

CHAPTER THREE

A Bird's-Eye View of the USA National Phenology Network*

AN OFF-THE-SHELF MONITORING PROGRAM

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Abstract. Phenology is central to the biology and ecology of organisms and highly sensitive to climate. Differential responses to climate change are impacting phenological synchrony of interacting species, which has been implicated in the decline of migratory birds that rely on seasonal resources. However, few studies explicitly measure phenology of seasonal habitat resources on the breeding and wintering grounds and at stopover sites. While avian monitoring methods are widely standardized, methods of monitoring resource phenology can be highly variable and difficult to integrate. The USA National Phenology Network (USA-NPN) has developed standardized plant and animal phenology protocols and a robust information management system to support a range of stakeholders in collecting, storing, and sharing phenology data, at the appropriate scale, to shed

light on phenological synchrony. The USA-NPN's *Nature's Notebook* can be integrated into established research programs, ensuring that data will be comparable over time and across projects, taxa, regions, and research objectives. We use two case studies to illustrate the application of USA-NPN methods and protocols to established long-term landbird research programs. By integrating phenology into these programs, avian ecologists are increasing their ability to understand the magnitude and consequences of phenological responses to climate change.

Key Words: citizen science, climate change, phenological mismatch, phenology monitoring, phenology protocol, Ruby-throated Hummingbird, stopover habitat.

Phenology, the timing of reoccurring life cycle events, is integral to plant and animal physiology, ecology, population and community dynamics, and adaptive evolution as well as nutrient, carbon, and water cycles (Chuine 2010,

Forrest and Miller-Rushing 2010, Pau et al. 2011). Phenology can be highly responsive to climate change and thus provides a valuable indicator of effects across spatial and temporal scales (Walther 2010, Yang and Rudolf 2010). Although not all

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species are exhibiting shifts in their phenology, those that are responding often vary in their rate, direction, and magnitude of change (Parmesan 2007, Møller et al. 2008, Both et al. 2009). Visser and Both (2005) emphasized that understanding the significance of phenological changes in any particular species must be in context of the phenology of resources necessary to sustain demanding life-cycle periods. For example, bird migration is a seasonal period of extremely high physiological demand (McWilliams and Karasov 2001) that can have significant impacts on annual survival (Silllett and Holmes 2002).

Differential impacts of climate change on migratory birds and their seasonal resources are creating or exaggerating phenological mismatches (Jones and Cresswell 2010, Saino et al. 2011), especially in long-distance migrants (Coppack and Both 2002, Both et al. 2006). Migration includes three distinct stages: departure, the migratory journey, and arrival. Advances or delays in departure dates or duration of the migratory period in response to climate change can alter arrival dates (Marra et al. 2005, Ballbontin et al. 2009, Both 2010), ultimately affecting reproductive success, fitness, and population dynamics (Møller 2001, Baker et al. 2004, Both et al. 2006). Migratory responses vary geographically and ecologically within and among bird populations and species, depending on sex, diet, migration distance, migration timing, brood size, population size, and phenotypic plasticity (Jenni and Kery 2003, MacMynowski and Root 2007, Vegvari et al. 2010, Gordo and Doi 2012). Selective pressures on birds to maintain phenological synchrony within seasonal communities under climate change may come from lower (e.g., food resources) or upper trophic levels (e.g., predators; Both et al. 2009). Thus, documenting species phenology across trophic levels is critical to understanding avian responses to climate change during all stages of migration.

Changing phenology is altering seasonal vegetation condition and food availability, causing mismatch across trophic levels on breeding grounds and resulting in avian population declines (Jones and Cresswell 2010, Saino et al. 2011). Migratory birds time their arrival at breeding grounds to obtain high-quality territories and take advantage of seasonal food resources necessary to reproduce and fledge young successfully (Møller 2001). Important components of

landbird breeding habitat quality include vegetation condition and food availability (Sherry and Holmes 1996, Smith and Moore 2005). Across the Northern Hemisphere, spring phenology of plants (e.g., flowering, leafing) has been advancing with warming trends during the past century (Menzel et al. 2006, Ellwood et al. 2013). Strong evolutionary selection for herbivorous insects to respond to cues that allow synchronization with host plant phenology (Bale et al. 2002, van Asch and Visser 2007) is also resulting in advancement of spring insect phenology, although mismatch may be occurring and even increasing (Parmesan 2007, Singer and Parmesan 2010).

