Climate change and the advance of laying dates in Pied Flycatchers *Ficedula hypoleuca*: the Harz and the rest of Europe

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It is not easy to show how birds react to climate change. For this, one needs long lasting population studies, and preferentially in areas both with, and without local temperature change. Here data for pied flycatchers *Ficedula hypoleuca* are presented, showing that they have advanced their breeding dates during the last 25 years in the Harz and in the Netherlands. Pied flycatchers lay earlier in warmer springs, but springs have not warmed to a similar degree across their breeding range. As a consequence, pied flycatchers have only advanced their breeding dates where temperatures increased, without any advance in laying dates in Scandinavia and Russia. The response to climate change may differ between species, as the comparison between European starlings *Sturnus vulgaris* and pied flycatchers shows. Starlings breed earlier in the year, and temperatures during this period have changed differently, and on the basis of temperature trends starlings were expected to advance their breeding dates in Russia, but not in central Europe. Climate change thus affects species differently at different places of their breeding range.

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The time scales that we experience depend largely on our age. As a child, one of the most striking features of nature is the change of seasons. When one grows older, nature appears to change more than just seasonally: the trees in the garden grow, and where once all the trees were cut, new saplings sprout and a forest grows. When one comes of age, the landscape appears no longer as it was in one's youth. Some changes, such as the rapid transition from a rural to an urban landscape, are obvious. Others are more subtle. During a hot summer month most of us 'believe' in global warming, but when the next summer is miserable, it is difficult to judge from mere experience whether we witness a directional change or not. And of course there are phenomena with time scales that we cannot directly observe during a lifetime.

The longer the time scale, the more difficult it is to detect how changes affect the life of birds. The fossil record is usually unhelpful, the genetic record hard to access, and on the ground we are often too late to observe how birds have responded. The moment we realise that the world is changing, many birds have already anticipated or disappeared from the scene. Glimpses from the past can be gleaned from comparisons between published data and current observations, and the best observations come from determined people that have collected the same data year after year in a consistent way. With respect to the arrival and breeding dates of birds we are fortunate that amateur and professional biologists have collected data for decades. One of these determined persons is Herwig Zang, who collected impressive long-term data on reproductive parameters of among others, pied flycatchers *Ficedula hypoleuca*. His continuous effort for decades, together with similar efforts of other amateur and professional ornithologists across Europe, allow us now to give an impressively complete picture of how flycatchers have adapted their breeding time to climate change.

During the 1990's the first evidence was published that birds were advancing their laying dates in response to climate change. The first decade-long time series of laying date were published from the UK, where many species

have advanced their egg laying date (CRICK & SPARKS 1999, CRICK et al. 1997, MCCLEERY & PERRINS 1998). There were some species that had exceptionally good data on annual laying dates from several populations, because they were easily accessible because they breed in nest boxes. One of these was the migratory pied flycatcher and at the turn of the century three separate studies did show that since 1980 pied flycatchers in both the UK (SLATER 1999), Germany (WINKEL & HUDDE 1997) and the Netherlands (BOTH & VISSER 2001) were laying progressively earlier over two decades. Although this pattern nicely fitted the idea of ongoing climate change, it is not easy to actually prove that climate change causes this change in laying date, rather than some other changes in the environment. In fact, there was indeed also a population in Russia that did not show any change in laying date over the years (SOKOLOV 2000), suggesting at least that it was not a uniformly global change in laying dates. One of the points I want to show here with the use of data of the Harz flycatcher population collected by H. Zang, together with other flycatcher populations across Europe, is that climate change indeed is the most likely cause of the advance in laying dates in birds.

Global climate change has the connotation of rising temperatures at all places and during the whole year. I want to stress that this is not the case (IPCC 2001), and this could have enormous consequences of how laying dates of birds are affected by local climate change, depending where and when they breed and where and when they migrate (SPARKS & TRYJANOWKSI 2007). More importantly, also within species, populations differ in their response, because they breed at different places and other periods of the year. We explore the effects of this spatial-temporal variation in temperature changes during the last 25 years on breeding dates in both a long-distance migrant, the pied flycatcher, and compare this with the short-distance migratory European Starling *Sturnus vulgaris*.

