The Phenology Handbook

A guide to phenological monitoring for students, teachers, families, and nature enthusiasts

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WHAT IS PHENOLOGY?

Phenology is the observation and measurement of events in time.

The passing of the seasons is one of the most familiar phenomena on Earth. Consider, for example, the onset of spring in temperate climates. As winter ends, our surroundings burst with new life — forest canopies fill with vibrant greens, flocks of birds migrate in formation to northern breeding grounds, and brilliant wildflowers and their insect pollinators appear in rapid succession across hillsides, roadsides, lake margins, and fields. Similarly, as autumn approaches, the deciduous forest canopy progresses towards a colorful demise, birds navigate their return to southern wintering grounds, mammals gorge on the summer’s bounty to prepare for their winter hibernation, and many plants ripen their last fruits before the onset of winter.

Whether we live in urban or rural environments, there are constant reminders of the changing of the seasons. Many of us notice when the first wildflowers appear in the spring, when our favorite fruits are available in the local farmers’ markets or supermarket, when trees change color or lose their leaves in the fall, when wildfire risk is highest due to the drying of our forests’ fuels, or when frost first appears in the fall or winter. By studying the seasons in greater detail over the course of our lives, we can deepen our connection with, and understanding of, the landscapes we inhabit. We also develop our ability to observe and to measure the pace and the timing of the seasons, the onset and duration of which are shifting with the changing climate.

Scientists refer to the study of the timing of seasonal biological activities as phenology. This term was first introduced in 1853 by the Belgian botanist Charles Morren and is derived from the Greek words phainos, meaning “to appear, to come into view” and logos, meaning “to study.” Phenology is the science that measures the timing of life cycle events in plants, animals, and microbes, and detects how the environment influences the timing of those events. In the case of flowering plants, these life cycle events, or phenophases, include leaf budburst, first flower, last flower, first ripe fruit, and leaf shedding, among others. Phenophases commonly observed in animals include molting, mating, egg-laying or birthing, fledging, emergence from hibernation, and migration.

To characterize and to describe phenophases, phenologists record the dates that these events occur, and they study how environmental conditions such as temperature and precipitation affect their timing. In addition, phenology may include the study of how the timing of phenophases evolves by natural selection in response to periodic environmental conditions such as winter cold, summer drought, and the emergence of pests and predators. The timing of phenological events can be quite sensitive to environmental conditions. For example, in a particularly warm and dry spring, leaf budburst and first flower might occur weeks earlier than usual, whereas in an exceptionally cool and wet spring they could be equally delayed. As a result, the timing of phenophases tends to vary among years based on patterns of weather, climate and resource availability. Phenological observations are therefore integrative measures of the condition of the physical, chemical, and biological environment. This environmental sensitivity means that phenological studies are simple and cost-effective ways to measure environmental changes, including climate change, over the long-term.

Weather is defined as the near-term atmospheric conditions of a region, such as temperature, precipitation, humidity, wind, and sunshine. The climate of a region, on the other hand, is characterized by the generally-prevailing weather conditions. For example, Santa Barbara, California is characterized by a Mediterranean climate — warm, dry summers and cool, moist winters. There are, however, daily and weekly changes in the weather that can rapidly change the temperature, sunshine, and wind conditions.
Phenology is a science for all seasons, locations, and species. From the leafing, flowering, and fruiting times of plants to the molting, mating, and migration times of the animals they support, the phenological progression of an individual, a population, or an entire species may occur rapidly or slowly, and synchronously or asynchronously with other organisms. How, then, can we measure and compare phenological patterns for a wide variety of organisms that exhibit different phenophases and at different time scales? The answers rest in the scale of our observations and in the ways that we record and describe them.

Phenology, as all environmental sciences, uses quantitative methods to measure and to describe the occurrence of events and patterns in the natural world. Phenologists are interested in the dates when phenophases occur, their duration, and the pace of transitions between phenophases, and these observations can take place at multiple biological and geographical scales. For example, a phenologist may record the dates that a plant opens its first and last flowers (from which the duration of flowering can be calculated), as well as the number of flowers that are open each day or week during the flowering period. This can be done for one or many individuals of the same species in one population, for multiple populations of a species that occupies different habitats or locations, and for multiple populations of different species that coexist in one habitat.

