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Authors: Coppack, Timothy, and Both, Christiaan

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PREDICTING LIFE-CYCLE ADAPTATION OF MIGRATORY BIRDS TO GLOBAL CLIMATE CHANGE

TIMOTHY COPPACK[1,2] & CHRISTIAAN BOTH[3,4]

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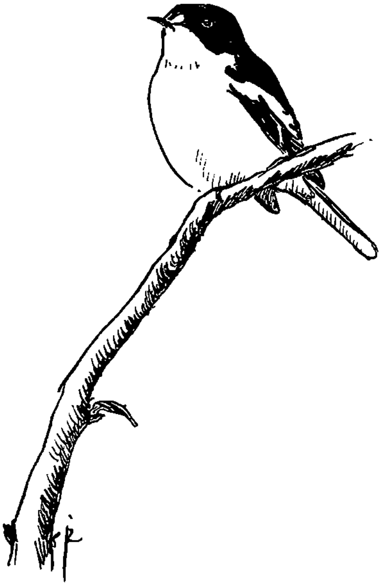
Analyses of long-term data indicate that human-caused climatic changes are affecting bird phenology in directions consistent with theoretical predictions. Here, we report on recent trends in the timing of spring arrival and egg laying found within a western European Pied Flycatcher *Ficedula hypoleuca* population. Mean egg laying date has advanced over the past 20 years in this population. The advancement in egg laying date was stronger than the advancement of spring arrival, suggesting that Pied Flycatchers are changing these stages of their annual cycle at different rates. It could be shown that selection for earlier breeding had increased. Hence, the observed adjustment in laying date did not match the advancement of spring. Our findings raise general questions about the adaptability of migratory birds to rapid environmental changes. Adaptive advancement of reproduction in response to increasing spring temperatures and to the concomitant advancement of food supply could be held back, because annual breeding and migration cycles are controlled primarily by endogenous rhythms and photoperiodic cues which do not relate to temperature. Migrants may have several options for arriving earlier on the breeding grounds, including an increase in migration speed, earlier departure from the wintering area or a shortening of migration distance. Changes in migratory behaviour could be accomplished either by phenotypic plasticity or by selection on different genotypes. Although descriptive field data provide compelling evidence for changes in, and possible constraints on, the timing of breeding and migration, their explanatory power in predicting the limits of adaptation remains restricted. We review recent experimental approaches, which explicitly test the relative roles of genetic versus environmental factors in the adaptation of life-cycle timing to global environmental changes.

Key-words: *Ficedula hypoleuca* – biological rhythms – climate change – migration – moult – photoperiod – reproduction

[1]Max Planck Research Centre for Ornithology, Vogelwarte Radolfzell, 78315 Radolfzell, Germany; [2]Institute for Avian Research, Vogelwarte Helgoland, P.O. Box 1220, 27494 Helgoland, Germany; E-mail: coppack@vogelwarte-helgoland.de; [3]Biologisch Centrum Rijksuniversiteit Groningen, P.O. Box 14, 9750 AA Haren, Netherlands; [4]Netherlands Institute of Ecology, P.O. Box 40, 6666 ZG Heteren, The Netherlands



INTRODUCTION

Bird migration is all about 'being in the right place at the right time'. Migratory birds are adapted to using the best sources of food for breeding and avoid harsh winter conditions by moving to habitats that are more hospitable (Alerstam 1990). The 'right time' to be in a certain breeding or wintering area, however, is far from constant on a geological time-scale. There have been two Ice

Ages within the past 150 000 years during which the areas where birds could breed were limited to a narrow space on either side of the Equator. But as global temperatures increased, their range margins expanded and the journeys to reach the summer breeding grounds became longer. Birds must have been extremely flexible in adapting the timing of breeding and migration to shifts in global climate patterns. All extant species have (by definition) survived the turbulent years of the post-Pleistocene period – although it may have been a 'narrow escape' for some of them. The Red Knot *Calidris canutus*, for instance, most probably went through a severe populational bottleneck in the late Pleistocene (Baker *et al.* 1994). Nevertheless, one could argue that most species will persist in the face of human-caused climatic changes, because so many have survived numerous episodes of climatic shifts before. In this paper, we explore whether long-distance passerine migrants are indeed flexible enough in their response to rapid environmental change, and we discuss several ways these birds could adapt to recent climatic trends.