Methods

First I want to show the trends in annual median laying dates of two pied flycatcher populations that were both collected by dedicated amateur bird researchers. The first is the well-known population of Herwig Zang, which started in 1970 and has been continued to the present date. This population is located in mainly beech forest at 51.53° N and 10.53° E, and during most of the period 1980-2003 about 400 nest boxes were provided in about 36 ha forest, which contained on average 43 pairs of pied flycatchers. The second population is studied by Bert Blaauw (now 87 years old!) and his team of co-workers in boswachterij Staphorst in the Netherlands (52.37° N, 6.17° E), and this population study started in 1960. This area contains about 1000 nest boxes with annually on average 240 breeding pairs of pied flycatchers in the period since 1980.

Next I want to compare the trends we found in these populations with other populations of both pied and collared flycatchers everywhere in Europe. To avoid any reporting bias in the response of flycatcher populations to climate change we used all populations we knew for which accurate laying dates were collected for at least 10 years in the period 1990-2002 (BOTH et al. 2004). Longer time series are used only from 1980 onwards, since most warming occurred after this year (IPCC 2001). In the study sites nest boxes were checked weekly in most instances, and the laying date of each nest was calculated assuming that one egg was laid every day. In cases where the laying date could not be determined this way, but the hatching date was known (only in three study sites, and a rather small percentage of nests within these sites), we calculated the laying date by assuming 13 days of incubation (beginning on the last egg) and again that one egg was laid per day. For each year and study site combination, we calculated the median laying date. Only first broods were included, which excluded broods of females that were previously known to have started a brood in that year, as well as broods that were started later than 30 days after the very first brood in that year for each study site. The first year that nest boxes were provided on a study site is excluded from the analyses, because newly established populations contain a high proportion of young birds that tend to lay later in the season (LUNDBERG & ALATALO 1992).

Study sites covered most of the species' breeding range, from Spain in the south to Northern Finland in the north, and from Wales in the west to Moscow in the east. Study sites were not spread evenly over Europe because we used

existing datasets collected for other purposes. Daily mean temperatures were obtained from meteorological stations close to the study sites. Details on how we averaged temperatures for each study site and over which period are given in BOTH et al. (2004). What I aim to give here is not so much the actual responses of pied flycatcher populations in the 25 different study sites, but want to use all these data from laying dates, and from meteorological stations across Europe to show the geographic variation in trends in laying date of pied flycatchers, and compare this with a resident or short-distance migrant bird species that breeds earlier in the season: the European starling (see for details BOTH & TE MARVELDE 2007).

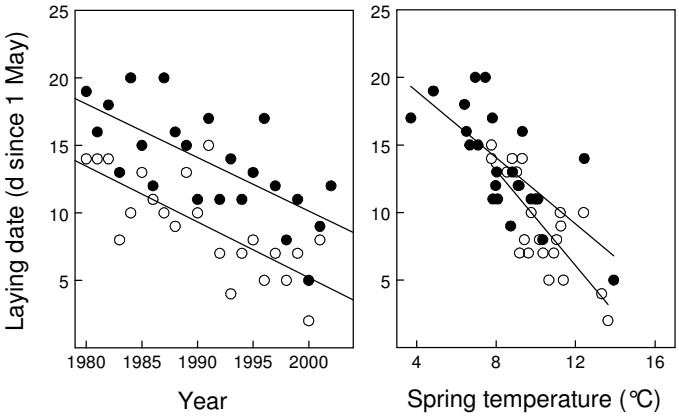

Fig. 1: Annual median laying dates of two Pied Flycatcher *Ficedula hypoleuca* populations during the last 25 years. (left) trends over the years, (right) effect of local annual mean spring temperature on laying date. Closed symbols: Harz (D), open symbols: Staphorst (NL). – *Mittlerer jährlicher Legebeginn in zwei Populationen des Trauerschnäppers Ficedula hypoleuca während der letzten 25 Jahre. Links: Veränderungen über die Zeit, rechts: Einfluss der lokalen jährlichen mittleren Frühlingstemperatur auf den Brutbeginn. Gefüllte Symbole: Harz (D), offene Symbole: Staphorst (NL).*