Levels Of Biological Organization

The biological world can be observed at a variety of “scales” — ranging from long-distance observations to close-up and detailed views. Each scale generally requires a different set of tools, from satellites to magnifying glasses to microscopes. Phenology is one of the few sciences that routinely measure patterns at many of these scales. The levels of biological observation that are most important to the global and local study of phenology are shown below.

**Biome**
A group of co-occurring plant, animal, and microbial communities that live in the same type of climate, share a well-defined geographic area, are adapted to a particular substrate and level of nutrient cycling, and exhibit a recognizable set of dominant life forms and habitats.

**Community**
A group of co-occurring populations of different species, each of which interacts with some proportion of the other species.

**Population**
A collection of individuals of one species inhabiting the same general area or sharing a common environment.

**Organism (Individual)**
One member of a population or species that may or may not depend on other members of its population in order to survive.

Remote sensing technologies allow for the detection of geographically extensive phenological patterns.

Observational studies performed by on-the-ground phenologists provide site intensive documentation of phenological patterns.
Phenology Across Levels Of Biological Organization

**Individual:** One member of a population or species that may or may not depend on other members of its population to survive. Individuals of the same species that live in the same location and that have the potential to mate with each other belong to the same “population”. Nevertheless, they may exhibit great variation in the timing of their phenophases. The particular phenological pattern that an individual exhibits (e.g., the date of germination; the onset and duration of flowering; the average number of flowers open per day during the flowering season; and the time of seed dispersal) is usually due to both genetic and environmental influences.

The timing of an individual plant’s phenophases can have a profound effect on its reproductive success, as it is likely to determine whether: it survives to flower; its flowers are pollinated; its flowers develop successfully into seed-bearing fruits; its fruits ripen fully and are successfully dispersed; and whether most of its seeds will germinate and produce seedlings that survive to adulthood. As for all traits that are determined by an individual’s genes and that affect success in reproducing, the timing of phenophases in plants and animals is subject to evolution by natural selection.

If the climate changes gradually, and if populations contain enough genetic variation in phenological traits such as the date of first flower, they will be able to adapt as natural selection favors individuals (and their genes) with phenological schedules that perform well under the new environmental conditions. Evolutionary biologists are concerned, however, that if climate change progresses too rapidly, many populations will not be able to adapt because they will not contain any genetic variants that perform well under the new conditions. Climate change has been associated with species’ extinctions in the past.

**Population:** A group of individuals of one species inhabiting the same general area or sharing a common environment, and with the biological ability to mate with each other. The phenological patterns exhibited by the members of a population are important because they determine: whether individuals are available for mating with each other; whether individuals compete for resources such as moisture in the soil or food; which individuals are exposed to (or escape from) flower- and seed-eating predators; and whether individuals can cooperate to deter herbivores or predators.

**Species:** Species is a collective term that usually refers either to one or to all of the populations of a given species. Populations of a given species may be large or small, closely spaced or highly isolated, and composed of individuals that occur in clumped, uniform, or random distributions. Where multiple populations of a given species are phenologically synchronized and not too far away from each other, the potential for migration and mating between populations is much higher than when they are phenologically mismatched. The exchange of individuals among populations can be very important, as it is one the most common mechanisms that maintains genetic diversity within them.

**Community:** A community is a group of co-occurring populations of different species, each of which interacts with some proportion of the other species in the community. Some of the interactions are positive, in which both species benefit (examples include pollination and seed dispersal). Other interactions benefit one species but harm the other(s), including predator-prey interactions, host-parasite relationships, and harmful microbial infections of plants and animals. The phenology of interacting species can be crucial to their survival, as the survival of mutually dependent members will be strongly influenced by whether and how their phenophases overlap. For example, if a pollinator emerges from winter dormancy and its nectar sources aren’t flowering yet, both the pollinator and the plant on which it depends will suffer. The pollinator will have no food source, and the plant will not produce seeds.

