CHAPTER 11

Food availability, mistiming, and climatic change

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11.1 Timing of breeding, food peaks, and fitness

Most bird species do not breed at just any moment in the year: breeding is mostly confined to a restricted period and is rather synchronized within populations. Seemingly, each species breeds at the period when benefits in fitness terms are maximal, and one of the major ultimate factors is food availability. For example, brent geese *Branta bernicla* migrate thousands of kilometres to the High Arctic to breed there in mid-summer, profiting from the high quality of the growing vegetation. Eleonora's falcons *Falco eleonorae* breed exclusively in the fall on Mediterranean islands, to match the nestling phase with the mass migration of passerines to their African wintering grounds. Honey buzzards *Pernis apivorus* have their chicks in the nest in mid-summer, when bee nests reach their maximal size. Great tits *Parus major* breed in the early spring in temperate forests, where they profit from the bonanza formed by herbivorous caterpillars that forage on young oak leaves. It is not just temperate and arctic species that exhibit well-defined breeding seasons, many tropical birds also breed at certain periods in the year, for example when food is most abundant due to seasonality in rainfall (Hau *et al.*, 2008). The restricted temporal abundance of food supplies within years shapes avian breeding cycles to a large extent, and understanding the effects of climate change on avian calendars therefore requires good knowledge of how the timing and abundance of food supplies changes along with climatic change.

Whereas birds are normally well adapted to breed on average at the time with most abundant food, the exact timing of these food peaks could vary considerably between years. This between-year variation is to a large extent determined by local weather conditions. For instance, in warm springs the caterpillar peak in Wytham Wood (Oxfordshire, UK) could occur as early as mid-May, whereas in exceptionally cold springs it is a month later (Charmantier *et al.*, 2008). The Wytham great tits track this between-year variation in their food supply very well: in the warmest springs they lay about 25 days earlier than in the coldest springs (Perrins, 1965; Charmantier *et al.*, 2008). Later we will see that not all species are able to track annual variation in the timing of their food supply so well.

For a bird it is not an easy task to match the timing of its greatest food requirements with the peak in food availability. Nestlings need most food in the second half of the nestling phase. To reach this stage, parents should already have built the nest, and laid and incubated the eggs. After the start of egg-laying, birds have little scope for speeding up the hatching date of their eggs, except from reducing clutch size. Thus, parents predict when the food peak will occur at the time of egg-laying. For a female great tit that lays nine eggs, incubates 13 days and whose chicks reach maximal food needs at about 10 days after hatching, this means that she should start laying 32 days before the expected food peak. This necessitates considerable predictive power. If temperatures are higher than normal after the female started, caterpillars develop faster, pupation dates advance, and, hence, the caterpillar peak is earlier, her chicks will hatch too late to

fully profit from the caterpillar peak (van Noordwijk *et al.*, 1995; Visser *et al.*, 2004). Larger species normally have longer incubation periods and therefore would have even greater problems in anticipating future conditions (Both *et al.*, 2009). The predictability of the food peak thus depends on the time interval between the decision moment (egg-laying) and when food is needed most, and whether reliable cues are available at the moment of egg-laying.

There is a clear paradox in the relationship between avian breeding dates in response to annual variation in food peaks: on average populations adjust laying dates to variation in food supply, but within any year almost all pairs have their chicks too late in the nest to fully profit from the food peak (Perrins, 1965; Drent, 2006). Within populations the earliest breeders normally produce most surviving offspring, and late breeders normally fare badly in fitness terms. This is not just because early breeders are better parents than late breeders, because if you exchange clutches between late and early clutches, the originally early parents perform badly with a late brood, whereas the originally late parents perform well with an early brood (Verhulst and Nilsson, 2008). That this decline in performance with date is because late broods are badly timed with the food peak was nicely demonstrated in pied flycatchers *Ficedula hypoleuca*: broods with delayed hatching did worse than early control broods, but the effect disappeared when these late broods were provided with supplementary food (Siikamäki, 1998). The reason that most birds lay too late to profit fully from the food peak is to a large extent because at the time of laying, food supplies are scarce, either preventing females from producing eggs (Perrins, 1970) or doing so at such a high cost in terms of female survival that there is selection against such a strategy (Brinkhof *et al.*, 2002; Visser *et al.*, 2004). Support for this notion comes from numerous food supplementation studies prior to egg-laying, which generally resulted in advances in laying dates (Drent, 2006), especially for females in poor-quality territories (Svensson and Nilsson, 1995; Nager *et al.*, 1997). On an individual level, a large part of most bird populations breeds later than optimal from the chicks' perspective because parents cannot lay earlier or choose not to do so.

11.2   Climate change and unequal responses across trophic levels: what is sufficient change in breeding phenology?

Many bird species have advanced their laying date during the last few decades (Chapter 10). This effect is seen in different genera and at different places around the globe, although data from the tropics are still lacking. One of the best pieces of evidence that local changes in pre-breeding temperature are responsible for this advance in breeding season comes from a comprehensive analysis of temporal trends in laying dates of 25 populations of pied flycatchers and collared flycatchers *Ficedula albicollis* across Europe (Figure 11.1). Mean breeding dates differed by about a month between populations depending on latitude and altitude. For each population, the annual mean laying date strongly correlated with the annual mean temperature during a 30-day window before the site-specific breeding date: birds bred earlier in warmer springs. Temperature trends over the period 1980–2001 for this site-specific time-window were very different, with no increase in northern and southern Europe, and clear warming in western Europe. The observed laying date trends were highly consistent with temperature trends: no advance in laying date in areas without warming, whereas birds advanced more, the stronger the increase in temperature (Both *et al.*, 2004). More support for an effect of temperature comes from Dunn (2004), who reviewed the effect of spring temperature on annual breeding dates and found that in 79% of 57 species birds laid significantly earlier in warmer years. Additional laboratory evidence now has indeed shown that birds' laying dates are directly related to temperature (Visser *et al.*, 2009).

