basalts is expected in subarcs. Barring extensive infiltration of externally derived fluids, our study implies marked devolatilization under forearcs (for clay-rich marls with high-temperature geotherms) or retention of H2O and CO2 to depths well beyond subarcs (for siliceous limestones in all geotherms and clay-rich marls with low-temperature geotherms). Accordingly, most of the initial CO2 and H2O in subducted marine sediments will not be released beneath volcanic arcs. This inference is consistent with both the deficiency in the amount of CO2 released from arc volcanoes compared to the amount of CO2 contained within subducted carbonates (Table 1) and with the imbalance between subducted versus expelled H2O (ref. 1).

Our equilibrium analysis implicitly assumes that there is no significant kinetic overstepping and metastability of metamorphic reactions. Although significant disequilibrium has been suggested for the transformation of anhydrous oceanic basalts and gabbros to eclogites19, the catalytic effect of H2O (ref. 15) implies that equilibrium is more likely in dehydrating systems such as subducted sediments.

Melting is an alternative mechanism for release of volatiles from subducted sediment. Recent experiments using marine red clay16 suggest that sediment melting does not occur for the geotherms that we consider here. However, because metamorphic reactions (for example, red clay) are unsuitable models for subduction-zone geotherms (for arc magma generation, the catalytic effect of H2O will be more important than it is for arc magma generation). The equilibrium analysis implicitly assumes that there is no kinetic overstepping and metastability of metamorphic reactions. Although significant disequilibrium has been suggested for the transformation of anhydrous oceanic basalts and gabbros to eclogites19, the catalytic effect of H2O (ref. 15) implies that equilibrium is more likely in dehydrating systems such as subducted sediments.

As shown in Fig. 2, fluids produced by metamorphism of subducted marine sediments are H2O-rich. Consequently, expulsion of such fluids to the overlying mantle wedge would not substantially affect the P–T conditions of melting (solidus) of the mantle wedge compared to those expected in the presence of a pure H2O fluid.

Devolatilization of subducted sediment could contribute to seismicity along the tops of subducted slabs. The continuous nature of devolatilization is compatible with the spread of earthquake hypocentres along individual subduction zones22. However, correlation of slab seismicity with metamorphic devolatilization of subducted sediments needs to consider the marked differences in devolatilization for different bulk compositions and geotherms.

Table 1 Subduction zone carbon budget

<table>
<thead>
<tr>
<th>Subducted carbon (Tmol yr−1)</th>
<th>Sediment carbonate</th>
<th>Sediment organic carbon</th>
<th>Oceanic metabasalts</th>
<th>Total</th>
<th>Expelled carbon (Tmol yr−1)</th>
<th>Arc: magnatium</th>
<th>Carbon imbalance (Tmol yr−1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1.2</td>
<td>0.8</td>
<td>3.4</td>
<td>5.4</td>
<td>2.5–3.5</td>
<td>2.5–3.5</td>
<td></td>
</tr>
</tbody>
</table>

*1 Tmol = 10¹² mol.
†(Subducted carbon) = (expelled carbon).

Adjustment to climate change is constrained by arrival date in a long-distance migrant bird

Christian Both* & Marcel E. Visser†

* Zoological Laboratory, Groningen University, PO Box 14, 9750 AA Haren, The Netherlands
† Netherlands Institute of Ecology, PO Box 40, 6666 ZG Heteren, The Netherlands

Spring temperatures in temperate regions have increased over the past 20 years1, and many organisms have responded to this increase by advancing the date of their growth and reproduction2. Here we show that adaptation to climate change in a long-distance migrant is constrained by the timing of its migratory journey. For long-distance migrants climate change may advance the phenology of their breeding areas, but the timing of some species' spring migration relies on endogenous rhythms that are not affected by climate change1. Thus, the spring migration of these species will not advance even though they need to arrive earlier on their breeding grounds to breed at the appropriate time. We show that the migratory pied flycatcher Ficedula hypoleuca has advanced its laying date over the past 20 years. This temporal shift has been insufficient, however, as indicated by increased selection for earlier breeding over the same period. The shift is hampered by its spring arrival date, which has not advanced. Some of the numerous long-distance migrants will suffer from

Received 7 June 2000; accepted 28 February 2001.


Supplementary information is available on Nature's World-Wide Web Site (http://www.nature.com) or as paper copy from the London editorial office of Nature.

Acknowledgements

We thank S. Peacock for advice about subduction zone geotherms, and G. Bebout, K. Caldeira and M. Schmidt for comments and suggestions. This work was supported by the MARGINS program of the NSF.

Correspondence and requests for materials should be addressed to D.M.K.
(e-mail: kerrick@geosc.psu.edu).

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climate change, because either their migration strategy is unaffected by climate change, or the climate in breeding and wintering areas are changing at different speeds, preventing adequate adaptation.

