack locally adapted genes. Long-distance dispersers could introduce new genes for earlier migration that allow a population to adapt to advances in the phenology of their habitat but, conversely, these immigrants may also have genes that are disadvantageous in their new breeding area. The success from an evolutionary perspective will evidently depend on the balance between such advantages and disadvantages, and translocation experiments are needed to examine this balance for immigrating individuals.

Another problem may arise from the spatial variation in phenology changes across the breeding areas. Whereas Dutch birds have become mismatched with their primary food source, Swedish birds probably have not, because spring temperatures did not rise so steeply there (Both *et al.*, 2004; Both and te Marvelde, 2007). In fact, if immigrants of southern origin arrive in these more northern places before the arrival of the philopatric individuals, they may encounter detrimental ecological circumstances because it is too cold for most insects to be active, and hence insectivorous birds may starve (Møller, 1994; Brown and Brown, 2000; Newton, 2007). Furthermore, in these more northern areas long-distance migrants arrive with larger body stores as an insurance against more adverse circumstances at arrival (Sandberg and Moore, 1996). This means that birds aiming to continue migration to more northern areas should obtain these stores before moving on.

The logic of latitudinal dispersal as an adaptation to climate change may be appealing, but in reality it may have drawbacks. There is abundant evidence that the decline in reproductive success over the season is a general phenomenon operating in the absence of climate change that is related to late birds being generally mismatched with the local food peak (Lack, 1966; Siikamäki, 1998; Charmantier *et al.*, 2008; Verhulst and Nilsson, 2008). Late arriving and late breeding individuals with poor success continue to persist in populations (Fig. 17.5), whereas (especially in migratory species) they also could have moved to a more northerly site and bred there in synchrony with the food peak. This suggests that the costs of continuation of migration must be rather high. However, there is some compelling evidence for latitudinal (or altitudinal) dispersal related to timing of spring migration from North America. American redstarts *Setophaga ruticilla* that spent the winter in the richest territories departed first in spring and subsequently selected breeding areas to the south of areas where they were born the previous year. In contrast, individuals wintering in low-quality habitat departed later, and tended to disperse to more northerly areas relative to their natal site (Studds *et al.*, 2008). Within the same breeding habitat, redstarts that had wintered in high-quality habitat arrived earlier in spring, bred earlier and hence fledged more offspring than those from low-quality winter habitat (Norris *et al.*, 2004). Thus, although the data on natal dispersal for this species suggested that birds can track the phenology of their breeding areas relative to their own departure date, it seems that many birds wintering in low-quality habitat should breed even further to the north in order to have timed their breeding season optimally. Their failure to do so suggests that the costs of dispersal could be too high, and/or that fitness in more southerly breeding areas is generally higher than in more northerly areas.

Habitat choice and local adaptation

Although we have little direct evidence that birds perform latitudinal dispersal to adapt to climate change, how much evidence is there in general that locally maladapted individuals show higher dispersal tendencies? The first problem we encounter here is how to define locally maladapted. Here I assume that young that grow poorly and/or hatch late in the season relative to the local food phenology are less well tuned to the local environment than other young, and therefore consider them locally maladapted. The question is whether these young are more likely to disperse to other areas? If this is so, the next question is whether these individuals are excluded from the better sites where they were born and therefore are ‘forced’ to disperse, or whether they disperse to areas that fit their needs better. Then we would expect that dispersal does indeed improve their fitness.

A number of studies have shown that young fledged in poor condition are more likely to disperse (Verhulst *et al.*, 1997; Tinbergen, 2005), and that individuals born late in the season disperse more (Pärt, 1990; Hansson *et al.*, 2002). However, examples for opposite patterns are available as well; sometimes early born fledglings disperse further, especially if in low condition (Altwegg *et al.*, 2000), or individuals in good condition can disperse more (Tilgar *et al.*, 2010), and date effects are not always found (Verhulst *et al.*, 1997). Most of these studies involve correlations between dispersal propensity/distance and phenotypic traits, not knowing the causes of individual variation and their effect on dispersal (but see Tinbergen, 2005). There are no studies that specifically addressed whether it is the locally maladapted individuals that disperse, which then also should show that these individuals are performing better in other habitats.