Phenological changes in resources are also occurring along migration routes, which can affect stopover duration and frequency, arrival timing, body condition upon arrival, and reproductive success during the breeding season (Sandberg and Moore 1996, Smith and Moore 2005, Norris and Marra 2007, Seewagen et al. 2013). Over the course of successive stopover events, birds repeatedly encounter novel habitats and unpredictable environmental conditions (Nemeth and Moore 2007, Gillies and St. Clair 2010), where they attempt to maximize food acquisition and fat accumulation while balancing search-time costs (Aborn and Moore 1997, Paxton et al. 2008). The ability to identify patches of local food availability quickly based on habitat characteristics detectable across scales should shorten stopover duration and migration timing and improve fitness. Birds likely select stopover sites through a top-down hierarchical process (Chernetsov 2006), advancing from coarse- to fine-scale features (Buler et al. 2007). Plant phenology may be a direct indicator of food availability for birds that consume plant resources such as nectar or fruits (Smith et al. 2007, McKinney et al. 2012), or an index of availability of herbivorous insect prey synchronized with plant phenology (van Asch and Visser 2007, McGrath et al. 2009). Therefore, changes in plant phenology and phenological mismatch at stopover sites could affect avian fitness directly through decreased food abundance and indirectly through loss of habitat selection cues at stopover sites.

In contrast to arrival and stopover ecology, the dynamics of migratory departure are poorly understood; however, departure dates of migrants from both ends of their migratory range are undoubtedly being affected by climate-driven

habitat condition and resource phenology. For example, American Redstarts (*Setophaga ruticilla*) wintering in tropical regions have later departure in dry years or when relegated to drier sub-optimal habitats (Marra and Holberton 1998, McKellar et al. 2013) and show increased abundance on the breeding grounds in years following high plant productivity in wintering areas (Wilson et al. 2011). In many parts of Europe, timing of departure from breeding to wintering grounds is advancing (Cotton 2003). While long-distance migrants are advancing their fall departure in order to cross the Sahel before seasonal dry periods, multibrood species are taking advantage of longer growing seasons on breeding grounds and delaying their departure (Jenni and Kery 2003). Therefore, changes in departure may be related to changes in habitat and resources on the departure or arrival grounds or at stopover sites and depend on a species' migratory ecology and life history traits.

The complexity of avian phenological responses highlights the need for data on not only their temporal and spatial patterns, but also the critical seasonal resources upon which they depend. Most migration studies have been limited by logistics or funding to collect new phenological data, or to the availability of existing data at relevant ecological, spatial, or temporal scales. To fill this void, metrics of vegetation phenology for large-scale applications are often derived from remote sensing data, such as the normalized difference vegetation index (NDVI; Greenberg et al. 2008, Balbontin et al. 2009, Tottrup et al. 2010), which are available at large spatiotemporal scales but are limited in their spatial and ecological resolution relative to ground observations (White et al. 2009). However, the advent of the Internet combined with the growing popularity of citizen science campaigns is beginning to change the manner and scale at which we can collect and share data to address these problems at relevant scales and produce alternative metrics of vegetation phenology (Silvertown 2009, Dickinson et al. 2010).

OBSERVING PHENOLOGY FROM THE GROUND UP

Observational phenology monitoring can assist in downscaling and validation of remote sensing data (Kang et al. 2003, Kaheil et al. 2008) and

supply detailed site-specific information on species and species interactions at fine resolutions relevant to individual organisms, populations, and communities (Schwartz 1999). The benefits of using observational phenology monitoring to address regional to global-scale changes include its generalizability across scales, its ability to represent ecological diversity, and its ability to reveal physical mechanisms (Schwartz 1994). However, understanding the complex dynamics of climate change impacts on bird migration phenology under changing climate conditions will require data on birds and seasonal resources across broad spatiotemporal scales, from individual breeding, wintering, and stopover sites to species' entire annual migratory range while transcending biogeographic and political boundaries (Kelly and Hutto 2005, MacMynowski and Root 2007, Taylor et al. 2011). Collection of sufficient data necessitates a monumental collaborative effort.

