ORNITHOLOGICAL MASTERCLASS

35 PHENOLOGY

From watching eagerly for the first Swifts to waiting for fledglings to appear at the garden bird feeder, ornithologists are captivated by when different events happen in nature. **Megan Stamp** explains the fascinating field of phenology – the study of recurring seasonal events – and why understanding it matters more than ever.

GREAT TIT: DAVID TIPLING/BIRDPHOTO.CO.UK, SHAGS: EDMUND FELLOWES/BTO

Timing is everything, so they say, and for birds in highly seasonal environments, the timing of breeding and migration events is critical. When a bird decides to breed can mean life or death for its offspring – too early and the cost of keeping eggs and then chicks warm might be too high, but the late bird may struggle to find food for begging chicks. An individual bird can adjust timings by decisions about when to build a nest, lay eggs and start incubating. Migratory birds are also faced with a host of earlier decisions that ultimately constrain their breeding timing, such as when they leave their wintering site, when and where they stop off en route, and when they arrive at the breeding grounds.

◀ Great Tit breeding has been studied in Wytham Woods since 1947.

Phenological datasets: from diaries to radar

Though popularised by the likes of Springwatch and its nestcams, our shared interest in phenology is not a recent phenomenon. The nature calendars and diaries of Robert Marsham and Gilbert White offer examples of bird arrival and breeding time records dating back to the 1700s. The legacy of these records remains today, with nature diaries now in our hands as recording apps and websites. Perhaps you have submitted data to the BTO's Nest Record Scheme, a globally peerless citizen science scheme that has amassed more than 1.8 million observations of the timing of egg-laying, incubation and fledging of birds stretching right back to 1939. Or perhaps you record the birds you see via BirdTrack and eBird, which can be used to document the timing of waves of migration.

Technological advances since the days of Marsham and White are allowing us to collect previously unimaginable forms and quantities of information, meaning that phenology is now very much in the realm of 'big data'. Weather radars can be co-opted to track flocks of migrating birds by day or night, and even at high altitudes, and can follow the timing of movements over large distances. New acoustic monitoring methods present opportunities to identify bird species and record the timing of their migrations, while geolocators and GPS devices can also track migration timings, and time-lapse cameras at penguin colonies can monitor breeding phenology in some of the harshest conditions on Earth.

◀ Shags on the Isle of May have been monitored intensively and systemically since 1973.

There is also a great wealth of long-term scientific studies. The Great Tits at Wytham Woods, Oxfordshire (*BTO News* 342), Shags on the Isle of May in the Firth of Forth, and Pied Flycatchers of Yarner Woods, Devon, are amongst projects providing several decades of phenology data collected using standardised methods. These datasets, along with the advances in technology and analytical techniques, have allowed us to glean many exciting insights into the dynamic way in which phenologies of different species of birds have been adjusting to a changing climate.

SO WHAT IS CHANGING?

Any bird enthusiast, or just anyone who spends time outdoors, likely recognises that in warmer years birds breed earlier. For instance, when a spring is 1°C warmer than average, populations of Blue Tits across Europe are expected to advance their egg laying date by 0.7–7 days. Therefore, as climate change has been leading to a trend of warming springs in recent years, we are seeing birds breed earlier over time.

KNOWN UNKNOWNS

While clearly important for determining shifts in timing, temperature is not the only factor at play. A study of laying date for 60 bird species across the UK and the Netherlands found that on average 50% of the magnitude of advancements was due to rising spring temperatures, but the remaining 50% was due to 'other factors'. These may include other environmental drivers, such as rainfall, or temperature effects acting at different times of year. They may also include non-climatic drivers such as urbanisation and habitat change, or even genetic change. For migratory birds, it may also be that temperature at wintering or stopover sites is additionally influencing migration and thereby breeding dates. We know more about bird phenology than we do for any other animal group, but there are big parts of the picture that we don't yet fully understand.

◀ Wheatears advanced their arrival to the UK by 10.7 days between 1971 and 2000.