Results and Discussion

Both in the Harz and Staphorst the pied flycatchers did clearly advance their laying dates between 1980-2003 by about 9 days (fig. 1). This was a rather gradual change over this period of time. Whereas both areas are at about the same latitude, the birds in the Harz were breeding four days later, because they bred at a higher altitude. This trend in laying date was related to the trend to higher temperatures in spring, and indeed the annual laying dates were clearly earlier in warmer than in colder springs for both populations (fig. 1). Note that although the birds in the Harz were laying later, they also on average bred at lower temperatures than the birds in Staphorst. The advance in laying dates, and the strong correlation with local spring temperatures does suggest that indeed climate change is the cause of these changes.

In a second step we compared 25 time series of laying dates of Ficedula flycatchers across Europe. In contrast to the two populations shown above, only 9 of these 25 populations showed a significant advance in laying date (BOTH et al. 2004). This suggests that it is not just a global pattern that pied flycatchers are advancing their breeding dates, but there is clear geographic variation in the response: in central and western Europe pied flycatchers have advanced their laying dates, whereas in most of Scandinavia, Russia and Spain no advance in laying dates was observed. The explanation for this is that the spring temperature just at the moment of egg laying in these areas did not increase to any extent, or even decreased (fig. 2a). The geographic variation in responses of pied flycatcher laying dates is thus due to temperatures changing at different rates (and even directions) in different parts of Europe.

Climate change has not just led to variation in temperature trends between areas, but also within areas, some periods have warmed more than others. This can be nicely seen if we compare the map of predicted laying date changes in starlings and pied flycatchers (fig. 2). Starlings start laying about three weeks earlier than flycatchers, and therefore they experience different temperatures during the reproductive period. In areas where pied flycatchers have clearly advanced laying dates (e. g. central Europe) the starlings were not predicted to have changed their laying date, because temperature before laying did not increase in these areas. In Scandinavia the pattern is again diffe-

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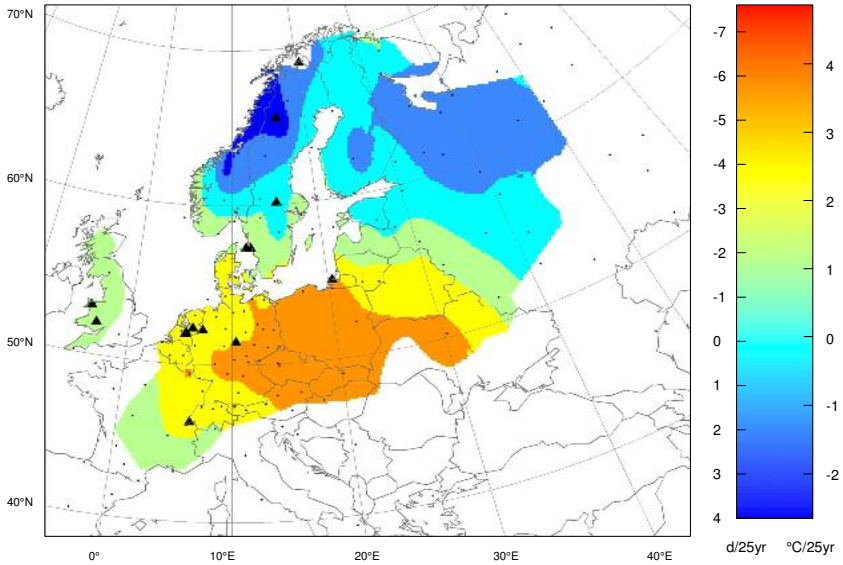

