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

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Chapter 1

General introduction

Claudia Burger

Seasonal timing and climate change

In temperate regions, organisms have evolved distinct annual cycles to perform the different life history events like reproduction, growth or migration. The timing of those events is shaped and optimized through the various trade-offs which occur between the different life-history stages, with the objective to maximise the fitness of an individual (Daan, Dijkstra & Tinbergen 1990; Roff 1992; Newton 2008).

Ecosystems are very dynamic, and this results in high between-year variation in the timing of seasonal events (Dunn 2004). The term ‘phenology’ describes the timing of seasonal events, like dates of budburst in trees or first-egg laying dates in birds. The study of phenologies has a long tradition with e.g. historic records of spring arrival dates of migratory birds dating back to the 18th century (Lehikoinen, Sparks & Zalakevicius 2004; see also Ellwood, Primack & Talmadge 2010). In recent years, phenologies have received particular interest because, in addition to fluctuations around a mean date (‘warm and cold years’), climate warming currently leads to strong directional changes (advancements) in the timing of seasonal events in many species.

During the last decades, climate change started to impact on ecosystems in various ways (IPCC 2007) and there is a strong need for species to adapt to those changes. Climate warming has already led to significant range shifts towards the poles in many species (Parmesan & Yohe 2003), and birds and butterflies sometimes lag behind in their northward range expansion relative to increasing temperatures, they have a “climatic debt” (Devictor et al. 2012). In addition, there is overwhelming evidence that climate warming advanced the timing of seasonal events on a broad scale (Thackeray et al. 2010). In many bird species, laying dates are related to spring temperatures and climate warming has thus led to directional shifts in recent years, towards earlier laying dates (Crick et al. 1997; Dunn 2004). Across Europe, populations of pied flycatchers (*Ficedula hypoleuca*) advanced laying dates differentially, depending on the amount of spring warming, thus showing stronger advances in areas with a stronger increase in spring temperatures (Both et al. 2004). However, interpreting the adaptive value of those advancements is often difficult, because, for most populations, information on the phenologies of other trophic levels that a species depends on is missing (Visser & Both 2005).

For certain species, a main problem with phenological shifts is the variation in the speed of advancement, which often differs between species of different trophic levels, e.g. birds and their insect prey (Thackeray et al. 2010; Both et al. 2009). In ecosystems, trophic levels depend on each other, thus if predators advance less than their prey, this can result in mismatches and impose fitness costs for predators due to food shortage. Although mismatches could occur and affect species in many stages of the annual cycle, e.g. during wintering, a main focus of ecological research is on the mistiming between predators and prey during the period of reproduction. Reproductive output is crucial in determining lifetime fitness of individuals. Mismatches have been

shown to result in seasonal declines in reproductive success and reduced survival to the next year in late breeders or late-born offspring (Charmantier et al. 2008; Visser et al. 1998). As a consequence, climate warming during that period was suggested to be an important driver of recent population declines in some species (Both et al. 2006; Saino et al. 2011).

Timing of reproduction with the food peak

In general, those individuals breeding relatively early are assumed to have higher fitness: they usually lay larger clutches (Klomp 1970), produce more surviving offspring, and have a higher chance of producing a second clutch (Brinkhof et al. 2002; Perrins 1970). The optimal period for reproduction depends however on the specific ecology of a species. A range of environmental parameters shape and constrain the phase during which reproduction yields maximum fitness gains (Dunn & Winkler 2010; Roff 2002). Food abundance during offspring rearing has often been hypothesized to be one of the main determinants of reproductive success in birds (Martin 1987; Lack 1968), because food demands are high during that period. Food limitation either results in parents needing to work harder (higher DEE, te Marvelde et al. 2011; Daan et al. 1996), which increases adult mortality, or reduced reproductive output when parental effort remains constant (Sanz et al. 2003). Most current studies on the timing of avian breeding is focussed on the synchrony with the food peak, but this is not the only selection pressure at work.

