How do birds adapt to a changing climate?

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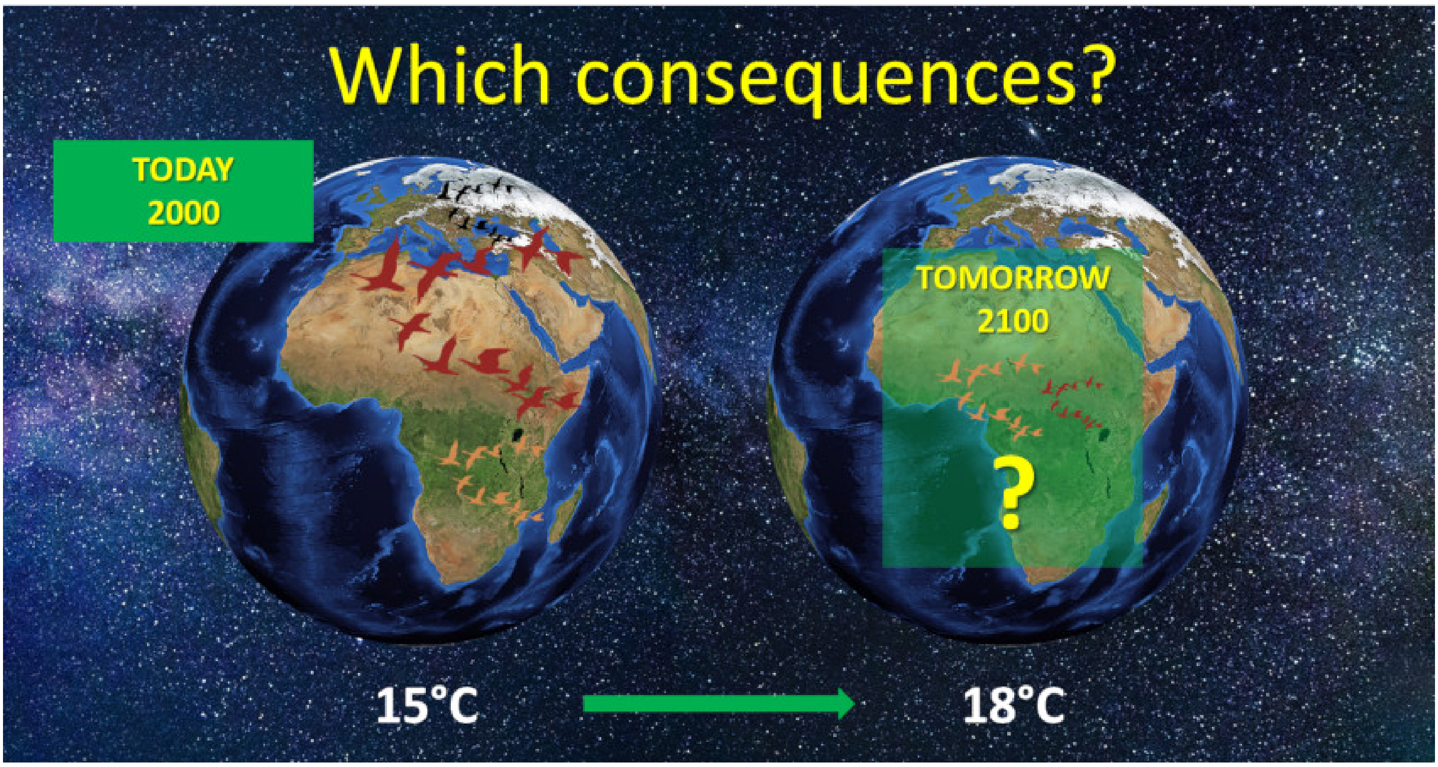

What can be done, being a bird, to adapt to a climate that is inexorably warming? Three solutions: fleeing under milder skies, adapting locally or disappearing. The best-known mechanism is the so-called "habitat tracking": the bird follows the thermal envelope to which it is adapted, going up in latitude or altitude. Another solution is to adapt to rising temperatures if warming is neither too fast nor too high. But the safest mechanism is to adapt through microevolution, i.e. by modifying the genetic structure of the population. When, for some reason, none of these mechanisms is possible, extinction is inevitable. Species living in extreme environments (such as the tundra or high mountains) are particularly vulnerable to extinction because the movement of their habitats is constrained by geographical limits. Some categories of birds, particularly long-distance migrants frequenting many habitats during their travel, are hardly hit by the new constraints they face.