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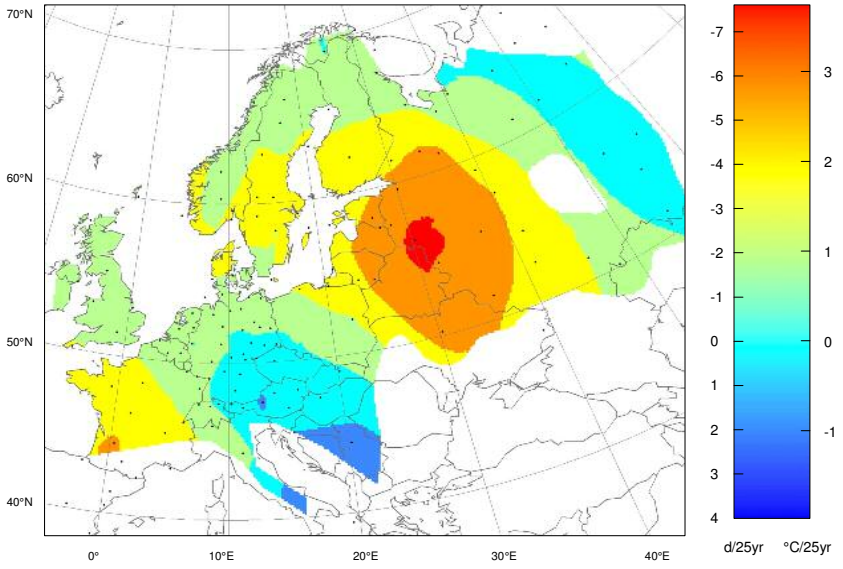

Fig. 2: Spatial variation in predicted laying date trend (1980-2004) in Pied Flycatchers *Ficedula hypoleuca* (a) and European Starlings *Sturnus vulgaris* (b). Dots represent the location of weather stations used in the calculation of the local trend in laying date on the basis of temperature, and triangles are the sites where time series of pied flycatcher laying date originate. – *Räumliche Variabilität im vorhergesagten Trend des Brutbeginns bei a) Trauerschnäpper Ficedula hypoleuca und b) Star Sturnus vulgaris. Punkte bezeichnen Wetterstationen, die für die Berechnung des lokalen Trends beim Brutbeginn auf Basis der Temperaturänderungen herangezogen wurden. Dreiecke bezeichnen die Orte, an denen Zeitreihen zum Brutbeginn des Trauerschnäppers ermittelt wurden.*

rent, where flycatchers have slightly delayed laying and starlings advanced laying. This variation was also partly observed in laying date changes in great tits *Parus major* and blue tits *Parus caeruleus* (Visser et al. 2003). Our data from long-term studies of nest box breeding passerines thus have allowed us to show that birds are really affected in their laying date by climate change, but that this differs among sites because of different patterns in warming, and between different species that breed at different times in the year.

The mere fact that birds change their laying date to climate change, does not automatically mean that this response is also sufficient to keep up with this environmental change. This brings me to the question why birds breed at a particular moment in the year. For forest breeding passerines the most important reason to breed in spring is that caterpillars and other herbivorous insects are superabundant during a short period when the leaves are young and fresh. If the birds can match the timing of when they need food most for their nestlings with the time of maximal availability, they can raise a large successful brood. If they fail to do so, they produce fewer offspring for the next generation (Perrins 1970). As a result of climate change, this caterpillar peak is advancing at least in western Europe, and in the Netherlands this advance is stronger than the advance in laying dates of both great and blue tits and pied flycatchers (Visser et al. 1998, Both & Visser 2001, Both et al. 2009). Interestingly, in the UK the great tits respond slightly stronger than the caterpillars (Cresswell & McCleery 2003), again indicating that responses in timing of different trophic levels could differ quite a bit across the continent.