The predicted rate of human-caused climate change is worrying. Anthropogenic climate change will lead to an increase of about 3.6°C (range 1.4 - 5.8°C) in mean surface air temperature within the next 100 years, mainly as a response to a doubling of atmospheric CO_2 from pre-industrial levels (Crowley 2000; Houghton *et al.* 2001). The expected average rate of temperature change far exceeds the natural variability of the past 1000 years and is higher than estimates of global temperature change for the last interglacial period (about 120 000 to 130 000 years ago) - the warmest interval within the past 400 000 years (Crowley 2000). This dramatic change in climate, in combination with the large-scale habitat loss that human-kind is causing, may be more difficult to survive than the natural environmental fluctuations bird species were confronted with during their evolutionary history. Predicting the consequences of global climate change for migratory birds is difficult, because individuals spend different parts of their annual cycle at different localities where the environment may be changing in different directions. In the temperate-zone, increasing winter and spring temperatures could generally promote residency and earlier breeding, whereas in tropical wintering sites desertification could lead to higher winter mortality. There is considerable concern that long-distance migrants, some of which are already facing severe population declines (Robbins *et al.* 1989; Berthold *et al.* 1998), could continually suffer from rapid climatic shifts, because their annual cycles of migration and reproduction are rigidly controlled by endogenous timing factors and responses to photoperiodic stimuli which do not relate to temperature (cf. Bradley *et al.* 1999; Both & Visser 2001).

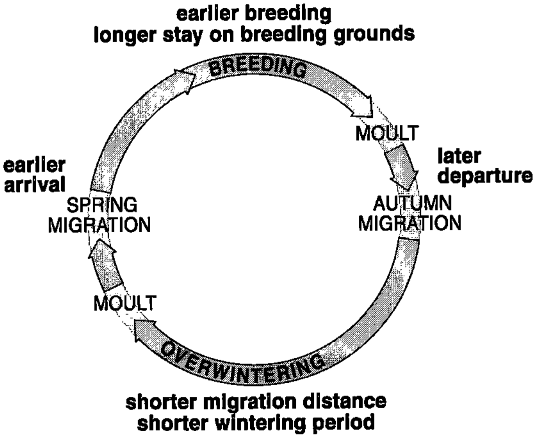


Fig. 1. The annual cycle of a migratory bird with observed and expected changes in the timing of life-cycle stages in the course of climate warming (adapted from Pulido & Berthold 1998; Jacobs & Wingfield 2000).

During the last decades, many bird species have responded to increasing spring temperatures by advancing life-cycle events or changing their distributions (Berthold 1991, 1998; Hughes 2000, Ottersen *et al.* 2001). For passerine birds breeding at mid- to high latitudes, the following trends have been reported (Fig. 1): (1) earlier spring-migration and arrival (Moritz 1993; Mason 1995; Sokolov *et al.* 1998; Sparks 1999; Jenkins & Watson 2000; Tryjanowski *et al.* 2002; Hüppop & Hüppop 2003), (2) earlier breeding (Crick *et al.* 1997; Winkel & Hudde 1997; Forchhammer *et al.* 1998; Sokolov & Payevsky 1998; Visser *et al.* 1998; Brown *et al.* 1999; Crick & Sparks 1999; Dunn & Winkler 1999; Both & Visser 2001), (3) later departure in autumn (Enquist & Petterson 1986; Gatter 1992; Bezzel & Jetz 1995; Vogel & Moritz 1995; Bergmann 1998), (4) shortening of migration distances / reduction of migratoriness (Sutherland 1998; Berthold 2001a,b). Although long-term trends reflect responses to environmental change, their explanatory power in predicting the adaptability of migratory birds to a rapidly warming climate remains limited. Most studies do not show whether the observed responses are indeed strong enough to track the current rate of climate change.