Move more, change less

The phenology of migratory birds is subject to unique constraints. A study of 684 species found that the shorter the distance a bird migrates, the greater the tendency to advance their breeding date in warmer years. Birds that coincide their arrival date with conditions conducive to breeding (when environmental conditions are favourable, there is plentiful food, and the best nesting spots have not been taken) tend to fledge more offspring. It is not surprising that long-distance migrants are advancing their breeding by less than residents – non-migratory birds can track the climate at their breeding site much better because they are already there. While birds that overwinter closer to their breeding site may use changes in climatic conditions at their wintering site to predict conditions at their breeding site and time their migration accordingly, long-distance migrants do not have this luxury. Imagine a bird wintering in Sierra Leone; year-to-year fluctuations in the winter climate will not be at all informative about year-to-year fluctuations in conditions on breeding grounds thousands of miles away! We think such species use some combination of photoperiod (the number of daylight hours) and an internal clock to decide when to migrate, and thus individuals cannot track the optimum breeding window as well as their counterparts with shorter commutes.

Maybe she's born with it? Maybe it's plasticity

So we know that many bird populations are changing their phenologies, and in some circumstances we can tell that climate change is responsible; but the question that remains is how are they changing their phenologies? It may be that an individual bird is plastic in its phenology – in a warm year it 'decides' to breed earlier and then in a cold year the same bird may breed later. This plasticity is perhaps most familiar to all of us by looking not at birds, but at trees, and the variation in leafing times from year to year. Plastic responses can be very useful in the face of rapid shifts (such as rapid temperature increases or large weather fluctuations associated with climate change), as it can give the birds a buffer to deal with this short sharp change. We think however that plasticity can only stretch so far, so if the change eventually gets too drastic then the birds might not be able to flexibly shift their phenologies to the necessary extent. Another way of advancing breeding phenology is via evolution – if the birds that breed earlier fledge the most offspring, this could lead to genes that favour early breeding becoming more common in a particular population.

Plastic responses can be very useful in the face of rapid shifts, as it can give the birds a buffer to deal with this short sharp change

Identifying how much birds can track changing climate through plasticity or whether they will need to evolve has major implications for assessing the challenges that populations face – with evolution via natural selection typically being much the slower process. We can test whether a response is plastic by observing the same individuals in different years – if a single bird changes

◀ UK Pied Flycatcher numbers fell by 59.4% between 1995 and 2022.

Migration factors

Species with longer northward migration routes are more likely to encounter weather-related delays

Can move quickly to breeding sites once conditions are ideal

IN EUROPE
Close to breeding sites

CROSSING TO EUROPE
Waiting for good weather

CROSSING THE SAHARA
Waiting for the winds

TROPICAL AFRICA
Waiting for rain

No knowledge of European breeding conditions, cannot move quickly

Phenology beyond temperate regions

IN THE TROPICS

In temperate regions, temperature is the most important driver of breeding phenology but in the tropics and subtropics rainfall is the bigger determinant. In these environments, precipitation helps drive insect abundance in the same way that temperature does in temperate regions. Purple-crowned Fairywrens in the monsoonal tropics of Australia have a rapid onset of breeding following rainfall. This is because insect prey emerges several weeks after such rainfall, coinciding with the fledging of the chicks.

ANTARCTICA

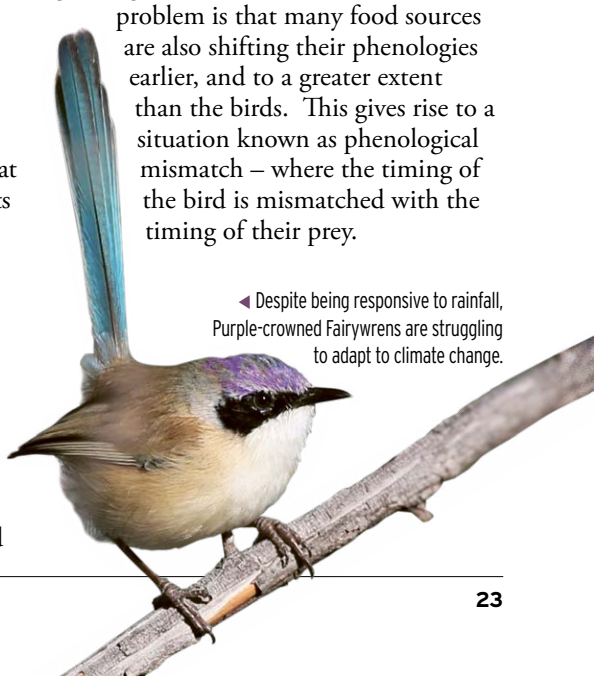
In Antarctica, some seabirds are bucking the general global trend by showing delays in arrival to their breeding grounds and in breeding phenology. Records of nine seabird species between 1950 and 2005 showed an average delay in arrival of 9.1 days, and the five of these species that had breeding records showed an average delay of 2.1 days for egg-laying date in the same period. This seems to be connected to a reduction in sea ice, which in turn decreases the availability of these birds' marine food sources.

