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# Understanding Phenology's Significance in Ecology and Evolution Holistically

**Rabia Lone**

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**ABSTRACT**

Nearly every element of ecology and evolution is impacted by phenology. Almost all biological phenomena have yearly cycles and are impacted by the timing of abiotic events, from individual physiology to interspecific connections to global nutrient flows. Interest in this subject has increased recently as more research have shown phenological responses to climate change. The genetic influences on phenology, modelling methods, ecosystem-level effects of phenological change, and evolutionary implications have all been the subject of extensive recent research. Yet up until now, these initiatives have often developed on their own. Here, we combine some of these distinct lines of research to decipher terminology, enable habitat type comparisons, and encourage the fusion of concepts and approaches across several sizes and disciplines. We go through the connection between phenology and life history, the contrast between phenology from an organismal and population level, and how phenology affects communities, ecosystems, and evolutionary processes. Future research should concentrate on tying together the ecological and physiological aspects of phenology, comprehending the effects of phenological change on the population, and explicitly accounting for seasonality and phenology in predictions of ecological and evolutionary responses to climate change.

***KEYWORDS:*** *climate change, life history, natural selection, phenology, synchrony*

## INTRODUCTION

The terms "phenomenon" and "phenotype" share the same Greek origin, phainomai (meaning"to appear"), as does the word "phenology." Phenology, the study of the timing of recurrent seasonal biological phenomena, has been an area of study for centuries, despite the fact that the latter two words may be more well-known. Humans have long been interested in recordingthe more-or-fewer regular appearances of things like the first flower blossoms of spring, the first migrating birds, or the first frost-damaged leaves of fall, whether for agricultural or religious reasons, or simply as a way to mark the passage of the seasons. When deciding when to plant winter crops, the ancient Greeks themselves utilised the time of leaf fall as a guidance.They understood the usefulness of phenology as a more accurate predictor of local weather than the movement of the stars. Phenology is essentially the temporal component of natural history at its most basic. Yet this temporal dimension is crucial because it establishes the developmental stage that an organism or population has reached at the moment when it crosses paths with specific elements of its environment. Thus, phenology plays a key organising role in almost all branches of ecology and evolution. A lot of phenological study has historically been centred on agricultural applications including pest control, agricultural meteorology, andhorticulture due of its practical significance for plant production. Studies on phenology in ecology and evolution have a long history, although many of these studies with significant phenological components did not refer to these as phenology in and of themselves (e.g. Clausenet al. 1941; Corbet 1954; Janzen 1967).

The last two decades have seen a rise in interest in phenology's function in ecology and evolution as a result of rising worries about recording and predicting the effects of climate change. The most blatant and well-researched biological reactions to the global warming overthe past 150 years have been phenological alterations. A better mechanistic knowledge of phenology is also becoming more attainable as research on the genetic basis of plant blooming time, insect diapause induction, and bird egg hatching time (Liedvogel et al. 2009) advances. The recent expansion of phenological study has also been facilitated by developments in the domains of quantitative genetics, phylogenetics, molecular and developmental biology, and ecosystem ecology. These diverse branches of phenology study have, up to now, tended to go forward separately and have used distinct terminology. By assembling this special issue, we hope to bring together some of these divergent areas of investigation, simplify terminology, make it easier to compare various habitat types, and—most importantly—promote the integration of concepts and methods across many sizes and disciplines. This article also underlines how crucial phenology is to almost every facet of ecology and evolution. We begin this introduction by defining the connection between phenology and life history and by quickly going through the physiological mechanisms and environmental signals that control phenology in various species. Finally, we explore how to define the form of the population-level phenological distribution—and why it matters—moving from the level of the individual organism to the population. Last but not least, we give a general review of how phenology affects the ecology of communities and ecosystems as well as the development of adaptation (or, sometimes, maladaptation). Along the way, we discuss some of the most pressing issues and potential topics for more research in this area.

## PHENOLOGY AND LIFE HISTORY

The majority of current ecological research and historical observations of phenology have focused on trends at the population level. These studies explore issues like how temperature affects the timing of leaf unfolding in a group of plants. Or has the time since the first frog crymoved forward over decades? On a more personal level, an intriguing inquiry may be: Why does an individual of a certain size or sex start growing or reproducing at a specific time of year? As many population-level patterns ultimately represent the combined activity schedules of many individuals, individual-level patterns are less frequently equated with phenology (Visser et al. 2010). Yet, comprehending them is crucial for making sense of many population- level patterns. Given that both terms take into account the timing of growth, reproduction, and senescence, the terms phenology and life history are occasionally used interchangeably. Of course, non-temporal features of life history like size at reproductive maturity and brood size are not included in phenology. However, by interpreting phenology in the context of life history, we are able to integrate phenological investigations with the theory and experiments that already exist to describe life-history evolution, such as the trade-offs that ultimately determine when annual plants flower or when tadpoles undergo metamorphosis. However, research examining species variety in recent phenological transitions seldom take life-history theory and the consequences of pertinent trade-offs into account.