1. Huge challenges

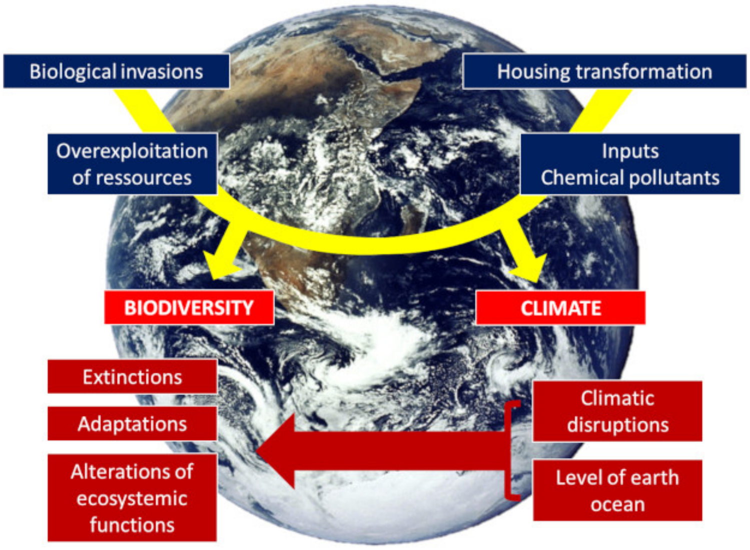

Figure 1. The different components of global change. The combination of climate change and its consequences affect biodiversity. [Source: © Jacques Blondel]

Climate change, which is no longer disputable, is one of the six components of what is called "**global change**", the other components being habitat alteration, chemical inputs, overexploitation of natural resources, and biological invasions (Figure 1). Their main characteristics, which earned them the title "global", is that they concern the whole planet; most of their effects being felt all over the world (see Biodiversity is not a luxury but a necessity). Climate change includes six phenomena: carbon dioxide concentrations, rising temperatures, rising global sea level, melting polar packs ice, expanding drylands and deserts, and an increase in extreme events (heat waves, floods, storms and cyclones). These upheavals are the symptoms of**anthropocenization** [1] of the planet and have serious consequences on many aspects of the life histories of organisms, at all scales of space, from local to global [2].

The pace of change is so rapid and abrupt that we are faced with a new set of "**natural experiments**" that illustrate the challenges encountered by populations of organisms facing completely new environments. These new living conditions may lead organisms to extinction, but they can also offer them new opportunities depending on how they respond (or not) to these changes (see The adaptation of life to environmental constraints). Birds have been subject of a large number of studies on their vulnerability and responses to global warming. They are expected to be particularly affected [3] to the point that **each degree Celsius increase in global temperature could lead to the extinction of 100 to 500 species** [4].

2. Temperature, a key factor in physiology and ecology

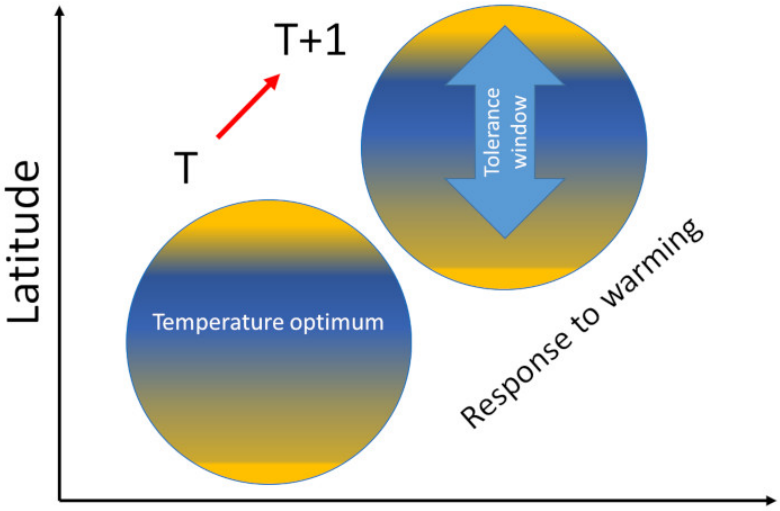

Figure 2. Response to warming from Time T to time T+1. Organisms live within a thermal window whose limits cannot be overshot. [Source: © Jacques Blondel]

According to the metabolic theory of ecology, the **metabolic profile of organisms controls all physiological and ecological processes at the level of individuals, populations and ecosystems** [5]. This macroecological constant, which applies to both macro- and microorganisms, varies with the size of the organism in a linear relationship when body masses and metabolic rates are expressed in logarithms. The sensitivity of birds to temperature makes it possible to define for each species a **thermal tolerance threshold** that defines the thermal envelope to which it is adapted (Figure 2). **Any crossing of this threshold results in cascading effects on a set of morphological, physiological and demographic traits associated with metabolism**. These effects are at the origin of the **biogeographic distribution of organisms**.

The responses of organisms to global warming show cascading effects from a given level of resolution of life to the next:

At the individual level, temperature affects growth, size, reproduction, and therefore the individual's fitness;

Then individual responses translate at the population level through their consequences on demographics, density and diversity, both phenotypic and genetic.

Next, at the level of species assemblages, performance is translated at the **population** level by influencing its composition, structure, energy production, specific diversity and dynamics.

Finally, what happens at the population level determines the functioning of the **ecosystem**.

Many examples, particularly in birds, illustrate the **vulnerability of organisms to temperature variations**, either when the **thermal tolerance threshold** is reached and then **exceeded**, or by **decreasing ecosystem productivity**, or by **disrupting interactions between species thus disorganizing food webs**.