Historic plant phenology data sets exist for North America, including data from legendary naturalists such as Henry David Thoreau and Aldo Leopold (Miller-Rushing and Primack 2008) and the cloned lilac and honeysuckle phenology programs initiated in the mid-1950s (Schwartz et al. 2012). Europe has a somewhat richer trove of historic phenology data on a relatively wide range of species (Ahas et al. 2002), including data sets on grape harvest that span more than 500 years (Chuine et al. 2004, Menzel 2005). Despite the immense value of these data for examining long-term variation, trends, and extremes in biotic responses to climate (Bradley et al. 1999, Miller-Rushing and Primack 2008, Ellwood et al. 2013), they focus on either small geographic regions, a relatively narrow range of species, or species that may not be ecologically relevant to bird migration habitats (Marra et al. 2005).

Over the past decade, there has been a boon in the collection of ecological data by citizen scientists, especially with the advent of online science initiatives (Dickinson et al. 2010). New citizen science programs such as eBird have provided vast amounts of data on migratory birds in North America that are being used to explore spatiotemporal patterns of bird migration and responses to climate change at unprecedented scale and resolution (Sullivan et al. 2009, Fink et al. 2010, Hurlbert and Liang 2012). Arguably, additional observational data at similar spatiotemporal scales

and ecological resolutions on the phenology of seasonal resources relevant to migratory birds at breeding, wintering, and stopover sites would be of significant value to understanding migratory habitat ecology, especially once integrated with bird monitoring data.

USA National Phenology Network and *Nature's Notebook*

In 2007, the USA-NPN (www.usanpn.org) was formed to track plant and animal phenology and ecological responses to climate change at a continental scale. The USA-NPN engages a diverse range of citizen scientist volunteers; federal, state, and nongovernmental organizations; professional research scientists; and educators to conduct monitoring as well as outreach and education. To guide this effort, the USA-NPN implemented *Nature's Notebook* in 2009, an online monitoring program comprising scientifically vetted protocols, observation guidelines, and interfaces for data entry and retrieval (the national phenology database, NPDb), in addition to a growing range of data products, educational materials, and support tools (Rosemartin et al. 2013, Denny et al. 2014).

Nature's Notebook provides all of the materials and tools necessary to implement phenology monitoring as an “off-the-shelf” package, ready for use and application to meet a wide range of monitoring and research goals and objectives (www.nn.usanpn.org). Through *Nature's Notebook*, people can create monitoring groups, register sites, plants, and animals to be observed; create and print standardized data sheets; and submit their observations. The methods and protocols explain and utilize species-specific phenophases for commonly occurring functional groups. Data can be collected throughout the year, and the methods and protocols help to minimize differences in terminology and phenological categories that regularly occur across projects using different protocols that later create challenges for data integration and analysis (Freeman et al. 2007).

All data submitted through *Nature's Notebook* are housed in the NPDb and, along with supporting metadata, are freely available online for download (www.usanpn.org/results/data). Registered sites are georeferenced and observers can record a range of supplemental details about the site such as slope, aspect, irrigation, landcover, development, and distance to nearest road or body of water. As

of May 2014, there were 673 plant and 272 animal species available for observation with detailed description pages of the organisms and their phenophases (www.usanpn.org/nn/species_search).

The *Nature's Notebook* program employs “status” monitoring, whereby observers record the phenological status for a suite of species-specific phenophases on every observation date. Such repeated sampling can reveal trends throughout the annual life cycle of a species and has greater predictive power, in contrast to “event” monitoring, which typically only captures the date on which a phenological event first occurs (Denny et al. 2014). Observers can also record abundance or intensity measures for many plant phenophases such as the number of flowers per plant or the percent of flowers that are open (Table 3.1), which can provide data on the relative abundance of plant resources potentially available at a given location and time.