Here, we illustrate the potential effects of climate change on the timing of breeding and migration with our work on the Pied Flycatcher *Ficedula hypoleuca*. This species winters in western Africa and breeds over a vast area throughout Europe (Lundberg & Alatalo 1992). Twice a year each individual has to fly thousands of kilometres between wintering and breeding sites. Being on schedule is crucial to a migrant. Arriving too late on the breeding grounds reduces the probability of finding a mate, and arriving too early in the season may bear high costs in view of the adverse climatic conditions and limited food resources in early spring. Similar time constraints probably also exist for the wintering period, because during this time Pied Flycatchers also defend territories, and the best ones are likely to be occupied first. High quality wintering territories may enable birds to grow a better plumage and to arrive in prime condition on the breeding site the following season. We stress that for a good understanding of how long-distance migrants can adapt to climate change we need to consider all intrinsically linked stages of their annual cycle (cf. Ens *et al.* 1994).

THE CASE OF THE PIED FLYCATCHER IN THE HOGE VELUWE

The fitness of birds breeding in seasonal environments often depends on the date they start breeding. Food may only be super-abundant for a short period in spring. Matching the energy-demanding breeding period with the peak in food availability enhances breeding success (Lack 1968; Perrins 1970; Van Noordwijk *et al.* 1995). The time at which food is most plentiful depends to a large extent on spring temperatures (Visser *et al.* 1998; Visser & Holleman 2001), and the response of many bird species that lay earlier in warmer years can be regarded as an adaptive response to this temperature-dependent food peak. In most cases, early egg laying has clear advantages (Daan *et al.* 1988; Verhulst *et al.* 1995; Siikamäki 1998).

The observation that a number of bird species have advanced their laying date with increasing spring temperatures (Crick *et al.* 1997; McCleery & Perrins 1998; Crick & Sparks 1999) does not necessarily mean that these birds are responding adequately to climatic shifts. To evaluate this, we have to examine the fitness consequences of alternative laying dates. The only example so far of a migratory bird species that has advanced its egg-laying date strongly, and of which the adequacy of this advancement was tested, is the Pied flycatcher (Both & Visser 2001). This species has advanced its laying date by more than a week during the last two decades in a Dutch population (Fig. 2; Both & Visser 2001), and the same strong advancement was reported independently for hatching dates in a German population (Winkel & Hudde 1997). Further support for the hypothesis that the observed advancement is indeed caused by rising temperatures comes from a Russian study in which neither an advancement of laying date nor a rise in temperature was found over the last two decades (Sokolov & Payevsky 1998). The observed advancement in The Netherlands was shown to be mainly a phenotypic response of individual females laying earlier in warmer years, but this response was not sufficient to track the advancement of spring (Fig. 2). So, despite the advancement of laying date, selection for the earliest laying females has increased over the last few years (Both & Visser 2001). This selection for laying date was stronger in warmer years with an early caterpillar peak than in colder years with a late caterpillar peak (Fig. 3).

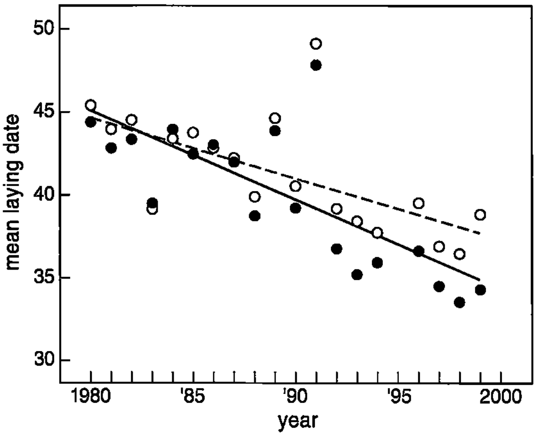


Fig. 2. Annual mean laying date (open circles and dashed line) and annual mean laying date weighted for the number of recruits produced per brood (filled circles and solid line) for the Pied Flycatchers in the Hoge Veluwe (The Netherlands). The weighted mean gives an approximation of where the population's optimal laying date may be, and the divergence of both means shows that in the course of the years the mean laying date deviates more and more from the optimal laying date. The difference between the means is the selection differential for laying date, which significantly increases over the years (r_s = -0.70, n = 19, P < 0.001).