Matching brood rearing with maximum food abundance might be constrained by other environmental or life-history factors which shape the optimal timing of breeding: temperature, population densities, inter- and intraspecific competition, as well as predation pressure might affect timing decisions (Dunn & Winkler 2010). Especially migratory birds might be constrained in their start of reproduction by their late arrival date (Both & Visser 2001), while, on the other hand, late reproduction is in conflict with the start of pre-migratory moult (Siikamäki 1998). For migratory birds, which cannot easily predict conditions at breeding grounds in advance (Coppack & Both 2002), arriving and breeding too early increases the risk of suffering from serious fitness costs. Exceptional cold spells upon arrival can result in high mortality, as shown in a migratory passerine (Brown & Brown 2000). Also Brinkhof et al. (2002) showed in coots (*Fulica atra*), that trade-offs exist for early breeding: although early breeding improved reproductive output, it also resulted in reduced adult survival.

To gain further insight into the optimal timing of breeding, Daan et al. (1990) developed a model on individual optimization in birds. An assumption of this model was, that both clutch size and laying date are important for maximising fitness. Using this model in a study on kestrels (*Falco tinnunculus*), Daan et al. (1990) found that, if fitness declines with date, birds should breed before the food peak (of rodents, which peak in autumn), to maximise their fitness. Only if no seasonal change in fitness

consequences of breeding time occurs, birds should match breeding with the food peak. A study on insectivorous tree swallows (*Tachycineta bicolor*) also demonstrated, that although birds bred before the food peak (of flying insects), selection for early breeding occurred, and thus no correlations between food abundance and fitness parameters were found (Dunn et al. 2011). Here, just like for kestrels feeding on rodents, prey phenology showed an increase throughout the season rather than a sharp peak in spring. The model of Daan (1990) is complicated in species with multiple broods, like some populations of great tits (*Parus major*): those species are expected to raise their first brood well before the peak to ensure sufficient resources also for second broods, which is in contrast to studies proposing perfect synchrony of first broods with the food peak as the optimal response (Visser, Holleman & Gienapp 2006). In great tits, birds produced second broods less often when caterpillar peaks occurred relatively early in spring, showing that climate change can also affect other life-history traits than just the timing of breeding (Verboven, Tinbergen & Verhulst 2001; Husby, Kruuk & Visser 2009). In summary, the studies of Daan (1990) and Dunn et al. (2011) show, how fitness components interact with seasonal variation in resources, and they make clear that matching brood rearing with the food peak is not always the optimal response.

The assumption that breeding schedules should coincide with the peak in food abundance in order to maximise fitness mostly stems from studies on temperate-forest passerines (Visser, Holleman & Gienapp 2006; Liedvogel et al. 2012 and references therein). In those species, food supplementation experiments supported the idea of food limitation: food supplemented broods grew better, fledged more offspring, and parents had a higher chance of survival to the next year (Verhulst 1994; Siikamäki 1998; Eeva, Lehikoinen & Nikinmaa 2003; Martin 1987). In single populations of forest passerines, the timing of reproduction with the caterpillar peak is well-studied (Both et al. 2009; Charmantier et al. 2008; Visser, Holleman & Gienapp 2006; Goodenough, Hart & Stafford 2010; Nussey et al. 2005). For example, in studies on great tits in The Netherlands and the UK, it was demonstrated that fitness parameters were positively correlated with caterpillar synchrony of broods (Charmantier et al. 2008; Visser et al. 1998; Visser, Holleman & Gienapp 2006). Forest passerines are commonly used as a classic example for the occurrence of phenological mismatches due to climate change (Both et al. 2009; Visser, Holleman & Gienapp 2006; Nussey et al. 2005). Most of this work was conducted in temperate deciduous forests of Central and Western Europe, containing oak trees (*Quercus* spp.). Here, the major peak in food abundance is assumed to be formed by caterpillars feeding on emerging leaves of deciduous (oak) trees (Southwood et al. 2005), and passerines like great tits and pied flycatchers use those caterpillars as nestling food (Perrins 1970; van Balen 1973; Sanz 1998; Lundberg & Alatalo 1992).