**Biome:** A biome is a group of co-occurring plant, animal, and microbial communities that live in the same type of climate, share a well-defined geographic area, are adapted to a particular substrate and level of nutrient cycling, and exhibit a recognizable set of dominant life forms and habits. Examples include: deciduous forests, woodlands, coastal dunes, shrublands, tropical forests, boreal (subarctic) forests, mangroves, grasslands, and deserts.
As you can see, phenology can be observed and measured at multiple levels of biological and geographical organization. Information from each of these levels provides fundamental knowledge about patterns and processes in nature. Phenological studies can inform us about the timing and duration of resource availability in ecological communities, including: when pollen and nectar are available to pollinators; when fruits are available to fruit-eating animals (including humans!); when leaves are available for herbivorous insects and mammals; and whether plants must compete with each other for the services of pollinators and seed dispersers. Phenological studies can also help to inform agricultural planning, the implementation and timing of disease and pest control methods, and eco-tourism industries, as well as the anticipation of allergy seasons.

The first goal of this section is to demonstrate how variation in phenological patterns can be described and measured at multiple levels, including:

- within and among individuals;
- within and among populations;
- within a community of coexisting species; and
- across large geographic regions such as states, continents, hemispheres, and even the entire planet

The second goal is to help you understand how the phenological progression of an individual, population, or community can influence its ability to survive and to reproduce.

This background in phenological variation will help you to develop a framework for understanding the variation that you observe in your backyard, school yard, or natural area. It will also provide you with some terminology that will allow you more easily to communicate your observations with other phenologists. Although we use flowering phenology as our primary example, keep in mind that the principles presented in this section can easily be applied to other organisms that may or may not exhibit similar phenophases (e.g., birthing times of mammals, migration and egg-laying times of birds, spawning times of fish, hibernation schedules of mammals, and pollen-producing times of non-flowering plants like Pine trees).

**Phenological variation within and among individuals - flowering curves**

Scientists have described over 250,000 species of flowering plants in the world. Although some species flower irregularly or continuously (e.g., in tropical biomes where environmental conditions are more or less constant), most flowering plants in the temperate zone exhibit conspicuous flowering phenophases that start and stop at predictable times of the year and in response to local climatic cues. The timing of these phenophases, and especially the pace of flowering, is highly variable among individuals, populations, and species. While some species (or individuals or populations) produce only a few flowers over a short period of time, others produce many flowers over the course of months. These patterns can be captured by graphs of **flowering curves**, from which it is easy to visualize the dates of key phenophases and to make comparisons among individuals (Figure 1).

Figure 1 shows the flowering curve for an individual plant that opens its first flower on April 15. For this individual poppy, the date of peak flowering is May 6, and the date of last flower (defined as the date when the last flower opens) is June 10. This means that the duration of flowering was 8 weeks (or 56 days). If floral display surveys were conducted for more California Poppy individuals in the same population, the resulting flowering curves would reveal variation in flowering phenology (Figure 2).

Figure 2 shows three hypothetical flowering curves, each curve representing a different individual of California Poppy. First, notice the variation among the three individuals for the dates of first flower, peak flowering, and last flower. The shapes of the three flowering curves also differ— the blue curve is the same shape as the black curve but shifted two weeks later, whereas the red curve exhibits a different shape altogether. Also
notice that even though the red curve differs in shape from the black curve, the date of peak flowering is the same. Lastly, notice that the duration of flowering is shortest for the individual plant represented by the black curve and longest for the individual represented by the red curve. Overall, the flowering curves of these three individuals overlap, which means that these individuals might compete for pollination service. Alternatively, the simultaneous flowering of these plants might help to attract pollinators, as they will present a more conspicuous display of flowers and provide more nectar than an individual plant. The overlap in flowering times also means that pollinators could be transferring pollen among these plants.