Costs and benefits of dispersal are not easily measured, especially because individuals that successfully immigrated into a population are normally compared with philopatric individuals, without taking the cost into account of finding and establishing a breeding territory elsewhere (Marr *et al.*, 2002; Møller *et al.*, 2006). Furthermore, studies of fitness consequences rarely measure all fitness components simultaneously, and again are mostly correlative (Doligez and Pärt, 2008). The fitness consequences of dispersal are variable when single fitness components are considered, but 8 out of 11 studies examining life-time reproductive success reported a decline in fitness of dispersing individuals of at least one sex (Doligez and Pärt, 2008). This suggests that dispersal is generally disadvantageous, but these fitness costs may be overestimated because dispersal tendency could have a genetic basis, and therefore young of dispersing individuals leave the study population more often, discounting the fitness of the dispersal genotype (Doligez and Pärt, 2008; Doligez *et al.*, 2009). Even if the fitness of dispersing individuals is generally lower, it still may be that for individuals that do disperse, their fitness is higher at the site of immigration, than at the natal site. Furthermore, there is the possibility that also for philopatric individuals, fitness is higher at another place, and the only way to discriminate these effects is by forcing individuals to disperse to another site, and measure the subsequent fitness consequences.

In our pied flycatcher study we found that chicks born later in the season dispersed further, which was even more pronounced in areas with an early tree phenology (Fig. 17.6). This suggests that young disperse more widely if they are locally maladapted with their hatching date to the local food peak, and therefore they grow up under low food conditions. For this reason one has to be cautious in interpreting trends towards higher local fitness penalties of breeding late as a maladaptive response to climate change (Both and Visser, 2001). Increased selection for early breeding may indeed even reduce local fitness (Charmantier *et al.*, 2008), but these changes in fitness consequences

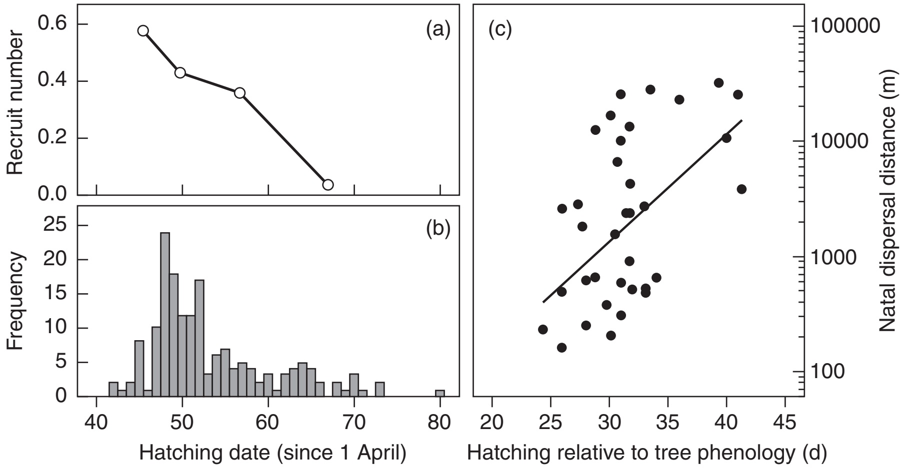

Figure 17.6 Effect of hatching date on local fitness (number of local recruits) (a) and natal dispersal distance (c) of pied flycatchers during the 2007 breeding season in Drenthe, the Netherlands. (b) gives the frequency distribution of hatching dates during this year. In 2007 the caterpillar peak was exceptionally early, with the peak date at 4 May. In (a) for each 25% percentile of hatching dates the mean number of recruits per brood is given (*y*-axis), and the mean hatch date for this group (*x*-axis). The *x*-axis in (c) gives the number of days between local budburst and hatching: higher values refer to larger asynchrony. Unpublished data.

are difficult to estimate if dispersal also changes at the same time, and especially late born young emigrate more due to their locally maladapted phenotype. The increased fitness penalty of breeding late could thus also partly be an adaptive response, because late young disperse to other habitats to which they are better adapted.