Seasonal changes in caterpillar abundance on trees can be measured relatively easily and accurately, so that long-term datasets on caterpillar peaks exist, for the Hoge Veluwe, The Netherlands (Visser et al. 1998), or for Wytham Woods,

Oxfordshire, UK (Charmantier et al. 2008). In oak and oak-mixed forests in The Netherlands, caterpillar peaks have advanced by about 2 weeks in the period from 1985-2005 (Both et al. 2009). This advance in caterpillars is considerably stronger than the advance seen in breeding dates of forest bird species (great tits, blue tits, coal tits and pied flycatchers), so that in the late years of this study only the earliest breeders profit from abundant caterpillars on trees. Based on the evidence of increasing mismatches, the increasing selection for early breeding (fecundity selection) over the last decades was thus attributed to those mismatches (Both & Visser 2001; Drent et al. 2003; and for UK: Goodenough, Hart & Stafford 2010). In this presumably simple system, caterpillar peaks were suggested as a yardstick for measuring mistiming in great tits (Visser & Both 2005), assuming that asynchrony with the peak would indicate maladaptation. However, in a follow-up study, it was recognized that such mismatches could also be adaptive if other constraints exist (Visser, te Marvelde & Lof 2012). In fact, there is little direct evidence that selection for early breeding is directly related to matching the food peak (but see Charmantier et al. 2008 for great tits) and there is only one experimental study in a wild passerine which showed that food abundance is the cause of a decline in nestling growth: delayed broods which were food-supplementation did not suffer from reduced nestling growth (Siikamäki 1998; additional evidence comes from a study on coots *Fulica atra*, Brinkhof & Cave 1997).

Fitness penalties of late breeding have been hypothesized to result from insufficient adaptation to advancing food phenology, but it is important to consider alternative explanations for the benefits of early breeding. Interestingly, already 60 years ago, before the onset of severe climate change, Lack (1966) reported that pied flycatchers breed on the declining slope of caterpillar abundance. It seemed a rather general pattern at that time, that those individuals breeding relatively early, benefited in terms of breeding success and survival (Perrins 1970). This suggests that benefits of early breeding did not solely arise as a consequence of shifting food peaks in recent years but are also related to other factors or trade-offs which shape timing of breeding.

Apart from food availability, other environmental conditions, e.g. lower predator or parasite abundance, might benefit early breeders (Both et al. 2009; Altizer et al. 2006). Moreover, early breeders might be of higher intrinsic quality and settle in the best territories (Verhulst & Nilsson 2008; Wardrop & Ydenberg 2003), resulting in an overall decline in reproductive success over the season. Experiments which investigated the quality versus date hypothesis found evidence for both processes, but more often the date hypothesis was supported, i.e. the decline in reproductive success was related to environmental factors which deteriorate with date *per se* (Verhulst & Nilsson 2008). It is however unclear how variation in quality could explain the increase in fecundity selection over the last years (data from 1974 to 2004, Goodenough, Hart & Stafford 2010; data from 1980- 1998: Both & Visser 2001) as there is no evidence for directional changes towards higher variation in individual or territory quality. Apart from the plausible relations with shifting food peaks, another possible explanation for

increases in fecundity selection for early breeding (using recruitment rates) is an increase in emigration rates of late-born offspring, e.g. because they react to increased mistiming by dispersing further away. The latter point will be introduced in more detail later on.

Habitat differences

The mismatch hypothesis is widely proposed as important driver of population declines in migratory passerines (Møller et al. 2008), although it is doubtful whether it is applicable to all populations, species or habitats. In general, forest habitats seem more sensitive to climatic changes compared to marsh habitats because marsh habitats have more constant food abundance without the typical, temperature-sensitive caterpillar peak as found in oak forests (Both et al. 2010). Little is known about the importance of mismatches across the range of forest breeding habitats for single species, and this has not been tested systematically.

