



Phenology



The study of recurring biological events in an organism's life cycle, particularly in relation to changes in climate, is called phenology. Environmental scientist **Hazel List Shipsey** explains how important it is to understand the environmental cues for events such as migration and flowering, and how this understanding can drive appropriate conservation strategies

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Have you ever wondered how ancient civilisations knew how to time agricultural practices and hunts? They relied on their understanding of plant and animal life cycle events, including budburst, flowering, insect emergence and animal migration. By observing and understanding these ecological cycles, past civilisations could survive and prosper within their environment. But what triggers recurring natural events?

Triggers for phenological events

Seasonal changes within plant and animal life cycles are largely driven by external environmental conditions. In terrestrial ecosystems, temperature, rainfall and day length are the most influential factors.

Changes to conditions act as environmental cues that can trigger distinct stages in an organism's life cycle, known as phenophases.

In temperate zones, for example, the cooler temperatures and shorter days of autumn cause plant growth regulator changes in deciduous trees. These changes trigger the colour change and eventual fall of leaves. This leaf senescence is largely driven by a rise in ethylene and a decline in auxins within the leaves (see *BIOLOGICAL SCIENCES REVIEW* Vol. 37, No. 1, pp. 2–6).

Leaf senescence is a phenophase



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Box 1 Plant–pollinator interactions

Almost 75% of all flowering plants (angiosperms) rely on pollination services from animals. These plant–pollinator interactions are not only vital for maintaining ecosystems, but also for supporting global food production and biodiversity. This is a mutualistic relationship, since both sides are provided with benefits. The pollinator is provided with food from nectar and pollen, while helping the plant reproduce by transferring pollen between flowers.

Some pollinator species – specialist pollinators – rely on specific plant species and, in turn, provide more efficient pollination for those plants. However, these specialist plant–pollinator interactions are especially vulnerable to shifting phenophases. If the flowering phenophase and pollinator emergence are mismatched, pollination may fail for that season. This threatens both plant reproduction and pollinator survival, which can have devastating effects on future populations and global biodiversity.

Plant–pollinator interactions are vulnerable to shifting phenophases



For species higher up the food chain, the triggers of phenological events are complex. Take migratory birds, for example, which travel thousands of miles between their overwintering and breeding grounds. Instead of responding directly to climatic conditions, their migrations are guided by endogenous cues (internal biological rhythms), which for many species are triggered by changes in day length.

However, changes in day length are not the only trigger. Behavioural scientists discovered this after observing that caged migratory birds kept in constant artificial daylength displayed two annual periods of heightened activity, known as ‘migratory restlessness’, in spring and autumn. It is hypothesised that migratory birds may also be responding to changes in air pressure to time their departure, explaining how birds from the tropics – where day length exhibits minimal change – know when to take flight.

These are examples of **proximate mechanisms** behind phenological events. Proximate mechanisms explain how phenophases occur, including the environmental cues and hormonal changes that trigger the expression of phenological traits. But this raises a question: why has natural selection favoured organisms that time their life cycle events to particular seasons?

Adaptive advantages of seasonal timing

From decomposers to apex predators, each group within a community plays a role in maintaining ecosystem structure. This balance within ecosystems depends heavily on the timing of life cycle events across taxa, which controls key biological interactions, such as predator–prey dynamics and plant–pollinator mutualisms (see Box 1).

TERMS EXPLAINED

Latitudinal gradient The spatial pattern of environmental conditions changing systematically with latitude.

Proximate mechanism The immediate, endogenous and exogenous factors that cause a plant or animal to exhibit a particular phenological event.

Ultimate mechanism The selective pressure that drives a plant or animal to exhibit a particular phenological event.

Over time, natural selection has favoured individuals with phenophases that maximise individual fitness, survival and reproductive success. Animal migration, for example, should maximise reproductive success and juvenile survival by ensuring that breeding happens in areas with abundant resource availability and favourable environmental conditions. These adaptive advantages are the **ultimate mechanisms** behind phenological events. These mechanisms explain why organisms benefit from timing their seasonal life cycle events to optimal environmental conditions.