We hypothesise that the apparently sub-optimal adjustment of laying date to rising temperatures is caused by the migratory strategy of Pied Flycatchers. This species normally arrives at the breeding grounds just shortly before the start of the breeding season (Lundberg & Alatalo 1992). The onset of spring migration is mainly controlled by an endogenous circannual rhythm, synchronised by daylength variation (Gwinner 1996) and unrelated to climatic factors at the breeding grounds. It is not surprising, therefore, that Pied Flycatchers' arrival date in spring has not advanced over the years, nor that it was unrelated to temperature (Both & Visser 2001). In our eyes, arrival date constrains a stronger advancement of breeding date than we observed and thus could be the cause of the insufficient adjustment. Because a Northern Hemisphere perspective often biases our understanding, we need to extend our perception and gather more knowledge on what happens outside the breeding period. We thus need to study the timing of several stages within the avian calendar and explore how flexible this calendar is (see Gwinner 1987, 1989 for experimental approaches).

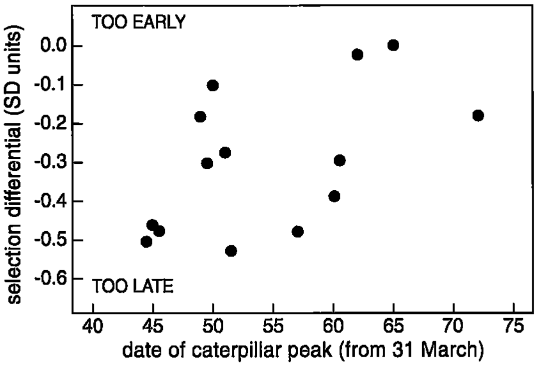


Fig. 3. Annual selection for laying date of Pied Flycatchers and the date of the caterpillar peak in the Hoge Veluwe (The Netherlands). The selection differential is the difference between the annual mean laying date and the annual laying date weighted for the number of recruits per brood, divided by the standard deviation of laying date. The caterpillar peak data were taken from Verboven *et al.* 2001. Data are from 1985-99 (r_s = 0.56, n = 14, P = 0.04).

ARRIVING IN THE RIGHT PLACE AT THE RIGHT TIME

Birds cannot reproduce before they have actually arrived on their breeding grounds. In order to predict whether long-distance migrants can adjust the timing of breeding to further advances in phenology we therefore need to understand what determines spring arrival. The timing of migration is linked to the timing of moult, which precedes migration (Fig. 1). The timing of pre-breeding moult and nocturnal migratory activity is proximately controlled by the photoperiodic conditions experienced during winter (Gwinner 1996). Food availability may affect the quality of replaced

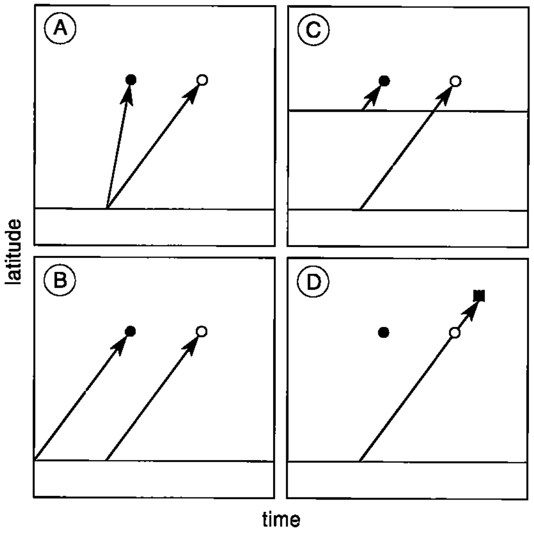


Fig. 4. Schematic depiction of four hypotheses on how migratory birds could adjust spring migration to advanced phenology on the breeding grounds. Open circles represent the existing optimal arrival date, and filled circles indicate the required earlier arrival to permit earlier breeding at the same latitude. Arrows show the timing and distance of migration starting from a given wintering latitude (horizontal lines). **(a)** Birds increase the rate of spring migration. **(b)** Birds leave the wintering grounds earlier and migrate at the same speed. **(c)** Birds winter closer to the breeding area (horizontal bold line) and migrate for a shorter period. **(d)** Birds prolong northward spring migration and move towards improving breeding conditions (square).

feathers, which in turn depends on climatic factors such as rainfall in Africa.