The trade-off between ideal age (young) and size (big) at maturity is one example. A balance between these is anticipated in the actual life-history strategy of an individual, with the precisepoint of compromise depending on variables like the individual's gender (Morbey & Ydenberg 2001; Nève & Singer 2008) or the relative risk of death in larval and adult settings (Werner 1986; Abrams & Rowe 1996). Environmental variables can mask the trade-off: people who grow up in a good environment have a higher chance of becoming large at maturity and maturing earlier (van Noordwijk & de Jong 1986).

Yet, the age-size compromise may have an impact on the kind or scope of evolutionary phenological change that would be anticipated in response to a warmer environment (Etterson& Shaw 2001). For instance, in annual plants (Mitchell-Olds 1996; Franks & Weis 2008), thereis typically a positive genetic link between age and size at blooming; in insects (many of whichare also annuals), a slower metamorphosis to adulthood provides more time for growth (Masaki 1967). The best phenological response to a longer growing season relies, in both situations, on the relative advantages of reaching reproductive maturity earlier in the season or developing larger offspring. The usefulness of this fundamental life-history concept hinges on how an organism's lifetime and reproductive schedule fit within the seasonal cycle. Iteroparous species,which can employ resources obtained in a prior growth season for reproduction in the current year, can exploit the predicted trade-off between optimum time and size during reproduction differently than other species. Because of this, big plants in temperate zones typically blossombefore smaller ones in the same populations (Forrest & Thomson 2010 and references therein).Similar to humans, healthy birds often lay eggs earlier in a given season than do birds in poor health (Price et al. 1988; Rowe et al. 1994). Maternal health, which is a reaction to food availability the year before, also affects the variance in breeding date in red squirrels (Tamiasciurus hudsonicus) (Réale et al. 2003). Because resources are not primarily controlled by an individual's capacity to obtain resources during a specific growth season, iteroparity andenvironmental fluctuation in resource availability confound the time-size trade-off.

## THE MECHANISTIC BASIS OF PHENOLOGY

Understanding the proximal determinants of phenology is crucial if we seek to forecast how phenological reactions to environmental change will pan out, just as it is necessary to comprehend the life-history trade-offs that are the ultimate causes of many phenological patterns. Understanding the genetics and physiology involved, especially the pleiotropic effects of alleles impacting phenological features, might influence predictions of evolutionary change in phenology based on straightforward optimality models (Metcalf & Mitchell-Olds 2009). Many phenological events, such as the beginning of reproduction or the transition into or out of a dormant state, are timed by a complicated interaction between an organism's genes and a number of external environmental stimuli. The time of biological processes may be directly influenced by certain external variables, such as temperature or precipitation, or they may operate as signals that establish the organism's internal "biological clock." However, for the majority of species, we are unsure of the following: I the precise environmental factors that have the greatest influence on phenology; (ii) the precise molecular and physiological mechanisms that control phenology; and (iii) whether variation in phenology over time or among individuals reflects genetic differences or merely plastic responses to environmental heterogeneity. Although there has been quick progress in addressing these ambiguities regarding the processes controlling phenology, they now severely restrict our capacity to predict how different climatic factors will affect future responses. Here, we go through a few of the most thoroughly researched elements that are thought to have an impact on both plant and animal phenology.

Due to the lack of accurate meteorological data, it is sometimes impossible to evaluate differentenvironmental determinants of phenology (such as temperature vs snowmelt). This exemplifiesa common drawback of descriptive phenological studies: while it is relatively simple to find a correlation between a given climate variable and a specific phenological response, this does not necessarily show that the relevant climate variable is the primary cue controlling phenology. Many climatic factors are likely to be correlated, and although conventional experimental designs (such snow removal or warming buildings), while useful in and of itself,may not be sufficient to disentangle these variables. This is just another example of correlationnot implying causality. To definitively establish which environmental elements govern phenology, more carefully regulated studies are required (e.g. Cleland et al. 2006; Sherry et al.2007). Statistical modelling to assess the efficacy of several predictors might at least give hintsas to which cues are most likely involved in cases when studies are not available. Phylogenetic conservatism in phenological changes, which suggests shared causes of phenology within clades, suggests similar reactions to recent climate change among groups of related species (Davis et al. 2010); this may allow conclusions regarding mechanism in taxa that have not yetbeen examined. If we are to make predictions regarding phenological reactions to future, unexpected climates and the likelihood of phenological decoupling among interacting species (see below; Arajo & Luoto 2007), a deeper mechanistic understanding is required.