Genetic diversity within ecosystems also means that certain species have evolved in a way that allows them to better detect and respond to environmental change. For example, genetic adaptations have been found in thale cress (*Arabidopsis thaliana*) that allow the species to be more responsive to changes in day length and to flower earlier. These adaptations resulted from allelic variation in the gene encoding the photoreceptor. Genetic adaptations like this allow certain organisms to stay better in tune with environmental change.

Spring events

In temperate zones, spring brings a rise in temperatures and days get longer. Key life cycle events unfold across ecosystems. The timing of these events is crucial for the reproductive success and overall survival of countless species across trophic levels. Over time, selection has favoured individuals able to navigate a delicate balance of trade-offs.

The weather in spring is notoriously unpredictable. If phenological events occur too early, organisms risk increased exposure to harsh environmental conditions and limited resource availability, which can be fatal. But an earlier onset of spring events offers advantages, such as longer growing or breeding seasons. For example, early leaf growth in plants provides benefits from the prolonged sugar production (from photosynthesis) and reduced interspecific

competition for resources, but risks damage to leaf tissue from late spring frosts (see *BIOLOGICAL SCIENCES REVIEW* Vol. 38, No. 2, p. 19).

If phenological events are delayed to later in spring, organisms may benefit from improved environmental conditions and have improved chances of survival. But a later onset of events will likely reduce individual competitive success for territory and/or mates. After migration, for example, a late arrival usually means birds struggle to establish nest sites and find mates – reducing their reproductive success. Over time, selective pressure has favoured organisms able to balance trade-offs.

Phenological mismatch

If interacting events are mistimed within a year, such as pollinator emergence misaligning with the blooming of flowers, there are phenological mismatches (see Figure 1). These can have severe consequences for individual fitness and survival.

Winter moths (*Opheroptera brumata*), for example, experience mismatch in warmer winters. Warmth triggers their eggs to hatch before the oak leaves upon which the larvae feed have emerged. Researchers in the Netherlands found that years with greater mismatch cause a decline in population density, due to juvenile

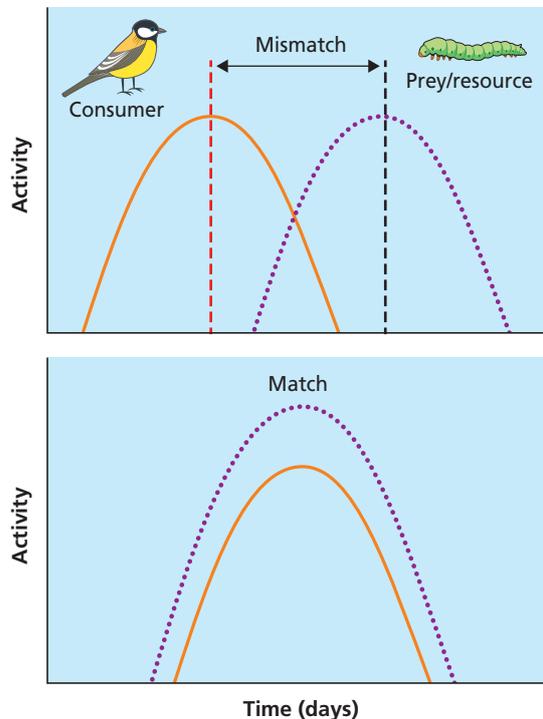


Figure 1 Phenological mismatch. The dashed black line shows the timing of peak resource availability (e.g. insects). The dashed red line shows the timing of peak consumer activity (e.g. migratory birds). When these peaks are misaligned, phenological mismatch happens, because peak consumer activity does not synchronise with peak resource availability

mortality. Such fluctuations in insect populations can have cascading ecological consequences for species in higher trophic levels, such as insectivorous birds.