The mere fact that so many bird species have advanced their breeding phenology in response to climate change (Crick *et al.*, 1997; Crick and Sparks, 1999; Parmesan and Yohe, 2003; Chapter 10) does not automatically imply that these changes are sufficient to cope with climate change (Visser *et al.*, 1998, 2004; Visser and Both, 2005). As argued before, the value of breeding on a particular day depends largely on its relative timing to other trophic levels (most notably food, but also predators and parasites), and if these other levels have shifted at a different rate, the advance in laying date may be sub-optimal. It could
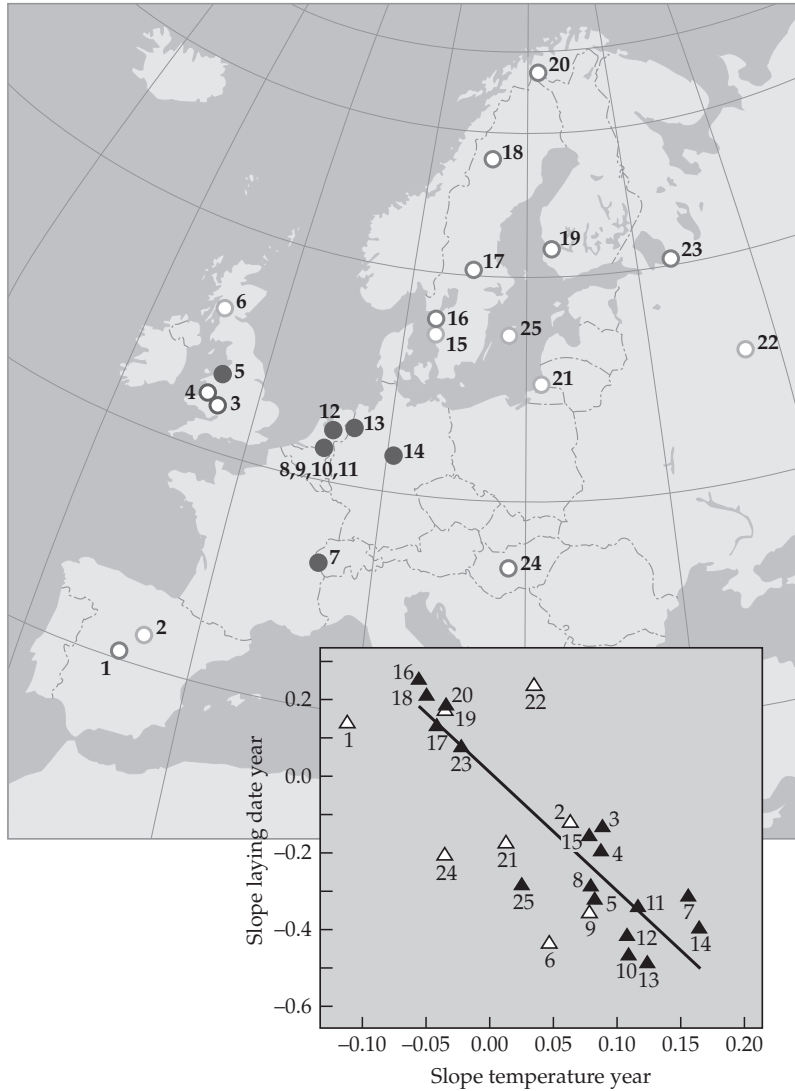
Figure 11.1   Laying date trends over time in 25 populations of pied and collared flycatchers, and their relationship with local temperature changes during 1980–2001. Reproduced from Both *et al.* (2004).

be either too small, in which case laying dates advance less than that of the food peak, or too strong, if laying dates advance more. Thus, the question is how to measure whether responses are sufficient.

11.2.1   Timing of breeding relative to food peak

The timing of the food peak can be used as a yardstick for determining whether birds have adapted

sufficiently to climate change. If the match between the food peak and the hatching dates does not change, then this can be interpreted as birds maintaining a match in breeding synchrony and adjusting well to the change (Figure 11.2a). In contrast, if the food peak shifts more than the birds' breeding date, they become mistimed (Figure 11.2b). The problem with this approach is that it relies on the assumption that reproductive success is, to a large
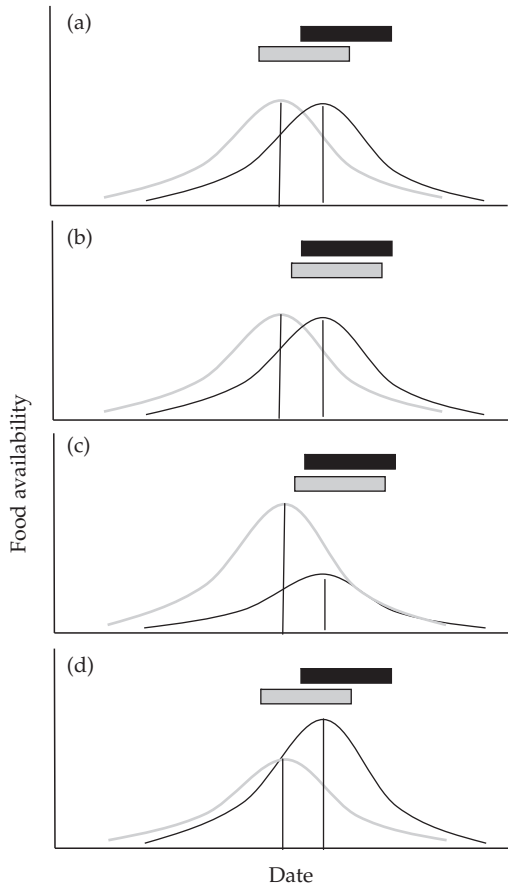
Figure 11.2 Possible changes in food peak (lines) and avian breeding dates (boxes) in response to climate change. Black lines and boxes represent the situation before warming, and the grey symbols after a certain period of warming. (a) Birds change in synchrony with the food peak; (b) food peak changes more than the birds, leading to mistiming; (c) a similar degree of mistiming, but food peak becomes larger, and therefore birds do not suffer relative to (b); and (d) birds change in synchrony with the timing of the food peak, but peaks get lower, and birds suffer reproductive consequences.

extent, determined by the temporal match between the chick rearing phase and the peak of a single group of prey. If multiple prey groups are important for a breeding bird with all of these prey varying in their responses to climate change, then a simple yardstick may not exist. Furthermore, so far most work has concentrated on the mere timing of peak food availability and not considered the width and the height of the food peak (Durant *et al.*, 2005; Jonzén *et al.*, 2007; Visser, 2008). There is a possibility that peak date advances, but the peak simultane-

ously becomes larger, and even an insufficient advance of breeding date relative to the food peak may not cause problems because birds have as much food available as before (Figure 11.2c). The reverse could also happen: birds keep the temporal match with the food peak date, but peaks become lower or narrower, and hence less food is available for birds to feed their chicks (Figure 11.2d). A change in shape in food peaks may well exist because invertebrates grow faster at higher temperatures and therefore may become unavailable after pupation, as suggested for caterpillars (Buse *et al.*, 1999). The reverse could also happen: weather-mediated mortality in (adult) insects is probably lower at higher temperatures, and a longer average life span may widen the food peak for birds. Warm springs and summers may also allow insects to have more generations, and hence food is available for longer periods. These issues of how climate change affects the width of the food peak have rarely been addressed empirically, although in a field study on caterpillar peaks there was no significant correlation between the peak date and the height or width of the peak (Visser *et al.*, 2006).