Migrants may have several options to achieve an earlier arrival on the breeding grounds. They might increase the speed of spring migration, advance the onset of migration or shorten migration distances (Fig. 4a-c). In addition, migrants could prolong their northward migration and move to higher latitudes where the phenology matches their reproductive demands (Fig. 4d). It is important to state that the four potential solutions for adjusting spring migration to phenological shifts on the breeding grounds are not necessarily mutually exclusive. Migrants could, for example, shift both wintering and breeding ranges northwards.

In the discussion of the different solutions, we assume that long-distance migrants rely primarily on endogenous timing factors and/or responses to the annual change in day length (Berthold 1996; Gwinner 1996). Although the onset of spring migration may also be affected by other environmental factors, we consider it unlikely that these can be used as predictive cues for anticipating conditions on the breeding grounds.

An increase in the speed of migration (Fig. 4a) would involve shorter stopover visits or accelerated flight en route. Especially in long-distance passerine migrants, spring migration may already be taking place at maximum speed, and further acceleration seems unlikely in view of the high energetic and behavioural demands this would involve. However, climate change will influence food availability and weather conditions in habitats used as stopover sites. If climate change causes earlier peaks in food abundance, and if the weather in spring generally improves, migrants could potentially increase fuelling rates and shorten the time spent on stopover sites.

An earlier onset of spring migration (Fig. 4b) from current wintering areas would require rearrangements of the endogenous circannual cycle or its responsiveness to photoperiodic cues. Evolutionary changes of the annual cycle may be slow and constrained by the lack of genetic variation, by genetic correlations and/or reaction norms that are not in accord with the direction of selection. In general, we expect genetic variation to be low within local populations, because of the severe fitness consequences of arriving either too early or too late. Genetic variation for the timing of spring migration has been found in some species (Brown & Brown 2000; Møller 2001), but not in the Pied Flycatcher (Potti 1998).

Long-distance migrants could winter closer to the breeding grounds (Fig. 4c), provided the spatio-temporal programme controlling their migration schedule can be altered. However, individuals that manage to overwinter at higher latitudes will experience photoperiodic conditions very dif-

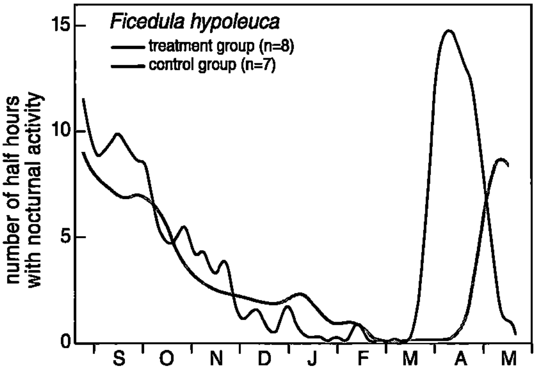


Fig. 5. Temporal pattern of nocturnal (migratory) activity in two groups of hand-raised male Pied Flycatchers from a southern German population held from September to May under photoperiodic conditions mimicking wintering at 37.5°N (treatment group: n_T = 8; *solid line*) and at 10.0°N latitude (control group: n_C = 7; grey line). Locally weighted regression lines with bandwidth λ_T = 3.18; λ_C = 6.06. Data from Coppack *et al.* (2003).