How climate change affects spring events

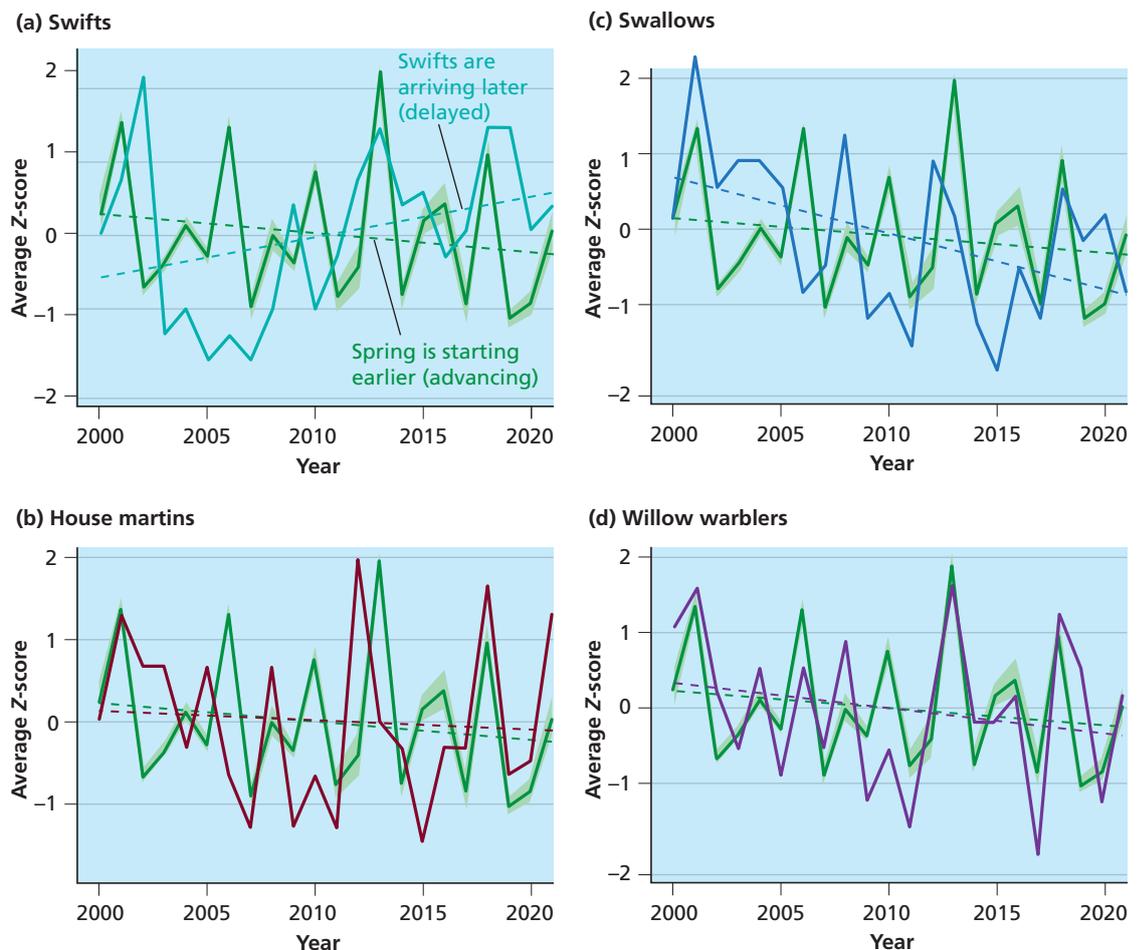
In recent decades evidence has amassed across the world of uneven shifts in the timing of life cycle events across trophic levels. These changes are directly linked to rising global temperatures, because biological processes are highly responsive to temperature change. In the UK, spring events are particularly vulnerable to long-term change since the season is undergoing the fastest annual increase in temperature in comparison with the other three seasons.

Published global studies, which have combined data from around the world (meta-analyses), have estimated that spring life cycle events in terrestrial ecosystems are advancing by as much as 5.1 days per decade. However, there

is a clear **latitudinal gradient** in phenological advancement across the globe, which is in line with the spatial variation in global warming. This is most evident in the Arctic, where phenological events for some species are advancing by 30 days per decade, with regional warming occurring almost four times faster than the global average.