The last two questions I want to address here is why the flycatchers have not responded sufficiently with their laying dates to the advance in the caterpillar peak, and whether this could be a cause of the decline in numbers in some areas. One of the reason why the flycatchers have not advanced their laying dates more is most probably because they have not adjusted their spring arrival dates sufficiently. Compared with the laying dates, we have rather poor data on arrival dates of pied flycatcher populations as a whole. Data on arrivals of the first males or the first cohort of males, has shown that both in Germany (Hüppop & Winkel 2006) and the Netherlands (Both et al. 2005) spring arrival has not advanced since 1980. It may however be, that part of the late birds, and especially females, have advanced their arrival, and that as a consequence the median laying date also could advance. At the moment, birds that arrive start immediately breeding, and for a further advance in breeding dates an advance in arrival dates is necessary. However, the problem for these birds is that they do not know at their African wintering sites when spring starts at their breeding grounds, and therefore they probably have difficulties in responding to climate change. Because these birds use day length variation (probably amongst other cues; Gwinner 1996), an appropriate response to climate change is not very easy.

Do populations of pied flycatchers decline as a result of climate change, and may this also be the reason why Herwig Zang has seen his population decline? I do think that the insufficient response relative to the caterpillars indeed is part of the reason of the local decline in flycatcher populations. In the Netherlands we have seen the species declining more strongly in rich deciduous forest, compared to mixed pine and oak forests (Visser et al 2004). In these rich deciduous forests the caterpillar peak in oak trees also happens to be earlier than in the mixed forests, and the decline in local flycatcher populations was up to 90 % in forests with such early food peaks (1987-2003), whereas the declines were only marginal in areas with late food peaks (Both et al. 2006). This decline is probably not confined to flycatchers, but may be an important reason why so many forest breeding long-distance migrants have declined during the last decades. This decline probably continues if the birds do not manage to adapt their timing sufficiently to the timing of their main food source.

Acknowledgements

I want to express my great gratitude to Herwig Zang who I admire strongly because of his continuous effort in collecting a really great data set on pied flycatcher. He has been very willing in sharing his data for this project, and without him and all the other collaborators across Europe we now would not have understood as much about how birds adapt to climate change. I think

Herwig must be held up as an example to younger researchers to start their population study and continue long and work as meticulously as he is still doing.

Zusammenfassung – Klimawandel und die Vorverlegung des Brutbeginns beim Trauerschnäpper *Ficedula hypoleuca*: Der Harz und der Rest von Europa

Es ist nicht leicht zu zeigen, wie Vögel auf den Klimawandel reagieren. Dafür benötigt man langjährige Populationsstudien, bevorzugt sowohl aus Gebieten mit lokalen Temperaturveränderungen als auch aus solchen ohne. In dieser Arbeit werden Daten über den Trauerschnäpper *Ficedula hypoleuca* vorgestellt, die zeigen, dass während der letzten 25 Jahre der Brutbeginn sowohl in den Niederlanden als auch im Harz vorverlegt wurde. Trauerschnäpper beginnen in wärmeren Frühjahren früher mit der Brut, aber die Frühjahre sind nicht überall im Areal der Art gleichermaßen wärmer geworden. Eine Vorverlegung der Eiablage ist daher auch nur in solchen Gebieten erfolgt, in denen die Temperaturen anstiegen, nicht dagegen in Skandinavien oder in Russland.

Die Reaktionen auf den Klimawandel können auch zwischen Arten unterschiedlich sein, wie ein Vergleich zwischen Trauerschnäpper und Star *Sturnus vulgaris* zeigt. Stare brüten früher im Jahr, die Temperaturänderungen während dieser Zeit sind unterschiedlich gegenüber späteren Phasen im Jahr. Auf der Basis der Temperaturtrends wird erwartet, dass Stare in Russland zunehmend früher brüten, aber nicht in Zentraleuropa. Klimawandel wirkt somit auf Arten unterschiedlich in unterschiedlichen Gebietes ihres Verbreitungsgebietes.

References

BOTH, C., A. A. ARTEMYEV, B. BLAAUW, R. J. COWIE, A. J. DEKHUIJZEN, T. EEVA, A. ENEMAR, L. GUSTAFSSON, E. V. IVANKINA, A. JÄRVINEN, N. B. METCALFE, N. E. I. NYHOLM, J. POTTI, P.-A. RAVUSSIN, J. J. SANZ, B. SILVERIN, F. M. SLATER, L. V. SOKOLOV, W. WINKEL, J. WRIGHT, H. ZANG & M. E. VISSER (2004): Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proc. R. Soc. Lond., Ser. B 271: 1657-1662.