3. What are birds' responses to global warming?

Two main types of responses to global warming are provided by birds. The first is an **immediate response**, of phenotypic nature, whereby the **bird immediately adjusts** its behaviour to **temperature variation** (see (see The adaptation of life to environmental constraints). This type of response is possible because each life history trait is expressed within a "window of phenotypic plasticity", the so-called reaction norm (see Focus Acclimation or adaptation?) that allows the body to respond immediately to the state of the environment. The second, much more difficult to démonstrate, is an **adaptive response** to new selection regimes. It is then a matter of microevolutionary adaptation, and therefore of **genetic nature**, in response to the new selection pressures exerted by the environment. While a phenotypic response is immediate, the microevolutionary response is **trans-generational** because it passes through a selective directional screening that happens on the descendants of genetic variants which present an advantageous variation for the trait in question, for example laying date or migration departure.

3.1. The "habitat tracking"

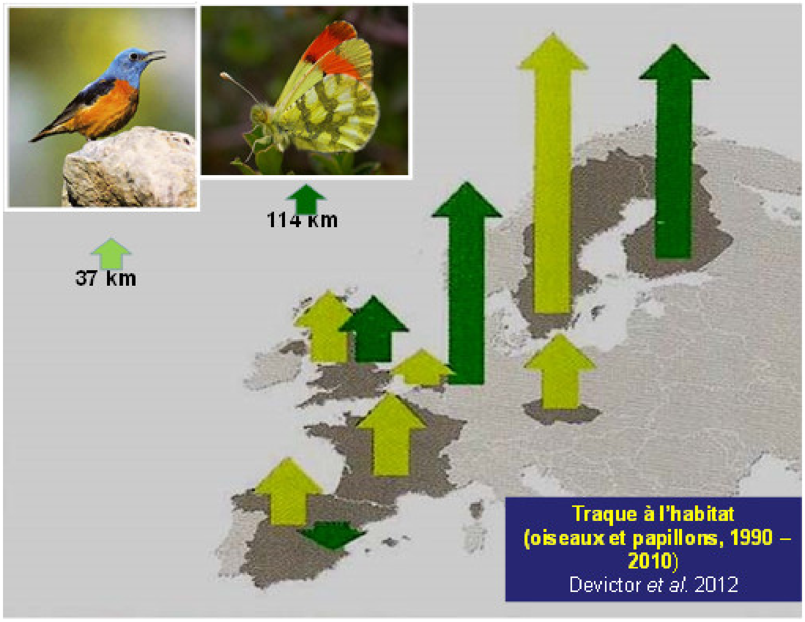

Figure 3.Northward geographical shifts of birds and butterflies between 1990 & 2010. According to ref. [8]. [Source: © Jacques Blondel]

Moving upward in latitude or altitude to follow the movements of the climate envelope to which one is adapted seems to be a logical and expected response. Indeed, the most immediately visible aspect of climate change consequences is the **change in distribution areas**. At wide scales of space and time, the comings up and down of vegetation belts and their associated fauna during the Pleistocene have been demonstrated in response to the alternation of glacial and interglacial phases that punctuated the last two million years at a frequency of about 100,000 years [6]. The routes used by organisms and their travel speeds have been specified using palaeobiogeography and phylogeography. This genetic method makes it possible to follow in time and space the organisms carrying molecular markers called haplotypes when mitochondrial DNA is used for animals and chloroplastic DNA for plants.

A **rise in latitude in response to contemporary warming** is obvious in most species of the two best studied terrestrial animal groups, birds and butterflies [7],[8] (Figure 3). This increase in latitude, which has been significant since the 1990s for 200 of the 500 breeding bird species in Europe for which data are available [9], is largely confirmed, with a strong acceleration from the 2000s. However, while climate warming plays a significant role in observed and measured movements, great care should be taken to balance climate with other environmental factors, particularly changes in habitats.

However any interpretations from correlative data involves some uncertainty because distribution envelopes of organisms may change without always having good arguments to explain them. Many changes in distribution areas cannot be explained as responses to climate change.

Hence the importance of being able to formally demonstrate the role of temperature rise in the movement of organisms.

How to measure the extent and speed of range shifts in response to climate warming?

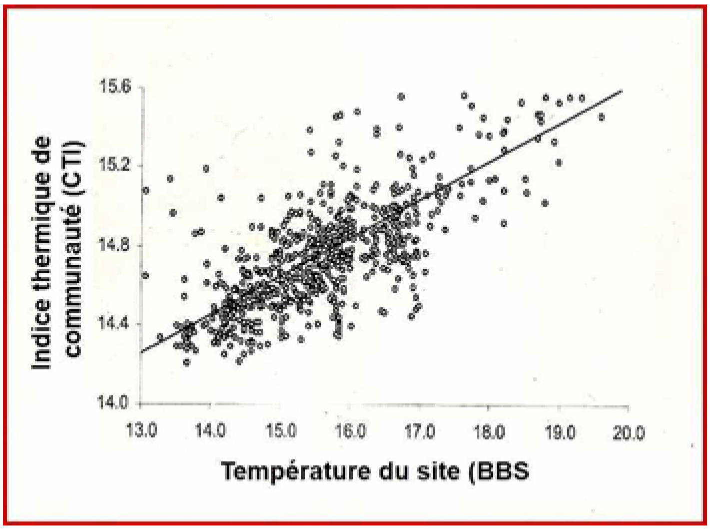

Figure 4. Relationship between the community temperature index (CTI) and the average temperature of the site where each survey was conducted (based on ref [10]). [Source: © Jacques Blondel]