At this moment it is impossible to evaluate the different habitat selection options that birds face in order to successfully adjust their timing of breeding when they arrive too late to profit from the local food peak. Fitness evaluations can only be done if we are able to track long-distance dispersal (e.g. by using stable isotopes, Hobson, 2005) and relate this to the timing of the annual cycle. It also requires manipulation of individual birds, to force them to breed at other (more northerly) sites and compare their breeding success to that of birds breeding in their familiar area. Although this seems a daunting task for most species, we have successfully translocated pairs of pied flycatchers to other breeding sites where they eventually reproduced successfully under natural conditions (Burger and Both, 2011). This experimental setup allows the study of fitness consequences of alternative breeding sites, including the effects of unfamiliarity with the local habitat. The next step would be to perform this experiment, including controls, over longer distances: do birds translocated to more northerly breeding areas breed earlier than local birds, and what is their reproductive success in comparison to local, non-manipulated birds? For dispersal to be advantageous, and mistiming occurring at both sites, we expect translocated birds of southern origin to breed earlier at the northern release site than local birds, and to reproduce better than the controls in both capture and release sites. This result would indicate that dispersal is a viable option for adaptation to mismatched phenology resulting from climate change. The alternative would be that translocated birds perform worse than control birds, which would strongly suggest that long-distance dispersal may not be an easy way to adapt to climate change.

The evolutionary potential of long-distance dispersal not only depends on the fitness consequences for dispersers, but also on the timing of arrival and breeding being heritable. Evidence for additive genetic inheritance of laying date within populations is available for several bird species (van Noordwijk, 1984; Sheldon *et al.*, 2003), but it is not always found (Both and Visser, 2001). Within-population genetic variation, together with the among-population variation in laying date, especially along a latitudinal gradient (Sanz, 1997), would suggest that birds in the north breed later than more southerly breeding birds because they are genetically programmed to do so. For great tits there is evidence that, given exactly the same aviary conditions, individuals of southern origin do indeed breed at shorter photoperiods than individuals of northern origin (Silverin *et al.*, 1993); this difference in photoperiodic response could well have a genetic basis. For pied flycatchers, we found that the timing of spring migration through North Africa was related to latitude, but also to birth date; these effects interacted in a complicated way. In western Europe birth date had a clear positive effect on migration date, but the effect was reversed in northern Europe, where later-born individuals migrated earlier through North Africa in spring (Both, 2010a). As a potential mechanism I hypothesised that photoperiod at birth sets the individual annual clock, and birds from more southern origins (west Europe) are born before the longest day, and thus experience longer days the later they are born (Both, 2010a). For northern Europe the reverse is true: virtually all young are born after the solstice, and hence the later born birds experience shorter photoperiods. This possible effect of photoperiod at birth on annual timing has some experimental support (Coppack *et al.*, 2001), but requires further investigation. It is important in this context because if birds do disperse to more northerly sites, and the timing of the annual cycle is mostly determined by environmental conditions at the natal site, the young of these dispersers may not behave differently from the original birds at this site (apart from hatching earlier in the season). The phenotypic effect of birth date, via photoperiod on the timing of the annual cycle, may be a nice adaptation to breeding at different latitudes, and also to allow earlier migration, arrival and breeding if phenology changes directionally. But at the same time it may hamper (genetic) adaptation to changed circumstances by latitudinal dispersal, because the young of the dispersers may not be phenotypically very different from the local population.

Concluding remarks and future directions

Climate change has multiple effects on the suitability of habitats for bird species, and the change in phenology of essential resources for important life stages of birds has been emphasised here. For some bird species there is clear proof that the phenology of their food is changing at a different pace than the timing of breeding, but examples of both compensatory timing and increased mismatches are available. Meta-analyses in general show that invertebrate phenology advances more strongly than vertebrate phenology (Root *et al.*, 2003; Thackeray *et al.*, 2010), implying that trophic mismatches are expected to become more frequent with ongoing climate change (Visser and Both, 2005). The first population consequences of trophic mismatches are beginning to show themselves, albeit only in long-distance migrants because these species are probably least flexible in adjusting their timing sufficiently to changes in the underlying trophic levels (Both *et al.*, 2006; Møller *et al.*, 2008; Both *et al.*, 2010). There are several ways to adapt to changes in phenology, and a change in habitat selection is one of the most promising. This may occur at small spatial scales if phenology varies among habitats, but this would solve the problem only temporarily. Changes in habitat selection on larger spatial scales may allow birds to adapt to advances in phenology on longer time scales, but we need more data on the frequency of long-distance dispersal and the fitness consequences of the improved phenological match relative to potentially detrimental effects of lack of local (genetic) adaptation. Technological novelties to track long-distance dispersal, and translocation experiments to investigate fitness consequences of dispersal, will allow us to predict the adaptive ability of species to adjust to climate change.

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