BOTH, C., R. G. BIJLSMA, & M. E. VISSER (2005): Climatic effects on spring migration and breeding in a long distance migrant. J. Avian Biol. 36: 368-373.

BOTH, C., S. BOUWHUIS, C. M. LESSELLS & M. E. VISSER (2006): Climate change and population declines in a long distance migratory bird. Nature 441: 81-83.

BOTH, C., & L. TE MARVELDE (2007): Climate change and timing of avian breeding and migration throughout Europe. Clim. Res. 35: 93-105.

BOTH, C., M. VAN ASCH, R. G. BIJLSMA, A. B. VAN DEN BURG & M. E. VISSER (2009): Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? J. Anim. Ecol. 78.

BOTH, C., & M. E. VISSER (2001): Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 296-298.

CRESSWELL, W., & R. H. MCCLEERY (2003): How great tits maintain synchronization of their hatch date with food supply to long-term variability in temperature. J. Anim. Ecol. 72: 356-366.

CRICK, H. Q. P., C. DUDLEY, D. E. GLUE. & D. L. THOMSON (1997): UK birds are laying eggs earlier. Nature 388: 526.

CRICK, H. Q. P., & T. H. SPARKS (1999): Climate change related to egg-laying trends. Nature 399: 423-424.

GWINNER, E. (1996): Circannual clocks in avian reproduction and migration. Ibis 138: 47-63.

HÜPPOP, O., & W. WINKEL (2006): Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migration routes. J. Ornithol. 147: 326-343.

IPCC (2001): Climate change 2001: The scientific basis. Contribution of Working groups to the Third Assessment report of the Intergovernmental Panel on Climate Change. Cambridge, UK.

LUNDBERG, A., & R. V. ALATALO (1992): The Pied Flycatcher. London.

MCCLEERY, R. H., & C. M. PERRINS (1998): Temperature and egg-laying trends. Nature 391: 30-31.

PERRINS, C. M. (1970): The timing of birds' breeding seasons. Ibis 112: 242-255.

SLATER, F. M. (1999): First-egg date fluctuations for the Pied Flycatcher *Ficedula hypoleuca* in the woodlands of mid-Wales in the twentieth century. Ibis 141: 497-499.

SOKOLOV, L. V. (2000): Spring ambient temperature as an important factor controlling timing of arrival, breeding, post fledging dispersal and breeding success of Pied Flycatchers *Ficedula hypoleuca*. Avian Ecol. Behav. 5: 79-104.

SPARKS, T. H., & P. TRYJANOWKSI (2007): Rapid (but differential) advance of spring arrival dates in two hirundines. Clim. Res. in press.

VISSER, M. E., F. ADRIAENSEN, J. H. VAN BALEN, J. BLONDEL, A. A. DHONDT, S. VAN DONGEN, C. DU FEAU, E. V. IVANKINA, A. B. KERIMOV, J. DE LAET, E. MATTHYSEN, R. H. MCCLEERY, M. ORELL & D. L. THOMSON (2003): Variable responses to large-scale climate change in European Parus populations. Proc. R. Soc. Lond., Ser. B 270: 367-372.

VISSER, M. E., C. BOTH & M. M. LAMBRECHTS (2004): Global climate change leads to mistimed avian reproduction. Adv. Ecol. Res. 35: 89-110.

VISSER, M. E., A. J. VAN NOORDWIJK, J. M. TINBERGEN & C. M. LESSELLS (1998): Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proc. R. Soc. Lond. Ser. B 265: 1867-1870.

WINKEL, W., & H. HUDDE (1997): Long-term trends in reproductive traits of tits (*Parus major, P. caeruleus*) and Pied flycatchers (*Ficedula hypoleuca*). J. Avian Biol. 28: 187-190.