Based on the robustness of temperature as a predictor of bird distribution envelopes, Devictor *et al* [10] used the databases of the STOC (acronym for *Suivi Temporel des Oiseaux Communs* i.e. Common Birds Temporal Monitoring) program conducted by the *Muséum national d'Histoire naturelle* (Paris), which consists of identifying the species that breed each year and always at the same place. They examined the response of these species (105 in total) to climate warming. To do this, they calculated the average temperature (between March and August) of the whole **distributional area of each species** (**STI**, *Species Temperature Index*). Then, they averaged the temperature indices of all the species of each assemblage of species recorded at a given point in the French territory, thus obtaining a **community temperature index** (**CTI**). This index, which is the average of all the STIs of the species that make up a local bird community, weighted by the abundance of each, was calculated for each of the 722 species assemblages recorded in the metropolitan area. These CTI values provide information on the average degree of "thermophilia" of the species that make up each local assemblage of species, with a high CTI indicating that the population contains many thermophilic species and that the site temperature is high (Figure 4, [10]).

These data allowed these authors to calculate the response of bird communities to global warming: the increase over time in the CTI value of a local population indicates that this population contains an increasing number of thermophilic species (i.e. living more southerly) or, in other words, that thermophilic species have replaced less southern species, the latter having moved further north. Changes in CTIs over time provide information on the extent of average movement of each species assemblage when CTI values are reported at the sites where populations have been surveyed.

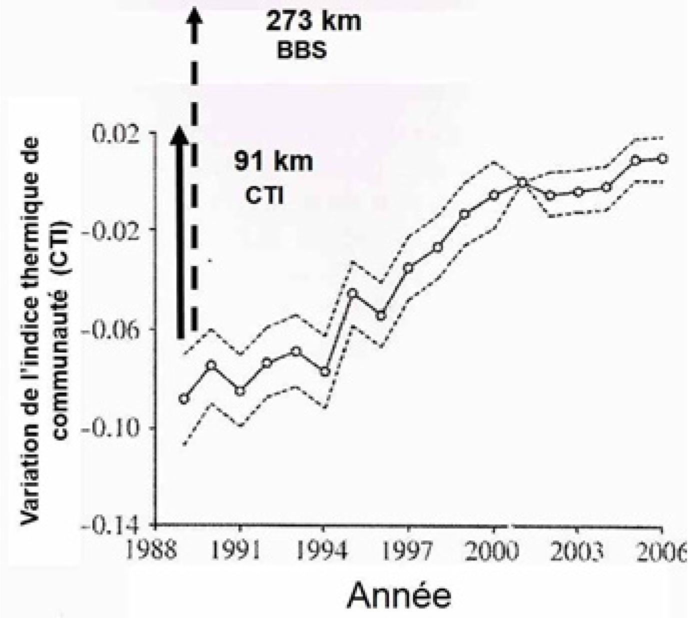

Figure 5. Evolution of the community thermal index (CTI) of bird populations in France between 1989 and 2006. The arrows indicate the northward ascent, in kilometres, of bird communities (continuous black arrow) and isotherms (dashed arrow) (completed from ref. [7]). [Source: © Jacques Blondel]

The same exercise was done for ambient temperatures by calculating for each of the 722 sites where the CTIs were obtained the local temperature differential (from March to August) over a series of 5-year period intervals between 1961 and 1990. As for the CTIs, **local temperature changes** were projected on the **climate map of France** (isothermal map) so that the comparison of the position of the CTIs and that of the local temperatures on their respective gradients gives a measure of their **respective displacement speed**. The spatial variation of the 722 CTIs distributed throughout France over a 2x2 km grid was calculated between 1989 and 2006, revealing that, as expected, the CTI of each point increases steadily over time, reflecting changes in the composition of local species assemblages in the direction of thermophilic species enrichment (northward shift of southern species). This variation corresponds to an average displacement of 91 ± 11 km. Meanwhile, the increase in local temperatures corresponded to a northward displacement of isotherms of 273 km (Figure 5, [7]). The authors conclude that, as expected, **birds move well north in response to warming, but they do so less quickly than they should** because the difference between the distance flown by birds and the distance between isotherms in the two periods is 182 km.

For many reasons that cannot be developed here, movements resulting from habitat tracking are highly variable depending on species, so that local species assemblages of any given habitat change over time. While latitudinal movements of birds are regularly observed, **habitat tracking also occurs along mountain slopes**when birds move up to follow **altitudinal shifts of their habitats**.

And in extreme environments?