For some populations of blue tits and pied flycatchers, no, or varying correlations between caterpillar peaks and breeding success were found (Garcia-Navas & Sanz 2011; Eeva, Ryömä & Riihimäki 2005; Veen et al. 2010), which might be related to habitat characteristics affecting the timing, width and species composition of food peaks. Steep caterpillar peaks have mainly been shown to occur on oak trees (*Quercus robur* ssp.; Veen et al. 2008; Visser, Holleman & Gienapp 2006), while caterpillar abundance on other deciduous and coniferous tree species is usually lower, peaks occur later or peaks are wider (e.g. van Balen 1973; Mägi et al. 2009). The type of habitat that a species occurs in is therefore an important ecological component in shaping timing of breeding in birds. I propose that, especially within species, the influence of habitat differences is highly underestimated while it could explain a large amount of the variation in fitness consequences of mismatched breeding, which has been found between studies.

Different ways of adapting to climate change

In many bird species, laying dates have advanced along with increasing temperatures (Crick et al. 1997; Dunn 2004). Most of those advances have so far been explained by phenotypic plasticity while little evidence was found for evolutionary change (Gienapp et al. 2008). Species often show plasticity in their responses, because, apart from directional climate warming, spring temperatures vary considerably between years (Figure 1.1), which requires plastic responses to match environmental conditions in a certain year (Gienapp et al. 2008; Dunn et al. 2011). Plastic responses however differ between populations of the same species (Husby et al. 2010): While a population of great tits in the UK adjusted laying date well to the advancing caterpillar peak,

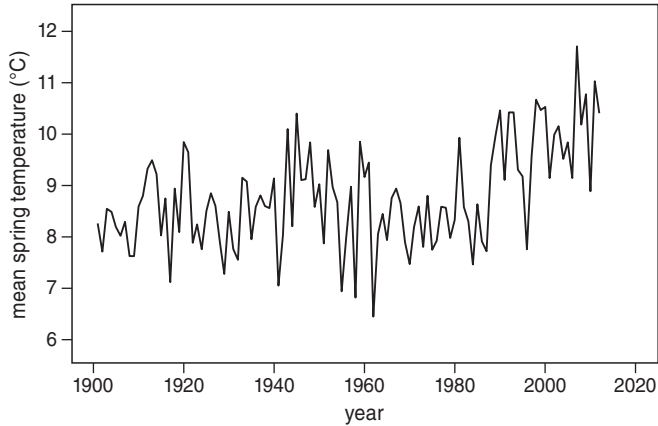


Figure 1.1 Mean spring temperatures (1st March – 31st May) between 1900 and 2012 at weather station De Bilt, The Netherlands. Data was obtained from the freely available dataset of the European Climate Assessment & Data set (<http://eca.knmi.nl>, Klein Tank et al. 2002).

a population in The Netherlands has not advanced their laying dates enough to remain in synchrony with the food peak. Phenotypic flexibility differs between populations, and in some cases, flexibility in adjusting breeding dates could become insufficient because climate change eventually shifts conditions outside of the reaction norm of a species (Visser 2008; Charmantier et al. 2008).

Selection for early breeding can also result in micro-evolution, if genetic variation exists. For instance, evolution on the sensitivity towards cues like temperature could enable an earlier start of egg-laying (Schaper et al. 2012). Evolutionary change might however be too slow to keep up with the rapid environmental changes through moderate heritabilities of life-history traits like laying dates (Sheldon et al. 2003). Whether the current speed of adaptation is sufficient for species to successfully cope with climate change likely depends on habitat type: in some habitats no or little response is needed when seasonal variation in food abundance is low.

Dispersal as a solution to overmisting?

Species should select the breeding habitat that is best suited to maximise their survival and reproductive success (Fretwell & Lucas 1970). Mobile species which fail to adapt locally have the option to move to new environments that match their phenotypes better (Edelaar, Siepielski & Clobert 2008). Dispersal, i.e. the movement between place of birth or previous breeding towards a new breeding location (Clobert et al. 2001), could thus play a key role in adapting to climate change. In a comparative study, those bird species with high natal dispersal rates showed lower population declines during recent climate change (Jiguet et al. 2007). Mistimed individuals could

use cues related to habitat, food or individual timing to perform conditional dispersal towards more favourable locations without the need to change their annual cycle. Conditional dispersal, depending on various parameters, like reproductive success, hatch date or habitat quality is not uncommon in birds (Paradis et al. 1998; Clobert et al. 2012; Eeva et al. 2008).