ferent from those that they encounter on their current wintering sites. At northern latitudes, birds are exposed to daylengths that decrease more rapidly in autumn, become substantially shorter in winter and increase faster in spring than more to the South. These conditions may set limits to the expression of endogenous rhythms, i.e. the range of photoperiods under which the successive stages of the circannual cycle can be completed may be limited. The rhythms of moult, migration and gonadal maturation may persist only if the photoperiodic conditions are similar to those a bird is normally exposed to during a given time of the year (Gwinner 1989, 1996). However, during their evolutionary history, long-distance migrants may have wintered at higher latitudes before, and their reaction norms might still include adaptive responses to photoperiodic variation. We recently tested this in an indoor experiment on southern German Pied Flycatchers. The results suggest that individuals wintering closer to the breeding grounds would instantaneously advance prebreeding moult, the onset of spring migratory activity, and gonadal maturation. Under a simulated Mediterranean photo-cycle, first-year male Pied Flycatchers initiated spring migratory activity approximately one month earlier than birds of the same age held under African photoperiods (Fig. 5). Since we have shown for the Dutch Pied Flycatcher population that earliness is becoming increasingly important and is associated with high fitness benefits, the observed direction of response indicates adaptive phenotypic plasticity, rather than maladaptedness. Hence, as far as the photoperiodic response mechanism is concerned, Pied Flycatchers could progressively establish wintering populations north of the Sahara desert and compete with short-distance migrants and all-year round residents. We consider it likely that the advancement of life-cycle events as measured under laboratory conditions may predispose individuals to react more instantly to a given environmental situation under natural conditions. While wintering closer to the breeding grounds, birds are less time-constrained, and being in an advanced state in early spring would allow them to arrive earlier in warm years and later in colder years. In fact, this is what short-distance migrants do and could be a reason why short-distance migrants generally show more year-to-year variation in spring arrival (Berthold 2001b).

Alternatively, long-distance migrants could extend breeding ranges to the North (Fig. 4d) and move to areas where the phenology suits their ecological and physiological requirements. In fact, the northern margins of many bird species breeding in Europe have moved further north over the past decades in the course of global warming (Burton 1995; Thomas & Lennon 1999). Avoiding increasingly unfavourable breeding areas in the South could be achieved by a facultative prolongation of the migration period (cf. Berthold 2001b).

CONCLUSION

Can a long-distance migrant like the Pied Flycatcher become an early-breeding short-distance migrant? To answer this question we need to gain deeper insight into the relative roles of genetic versus environmental factors that determine the timing of migration. Adaptive evolution of migratory behaviour requires genetically based variation among individuals. Low heritabilities reported for the date of spring arrival in the Pied Flycatcher (Potti 1998) have suggested that the evolution of the timing of migration may be genetically constrained. However, in European Barn Swallows *Hirundo rustica* (Møller 2001) and North American Cliff Swallows *Petrochelidon pyrrhonota* (Brown & Brown 2000) genetic variation in the timing of spring arrival is present. Common-garden experiments with Garden Warblers *Sylvia borin* from alpine and lowland populations suggest that the onset of spring migratory activity is genetically differentiated and that there is genetic variation in this trait on which selection could act (Widmer 1999).

Until now, experimental work on the genetics of bird migration has focussed primarily on one life-cycle stage in a single species. In selective breeding experiments with Blackcaps *Sylvia atricapilla* heritabilities have been found for the amount (Berthold & Pulido 1994) and the onset (Pulido *et al.* 2001) of autumn migratory activity, and for the frequency of migrants within populations (Pulido *et al.* 1996). Given that genetic and phenotypic variation in migratory traits is relatively high, we predict a strong response to selection. Nevertheless, even given the 'genetic substrate' for natural selection, adaptive evolution of migratory cycles could still be constrained by genetic correlation's with other life-history traits and/or reaction norms that are not in accord with the direction of selection. For instance, Coppack *et al.* 2001) were able to show that the photoperiodic response to earlier hatching dates disrupts the temporal organisation of juvenile Blackcaps, leading to unseasonably early migration in the middle of moult. This kind of reaction to day length could counteract the fitness benefits of earlier breeding. When relationships between the selective environment and proximate cues change there will be selection on reaction norms (Visser & Lambrechts 1999). However, responses to such selection may be slow, and in the long run, species may not keep pace with rapid environmental changes.