their phenology across time, then this must be due to them having a plastic response. Using this method, the Wytham Woods Great Tit study showed that the changes in female egg-laying dates are consistent with plasticity. In comparison, determining whether evolution has contributed to shifts in timings is much harder to test. Perhaps the best evidence we have is from an experiment carried out in Germany on Pied Flycatchers, first in 1981 and then again in 2002. Here, different birds were all raised in identical conditions in both years, and it was found that the more recent birds had shifted to breed 11 days earlier. Since they were all experiencing the same conditions, we can rule out plasticity as an explanation for the shift, and therefore we can infer that the shift is due to evolution and a genetic change.

It seems that for many species, plasticity is a major contributor to the shifts that we are seeing, whereas it is not yet clear how much of a contribution evolution is making and for which species it is most important. It may not be chance that the best evidence for evolution comes from a migratory species, the Pied Flycatcher, that is less able to rely on plasticity to adjust its breeding dates.

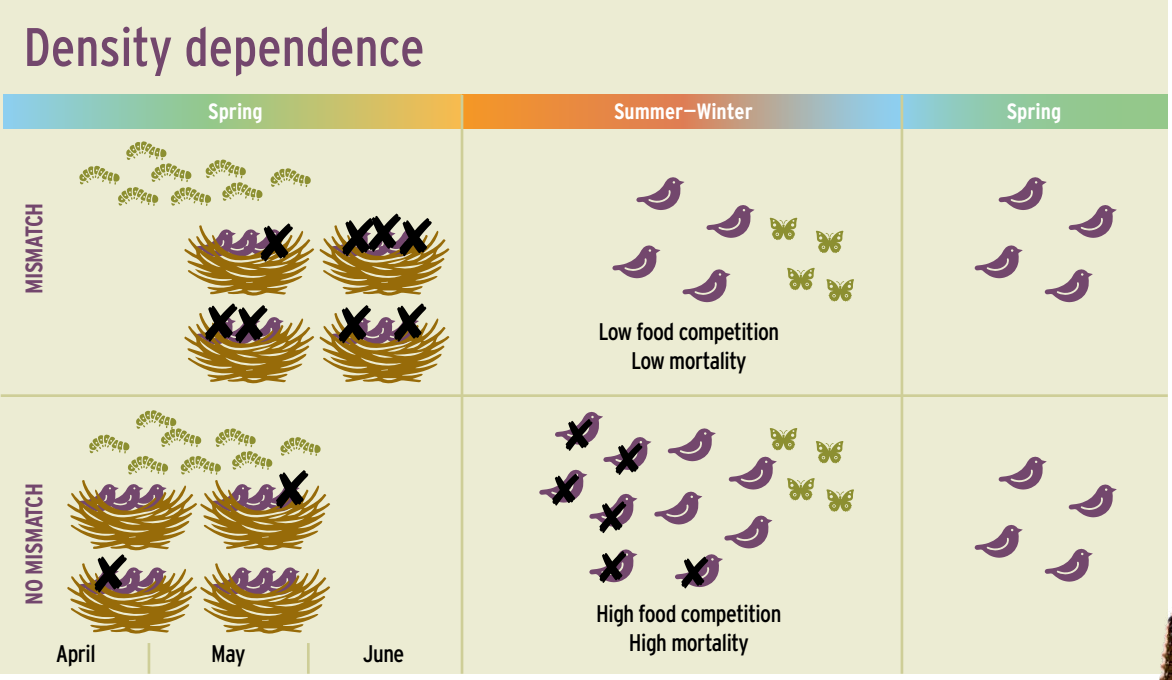
POSSIBLE CONSEQUENCES

So, what is the problem if birds are breeding or migrating earlier? Well, the problem is not that they are breeding earlier, it is that even with these advances they may not be breeding early enough. For many species, evolution over centuries has shaped bird breeding timing so that the peak of food availability coincides with when their growing chicks need it the most. The problem is that many food sources are also shifting their phenologies earlier, and to a greater extent than the birds. This gives rise to a situation known as phenological mismatch – where the timing of the bird is mismatched with the timing of their prey.