The problem with using food peak date as a yardstick for trends in laying dates is that at present few long-term studies on food peak dates are available. In fact, these are restricted to two studies on caterpillars, one in The Netherlands (Visser *et al.*, 2006) and the other in England (Cresswell and McCleery, 2003), and these are used as a yardstick for the timing of nest box breeding passerines. Food peaks at shorter time scales are measured in species like Arctic breeding geese, but how these have shifted as a result of climate change has not been measured directly (van der Graaf *et al.*, 2006). Recently some estimates of the timing of food peaks for sparrowhawks *Accipiter nisus* were made by calculating the mean timing of breeding or fledging of some of their main prey species (Nielsen and Møller, 2006; Both *et al.*, 2009a). Interestingly, in both cases the peak in prey availability advanced, in contrast to sparrowhawk breeding dates, and sparrowhawks did not breed earlier in years with an early food peak. Because real measurements of food peaks are lacking, sometimes proxies for timing in other trophic levels are being used for which data are available, such as plant phenology for

insectivorous birds (Marra *et al.*, 2005; Møller, 2008), but it remains unknown how well these correlate with food abundance. There is definitely an urgent need for documenting how the temporal abundance of prey populations is changing relative to their avian predators in response to climate change, and also whether this would lead to diet shifts in these birds.

11.2.2 Changing selection on timing of breeding

Birds should aim to breed at the time that maximizes their fitness, and we have already seen that in many cases the earliest breeders gained highest reproductive success because they matched their chick rearing time best with the food peak. An indirect way to estimate whether birds adjusted sufficiently to advances in their food peak is to assess whether this effect of breeding date on fitness has changed over the years. The reasoning is that if the food peak advances more than the birds' breeding seasons, the fitness for late-breeding birds is more reduced than for early breeders, and hence the effect of breeding date on fitness becomes steeper. There is only one study that actually has demonstrated that selection for early breeding became stronger in years with a larger mismatch between breeding date and the food peak: the case of the Wytham great tits (van Noordwijk *et al.*, 1995; Charmantier *et al.*, 2008). Interestingly, this was not the case for the Dutch great tit population (Visser *et al.*, 2006), although here selection for early laying did increase, as did the mismatch between food peak and the birds' breeding season (Visser *et al.*, 1998). It should also be noted that just a negative effect of breeding date on fitness is not necessarily an indication of an increased mismatch between food peak and hatching dates because this pattern of the earliest breeders performing best is a general rule that has existed before the recent rapid increase in spring temperatures (Perrins, 1965).

Increased asynchrony between food peak and breeding dates may result in stronger selection for early breeding, but increased selection is not necessarily the result of an increased temporal mismatch. If the food peak becomes narrower, and birds breed at the descending slope of the peak, this would lead to increased selection for early breeding, even if the match between peak date and breeding date remains unchanged.

Using changes in the strength of selection as a proxy for changes in synchrony also has the problem that appropriate fitness consequences are difficult to measure. In some cases, the number of fledglings is used (van der Jeugd *et al.*, 2009; Ahola *et al.*, 2009), which has the problem that quality differences among fledglings often lead to variation in survival. In other cases, researchers have been using the number of offspring recruited to the local population (Visser *et al.*, 1998; Both and Visser, 2001; Charmantier *et al.*, 2008), not accounting for dispersal out of the study area. It is conceivable that late-born offspring are more likely to disperse out of the study area in regions where birds are becoming more mistimed with their food supply. Thus, if late-hatched offspring have a stronger tendency to disperse out of the area, this results in stronger selection for early breeding at the local scale, without these late-breeding individuals actually having reduced fitness. These movements could indeed be a sign of increased mismatch, but the effect may be more subtle than what is measured in local fitness terms. Evidence for climate change affecting dispersal rates is scarce, with both an example of increased dispersal in Arctic terns *Sterna paradisaea* (Møller *et al.*, 2006) and a decrease in dispersal in common lizards *Lacerta vivipara* (Massot *et al.*, 2008). Any change in dispersal also makes it difficult to measure potential survival costs of early laying to the adult female under harsh conditions, because dispersing females remain unidentified (Sheldon *et al.*, 2003). As a result, selection for laying date may differ between male and female parents and the effect of climate change on selection for phenological traits may differ between the sexes (Møller, 2007).

11.3 Case studies

There are few good examples of the effects of climate change on the timing of breeding in birds, how this changed relative to the timing of the birds' main food supply, and its subsequent fitness consequences. I will discuss three examples in some detail below because these illustrate well the problems

that birds may face in responding to climate change, as well the problems researchers have in documenting what happens and interpreting the results.

11.3.1   The great tit

Great tits are convenient for studies of the effects of climate change because long-term population studies are available from many populations across Europe, enabling us to look back in time and examine the response of birds to changed temperatures. This species is not more (or less) interesting than other species, but it happens to breed in nest boxes and hence basic life-history data have been collected for many years, often on populations in which all breeding pairs and their young are ringed. Furthermore, in deciduous forests about 80% of the food mass brought to the chicks consists of caterpillars, and early broods in particular are fed with high proportions of caterpillars (Perrins, 1965; van Balen, 1973; Naef-Daenzer et al., 2000; Wilkin et al., 2009). During the peak, caterpillars can be so abundant that food seems unlimited, but caterpillar peaks normally only last about 3 weeks, after which most caterpillars pupate and become difficult to obtain (Visser et al., 2006). Caterpillar peaks are rather easily measured by either catching winter moth caterpillars when they descend the trees to pupate in the ground (half-fall dates are used (Perrins, 1965)), or by collecting caterpillar frass underneath trees on a regular basis during the season (Tinbergen, 1960; Visser et al., 2006). For two areas in Europe, long-term data on both caterpillar peak dates and great tit breeding dates are available: the Hoge Veluwe area in The Netherlands from 1985 to 2005 (Both et al., 2009) and Wytham Woods in the UK from 1961 to 2007 (Charmantier et al., 2008).

Caterpillar peaks have advanced in both the UK and The Netherlands, and although the methods differed, the rate of advance is roughly similar for the period 1985–2005: about 15 days. In both areas, great tits started egg-laying progressively earlier over the study period, and both annual caterpillar peak dates and annual mean great tit egg-laying dates were highly correlated with local temperatures in the period prior to egg-laying. Whereas in Oxford the time interval between the food peak and the birds' breeding dates remained unchanged over the years (Figure 11.3a, b; Cresswell and McCleery, 2003; Charmantier et al., 2008), the birds in The Netherlands became more asynchronous with their food peak because their breeding dates advanced less than that of the caterpillars (Figure 11.3d, e; Visser et al., 1998; Both et al., 2009a). In The Netherlands, this increased mismatch was also reflected in increased selection for early breeding: early breeders now have a higher fitness benefit compared to late breeders than in the past (Figure 11.3f; Visser et al., 1998; Gienapp et al., 2006). In contrast, Oxford great tits increased synchrony with their prey, partly because they shortened their incubation period. Whereas in the past there was strong selection for the earliest breeders, at present the fitness penalties of breeding late are less severe, and selection became stabilizing (Figure 11.3c; Charmantier et al., 2008). These contrasting results between the two populations are interesting because they have a certain consistency: if birds on average hatch synchronously, there is not strong selection for breeding early (or there is stabilizing selection), whereas if they hatch too late, there is selection for early breeding (van Noordwijk et al., 1995). The question, however, is why British great tits were able to adjust better to the advancement of the caterpillar peak than the Dutch population?