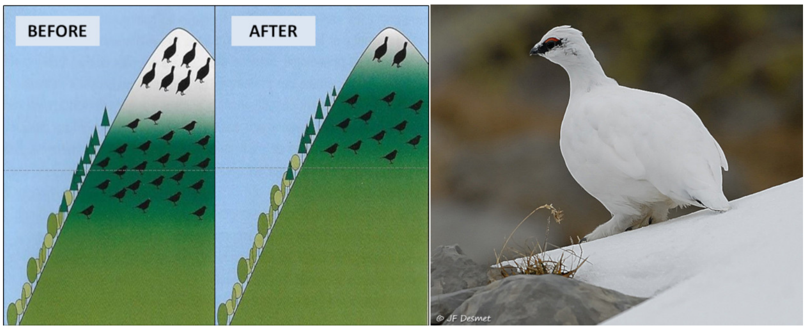

Figure 6. Populations of the rock ptarmigan (Lagopus muta), the most cold-adapted bird in the French birdlife, are declining as their habitats shrink. Upward shifts of the habitats of mountain species such as the rock ptarmigan result in the fragmentation, then the decrease and ultimately the extinction of their populations. [Source: diagrams © Jacques Blondel, photo © Jean-François Desmet/reserved rights]

When habitat tracking that allows the organism to "stick" as close as possible to the climatic envelope to which it is adapted is **no longer possible**, as it is the case for bird populations breeding in **extreme environments** such as the Arctic, Antarctica or in high mountain environments, their numbers are expected to collapse if no adaptive response is possible. This is observed in populations of the rock ptarmigan *Lagopus muta* (Figure 6) whose **habitats shrink from year to year** as they move upwards as a result of climate warming. Over the past three or four decades, Arctic ice areas have declined at a rate of 45,000 km^2 per year. These impressive figures are associated with many other phenomena such as permafrost melting, the northerly rise of subforest formations, narrowing tundra habitats areas accordingly. In response to climate warming, the extension of forested formations in latitude and altitude results in a shrinkage, estimated at 40% to 57% by the end of the 21th century, of habitats specific to many goose and shorebird species, half of which could disappear by the end of the century [11].

3.2. Climate warming and bird migration: new challenges

The **steady decline,** of about 1% per year for the last **twenty years**, of **trans-Saharan migratory species** is due to a number of constraints including a **deterioration of conditions for migration and wintering habitats that fragment**, desertify and transforms, as well as the worsening of metabolic constraints associated with crossing an expanding Sahara [12].

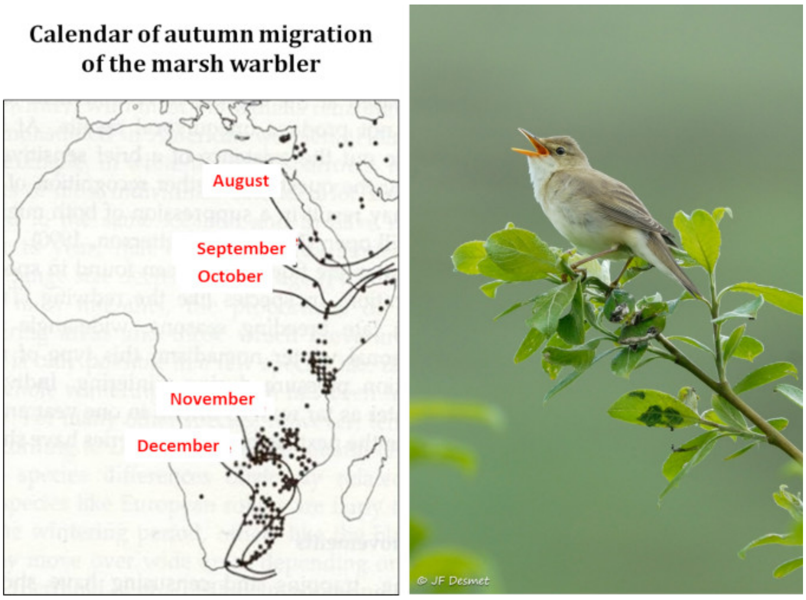

Figure 7. Calendar of autumn migration of the marsh warbler (Acrocephalus palustris). Like all trans-Saharan migrants breeding in Europe, this warbler faces new constraints due to the expansion of the Sahara and the degradation of habitats.]Source: diagram © Jacques Blondel, photo © Jean-François Desmet/reserved rights]

Migration (Figure 7) is a **complex phenomenon** governed by **sophisticated** behavioural, physiological and endocrine **adaptations**. It is achieved according to a rigorous timing and implies the existence, at the various stages of the journey, of resources allowing birds to reconstitute periodically their energy reserves in stopover sites. Climate change is disturbing the subtle balance that evolution has established between these different factors.

The **warbler** family is a **nice model** for studying these issues because of the seventeen species breeding in Europe, some are trans-Saharan migrants, some are partial migrants, and others are sedentary. A simulation of the response of the different species to global warming shows that, depending on various warming scenarios, breeding territories are expected to move northward by an average of 3.8 to 4.4 degrees latitude, which will increase the distances to be covered by highly migratory species such as the **garden warbler** (*Sylvia borin*) by some 400 to 600 kilometres because wintering habitats are not expected to change. It has been calculated that this **increase in the distances to be covered requires an increase in the bird's net mass of about 9%,** corresponding to the excess energy reserves that must be stored in the form of fat required for this journey. We know that a small sparrow weighing about fifteen grams consumes about 3.5 grams of fat to cover 1000 km. Such an additional cost implies finding more food during migration stopovers and being able to store it as fuel in the body, a challenge that is difficult to meet and presumably one of the causes of the observed decline of populations. It may also be that the process of becoming adapted to the new conditions imposed on migrants is not fast enough if genetic responses to new selection pressures are slower than required by the speed of temperatures rising [13].