## ECOLOGICAL EFFECTS OF PHENOLOGY

The anticipated ecological effects of changes in phenological distributions as a result of climatechange have received a lot of attention in recent research. Phenology plays a role in almost allecological connections, thus there is obviously room for significant effects. Here, we highlight a few effects of phenology change on population dynamics, interactions between species, and ecosystems. One often mentioned potential outcome of climate change is that species would vary in how much their phenologies fluctuate, which might have disastrous effects on interacting species (e.g. Harrington et al. 1999; Durant et al. 2007; Both et al. 2009; Hegland et al. 2009). Depending on whether the interaction in question is mutually beneficial (i.e., a mutualism), mutually detrimental (i.e., competition), or unilaterally beneficial (i.e., predation),as well as whether differential changes in phenology drive species closer together or further apart in time, these shifts could, in theory, have positive or negative effects on the populationsinvolved. Given that various signals are used by different species to control phenology, such changes in relationships appear inevitable (still something of an unanswered question; Aono & Kazui 2008; see above). Nonetheless, there are still few instances of such transitions having noticeable demographic effects in real life. Miller-Rushing et al. go through the causes of thisgap's persistence and potential remedies (2010). A strong argument must be made for a changein contact intensity or frequency, establish that the change is due to climate change, and showthat the change has changed one or more of the implicated species' vital rates. By demonstratingthat pollen limitation in a subalpine wildflower has increased over the last 17 years and posingthe possibility that plant-pollinator decoupling may be taking place, Thomson (2010) offers one of the few examples of a significant species interaction that has been documented over a long period of time. Several have anticipated this occurrence, including Dunne et al. in 2003 and Memmott et al. in 2007, but it has not yet been proven. The plant is a perennial, and we donot know whether population growth is constrained by seed availability, thus the findings are ambiguous as to whether climate change is to blame. Moreover, population losses have not yetbeen noticed. This demonstrates the challenges that come with this kind of job and points up areas where more work needs to be done.

The length of the growing season also affects the cycling of carbon, nutrients, and water at theecosystem level. Because of the conflicting impacts of increased photosynthesis and respiration, it is unclear whether changes in the duration of the growing season will result in a net gain or decrease in carbon fixation for carbon in particular. Phenology establishes the timeframe in which photosynthesis may take place, and this temporal influence can boost primary productivity more than the direct impact of temperature on photosynthetic rate (Piao et al. 2007). This issue's research by Richardson et al. (2010) examines how this phenological effecton ecosystem productivity varies across different types of temperate forests and between the spring and autumn seasons, demonstrating that an extended growing season can increase net productivity despite higher temperatures' increased carbon loss. Forecasting the duration of thegrowing season in different ecosystems under future climate change is so crucial. Forecasts ofphenological changes at the community level are challenging, nevertheless, since there are few comprehensive long-term records and because phenological responses varies between species and places. Ibáez et al. (2010) present a hierarchical Bayesian method for solving this issue that gets beyond some of the drawbacks of more traditional statistical methods.

## CONCLUSION

We have attempted to provide a thorough description of the mechanisms underlying phenology in this introduction, as well as the reasons why phenology is significant to both evolutionary and ecological study. Several of these issues are expanded upon in the pieces in this special edition, and we hope that the publication as a whole will encourage further synthetic work in this area. We identify several critical areas where future study might be particularly fruitful: first, deeper links between the ecology and physiology of phenology are required. As Visser et al. (2010) demonstrate, because ecologists and evolutionary biologists read separate publications and employ different terminologies, a sizable amount of physiological andchronobiological work pertinent to eco-evolutionary investigations of phenology has gone largely unreported. The effects of phenological variation at the population level require greater study. There are clear concerns regarding the effects of this seeming asynchrony on the vital rates of the populations involved since there are more and more recorded examples ofinteracting species that appear to be out of sync. Too often, it is impossible to provide an answerto these questions because we are unsure of the initial degree of synchrony, which must have existed given that weather conditions were variable even prior to recent accelerated climate change, as well as because we are unsure of how the particular interaction affects population growth rates. 'Mismatched' species or individuals may occasionally switch to different food sources or relocate. The population biology of phenology is a topic that needs a lot of attention,as stated by Miller-Rushing et al. There are several potentials for new synthetic research due to the multidisciplinary character of phenology and the prevalence of phenological reactions to climate change. Additionally, time is an exceptional biological phenomenon. Time is fully asymmetrical compared to other factors; early occurrences can have an impact on later ones, but not the other way around. Early-season bolters can alter the light conditions for their later-season neighbours, giving them a possible competitive edge. These temporal correlations willalter along with changing climatic conditions and season lengths. The publications gathered here should improve our comprehension of these shifts and pave the path for more investigation.

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