The common pattern among birds is that the earliest breeders have highest fitness, and a rather large fraction of each population breeds too late to gain maximal fitness from the current reproductive attempt because the energetic demand of their nestlings peaks as the food supply is declining (Drent, 2006; Verhulst and Nilsson, 2008). This pattern was first described for Oxford great tits by Perrins (1965), and he suggested that most females were food constrained early in the season, preventing them from breeding earlier (Perrins, 1970). Paradoxically, one year of food supplementation studies in Oxford around 1970 did not make great tits lay earlier, possibly because there was a cold spell around the normal laying dates (Perrins, 1979; C.M. Perrins, personal communication). For other areas, there has been evidence that great tits start laying earlier when supplied with extra food (Källander, 1974; Nager et al., 1997), suggesting that they are indeed either constrained by food or unwilling to pay the cost of early laying. The advance in the Oxford
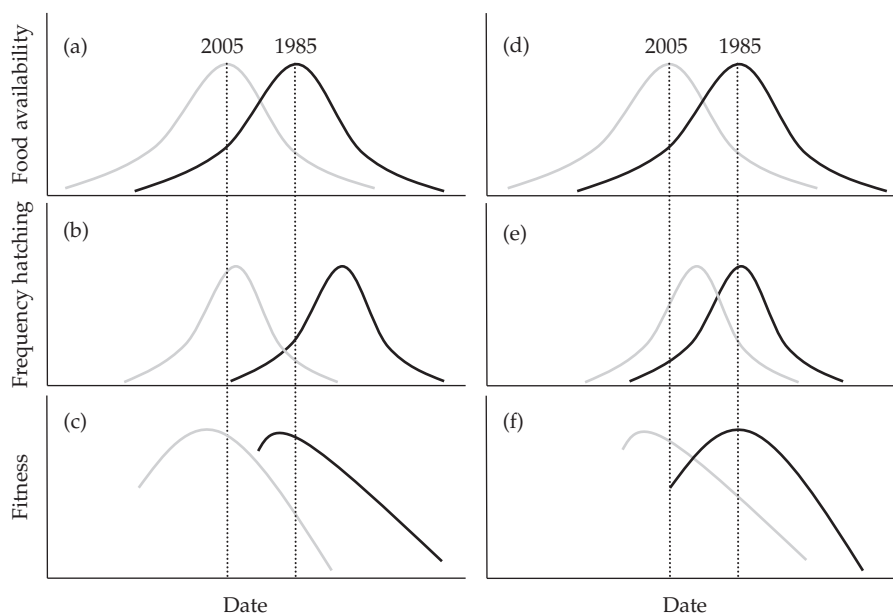
Figure 11.3   Schematic changes between 1985 and 2005 in caterpillar availability over the season (a and d), hatching date distributions (b and e), and fitness consequences of breeding date (c and f) in the great tit populations at Oxford (UK, a–c) and the Hoge Veluwe (The Netherlands, d–f). The black lines are for 1985, the grey lines for 2005. The thin hatched line delineates the caterpillar peak dates. Fitness consequences were measured as the number of local recruits. Data from Visser *et al.* (1998, 2006), Charmantier *et al.* (2008), and Both *et al.* (2009a).

population and the release in selection for early breeding suggest that the costs of early laying (or constraints) have been reduced to such an extent that the average bird is now breeding at a time to match the food peak (Cresswell and McCleery, 2003). It would be interesting to perform a food supplementation experiment now in the Oxford population because the patterns suggest that at this very moment a large fraction of the population is breeding at the right time relative to the food peak, and hence food supplementation is not expected to make birds lay earlier. One way or the other, climate change thus seems to have released birds from constraints on early laying in great tits in Oxford, allowing the average bird to profit more from the caterpillar peak than in the past.

The Dutch great tit population was rather exceptional in avian fitness studies because there was little selection for early breeding during the 1970s (Visser *et al.*, 1998). Apparently, the average bird at then laid at the right time, although it has not been described that there was indeed stabilizing selection (although there is a trend in the data presented

by Gienapp *et al.* (2006)). Whereas Oxford great tits improved their synchrony with their caterpillar food peak, Dutch tits showed the opposite tendency. At present, there is no single explanation for why Dutch tits responded less than the food peak, but I present three non-exclusive hypotheses, all of which have some empirical support. The first is that temperatures at different moments of the spring have been changing at different rates: in the period prior to egg-laying temperatures did not increase strongly, and since birds use these temperatures as a cue to start laying, there is only a limited degree of advance (Visser *et al.*, 2009). However, increase in temperatures has sped up caterpillar growth and hence advanced their peak date, more so than the tit breeding date, causing increased mismatch (Visser *et al.*, 1998, 2006). A second reason is that great tits have the opportunity to produce a second brood, and if they do so, they should time their first brood a bit early compared with the food peak in order to still profit from the very latest caterpillars in their second brood (Crick *et al.*, 1993). Thus, they should compromise their first brood by raising them before

the food peak, to give their second brood a better chance. If the likelihood of producing a second brood declines for whatever reason (e.g. narrower food peak), then birds should delay their laying date, to better match the nestling phase of their first brood with the food peak (Visser *et al.*, 2003). Thus, there may be two opposite trends: the food peak is advancing and thus the birds should breed earlier, but they are producing fewer second broods and in this case they could advance less than the caterpillar peak to achieve better synchrony. There is indeed evidence that across Europe great tit populations that used to have a high proportion of second broods have advanced their laying date less than populations not having changed their double broodedness (Visser *et al.*, 2003). However, this explanation would imply that the laying date of first clutches has become better synchronized with the food peak instead of worse, and it cannot explain the increased selection for early breeding. The third explanation is that the genetic make-up of the population is such that the way they respond to increased temperature limits an appropriate response. It has been shown that individual birds change their laying date depending on spring temperature: they lay late in a cold spring and early in a warm spring (Przybylo *et al.*, 2000). This response reflects a 'reaction norm', and it allows individuals to respond to environmental variation they could encounter during their life time (Stearns and Koella, 1986). Such reaction norms are evolved traits that maximize fitness within a certain range of environmental variation. If circumstances change much, existent reaction norms may become maladaptive, for example because the environment at the moment of decision making is not a reliable predictor for the timing of the food peak. However, there may be genetic variation for reaction norms of laying date on spring temperature, as suggested for the Hoge Veluwe population: some families respond stronger to temperature than others (Nussey *et al.*, 2005). The population may thus be in an evolutionary transition stage, with the most plastic reaction norms now leaving most surviving offspring and the mismatch being a temporary lag in evolutionary response. Indeed, the most plastic genotypes did best in fitness terms during the more recent period (Nussey *et al.*, 2005). The question is whether ongoing change

could still be matched with such an apparent evolutionary reaction because genetic variation for this trait may be locally depleted. A strikingly different result was found in Oxford where no genetic variation for reaction norms of laying date on temperature were found, and where the population response in laying date was completely attributed to the phenotypic plasticity of this one common reaction norm to increased temperatures (Charmantier *et al.*, 2008).