If a phenologist’s goal is to quantify and to summarize the phenological behavior of a population (such is often the case), a single graph that contains thirty or more flowering curves would be a bit overwhelming. Instead, the mean and variance of a phenophase of a population can be expressed in a different type of graph. In Figure 3, the mean date of first flower is April 8 for 30 individuals of the same California Poppy population in Santa Barbara. The error bars represent the variation among individuals within the population for date of first flower; there is a moderate amount of variation in this population (more about this shortly). If the pace and duration of flowering are tracked for each of these 30 individuals, the same graph could easily be constructed for other phenophases such as peak flowering and last flower.

**Phenological variation within a population – what does it mean?**

The variation in flowering phenology among individuals in this population of California Poppy could be due to different sources, including:

- **environmental factors** – the timing of an organism’s phenophases can change dramatically as a direct response to environmental conditions such as temperature or the microhabitat in which each individual plant lives (e.g., in the shade of another plant vs. direct sunlight, in a sandy soil vs. a clay soil, highly exposed to cold winds vs. protected from them);

- **genetic factors** – the genes inherited by, and expressed by, each individual (the flowering curves of siblings or other closely related individuals will tend to be more similar than the flowering curves of more distantly related individuals); or

- **a combination of environmental and genetic factors** - for many traits, the phenotype of an individual (e.g., its flowering time or duration) is determined by interactions between the genes that affect the trait and the environment in which they are expressed.
While more detailed observations and experiments could reveal the relative importance of each of these sources of variation in shaping flowering patterns, we can also think of the consequences of variation in flowering patterns.

Patterns of mating and reproductive success in flowering plants—and therefore the long-term sustainability of a population—are largely dependent on the timing of flowering. For example, individuals that initiate flowering before pollinators are active in the spring are likely to suffer low reproductive success due to a lack of pollen transfer. Similarly, if the beginning and the end of the flowering season are characterized by only a few individuals that are flowering, the availability of pollen during these periods may be relatively low, even if pollinators are abundant. If individual plants cannot attract pollinators when population sizes are low (e.g., at the beginning and end of the flowering season), natural selection will favor individuals that flower synchronously (e.g., at the time of a population’s peak flowering). In addition, during times of the season when only a few individuals are flowering, the probability of mating between close relatives increases, and this can reduce the genetic quality of the seeds produced.

On the other hand, if so many individuals of the same species flower at the same time that they compete for pollinators, then many of their flowers are likely to remain unpollinated. In this case, individuals that flower slightly “out of synch” (earlier or later) with the majority of their local population may benefit (have higher pollination success) because there is less competition for pollinators. In sum, variation in flowering patterns among individuals within populations will affect their visitation by both pollinators and seed dispersers, and this will affect the way that natural selection acts to favor particular phenophases.

Many plant biologists refer to plants as “phytometers” because their development and reproduction can provide excellent integrative information about ambient conditions.

**Phenological variation among populations**

Building upon this understanding of phenological variation within populations, we can continue to scale up our observations to compare phenological variation among populations. Let’s suppose that students from San Diego, San Francisco, and Arcata each conduct a within-population study. The onset of spring typically arrives earliest at southern latitudes (San Diego) and progresses northward (Santa Barbara, then San Francisco, then Arcata), so the students hypothesize that California Poppies will start flowering earliest in San Diego, followed by the next northern location (Santa Barbara), and so on. The results of this hypothetical study are graphed in Figure 4.

There are two major aspects of phenological variation that are illustrated in Figure 4. First, notice that the students discovered a latitudinal trend in flowering times, just as they expected. As mentioned above, this trend is also commonly observed along elevation gradients, where populations at higher elevations tend to flower later than populations at lower elevations. These phenological changes with latitude and elevation are commonly observed in a variety of plants and animals, and represent strong direct environmental regulation of biological activities, typically by temperature. This general principle is described by Hopkin’s Law: the date of first flowering
(and other phenophases) is delayed by approximately 4 days per degree latitude or 120 meters elevation (equivalent to 1 day per 100 feet elevation). While these trends reflect the sensitivity of phenophases to environmental factors, keep in mind that genetic factors also regulate the timing of phenophases and that the patterns we see in nature are largely the result of interactions between environmental and genetic factors.