For birds which became mismatched with the local food peak, dispersal to a “later” or less seasonal habitat might be advantageous, given that such habitat heterogeneity exists. For passerines like tits and flycatchers, coniferous habitats might be an increasingly favourable option, since they are less susceptible to climate change, as caterpillar peaks occur later and food abundance fluctuates less strongly over the season, compared to oak habitats (van Balen 1973; Veen et al. 2010). Emigration from unfavourable habitats like oak forests could also explain declines in bird densities in those areas (Both et al. 2006), and increased emigration of late born individual may explain some of the observed increases in selection for early breeding (e.g. Both & Visser 2001; Both 2012).

Ideally, to study whether species show adaptive responses, mismatches need to be induced by manipulating the environment, e.g. the timing of breeding, or food supply. Some experimental evidence exists that birds responded to manipulations by adjusting their dispersal distances (e.g. Doligez, Danchin & Clobert 2002; Nicolaus et al. 2012). Similar experiments can show if adaptation to environmental change is achieved via such small-scale dispersal events. Dispersal also comes with potential costs like survival costs during moving, or fitness consequences due to unfamiliarity with the new habitat, and this might counteract benefits due to improved timing (Ronce 2007; Doligez & Pärt 2008; Marr et al. 2002).

Dispersal occurs on different scales, locally, between habitats, but also over long distances (Paradis et al. 1998). While older birds are often rather philopatric and disperse only short distances between breeding attempts, the exchange of genes and phenotypes between populations will mainly occur through first-time breeders (natal dispersal), which usually show much higher dispersal distances (Clobert et al. 2001). If local habitat shifts are insufficient to restore synchrony (adaptation), populations could also successfully adapt to climate change through immigration of individuals from southern populations (Edelaar, Siepielski & Clobert 2008). Southern immigrants would introduce their genes and phenotypes for early laying into the Northern population. Selection can act on those immigrant genes and phenotypes which could speed up micro-evolution dramatically. Likewise, individuals dispersing to a more northern breeding location could catch up with spring phenology because they migrate much faster than spring phenology progresses, and thus likely benefit from improved timing with prey phenology. Individual benefits are however mostly expected in relatively warm springs when individuals would suffer from mistiming at their original location. In pied flycatchers, there is indeed evidence for occasional long-distance dispersal towards alternative breeding locations, but data are too scarce to address fitness consequences (Both et al. 2012).

Long-distance dispersal may not come without a cost: although phenological matches may be better, maladaptations to other environmental traits may induce fitness costs for long-distance dispersers (Clobert et al. 2001; Brown, Brown & Brazeal 2008). Little is known about such fitness consequences, especially survival costs, of individuals dispersing over hundreds of kilometres, and breeding at a new and distant site. Observations that immigrants apparently have lower reproductive success than philopatric birds may result from the non-randomness in intrinsic quality of dispersers versus philopatric individuals and incomplete fitness estimates (Doligez & Pärt 2008). Examples showing opposite patterns (dispersers are stronger or have higher reproductive success) also exist (e.g. Clobert et al. 2009; Eeva et al. 2008).

Patterns and consequences of long-distance dispersal are difficult to study: small songbirds can hardly be tracked over large distances, although some large-scale efforts have been made for getting unbiased estimates of natal dispersal distances and for studying consequences of dispersal (Winkler et al. 2005). Translocations could help simulating long-distance dispersal to study fitness consequences of breeding at a distant site. So far, these translocations have mostly been used as a conservation tool, for example, for reintroductions of species to islands (Brower et al. 2009; Armstrong & Seddon 2008). In one experiment, in which great reed warblers were translocated in order to subsequently study their behaviour, females could be followed and studied after translocation to a new location (Bensch & Hasselqvist 1992). However, for pied flycatchers, the rate of birds which settled at a new location after translocation has been rather low if birds were released immediately after moving (Pärt 1995; Slagsvold et al. 1988).

Long-distance dispersal could be a powerful mechanism through which species could adapt to climate change. This argues for a need to develop new methods for simulating long-distance movements to estimate costs, benefits and population consequences of dispersal in order to better predict its' potential important for species' adaptation to large scale environmental change.