It is clear that the adjustment of breeding date to climate change is not always an easy task for birds, and it also causes headaches for researchers if populations of the same species, living just about 500 km apart can react so differently. Apparently, local ecological conditions may be essential for understanding why one population responds in one direction, whereas another responds in a completely different direction. There is the possibility that the differential effects are not solely due to populations differing in their response to climate change, but that over the study period habitats also have changed and it is the interaction between habitat change and climate change that happens to lead to divergent directions of change in the birds. Although it is fortunate that we have two detailed long-term studies of the same species available, at present the apparently different responses make it impossible to generalize even to other populations of great tits, let alone to other species, because far more reactions to climate change may exist.

11.3.2 Pied flycatcher

The other species studied intensively with respect to timing of breeding and food availability is not a completely independent player from the great tit populations just described. It is the pied flycatcher: it also nests in boxes, which provides the same advantages for collecting long-term life-history data in many populations, but also the same disadvantage in that there is the artificiality of a nest box study (Møller, 1992). During the breeding season, pied flycatchers are in many ways ecologically similar to great tits: they breed in the spring in enclosed nest holes in forests and feed their offspring with a high proportion of caterpillars (Lack, 1966; Sanz, 1998). However, outside the breeding season they

live completely different lives: they leave Europe immediately after the breeding season to go to their wintering grounds in West Africa and return just before they start breeding. Pied flycatchers breeding in western Europe do not return before mid-April and leave again at the end of July, spending most of the year (September–March) in Africa. We know relatively little about their life in Africa: they live in savannah woodland and Guinea-type woodland, around 10° north of the equator, and forage exclusively on arthropods. In winter they seem to be philopatric, returning to the same site year after year (Salewski et al., 2002), which is in contrast to the breeding grounds where males are philopatric, but females and young birds often disperse to other breeding sites. Before they migrate from the breeding grounds they moult all their feathers, and before the onset of spring migration they moult their body feathers again to obtain their breeding plumage. This migratory life style makes pied flycatchers an interesting contrast to the great tit studies described above.

We have only a single study of long-term effects of climate change on the breeding phenology of the pied flycatcher and the timing of the peak caterpillar abundance, in the same area in The Netherlands as the great tit study. Pied flycatcher chicks hatch about 10 days later than great tit chicks, and whereas most great tits hatch late relative to the caterpillar peak, this is even more common for pied flycatchers. Early broods of flycatchers can still profit from the late part of the caterpillar peak, however, and chicks in these nests are fed with more than 70% caterpillars. Chick diet, however, changes rapidly with date: chicks that hatched 10 days later get less than 10% caterpillars in their diet (Figure 11.5c). This change in diet is also reflected in the fitness effects of hatching date: early broods have far more chicks that recruit to the breeding population than late broods (Figure 11.5a). It is not that these late-born chicks are starving in the nest: they are fed with a more varied diet and they grow only slightly slower on this diet, but for one reason or another they return far less often as breeders.

The effect of two decades of climate change on pied flycatcher breeding dates in The Netherlands has been very similar to that on great tits in the same area: they advanced their breeding dates by about half a day per year, but the advance in the date of the caterpillar food was even stronger (0.75 day/year, Figure 11.4). Thus, the interval increased between the caterpillar peak date and the date at which most flycatchers had young in their nest. This stronger asynchrony was also reflected in the change in selection for breeding date: in the early 1980s, birds that laid at the average date had highest fitness, whereas in the course of the following two decades the earliest broods were doing increasingly well compared with late broods (Both and Visser, 2001; Drent et al., 2003). Thus, pied flycatchers also adjusted their breeding dates to warmer springs, but not enough to keep up with their food supply.

Their complex annual cycle may explain why flycatchers failed to respond more to climate change. At the wintering grounds, they cannot easily (if at all) predict when spring starts at their distant breeding grounds, thousands of kilometres away. It is not just the distance that makes it impossible, but also the time, because it takes them at least 3 weeks to migrate from winter to breeding grounds. We know little about what cues trigger them to start migration in the field, but laboratory studies have clearly shown that they use at least photoperiod to prepare for migration (Gwinner, 1996). This means that they use an internal calendar, and natural selection has shaped this calendar response such that given the average migration time, birds on average arrive at the moment that maximizes their fitness. This is not too early, because insects do not emerge when it is cold, and an obligate insectivore such as a flycatcher would die. It also should not be too late, because then the caterpillar peak is missed completely, and birds fail to breed successfully. There is just a short time window that is optimal, and it is surprising that flycatchers (and many other long-distance migrants) manage to arrive neither too early nor too late, although sometimes the timing is wrong, and migrants hit cold weather after arrival, causing high mortality (Newton, 2007). In some swallow species, it has been shown that birds arriving early are at risk from extremes in spring weather (Møller, 1994; Brown and Brown, 2000). The reason why flycatchers breed later than tits and cannot fully profit from the caterpillar peak probably lies in this survival cost early in the season.
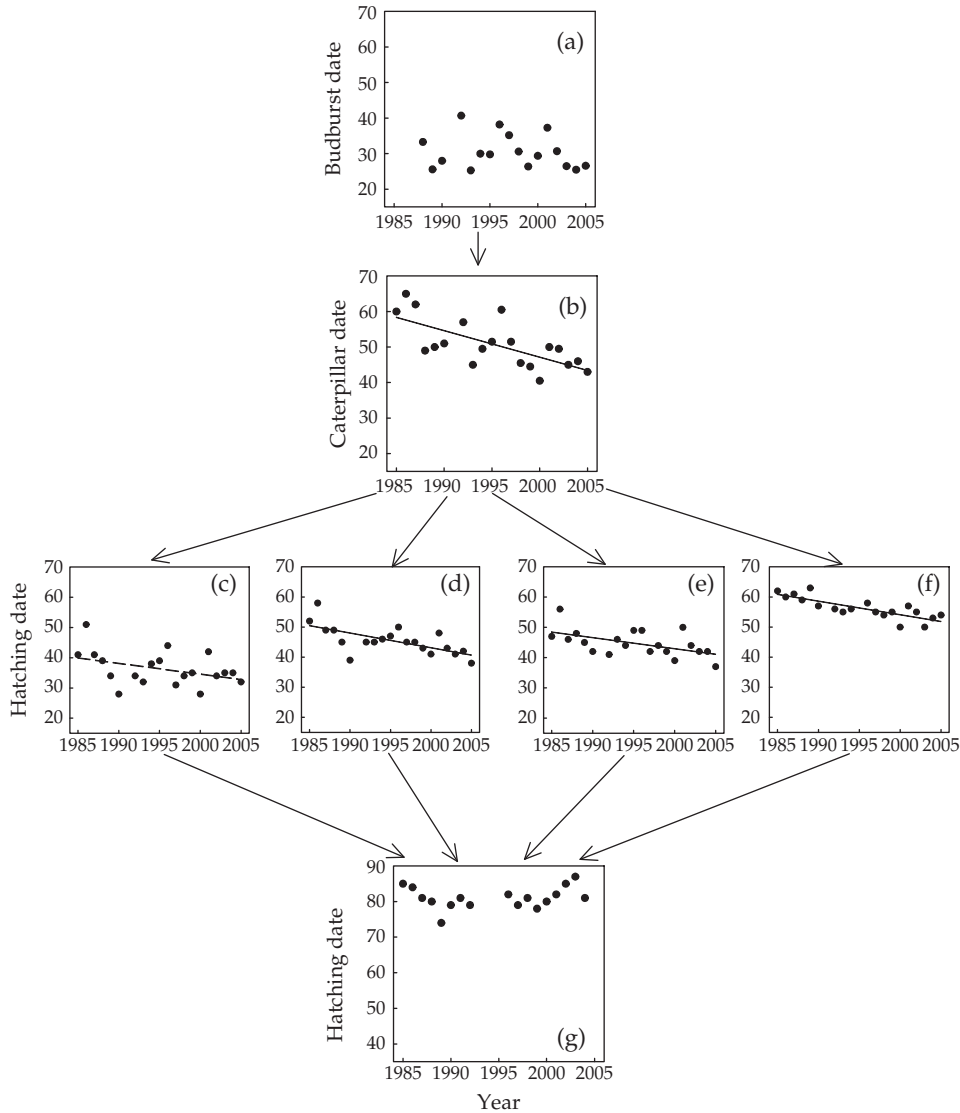
Figure 11.4 Trends in (a) annual budburst, (b) caterpillar peak date, mean hatching dates of (c) coal tits, (d) blue tits, (e) great tits, (f) pied flycatchers, and (g) hatching dates of sparrowhawks in the period 1985–2005 on the Veluwe area, The Netherlands. Reproduced from Both *et al.* (2009).