Figure 4 also illustrates different levels of within-population variation – the San Francisco population exhibits the greatest amount of variation among individuals in first flowering date, whereas the Arcata population exhibits the least amount of variation. Another way to describe this pattern is that the Arcata population exhibits the greatest amount of synchrony for first flowering date. As we discussed earlier, the amount of synchrony within populations can have important short- and long-term consequences for pollination success, seed production, and seed quality. As you will see in the next section, phenological variation among coexisting species can have important consequences for community dynamics.

**Figure 4.** Hypothetical mean date of first flower of California Poppy (for 30 individuals from each of four populations) increases with increasing latitude, from San Diego in the south to Arcata in the north. The Santa Barbara result is the same as in Figure 3. The y-axis should be labeled as “date of first flower”.

### Phenological variation among coexisting species: community-level phenology

A brief visit to any habitat, whether it’s a backyard, school yard, or park, can reveal community-level phenology. The casual observer is likely to find some plant species that are flowering and other species that are not. Of the species that are flowering, some are likely to be just starting to flower (these plants will bear a large proportion of closed flower buds relative to the proportions of open flowers and developing fruits) and others are likely to be finishing up (these plants will exhibit a very low proportions of closed flower buds and open flowers and a very high proportion of developing fruits). The more attentive observer will notice the distribution of pollinating insect species among the flowering plants, noting whether particular insects prefer the flowers of certain plant species. Similarly, some species of birds might tend to spend more time visiting certain plant species, foraging for nectar (hummingbirds) or dispersing fruits and seeds (many songbirds).

A repeated visit a week or two later will reveal changes that have occurred in the phenology of the plant community, and probably in the abundance or assemblage of insect and bird species as well. **Community-level phenology is quantified as the change over time in the appearance, activities, interactions, or diversity of the assemblage of coexisting species in one habitat** (Figure 5).

Figure 5 depicts the phenology of a portion of a hypothetical ecological community. For each of the five species of flowering plants, the length of the red line represents the duration of each species’ flowering period. For example, the starting point of each line represents the date when the first individual plant in that population started to flower, and the endpoint represents the date when the last plant produced its last flower. For insect pollinators (green lines), insectivorous birds (insect-eating; orange lines), and frugivorous birds (fruit-eating; blue lines). There are several ways to calculate variation among individuals that can be represented by the range bars shown in Figures 3 and 4. The most common estimate of variation is called the standard deviation. See the Activity Guide Chapter in this Handbook for instructions on how to calculate this and other measures of phenological variation.
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Figure 5. Graphical representation of the phenological progression of a biologically diverse community. Each horizontal line represents the timing and duration of a particular kind of phenological activity observed in a single species. For example, for flowering plants, each line may represent the duration of the flowering period of a given species. In this case, each line starts at the date of first flower among all monitored plants in the population, and the line ends at the date of the last flower produced by any of these plants. Similarly, for the species of insect pollinators, insectivorous birds, and frugivorous birds, the lines represent the first and last dates that any individual of these species is observed to be actively foraging. Drawing a vertical line across the graph at any date reveals the diversity and identity of coexisting (and potentially interacting) species; note that diversity and the composition of the community changes over the course of time.

Note that plants differ from animals in that, generally speaking, it is much more likely that individual plants can be monitored repeatedly within a growing season, recording the first and last flowering date of each individual plant. With this information, the start and end dates for the plant species in Figure 5 could, alternatively, represent the average dates of first and last flower, respectively. For example, we could calculate the average (mean) date of first flower if we recorded this date from multiple individuals. It’s much more challenging to do this for animals simply because they’re highly mobile and it’s difficult to identify different individuals.