Higher spring temperatures over the past two decades have led to advancing tree phenology and subsequently to earlier peaks in insect abundance\(^2\)\(^-\)\(^11\). Several bird species\(^3\)\(^-\)\(^8\), but not all\(^12\), have advanced their egg-laying date as a consequence of this advance in their food supply\(^6\)\(^-\)\(^9\). Advancement of laying has not kept up with selection for earlier laying in areas where early spring temperatures have not increased as much as those late in spring\(^13\). Adaptive advancement of reproduction may also be hampered in species that rely on endogenous rhythms or environmental stimuli unrelated to temperature\(^4\), such as day length. Long-distance migrants are extremely vulnerable in this sense, because in some well-studied species the timing of spring migration from the overwintering area is triggered by cues that are unlinked to the climate at their breeding grounds, and their breeding date is constrained by their arrival date.

We examined how a long-distance migrant bird, the pied flycatcher *Ficedula hypoleuca*, has responded to recent climate change, using data from a long-term study in the Hoge Veluwe (The Netherlands). Pied flycatchers overwinter in the zone of dry tropical forest at about 10° north in west Africa, and breed in temperate forests in Europe\(^14\). Males normally arrive before females, and females select males on the quality of their territory\(^15\).

Temperatures at the time of arrival and the start of breeding by pied flycatchers (16 April to 15 May) have increased significantly over the period 1980–2000 (Fig. 1a). Over the same period, the birds have not advanced the spring arrival on their breeding grounds (Fig. 1b), but have advanced their mean laying date by about 10 days (Fig. 1c). Mean laying date was unrelated to population size\(^16\), and population size did not show a significant trend (\(r = -0.08\), \(n = 21\), \(P = 0.72\)). Selection for early laying date has become stronger over the course of this 20-year period (Fig. 1d), indicating that early laying pairs do better than later pairs. Thus, the response in laying date has not been sufficiently strong to track the advancement of spring.

Mean laying date was strongly correlated with the mean temperature in the second half of April and the first half of May (Fig. 2a), but arrival date was not (Fig. 2b). Arrival and laying dates were furthermore uncorrelated with temperatures in the first half of April, just before arrival of most birds (arrival: \(r = -0.04\), \(n = 20\), \(P = 0.87\); laying: \(r = 0.30\), \(n = 21\), \(P = 0.20\)). The advancement of egg-laying date was, to a large extent, caused by plasticity of individual females to temperature\(^12\) (analysis of covariance (ANCOVA)); individual, \(F_{1,211} = 2.16\), \(P < 0.001\); age, \(F_{1,412} = 17.12\), \(P < 0.001\); temperature, \(F_{1,412} = 50.57\), \(P < 0.001\); average individual slope (\(-1.10 \pm 0.15\)) significantly differs from population slope (\(-1.67 \pm 0.24\), \(F_{1,413} = 13.55\), \(P < 0.001\)), and not by selection for genotypes for early breeding (heritability\(^2\) (\(h^2\)) for laying date (relative to yearly mean) calculated from mother–daughter regression is not significant: \(F_{1,223} = 1.11\), \(P = 0.29\), \(h^2 = 0.16 \pm 0.15\)). As a consequence of the correlation between laying and temperature (Fig. 2a) and the absence of a correlation between arrival date and temperature (Fig. 2b), the interval between arrival and egg-laying has decreased with increasing temperatures (linear regression: \(F_{1,19} = 9.73\), \(P = 0.006\)).

Pied flycatchers were able to advance their laying date because they normally arrive on their breeding grounds earlier than their average optimal laying date\(^14\). Their spring migration strategy, triggered by day-length variation on their wintering grounds\(^5\), enabled them to arrive in time to respond adaptively to the naturally occurring variation in the start of spring\(^14\), and thereby start egg-laying at the date that maximizes fitness\(^6\). Owing to the advanced phenology on their breeding grounds and their relatively inflexible arrival date, however, this window has become too narrow, and a significant part of the population is now laying too late to exploit the peak in insect abundance optimally (as shown by the increasing selection for early laying; Fig. 1d).

The strong response of laying date in the pied flycatcher seems at variance with the lack of response in the resident great tit *Parus major* population breeding in the same area\(^7\). In both cases, however, the advancement of laying date is insufficient, as indicated by the presence of increased selection for earlier breeding. For the great tits, which start egg-laying about 2 weeks earlier than the flycatchers, the lack of a sufficient response is due to increasing temperatures in late, but not in early spring. For the flycatchers, the advancement is not hampered by such temporal variation in climate change, but because their timing of spring migration is triggered by day length, which is not affected by spring temperatures on their breeding grounds. The decision when to start spring migration thus becomes maladaptive if the cue used for migration is independent of the environmental change in the breeding area.

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**Figure 1** Spring temperature, breeding and spring arrival date of a pied flycatcher population in the Netherlands from 1980 to 2000. a, Mean average daily temperature in the period of arrival increased (linear regression: \(F_{1,19} = 8.31\), \(P < 0.001\)). b, Median arrival date did not advance (\(F_{1,19} = 2.32\), \(P = 0.15\)). c, Mean laying date did advance (\(F_{1,20} = 17.14\), \(P < 0.001\)). d, Standardized selection differential for laying date decreased with year (\(F_{1,17} = 12.00\), \(P = 0.003\)) over this period.