Spring arrival dates of pied flycatcher males in western Europe have not clearly advanced, which could explain why their breeding dates did not advance in synchrony with the food peak (Both and Visser, 2001; Both *et al.*, 2005; Hüppop and Winkel, 2006). There are some difficulties with these data and the interpretation, which deserve attention. The data pertain to early arriving males because these can be easily monitored, whereas after a couple of

days one easily loses track of which individuals have been present and which just arrived. There are no long time series of arrival of a large fraction of breeding populations available, and it may very well be that the first birds have not advanced arrival, whereas later birds did so, and hence they are now arriving more synchronously. This is partly supported by the breeding data: we know that at least at this moment for females there is a tight correlation
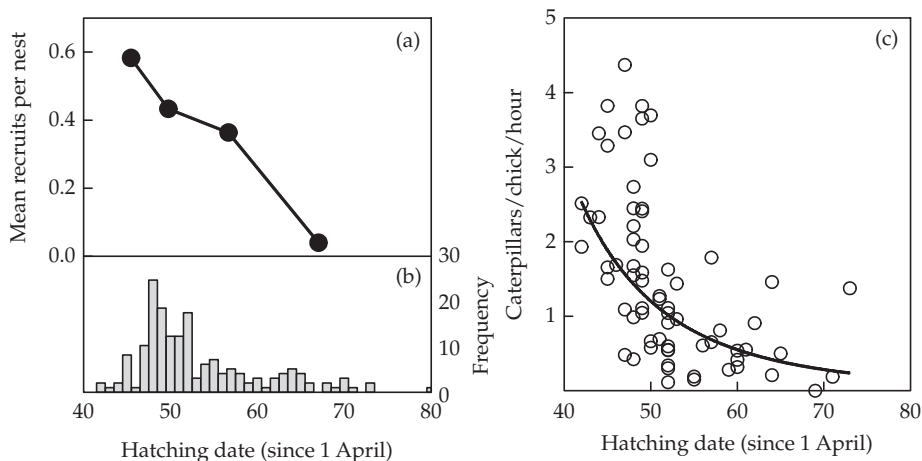
Figure 11.5 Effect of hatching date on (a) fitness and (c) diet composition of pied flycatchers during the 2007 breeding season in Drenthe, the Netherlands. (b) The frequency distribution of hatching dates during this year. This year the caterpillar peak was exceptionally early, with the peak date on 4 May (C. Both, unpublished data).

between arrival and first egg-laying date. This differs among years, with a shorter interval between arrival and laying in warmer springs and a longer one in colder springs. The mean laying date of pied flycatchers did not just advance over time, but it also became more peaked because late breeders advanced more (Both *et al.*, 2009a), which could be a sign of late birds advancing their arrival, in contrast to early arrivals. Laying date also advanced because birds shortened the interval between arrival and laying, and at present many females start laying about 5 days after arrival, which is about the minimal time needed for producing eggs. This suggests that arrival date is indeed constraining laying date, and we think that this is an important reason why flycatchers did not advance their laying date in synchrony with the caterpillar peak. They are just insufficiently flexible in migration date to react to warmer springs on their breeding grounds, which fits nicely with the idea that migration dates are mostly governed by photoperiod.

The hard-wired start of migration could explain why pied flycatchers have not adjusted their arrival time and hence lagged behind the food peak with their breeding time. This is in stark contrast with many other studies, which recorded that migrants have advanced their arrival dates in the last few decades (see, for example, Hüppop and Hüppop,

2003; Ahola *et al.*, 2004; Lehikoinen *et al.*, 2004; Marra *et al.*, 2005; Jonzén *et al.*, 2006; Rubolini *et al.*, 2007; Gordo, 2007). It is unclear whether these responses were due to an earlier start of migration or due to faster migration. Support for an increased speed of migration comes from correlations between temperatures *en route* and arrival or passage dates (Hüppop and Hüppop, 2003; Ahola *et al.*, 2004; Marra *et al.*, 2005), but data are lacking for changes in departure dates from tropical wintering grounds. Although the advances in arrival dates are thus not inconsistent with a hard-wired photoperiodic start of migration, there is a lot of variation around trends in arrival dates of migratory birds, both between and (to a lower extent) within species (Rubolini *et al.*, 2007). For example, why did Dutch pied flycatchers not advance their arrival date, in contrast to Finnish pied flycatchers, which did (but did not shift their breeding date!) (Ahola *et al.*, 2004)? The most likely reason is that these populations migrate at different times in the season: Dutch flycatchers pass through northern Africa on average around 20 April and Finnish flycatchers about 15 days later (Both and te Marvelde, 2007). Although this may not seem like a big difference, for the birds it probably is because temperatures throughout Europe have not increased equally in time and space. The period at which Dutch birds migrate from North

Africa to their breeding areas has not warmed, and advancing arrival consequently means encountering colder conditions *en route* and at arrival. For Finnish birds this is different: temperatures have risen during their journey through Europe, and consequently they can migrate faster and arrive earlier at their breeding grounds. Interestingly, after arrival in Finland, temperatures have not increased, and birds have not changed their laying dates. They are thus waiting longer before commencing breeding than in the past, again the opposite to the Dutch situation.