Starting at the earliest date in February (you can impose a vertical line across the entire graph to help visualize this), only one of the four monitored species of insect pollinator was active when the first plant species began to flower and when the first insectivorous bird species was observed to forage. Moving the date to mid-March, four of the five species of plants were flowering, three species of insect pollinators were active, four species of insectivorous birds were observed, and one species of frugivorous bird was actively foraging. Finally in late-July there were only two species of plants that were in flower, one species of insect pollinator, one species of insectivorous bird, and three species of frugivorous birds. Of these three time periods, biodiversity of the “active” community was highest in mid-March.

lines), each line represents the start and end of foraging activity (pollinating, insect-eating, fruit-eating). In other words, the lines show the start date and the end date of all monitored individuals in the population.
**Community-level phenology - what does it tell us?**

What does the phenology of ecological communities tell us beyond its approximate time schedule? To start, it describes the availability of resources in the community and sheds light on which species might be interacting most strongly with other species. For example, in the community represented by Figure 5, the two species of plants that were still flowering in July could be visited by only one species of insect pollinator (at least, among those pollinators observed); if this pollinator prefers to forage for pollen and nectar in one species over the other, then fruit and seed production of the neglected species is likely to suffer.

As a more complex example, the abundance of insectivorous bird species is highest in March and the foraging activities of these birds is likely to reduce the abundance of insect pollinators. This may, in turn, reduce pollination services for the plants that are in flower at that time, which could result in many flowers being left unpollinated. This reduction in pollination could then lead to a decrease in the availability of ripe fruits for the three species of frugivorous birds that appear later in the spring. If three species of frugivorous birds are actively foraging for a limited supply of fruits, then competitive interactions among them are likely to be intense, and this could potentially affect the reproductive success of either individual birds or an entire population.

Overall, ecological communities are dynamic assemblages of coexisting species that interact both directly and indirectly over time. Thus, the phenology of communities provides a measure of their diversity and productivity, the combination of which can contribute to the long-term stability of the community.

**Phenological variation among communities (across landscapes, continents, hemispheres, and the globe)**

The detection of phenological patterns across ecological communities and across broad geographic scales plays an important role in our understanding of global environmental changes. The recent development of new remote sensing technologies (e.g., satellite-based observations) as well as new information-sharing and analytical tools has enabled the integration of historically disparate environmental sciences (more about this later). The resulting multidisciplinary approach has led to the development of large databases that provide layers of information on physical, chemical, and biological processes across a variety of geographic scales. These efforts have helped to develop a stronger understanding of how environmental conditions, especially the climate system,
affect phenological patterns among ecological communities and biomes. Some questions that have emerged focus on determining which community types are most sensitive to environmental change, which communities are the most imperiled, and how changes in one community can affect the productivity and diversity of another community.

**SUMMARY - WHAT IS PHENOLOGY?**

From individuals and populations to communities and biomes, the phenological attributes of living systems influence their ecological interactions and therefore the probability of their long-term persistence. For example, if species that depend on each other (mutualists, such as a plant species and its pollinator) do not thrive at the same time (synchronously), then both species may suffer. The timing of an organism’s phenophases can change dramatically as a direct response to environmental conditions, and this can have larger effects in the community. For example, warmer weather at the onset of spring can cause the seeds of many species to germinate earlier than they ordinarily would. Some individuals and species are more malleable (or “plastic”) in this regard than others, and the asynchrony that may arise as a result of species-specific responses to environmental change can have cascading effects through the community.

The productivity and sustainability of ecological communities, whether wild or farmed, can be greatly diminished when the phenophases of interdependent populations or species become asynchronous. With these concepts in mind, we can now provide a more precise definition of phenology: Phenology is the study of the timing of recurring biological events, the interaction of biotic and abiotic forces that affect these events, and the interrelation among phases of the same or different species.

**SYNTHESIS - PHENOLOGICAL VARIATION**

With the introduction above, you’re now well aware of the ways in which the phenological schedule of an individual, population or species can affect its ability to persist in natural communities such as forests, fields, and streams, or in managed communities such as farms, local parks, or recreational areas.