At present, it is impossible to predict the future of long-distance migrants in a rapidly warming world. 'Historical' field data give us only an idea about the limits of adaptation. Reports of climate-related trends in the timing of migration and egg laying can be overestimated, and predictions for the twenty-first century could be biased by giving the date of events each year, rather than their timing relative to the vernal equinox (Sagarin 2001). Relationships between photoresponsiveness and the adaptability of avian reproduction and migration cycles are impossible to analyse in the field. On the other hand, questions on reproductive success, survival probability, and species-interactions can only be addressed using a field approach. Thus, we should encourage both laboratory and field investigations which help to predict whether or not migratory birds will be able to keep pace with changes in the timing of the seasons and the geography of suitable habitats. In addition, we have to maintain long-term phenological records so that future generations will be able to test today's hypotheses.

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SAMENVATTING

Lange fenologische tijdseries laten duidelijk zien dat sommige trekvogels tegenwoordig eerder uit hun winterkwartier aankomen en dat verschillende soorten eerder gaan broeden dan vroeger. Dit komt waarschijnlijk door een toename van de temperatuur op aarde. In deze bijdrage laten we zien dat Bonte Vliegenvangers *Ficedula hypoleuca* die in nestkasten op de Hoge Veluwe broeden, de laatste 20 jaar veel eerder zijn gaan broeden, maar niet eerder uit hun overwinteringsgebied aankomen. Dit betekent dat de verschillende stadia van de levenscyclus niet allemaal synchroon veranderen met

de toename van de temperatuur in ons land. Bij de Bonte Vliegenvanger nam de selectie op vroeg broeden toe. Dit betekent dat de waargenomen vervroeging in legdatum niet voldoende is om de verschuiving van het voorjaar bij te benen. We denken dat de aanpassing van legdatum beperkt wordt door de aankomstdatum, die in de loop der jaren, zoals we al zagen, niet veranderd is. Deze bevindingen leiden tot een aantal algemene vragen naar de vraag hoe goed langeafstandstrekkers zich kunnen aanpassen aan een snel veranderend klimaat. Wanneer de temperatuur stijgt, zouden vogels eerder moeten gaan broeden, omdat ook hun voedsel eerder beschikbaar komt. Deze reactie zou echter beperkt kunnen worden doordat onderdelen van de jaarcyclus, zoals trekken en broeden, niet worden bepaald door de temperatuur, maar door endogene ritmiek en een reactie op de variatie in daglengte. Bonte Vliegenvangers overwinteren in Afrika en het begin van hun voorjaarstrek wordt vooral bepaald door de verandering van de daglengte daar. Daarom is het niet verbazingwekkend dat ze niet eerder aankomen in het broedgebied. Om eerder te kunnen aankomen dan nu het geval is, zouden ze in plaats van een eerder vertrek uit het Afrikaanse winterkwartier, ook kunnen kiezen voor een hogere treksnelheid of voor een meer noordelijk gelegen overwinteringsgebied, waardoor de trekafstand verkleind wordt. Deze veranderingen in trekgedrag kunnen worden bewerkstelligd door fenotypische plasticiteit of door selectie op verschillende genotypen. In het veld zijn deze mogelijkheden vaak moeilijk te onderzoeken. Laboratoriumexperimenten kunnen echter uitsluitsel geven of een soort de mogelijkheid heeft om zijn trekstrategie aan te passen. Als voorbeeld laten we de resultaten van een experiment zien waarbij we Bonte Vliegenvangers in volières hebben laten overwinteren op een daglengtepatroon zoals in Zuid-Spanje wordt aangetroffen. Hiermee simuleerden we dus een noordelijker overwinteringsgebied. Tijdens het experiment is gemeten wanneer de vliegenvangers in het voorjaar gingen ruien en trekken. Het experiment laat zien dat Bonte Vliegenvangers die op een Spaanse daglengte overwinteren, eerder ruien en eerder in het voorjaar trekgedrag vertonen dan soortgenoten die op een daglengtepatroon worden gehouden dat overeenkomt met hun Afrikaanse overwinteringsgebieden. Het experiment toont aan dat Bonte Vliegenvangers plastisch op hun omgeving kunnen reageren. Dit biedt mogelijkheden voor verdere aanpassing van de soort aan klimaatsverandering.