There are striking similarities and differences between the tit and the flycatcher studies, but one major conclusion from both studies is that even within a single species the effects of climate change can differ dramatically between populations. The important similarity is that the timing of phenology at one trophic level may change at a different rate compared to timing at another trophic level, and this may have beneficial (Wytham great tits) or detrimental effects (Dutch tits and flycatchers) on individual birds. So far we have not been considering whether population sizes are also affected by becoming more or less mistimed due to climate change.

11.3.3 Barnacle geese and vegetation growth

Small herbivores depend on highly nutritious vegetation, which means that they preferentially select areas with growing vegetation as foraging sites. High Arctic breeding geese make use of different periods of new vegetation growth when they migrate up to their northern breeding sites, enabling them to store sufficient resources for early breeding when the tundra is still snow covered (van der Graaf *et al.*, 2006; Madsen and Klaassen, 2006). At the breeding grounds there is a short period of availability of high-quality vegetation, and geese hatching their offspring at this time have the highest fitness (van der Jeugd *et al.*, 2009). Hatching too late has severe fitness consequences because chicks survive badly after fledging. Although shifts in goose phenology relative to the food peak on the tundra have not been shown, gosling growth was remarkably lower during warm summers (Dickey

et al., 2008), suggesting that climate change may cause a mismatch here as well.

During the last few decades, barnacle geese *Branta leucopsis* have expanded their breeding ranges to the south and are now breeding in areas that once were only used for wintering or stop-over during migration. On the island of Gotland in the Baltic barnacle geese have been studied for decades, and during this period the geese started their laying progressively earlier during spring. At the same time, selection for early breeding increased, suggesting that the advance of breeding date lagged behind the advance in plant growth phenology (van der Jeugd *et al.*, 2009). Interestingly, the Baltic population of barnacle geese grew strongly during this period despite increased mismatch.

11.4 Population consequences

World-wide bird populations are under pressure because of ever-expanding human activities resulting in habitat destruction, degradation, and fragmentation. Climate change is an additional factor that could cause some species to increase and others to decline. One clear effect of climate change on bird populations is that ranges shift over latitudinal trends (Thomas and Lennon, 1999; Brommer, 2004; Chapter 18), and on local scales species that are at their lower latitudinal range margin decline, whereas species increase that are at their upper range margin (Reif *et al.*, 2008). On a European scale, species that have a low thermal maximum determining their distribution (i.e. more northern species) declined more strongly than species having a high thermal maximum (Jiguet *et al.*, 2010). The reason for these differential population trends and range changes could be both physiological (individuals cannot cope with the heath) and ecological. The ecological causes for climate change-related declines could include increases in predator/parasite abundance, inter-specific competition, lower absolute food abundance, but also differential changes in phenology across trophic levels (Chapters 15, 16, and 18). At present, it is impossible to judge the relative contributions of these different causes, especially because so far the scientific results are mainly descriptions of patterns in abundance

changes rather than measures of ecological relationships that may be important.

As already shown, climate change could lead to a stronger mismatch between breeding seasons of birds and their prey, resulting in fewer offspring produced, which subsequently could lead to declining population sizes. This detrimental effect of mismatch is not easily demonstrated because populations could decline for many other reasons as well, or could even grow, if other limiting factors are improving at the same time. For great tits it is highly conceivable that increased mismatch would not easily result in declining populations because population sizes are to a large extent determined by winter weather and especially winter food (Perrins, 1965; van Balen, 1980). Climate change may result in fewer chicks being raised successfully (although this has not really been shown!), but simultaneously may improve winter survival through increased winter temperatures and higher food abundance. The mean number of recruits produced may therefore not decline. Furthermore, density-dependent feedbacks may ameliorate the reduction in number of offspring by improving the survival of offspring (and adults) after fledging (Grøtan et al., 2009).

In pied flycatchers, increased mistiming seems to be responsible for geographic variation in population trends within The Netherlands (Both et al., 2006). Although the evidence is indirect, the first observation was that some nest box populations declined strongly between 1987 and 2004, whereas other populations were stable or even increased. The reason was not competition for nest boxes, and it also did not seem to be deterioration of habitat per se, because great tits and blue tits Cyanistes caeruleus did not show declines (or increases) in areas where flycatcher populations plummeted. It was mostly in the richer deciduous forests that populations crashed, whereas no such effect was found in mixed or coniferous forests (Visser et al., 2004). If an increased mismatch was the cause, we expected that in areas with a population decline the caterpillar peaks were earlier, or flycatchers bred later than in areas without such a decline. This was indeed what we found: in forests with the earliest food peaks flycatchers had virtually disappeared. Other areas had caterpillar peaks that were more than 2 weeks later, and in these areas flycatcher populations were still thriving. Unfortunately, we were not always able to relate this to flycatcher phenology at the time because flycatchers were no longer present in the early forests. With earlier data on breeding phenology, we could show that populations that had adjusted their mean laying date least to spring temperature had declined the most (Both et al., 2006). These areas had the highest caterpillar density, and flycatchers in the past probably had profited from the final part of this high caterpillar peak. Since their arrival in spring had not changed whereas the caterpillar peak did advance, these rich habitats became unsuitable. It was unclear whether this population decline in early forests was due to low breeding success or the result of individuals abandoning these former breeding grounds and moving towards later forests, although on a nationwide scale there was a decline as well. These data are strongly suggestive that populations could decline as a result of becoming more mistimed with their food supply through climate change.

Is the insufficient response to climate change in flycatchers unusual, or are other species as vulnerable, which species' attributes are expected to make them vulnerable to climate change, and are there species living in more and less sensitive habitats? One reason why flycatchers are sensitive is because of their migratory life style, and if indeed departure decisions in long-distance migrants are mostly steered by an internal calendar (modified by photoperiod), it is expected that these species will be more sensitive to climate-related shifts in their food peaks than resident species. Among migrant birds there is consistency among species in how strongly they have advanced their arrival dates during recent decades (Rubolini et al., 2007), and European species with no change in arrival date declined more between 1990 and 2000 than species showing a clear advance (Møller et al., 2008). This result could suggest that increased trophic mismatches are causing slowly responding species to decline, but it is also possible that declining species respond differently with their migration timing to non-declining species (Miller-Rushing et al., 2008).