Figure 8. Black-headed Warbler (Sylvia atricapilla). [Source: © Jean-François Desmet/reserved rights]

Indeed, since **migratory behaviour** is a **genetically determined and inheritable trait**, it is expected to evolve under the effects of directional selection pressures exerted by current warming. A team of German researchers has elegantly experimentally demonstrated on a partially migratory bird, the blackcap warbler *Sylvia atricapilla* (Figure 8), that migratory behaviour can disappear or appear as a result of selection pressures applied to back- crosses in aviaries. A small experimental population that was partially migratory at the beginning of the experiment was made totally migratory in three generations, or totally sedentary in six generations [14].

Under current selection pressures, **many partially migratory species** can be expected to **become resident**, as is already being observed, while many trans-Saharan migratory species will have to **modify their migratory performance** in order to **meet the new challenges** raised by the deterioration of their migration conditions. Huge variations in the intensity of migratory behaviour occurred repeatedly in the history of birds, especially during the Pleistocene with alternating glacial and interglacial periods that significantly altered the tempo and mode of migration.

3.3. An alternative to habitat tracking: local adaptation

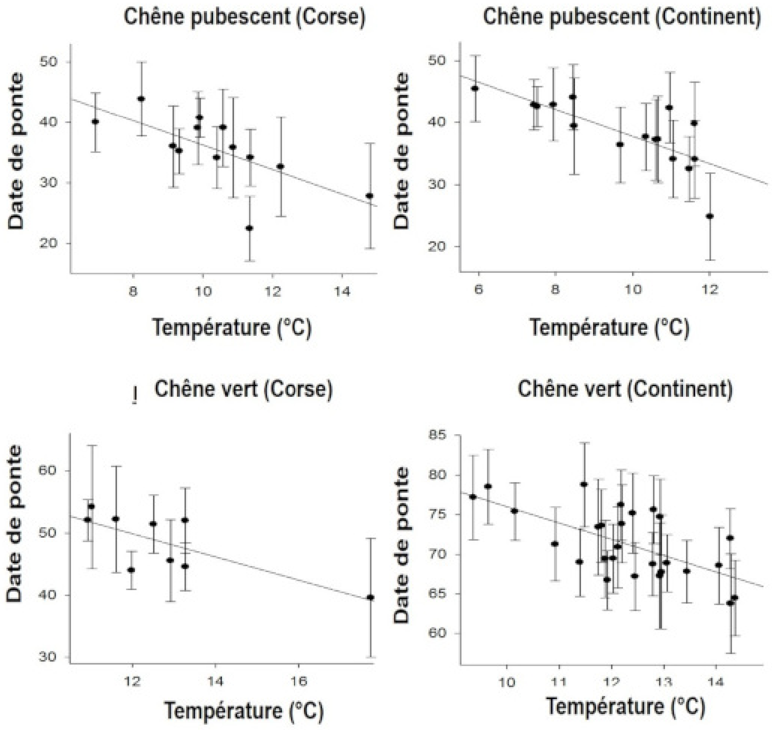

Figure 9. Relationship between the laying date and temperature at the beginning of spring in different habitats dominated by oaks in the surroundings of Montpellier and Corsica. The milder the temperatures, the earlier the tits lay their eggs. Modified according to ref. [16]. [Source: © Jacques Blondel]

Many life history traits respond with varying degrees of intensity to global warming. For example, **birds tend to nest earlier in spring** [15] but the complexity of the mechanisms involved explains the exceptions that are often observed.

Observed changes in life history traits may be related to phenotypic plasticity whereby individual proximately responds to an environmental signal, such as immediate temperature: birds tend to start laying later when spring is cold and a earlier when it is warm (Figure 9, [16]).

However this immediate response, which occurs within a "window of phenotypic plasticity", has its limits because this window is not extensible so that some kind of maladaptation occurs whenever the limits of the window are overshot. In a study on the variation in the laying date of the great tit *Parus major* (Figure 10), Visser *et al* [17] were surprised to find that the population did not respond to warming, although the peak of abundance of defoliating oak caterpillars these passerines feed upon in during the breeding season, had advanced by about ten days.