**Figure 2** Breeding date and spring arrival of a pied flycatcher population as a function of spring temperature in the Netherlands. a, Average laying date was significantly related to the mean average daily temperature (°C) in the second half of April and the first half of May (\(F_{1,20} = 37.59\), \(P < 0.001\)). b, Median arrival date was unrelated to spring temperature (\(F_{1,19} = 0.66\), \(P = 0.43\)).
In other long-distance migrants, the breeding grounds on which the breeding grounds is also relatively insensitive to the temperature on arrival, although in some species the temperature on journey is a good correlate of arrival date\(^6,19\). Climatic factors may be important in fine-tuning the onset and speed of migration, but climate change differs between temperate and tropical latitudes\(^1\), and therefore a response to environmental cues such as temperature for the onset and speed of migration may not lead to an adequate arrival date on the breeding grounds. Short-distance migrants may be more flexible in their response, because the circumstances on the wintering grounds will be a better predictor for the optimal arrival time on the breeding grounds and genetic variation has been shown for some of their migratory traits\(^22,23\).

Large-scale climate change may thus form a serious threat to at least some of the numerous species that migrate from tropical wintering grounds to temperate breeding areas\(^2\), because they arrive at an inappropriate time to exploit the habitat optimally, and face higher competition with resident species that may have increased in numbers through enhanced winter survival\(^3\). This may, in fact, be partly responsible for the decline of these species in western Europe\(^26\).

### Methods

#### Data collection

Data were collected from a nest-box breeding population of pied flycatchers in the Hoge Veluwe area, central Netherlands, between 1965 and 2000 (ref. 9). We analysed data from 1980 to 2000, because temperature increased most markedly after 1980. We used only nests that were considered to be first nesting attempts of females during that year (n = 1,892). Parents and chicks were reared with uniquely numbered aluminium rings. Arrival data were obtained from a local amateur bird group, working within 10 km from the study area\(^24\). Members of this bird group recorded each year the first singing pied flycatcher, and the median first arrival date was used as approximation of arrival in the study area. The lack of an advancement in arrival date was confirmed by analysing the arrival date of the first male recorded in the study area from 1992 to 2000 (\(F_{1,19} = 0.26, P = 0.63\)), the first ten males that arrived in an area nearby from 1980 to 1990 (\(F_{1,19} = 0.25, P = 0.62\)), and the mean start of nest building of the first ten pied flycatcher nests each year in 1980–2000 (\(F_{1,10} = 0.19, P = 0.69\); start of egg-laying was estimated from the state of the nest during weekly checks).

#### Analyses

All analyses were performed with linear regression using two-tailed \(P\) values. In most cases we used annual means. In the analysis of the response of individual females to temperature, we used females that bred in at least 2 years (n = 273). In this analysis, female age was a factor for first known breeding or later breeding in the area (real age was not determined), because first year breeders normally breed later\(^4\). Individual is used here as a factor in an ANCOVA. Temperature used is the average of the mean daily temperatures from 16 April to 15 May recorded by the Royal Dutch Meteorological Institute (KNMI) at De Bilt (The Netherlands). The standardized selection differential is the mean laying date - the median first arrival date was used as approximation of arrival in the study area. The standardized selection differential is the mean laying date - the median first arrival date was used as approximation of arrival in the study area. The standardized selection differential is the mean laying date - the median first arrival date was used as approximation of arrival in the study area.

Received 1 November 2000; accepted 28 February 2001.


Acknowledgements

I. van Balen and J. Visser managed the long-term study for many years. The board of National Park ‘De Hoge Veluwe’ kindly allowed us to work on their property. I. Pilzecker and R. Bijlsma allowed us to use some of their unpublished observations of flycatcher arrival. J. Harvey, C. M. Lessells and A. J. van Noordwijk commented on an earlier draft.

Correspondence and requests for materials should be addressed to M.E.V (e-mail: m.visser@tno.moon.knaw.nl).

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**Endosymbiotic sulphate-reducing and sulphide-oxidizing bacteria in an oligochaete worm**

**Nicole Dubillier**, Carole Müllers, Tim Ferdeman, Dirk de Beer, Annelie Pernthaler, Michael Klein, Michael Wagner, Christin Eresüs, Frank Thiermann, Jens Krieger, Olav Giere and Rudolf Amann

*Max Planck Institute of Marine Microbiology, Celsiusstrasse 1, D-28359 Bremen, Germany*  
†Department of Microbiology, Technical University of Munich, D-85350 Freising, Germany  
§Department of Invertebrate Zoology, Swedish Museum of Natural History, S-10405 Stockholm, Sweden  
∗Zoological Institute and Zoological Museum, University of Hamburg, D-20146 Hamburg, Germany

Stable associations of more than one species of symbiont within a single host cell or tissue are assumed to be rare in metazoans because competition for space and resources between symbionts can be detrimental to the host\(^1\). In animals with multiple endosymbionts, such as mussels from deep-sea hydrothermal vents\(^2\), and reef-building corals\(^3,4\), the costs of competition between the symbionts are outweighed by the ecological and physiological flexibility gained by the hosts. A further option for the coexistence of multiple symbionts within a host is if these benefit directly from one another, but such symbioses have not been previously described. Here we show that in the gutless marine oligochaete...