The rate and direction of shifts to spring events is also showing variation between organisms, meaning species interactions are falling out of sync. This variation comes down to phenotypic plasticity – the ability of a species to adjust its behaviour or traits in response to the environment (for example, see *BIOLOGICAL SCIENCES REVIEW* Vol. 38 No. 2, p. 19).

Some species are naturally better at sensing and responding to changes such as rising temperatures. These species can rapidly shift the timing of their phenophases without requiring generations of evolutionary change. Others may respond slowly to environmental change and fall



Source: Data from the Woodland Trust's Nature's Calendar database

Figure 2 Time-series data for migratory bird arrival dates to the UK from 2000 to 2021. Spring green-up is represented by the green line, while the other coloured lines show the arrival trends of four species: (a) swifts, (b) house martins, (c) swallows, and (d) willow warblers. Z-scores were used in the standardisation process because they provide a common yardstick, with positive values indicating a delayed arrival and negative values indicating an advanced arrival

out of sync with the optimal temporal niche for individual survival and reproduction.

This varying ability to respond to environmental change is driving increases in phenological mismatch across trophic levels in response to climate change. These differences are shaped by the genetic diversity across ecological communities, and even individuals within a species may show variance in phenotypic plasticity.

How mismatch is affecting migratory birds

Migration is a key biannual phenological event in which animals move between wintering and breeding grounds. Climate change poses a particularly significant threat to many migratory birds by disrupting arrival synchrony with breeding ground conditions and spring green-up (buddburst and insect emergence). Research shows that this mismatch is having an impact on long-distance migratory birds, such as those travelling between Sub-Saharan Africa and the UK, due to the weak climatic connectivity between wintering and breeding grounds.

The magnitude of mismatch varies between species, with some showing better adaptive ability to keep track of conditions in their breeding grounds (see Figure 2). The variation in arrival trends between species is complex, but it largely reflects differences in migration strategy and adaptive ability. For example, swifts remain airborne for the entirety of their migration route, whereas willow warblers take prolonged breaks at stopover sites to rebuild their energy stores. Such differences directly influence both the speed of migration and the environmental conditions faced along the route.

Species that rely on stopovers to build up their energy stores for migration are also particularly vulnerable to mismatch. For example, semipalmated sandpipers (*Calidris pusilla*), which migrate between the Arctic and South America, depend upon horseshoe crab eggs in Delaware Bay to replenish their fat stores during migration. Misalignment between stopover timing and horseshoe crab spawning (which is tied to lunar cycles) can limit the birds' ability to reach their breeding site, proving detrimental to the future population size of this species.

Why phenology is important

Phenology allows us to understand how climate change is impacting our natural world. Climate-induced changes to life cycle events are altering the structure and function of ecosystems around the world, with changes to species interactions and overall biodiversity loss being reported.



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Semipalmated sandpipers in Delaware Bay, USA

Increases in the abundance and distribution of invasive species are also occurring in many ecosystems. This is a result of new temporal niches, created by the changed seasonal rhythms of natural events, which can be exploited by invasive species with minimal competition. However, understanding the timing of life cycle events is also the key to developing effective conservation strategies. By aligning our actions with the seasonal timing of organisms, we will be in a better position to recover ecosystems and build up their resilience to the changing climate.

RESOURCES

Plant–pollinator interactions:

<https://tinyurl.com/plant-pollinator>

Additional information about bird migration:

<https://tinyurl.com/bird-migration-triggers>

<https://tinyurl.com/migration-mystery>

The impact of a warming spring in the UK:

<https://tinyurl.com/warming-spring>

Migration of the monarch butterfly:

<https://tinyurl.com/monarch-migration-mystery>

More about the role of horseshoe crabs in Delaware Bay for migratory birds:

<https://tinyurl.com/horseshoe-crabs-birds>

Hazel List Shipsey has a BSc (Hons) in environmental science from the University of Liverpool. She is currently taking a year out of her studies to gain hands-on experience in the field through volunteer work. She then plans to pursue a Master's degree in ecology, with the hope of going into a research career to help mitigate global biodiversity loss.