The explanation for this lack of adaptation was as follows: to **adjust their breeding time** to the optimal date which fits to the **peak abundance of the insects** they feed on, birds use **signals from the environment** (so-called proximal signals) that inform them on the **amount of food** they will find more than a month later (after laying and incubating the eggs). If the **ecological factor** that determines the window of phenotypic plasticity within which the bird decides to lay eggs, in this case the birch budburst, does not respond in the same way to the temperature increase that **triggers** the development of chick food, in this case the budburst of oaks that announces the hatching of defoliating caterpillars, there will be a **gap** between these two crucial stages of the reproductive cycle, namely **laying eggs** and **rearing young**. The bird's margin of manoeuvre is narrow because when the first egg is laid, the "blow is gone" so to say because the events inevitably follow one another: it takes four days to form an egg in the oviduct, the bird lays one egg a day and then incubates its clutch laying for 12 days. Since the young's needs are at their maximum eleven days after hatching, the bird must "decide" to lay 4+10+12+11 days = 37 days before the peak of abundance of the food resource if it lays 10 eggs. It does this by using signals "proximal" to the medium, in this case the **photoperiod**. [18]

Figure 10. Coal tit (Parus major). [Source: © Jean-François Desmet/reserved rights]

The challenge for the bird is to **adjust demand to supply**, a phenomenon of maladjustment taking place whenever supply is shifted in time in relation to demand. Such situations are not exceptional, particularly among trans-Saharan migrants because of a delay in the phenology of signals that occurs several thousand kilometres away. If the signal that triggers the return of a trans-Saharan migrant does not change while the signal that triggers the appearance of his food in Europe is advanced, the result is maladaptation. This was observed in a population of the European Pied Flycatcher *Ficedula hypoleuca* in the Netherlands, as the bird did not significantly advance its date of return from Africa, while the emergence of the caterpillars on which it feeds its young was advanced by about ten days in response to global warming [19].

Besides phenotypic plasticity that has its limits, **adaptive evolution** by **directional selection** can be rapid so that selective processes can significantly affect the dynamics of a population within a few generations [20]. Such an evolutionary change will, over time, **restore the broken synchronism**; a process known as "evolutionary rescue" by which the genetic structure of the population gradually changes over time as a result of directional selection that favours the least maladapted individuals.

Figure 11. Foggy moth (Operophtera brumata): left, caterpillar, food almost exclusive to coal titmice in some habitats in spring; right butterfly. [Source: Caterpillar © spacebirdy (CC BY-SA 3.0); butterfly : ©entomart (royalty-free)]

An example of directional selection in action is provided by the story of an English population of coal tit [21] (see Figure 10). Half-century monitoring of this population, all of whose breeding individuals are ringed, showed that between 1961 and 2007, the laying date advanced by 14 days, allowing birds to "shift" to the food supply provided by the caterpillars of the winter moth *Operophtera brumata* (Figure 11). Individual monitoring of each female showed that each year **individuals adjust their laying date** to **match the food supply and the demand expressed by the chicks**. The fact that the response is immediate with an excellent correlation between the peak demand period and the peak abundance of caterpillars points to phenotypic plasticity as an adjusting mechanism.

But the effectiveness of **phenotypic plasticity** is not indefinite. At some point, when the limit of the plasticity window has been reached, a **microevolutionary mechanism** comes into play to take over, one might say. Quantitative genetics methods that have been applied to this population since all individuals are ringed and therefore known, have demonstrated the effectiveness of this mechanism based on two key parameters, the **intensity of selection** imposed by the temperature differential and the **heritability** of laying date. The authors of the study showed that tits whose mothers nest a little earlier in the warm years are more likely to recruit their young into the population than others, with recruitment rates being in the average when the previous year's temperatures were in the average.

3.4. The cost of maladaptation

Figure 12. Blue tit (Cyanistes caeruleus). [Source: © Jean-François Desmet/reserved rights]

The vital importance for fitness of phenotypic adjustment and/or response to selection can be measured by estimating the **cost** of local **maladaptation**, for example when there is a **mismatch between food supply and demand**. Again, the tit model was used to analyse these costs based on measurements of the difference between the maximum feeding demand period of blue tit chicks *Cyanistes caeruleus* (Figure 12) and the peak abundance of caterpillars with which the chicks are fed. From methods using doubly labelled water (with oxygen and hydrogen isotopes) it has been possible to measure and express in terms of energy currency (e. g. kilojoules), the metabolic effort provided by a bird to raise its young. It was shown that, compared to well synchronize broods on the food availability window, **poorly synchronized broods** had:

lower quality offspring with little chance of survival,

a much higher cost of raising chicks (about 2 to 4 kilojoules spent to produce one gram of chicks compared to 1 to 2 kilojoules in well synchronized broods),

a metabolic effort provided by the parents almost twice as high (5 to 7 times the base metabolism compared to 3 to 4 times) to feed the mismatched broods [16].

The **consequences of** such a lack of synchronization between supply and demand could become **serious** if the acceleration of **global warming** were to become such that the expected response to selection was not fast enough to allow organisms to adapt in time to new environmental conditions.

4. Global changes and ecosystem functioning

Figure 13. Variable nozzle (Buteo buteo). [Source: © Jean-François Desmet/reserved rights]

As all species in a community do not all respond in the same way to climate forcing, disruptions in interspecific interactions could have unpredictable consequences on ecosystem functioning. This is a huge subject because while the **direct consequences of global warming** are fairly **well know**n at the *species lev*el, almost **nothing is known** on what happens to **interactions between species** within permanently reorganizing assemblages.