In this thesis I addressed the following objectives:

1. Is the selective disadvantage of late breeding a result of food limitation?

Here, I investigated the notion that the increase in selection for early breeding (data from 1974 until 2004, Goodenough, Hart & Stafford 2010; see also Both & Visser 2001) in pied flycatchers is related to the amount of mismatch with the food peak. As climate warming continued to take place in recent years, I expected that fitness penalties for late breeders have intensified relative to those earlier studies, because birds became more mismatched with the food peak. Direct evidence for food limitation of late breeders would thus support the mismatch hypothesis. Alternatively, quality differences between early and late breeders could as well result in reduced fitness of late breeders. Even without survival costs for late-born offspring, selection for early

breeding could arise from differential dispersal between early and late-born offspring because calculations are based on local recruitment rates.

To address this question, I took an experimental approach, which manipulated timing of breeding and food availability, in order to separate the contributions of food as an important date effect while controlling for individual quality (Fig. 1.2, and Chapter 2). Natal dispersal relative to timing of breeding and birth date was investigated within our large study area to rule out the possibility that selection for early breeding is caused by late birds dispersing further away (Chapter 4).

2. Some populations are well-adapted while others are not.

Can this variation be explained by habitat differences?

In chapter 3, I detail the trophic relationship between resource use and reproductive success across populations. Evidence that the synchrony with caterpillars is causally linked to fitness is mainly based on single, descriptive studies in oak habitat (Charmantier et al. 2008; Visser, Holleman & Gienapp 2006). Only a few studies address the trophic links in more detail, by studying how food abundance affects nestling diet in different habitats (Tremblay et al. 2005) and how caterpillars in the diet affect reproductive success (Garcia-Navas & Sanz 2011). Here, I systematically investigate the effects of habitat differences and spring temperature on seasonal changes in nestling diets for populations across Europe. I furthermore assess the importance of caterpillars in nestling diets for fitness and discuss the necessity of matching the caterpillar peak.

3. Is rapid adaptation possible through habitat shifts, and on a larger scale, through long-distance dispersal?

In chapter 4, I explored the hypothesis that birds respond to mistiming by dispersing further away and, especially, shift to breed in less seasonal habitats. I relate adult and natal dispersal distances within our large-scale study area to environmental and life-history parameters like timing, reproductive success and habitat, in order to investigate this notion. As individuals might have already chosen the best habitat for their individual phenotype, we experimentally created mismatches by delaying broods and manipulated food availability, to investigate whether this resulted in differential dispersal behaviour (see Chapter 2).

In order to study the fitness consequences of dispersal outside the study area, individuals have to be forced to breed elsewhere, because this avoids biases due to non-random dispersal and enables larger sample-sizes. In chapter 5, I describe a novel set-up for moving birds to a breeding location chosen by the experimenter. In chapter 6, this set-up is applied for simulating long-distance dispersal to a Northern breeding location. I studied, if birds benefit from improved timing in terms of reproductive success, or suffer because they lack certain adaptations to the new environment. I show, that such a novel experiment can give important insights into whether long-distance dispersal could speed up adaptation to climate change.

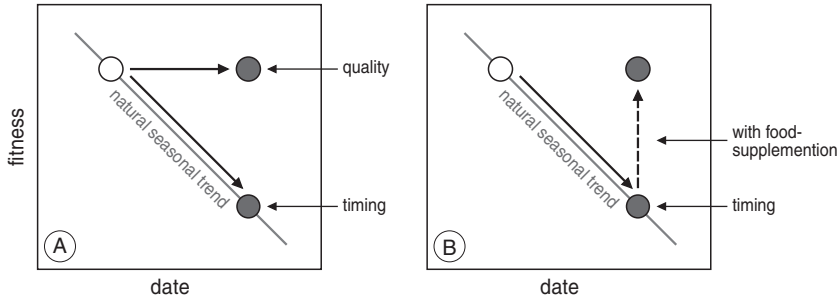


Figure 1.2 Hypothetical expectations for the different experimental treatments: filled circles indicate the outcome of the delay treatment, in terms of fitness, (A) if the decline in fitness of delayed broods is either due to date per se (timing), or quality. (B) if food-limitation is the cause of a decline in fitness, this decline should disappear when broods are food-supplemented. Figure adapted from Verhulst & Nilsson (2008).