For example, what are some ways in which an individual plant’s flowering schedule may result in lower fruit production or seed quality compared to that of other members of the same population? Flowering when pollinators or potential mates are scarce — or when flower-eating insects are particularly abundant — will reduce pollination and fruit production. Alternatively, when closely related individuals flower at the same time, the inbreeding that may result can lead to reduced genetic quality of the seeds produced in the same way that mating between close relatives in humans and other animals can increase the risk of genetic diseases. Delaying flowering until late in the season, when the risk of drought (in deserts and in Mediterranean climates) or frost (in seasonal temperate climates) increases, may prevent any successful seed production at all. The risks associated with flowering at the “wrong” time are many and sometimes fatal.

With these ideas in mind, you should have no trouble providing answers to the following questions:

**For a given plant species, how may populations that are spatially separated from each other benefit from being in phenological synchrony with each other?**

- Unless populations are so isolated from each other that they never come in contact through seed dispersal or through the movement of pollen by wind or by animal-transfer, populations often benefit from receiving genetically distinct seeds or pollen from other populations. This increases a population’s genetic diversity and may increase the probability that it can adapt to environmental change.
Within a given community, what are some additional ways in which one or more species are affected by the timing of the phenophases of other species?

- Pollinators that eat pollen (e.g., female bees and their offspring) will only have a food source if they are active during the flowering period of their favored plant species. Reciprocally, flowering plants that rely on animal pollinators will only produce fruits (and seeds) if they flower when their pollinators are abundant and searching for them.
- Nectar-eating birds, bees, and ants depend on the flowering time of their “prey”; plants that are attacked by these “nectar-robbers” will suffer reduced fruit and seed production, while plants that flower when such “thieves” are rare will enjoy higher reproduction (assuming that their pollinators are available).
- Flower- and bud-eating beetles, bugs, moth and butterfly larvae, and other insects depend on the flowering schedules of their prey. So, not only does the phenology of plants affect their exposure to nectar-thieves, but it also affects their exposure to flower- and bud-eating species.
- The phenology of moth and butterfly larvae not only affect the plants that they eat, but it has strong effects on the survivorship and reproductive success of the birds that eat them.
- Pest-controlling insects and birds eat agricultural pests that, in turn, can destroy crops. A well-known example is the lady bug, a type of beetle that eats aphids, which — if not controlled — will attack young flowers, stems, and leaves. If pest-controlling animals (lady bugs, in this case) are not active in synchrony with their prey, an entire season of a crop’s production may fail.

In sum, the phenology of plants influences the abundances of the insects that eat or pollinate them as well as of the birds and small mammals that depend on them for fruits and seeds. The phenology of plant-eating insects and small mammals, in turn, affects the reproduction of their plant prey. The phenology of pollinating insects affects the reproductive success of the plants that they visit. And, the phenology of insectivorous birds affects the larvae on which they depend and the plants on which those larvae are found!

The answers to the above questions can have important implications both for wild species and for managed crops. The long-term viability of many wild plant populations depends on successful pollination, which can be limited if plants flower when pollinators are scarce or unavailable. If fruit and seed production are diminished because of plant-pollinator asynchrony, food availability to frugivorous (fruit-eating) birds and mammals could be severely reduced. It is easy to imagine how food web dynamics in nature could be altered by asynchrony in the biological community. This is also true in the case of managed crops, where almost all of the farmed fruits that humans eat come from pollination services that are provided by insects. The synchrony of pollinator availability and flowering in farmed plants is therefore critical to our ability to produce food.

THE MODERN SCIENCE OF PHENOLOGY

A new era in seasonal studies

Modern phenological studies are thought to have been initiated in Europe in the mid-18th century. Beginning in 1736, Robert Marsham kept detailed records of “Indications of Spring” on his family estate in Norfolk, Britain with the goal of improving timber production by learning more about the timing of plant and animal life cycles. His annual observations included the first occurrences of leafing, flowering and insect emergence. His descendants maintained these records until 1947, making it one of Europe’s longest phenological monitoring records. Although he was equipped with only a notebook and a writing instrument, the “modern” aspect of Marsham’s approach was the systematic nature in which he recorded phenological events for many wild species living in a single ecosystem (27 phenophases for 20 plants and animals).