Here is an example [22]: the four-fold increase in the numbers of a German population of common buzzard *Buteo buteo* (Figure 13) over the past 20 years is the result of an improvement in the bird's survival from 0.63 to 0.74 in females and from 0.61 to 0.80 in males. Surprisingly, these **changes in survival** were associated with a considerable decrease over the same period in the values of the very general North Atlantic Oscillation climate metric (**NAO**, colder temperatures, less rain but more snow; see Climate Variability: the example of the North Atlantic Oscillation). Although the relationship between the variation in NAO and buzzard survival does not say anything on the mechanisms involved because **correlation does not mean causality**, these variations were confirmed on a larger spatial scale: when the **NAO decreases, buzzard survival increases** and vice versa. The mechanism involved is therefore somehow related to these climatic factors.

The authors of the study eventually discovered it: the main prey of buzzards, especially in winter, is the vole *Microtus arvalis* whose populations are climate sensitive. While rain and frost are very unfavourable to this small mammal, a snow cover protects it while allowing the predator to detect and capture it if the snowpack is not too thick. A small layer of snow, which has been quite frequent over the past two decades, was therefore very favourable to voles, and therefore to their predators. The close relationship between the **geographical variation in buzzard survival** and **climatic conditions** is a demonstration of the **interdependence** of the different levels of variation, that of **climate**, that of **voles** and that of their **predators**. But this example also illustrates the complexity and, often, the unexpected nature of the relationships that climate change may produce. This makes it very difficult to predict and model the changes expected from the reorganization of food webs within species assemblages and, more generally, the responses that organisms make to climate change.

5. To go further

The main **limitations** of **studies** on **organisms' responses** to climate change are due to their mostly **correlative nature**, which says **nothing** on the triggers and **mechanisms** involved. However, the involvement of several components of global change in changes in distribution areas or phenological events such as laying dates or migration departure dates in birds complicates the analysis of mechanisms. Three types of approaches can provide interesting answers:

The first is **modeling of niche envelopes** [23] which is based on a multivariate statistical representation of the organism's niche by relating its spatial distribution to key environmental variables. The niche thus defined is projected into the geographical space that the species should occupy in the future according to different expected scenarios of climate change as proposed by the IPCC *(Intergovernmental Panel on Climate Change*).

A second approach which is expected to be particularly promising, is **epigenetics**, namely the study of mechanisms of environmental origin (climate stress, disturbance events, maternal effects) that modulate the expression of coding genes without modifying the genetic structure of the organism (see Epigenetics, the genome and its environment). These mechanisms of non-mendelian heredity (sometimes named “soft heredity”) can play a considerable role in adapting organisms to environmental changes because they are expressed during the development of the individual without going through the intergenerational screening of natural selection. These changes of epigenetic origin, which, moreover, are heritable, have the evolutionary consequence of either shifting the mean of the line to a new optimum, or modifying its variance and therefore its fitness, or reducing its variance around a new optimum, what is called a "phenotypic channelling" process [24].

A third approach, still under-exploited but promising, is the **use of data from the past**. As soon as they can be identified, the responses of organisms to changes that took place in a more or less distant past represent "natural experiments" that allow ecological and evolutionary theories to be tested [25].

The fossil record can thus provide answers on adaptive evolution in response to climate change at time scales from a few years to about ten thousand years. It also provides answers on the reality of phenotypic plasticity at shorter time scales, of an order of one to a thousand years. Paleogenomics can also identify range shifts, population collapses and extinction events in response to climate change. Responses to variable climates have thus been explored using evolutionary genetics and experimental approaches to "resurrection ecology", which consist in resuscitating propagules in prolonged dormancy, sometimes for several centuries (diatoms, insects, fungal algae, bacteria) and then experimentally submitting them to climatic stress events [26]. The great merit of all these approaches, many of which are still at an exploratory stage, is that they allow to **move from correlative models** to **process models** that allow to **identify the mechanisms involved**.

6. Messages to remember

Organisms are adapted to live within a temperature window below or beyond which their survival is jeopardized,

Habitat tracking in response to warming is a classic response which varies from species to species,

Habitat tracking is no longer possible in extreme habitats (tundra, high mountains), hence the threats to birds in these environments,

Global warming is imposing new and severe constraints on migratory birds, especially trans-Saharan migrants,

An alternative to habitat tracking is local adaptation through phenotypic adjustment and/or or microevolution,

Global changes modify the interactions between species, and therefore the structure and dynamics of communities.

Notes and references

Cover illustration. [Source: © Jacques Blondel]

[1] The changes inflicted by humans on the Earth system have proved so profound and universally distributed that meteorologist and chemist Paul Josef Crutzen coined the term Anthropocene at the end of the 20th century (Crutzen & Stoermer, 2000, The "Anthropocene". *Global Change Newsletter* 41, 12-13), literally, "the era of man" to refer to that period in the history of the Earth from which human activities have irrevocably marked the Earth's crust, as well as powerful telluric forces. Although the International Commission on Stratigraphy was cautious about this new sequence of Earth's history, the term quickly became part of scientific vocabulary, including that of the life sciences.

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