The effects of increased trophic mismatches have mainly been studied in habitats that are characterized by short seasons with a highly

peaked food availability, like temperate forests (the tit and flycatcher examples), but also arctic tundras (Tulp and Schekkerman, 2008; Dickey *et al.*, 2008; van der Jeugd *et al.*, 2009), or higher altitude moorlands (Pearce-Higgins *et al.*, 2005). In these habitats, timing is at a premium, and if a bird misses the short time window, it will fail for that season. All habitats have a certain seasonality, but they can differ substantially in how wide food peaks can be for the birds living there. Marshes have a very wide food peak, and marsh-inhabiting migrants such as reed warblers *Acrocephalus scirpaceus* have in fact profited from climate change: They can start breeding earlier nowadays because reeds grow faster, providing safe nesting sites earlier in the year (Schaefer *et al.*, 2006; Halupka *et al.*, 2008; Dyrcz and Halupka, 2009). In a Polish population, the time window for breeding also increased, allowing more pairs to successfully raise two broods a year (Halupka *et al.*, 2008), in contrast to a German population where the duration of the breeding season was reduced, but reproductive success also increased (Schaefer *et al.*, 2006). Again populations of the same species show different responses! More generally, we have to be aware that habitats differ largely in width of seasonal food peaks and that the strongest effects of climate change on unequal phenological responses of different trophic levels depend on these habitat characteristics.

Marshes differ in seasonality from forests, and long-distance migrants may be more vulnerable to trophic mismatches than residents because their annual cycle constrains adjustment to advanced phenology in their breeding sites. To test this, we compared population trends of common insectivorous bird species in marshes and forests in The Netherlands between 1984 and 2004. Long-distance migrants all declined in forest, whereas such an effect was not observed for long-distance migrants in marshes. This effect was also present within some generalist long-distance migrants, which all showed a decline in forests, but an increase in marshes. In resident and short-distance migrants, we did not find any difference between trends in forest and marsh: on average they increased in both habitats to a similar extent, suggesting that there was not a general deterioration of forest

habitats (Both *et al.*, unpublished data). These data are consistent with the hypothesis that the effect of climate change on trophic mismatches is most prevalent in highly seasonal habitats and that species that have difficulties responding to advances of their food suffer the most. Thus, climate change-caused trophic mismatches may start to kick in as an important additional reason why long-distance migrants decline, and we are just at the start of even greater climate change in the next decades, which affects not just breeding grounds but also wintering areas.

11.5   Beyond two trophic levels

All the patterns described so far have been overly simplistic: they included two species (or at best two groups of species), with the predator trying to match its timing with the timing of their prey. However, ecology is far more complex than that, and here I present an example of the complexity that we should start to consider in terms of the effects of shifting trophic relationships and climate change (Chapter 18). Let us just think about three trophic levels, say a passerine bird eating a caterpillar and the passerine being eaten by a sparrowhawk. What the passerine should do is to time its hatching to the caterpillar peak, but also try not to match its fledging date to the nestling stage of the sparrowhawk. The sparrowhawk, on the other hand, should try to match its nestling time to the peak in fledging passerines, to have maximal food for its offspring. Caterpillars should try to have pupated before the peak in food requirements of passerines to reduce the likelihood of ending up as bird food. Thus, caterpillars should try to advance their phenology more than that of passerines if they can (this depends on the phenology of their food again). The optimal breeding date of passerines depends not just on their food but also on the timing of their predators. One could imagine that a passerine might breed a bit too early to let its offspring fully profit from the food peak, and in this way it may reduce predation on its offspring after fledging. If the timing of the sparrowhawk responds less to climate change than the passerine (Figure 11.4; see also Nielsen and Møller, 2006; Both *et al.*, 2009a), this may subsequently affect synchrony

between passerine and caterpillars. In this case, passerines could improve synchrony with their prey. The same argument holds if sparrowhawks decline: this could affect the optimal timing for passerines. We should start considering these more complex interactions between timing of multiple trophic levels because they can lead to counter-intuitive responses to climate change (Both *et al.*, 2009).

Within the same trophic level, species often interact for a certain resource, like food, and so far we have ignored inter-specific competition. Without pretending to cover this in any detail, the consequences of timing of one bird species not only depend on timing of its food but also on timing of its competitors. Blue tits eat smaller caterpillars than great tits and consequently can breed a bit earlier, and their breeding density therefore affects the reproductive success of great tits because they deplete part of caterpillars, but not vice versa (Dhondt, 1977). If these species would for one reason or another differ in phenological response to climate change, this could also affect reproductive success of other species.

Finally, unequal responses of different trophic levels may alter ecosystem functioning because some species may be released from predation by insufficient adjustment of their predators (Chapter 18). So far there are no good data showing such effects, but if insectivorous birds exhibit lower predation pressures on their caterpillar prey, then this could lead to outbreaks, damaging the trees on which they forage (Marquis and Whelan, 1994; Sanz, 2001). The strength of these effects depends not just on birds as predators, but of course also on a multitude of other interacting species, and especially if they are insects with a similar rapid response to warming they may respond as strongly as their prey, keeping them in check.

11.6   Conclusions and future directions

Adjustment to climate change is constrained in several bird species, leading to mismatches with their food, which could explain part of long-term population trends. We most likely will be witnessing accelerating climate change during the next few decades, and at present it is unclear how ecosystems will react. Adjustment to these new circumstances will probably require evolutionary responses (Møller *et al.*, 2004; Visser, 2008), but at present these have not been found in birds (Gienapp and Merilä, 2007). Such evolutionary responses could be working on genetic variation that may be present in populations (e.g. for laying date; Sheldon *et al.*, 2003), but insufficient responses seen so far suggest that we should have seen evolutionary changes happening already. Dispersal of individuals to more northern areas may also be an important mechanism of evolution because these individuals may, for example, introduce additional genetic material for an earlier breeding date.

It is important to emphasize that populations of the same species could show very different responses to climate change, as do different species. This means that we are just at the very beginning of understanding how climate change affects trophic relationships, and predictions of how any one species will be affected are impossible. There is an enormous need for more detailed and long-term ecological studies, examining how climate affects the timing and also abundance of different trophic levels, how intricate trophic levels are linked, and how individual fitness relates to the timing and abundance of lower and higher trophic levels. These studies are needed in species not yet studied, but also more replications of well-studied species like tits or flycatchers are important because they will lead to a better understanding of spatial and temporal variation in ecological responses to climate change. Studies should not just measure the timing of food availability and of breeding but should also focus on a quantitative approach to how food abundance at any time of the season affects fitness, the importance of prey abundance vs. prey quality, whether food peaks are changing in width, and whether birds can switch to alternative prey. Furthermore, we should aim to study not just a single trait (e.g. laying date) at a time, but more phenotypic traits should be considered simultaneously (e.g. energy expenditure, timing of migration, and morphology). Although politicians want quick answers about the ecological consequences of climate change, we need good science addressing the potential impacts, and for this reason it is never too late to start a new long-term study.

Currently, we can make certain predictions about the habitats and species that will be most vulnerable to the effects of trophic mismatches. Species living in habitats characterized by a short peak in food availability are expected to be most affected. Furthermore, species that are least flexible in their phenological response are vulnerable, and these include species with a long time needed for laying and incubation, and long-distance migrants. The population declines that we are now observing in migratory species that have adjusted their arrival dates very little to climate change (Møller *et al.*, 2008) and are breeding in the most seasonal habitats (Both *et al.*, unpublished data) may be just the start of even more severe ecological changes ahead.

11.7   Acknowledgements

11.8   References

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