Study system

Our study species, the pied flycatcher, is a small, hole-nesting, long-distance migratory passerine. Pied flycatchers breed in temperate and boreal forests across Europe and winter in sub-Saharan West Africa. Our population arrives in the breeding area from the first week of April, with most males arriving in the second 10-day period of April, and the females about five days later. Nest building starts quickly upon arrival, and during this study the earliest clutches started at the 20th of April, with the peak occurring in the first week of May.

The species is single-brooded and parents provide bi-parental brood care. Clutch sizes usually range from five to eight eggs, with an incubation time of 14 days and young fledge at about 15 days of age. Pied flycatchers are found in a variety of forest habitat, given suitable nesting opportunities (tree cavities), but are usually reported to prefer deciduous (oak) forests over coniferous forest types (Lundberg & Alatalo 1992; Siikamäki 1995). Their diet is variable: studies on nestling diets usually report considerable amounts of caterpillars (or adult *Lepidoptera*) in the diet, as well as *Coleoptera*, *Arachnida*, *Diptera* and *Hymenoptera*, besides other insect groups (Lundberg & Alatalo 1992). The main difference between deciduous and coniferous forests is a lower amount of caterpillars in nestling diets in coniferous woodlands (Sanz 1998).

Adult flycatchers are rather philopatric and return rates are often high, but female return rates drop with latitude (Sanz 2001). It is unclear if this is a result of differences in adult survival or differences in dispersal distances. In contrast, recruitment rates are rather low in all populations (usually below 10%), suggesting large dispersal distances for second-year birds (Chernetsov et al. 2006). In most populations (except some isolated ones in Spain), more than 50% of breeding birds in a year are immigrants (un-ringed individuals) from unknown origin.



Figure 1.3 Study area in Drenthe, The Netherlands. Icons indicate the locations of the 12 study plots, containing 50 or 100 nest boxes each.

Pied flycatchers are an ideal model species for studying how wild birds cope with climate change: the species is a long-distance migrant and breeds in seasonal habitats, and might thus be especially vulnerable to environmental changes. Population declines have indeed been found and have been related to mistiming of breeding with the food peak (Both et al. 2006). Pied flycatchers are single-brooded and should thus optimise the timing of this single breeding event. Furthermore, long-term data on environmental and breeding parameters exist, and populations of pied flycatchers are being studied across their breeding range and addressing different objectives, thus generating great knowledge about the ecology and life-history of the species. Finally, setting up new nest box-breeding populations is done relatively easily and this allows detailed studies of hundreds of breeding pairs per year.

The main study area was located in Drenthe, The Netherlands (Fig. 1.3). A nest box population was established in 2007. 12 study plots were divided up into a Northern part, located in the Drents-Friese-Wold, and a Southern part, National Park Dwingelderveld and Boswachterij Ruinen. Plots were separated by several kilometres,

and usually surrounded by forest which did not contain nest boxes but some natural cavities. In addition, an unknown number of nest boxes existed in the neighbourhood, e.g. in gardens). The study area consisted of nine plots with 100 boxes each and three plots with 50 boxes each, summing up to around 1050 boxes in total. All nest boxes had inner dimensions of 90×120×230 mm (entrance hole 32 mm). In each plot, nest boxes were placed in more or less regular grids with distances between boxes ranging between 40–100 m. Timing and food supplementation experiments were run in both the northern and southern part of the study plots, the most distant plots were however excluded for practical reasons. The habitat of the study area ranged from oak forest to coniferous woodlands with pine trees (*Pinus* spp.). Because oak forests differ strongly in their caterpillar phenology from other forest types, habitat was categorized into two types: oak or oak-mixed, and non-oak (mostly coniferous and birch) habitat.

Flycatcher occupation rates of the nest boxes varied between 10% and 60 % of boxes per plot, summing up to about 300 breeding pairs/year in the experimental years. The remaining boxes either remained empty or were occupied by great tits, blue tits and nuthatches.