◀ Despite being responsive to rainfall, Purple-crowned Fairywrens are struggling to adapt to climate change.

WHEATEAR: EDMUND FELLOWES/BTO, PIED FLYCATCHER: AMY LEWIS/BTO, PURPLE-CROWNED FAIRYWREN: NITRAUS/FLICKR



The author

Megan Stamp is a PhD student researching phenology of forest food webs at the University of Edinburgh. Her main focus is on exploring the impacts of phenological shifts between competing species, and she spends spring in the field working on the Phenoweb project in Scotland, collecting data on phenological mismatch between Blue Tits, caterpillars and trees across 44 sites between Edinburgh and Dornoch. She is a BTO-licenced Blue Tit ringer.

The early bird catches the caterpillar

One habitat where birds may be particularly susceptible to such mismatches is temperate forests. These habitats see a short-lived burst in the abundance of caterpillars, which time their development to coincide with the arrival of new leaves. In a warming climate the peak of caterpillar abundance can come and go before the peak of food demand from chicks, reducing the chances of chicks fledging.

Returning to the famous Wytham Woods Great Tits, researchers have been studying how the relationship between caterpillar and Great Tit timing impacts on breeding success for many decades and find that individual birds with broods that are most synchronous with the presence of caterpillars fledge more chicks. Similar patterns have been found in Blue Tits, Pied Flycatchers and Wood Warblers.

Impacts on the phenology of interactions is not entirely limited to diet either. Cuckoos have advanced their spring migration time very little, both in the UK and elsewhere in Europe. While previously Cuckoos laid eggs in the nests of non-migratory or short-distance migratory host species such as Robins, Dunnocks and Meadow Pipits, with climate change they appear now to be shifting more to laying their eggs in the nests of other long-distance migrants such as Reed Warblers. This suggests that Cuckoos are arriving too late to coincide their brood parasitism with the breeding period of their usual hosts.

In a warming climate the peak of caterpillar abundance can come and go before the peak of food demand from chicks

HOW BAD IS MISMATCH?

The natural conclusion upon hearing that increased mismatch leads to more offspring mortality is that populations of birds experiencing high levels of mismatch will be in trouble. So, do we see this? While there are many studies that show changes in breeding phenology, and a reasonable number that indicate that mismatched birds fledge fewer young, there are actually very few studies that manage to connect this to population trends. So as of now it is difficult to say how much of a concern mismatch is. One explanation for why we may not yet be seeing an impact on population sizes is a mechanism known as density dependence: if mismatch is bad and fewer chicks fledge one year, then these fledglings will have a greater abundance of food per bird and will therefore be more likely to survive to the next year. This was found to be the case in a population of Great Tits in the Netherlands, where the level of mismatch had no impact on population growth – the growth rate was the same size whether the birds were mismatched with the caterpillars or not.

The BTO Cuckoo Tracking Project has shown that Cuckoo spring arrival is largely determined by when birds leave their pre-Sahara crossing stopover in West Africa. This is dependent on the timing of rains, which dictate the birds' insect food supply. This timing is largely fixed, preventing Cuckoos from advancing their arrival in line with earlier European springs, leading to phenological mismatch with some host species: **www.bto.org/cuckoo-clocks**

We are, however, seeing decreases in populations of many birds. Breeding Bird Survey data show that the UK population of Pied Flycatchers (a species experiencing phenological mismatch with climate change) has been decreasing over the last few decades, but there is currently no hard evidence to say whether or not mismatch is playing a part in this decline. Against the backdrop of climate change, there is much work to do if we are to better understand the capacity of populations to adjust their timing to track changing conditions. Phenology is liable to remain a hot topic. ■

Find out more

https://bit.ly/4hToXbM

Thackeray *et al*. 2016. *Nature* **535**: 241–245.

Macphie & Phillimore 2024. *Current Biology* **34**: R183–R188.

Helm *et al*. 2019. *Current Biology* **29**: 3714–3719.

CUCKOO: EDMUND FELLOWES/BTO