Nature's Notebook: Relevance to Bird Migration

While *Nature's Notebook* involves monitoring of a wide range of plants and animals and their species-specific phenophases, events most relevant to the study of bird migration and habitat ecology are the presence and feeding of bird species, plant phenophases related to bird food resources (e.g., flowers, fruits) or resources used directly by herbivorous invertebrate prey (e.g., leaf buds, young leaves), and the presence or emergence of invertebrate prey such as lepidopteran larvae. Table 3.1 lists some of the phenophases most frequently recorded through *Nature's Notebook* for birds, plants, and insects that could be applied to research and monitoring of bird migration and seasonal resources at breeding, wintering, and stopover habitats.

While other broad-scale monitoring programs that focus on a single taxonomic group provide extremely valuable phenological data that can be overlaid with data from other programs (e.g., eBird, Frogwatch), a significant benefit of *Nature's Notebook* is that it can provide colocated data for multiple taxa and phenophases using nationally standardized protocols. Because the protocols used in *Nature's Notebook* have been specifically developed to address phenological questions, their use will reduce the challenges that can arise when comparing phenological data collected with different methods (Freeman et al. 2007).

TABLE 3.1

Bird, plant, and insect phenophases recorded through the USA-NPN's phenology monitoring program, Nature's Notebook, relevant to study of bird migration, seasonal resources, and condition of stopover habitats.

Taxa	Phenophase	Phenophase description	Abundance/intensity measures
Birds	Active individuals	One or more individuals seen moving or at rest	Number of birds in this phenophase
	Feeding	One or more individuals feeding; if possible, record species or substance being eaten	Number of birds in this phenophase
	Fruit/seed consumption	One or more individuals eating fruits, seeds, or cones of a plant; if possible, record plant name	Number of birds in this phenophase
	Insect consumption	One or more individuals seen eating insects; if possible, record insect or describe it	Number of birds in this phenophase
Plants	Flowers or flower buds	One or more fresh open or unopened flowers or flower buds visible	Number of flowers or flower buds
	Open flowers	One or more open, fresh flowers visible	Percentage open
	Pollen release	One or more flowers release visible pollen grains when gently shaken or blown onto a surface	Amount of pollen released
	Fruits	One or more fruits visible on the plant	Number of fruits
	Ripe fruits	One or more ripe fruits visible on the plant	Percentage ripe
	Recent fruit or seed drop	One or more mature fruits or seeds dropped or removed from the plant since last visit	Number mature fruits dropped seed
	Breaking leaf buds	One or more breaking leaf buds visible	Number of buds breaking
	Increasing leaf size	A majority of leaves have not yet reached full size and are still growing larger	Percentage of full size
Insects	Active caterpillars	One or more caterpillars (larvae) moving or at rest; when seen on a plant, record the name of the plant or describe it in the comments field	Number of individuals in this phenophase
	Caterpillars feeding	One or more caterpillars feeding; if possible, record species or substance being eaten	Number of individuals in this phenophase
	Flower visitation	One or more individuals visiting flowers or flying from flower to flower; if possible, record plant	Number of individuals in this phenophase
	Active subadults	One or more subadults moving or at rest	Number of individuals in this phenophase

Status of *Nature's Notebook* and the NPDb

As of 13 June 2014, over 3,629 registered observers had actively submitted over 3.5 million status records from 6,258 sites located across all 50 US states, the US Virgin Islands, and Puerto Rico. The species with the most observations in the NPDb recorded through *Nature's Notebook* include red maple (*Acer rubrum*), coyotebush (*Baccharis pilularis*), and quaking aspen (*Populus tremuloides*) for plants; bumblebees (*Bombus* spp.), monarch (*Danaus plexippus*), and red admiral (*Vanessa atalanta*) for insects; and American Robin (*Turdus migratorius*), Ruby-throated Hummingbird (*Archilochus colubris*), and Black-capped Chickadee (*Parus atricapillus*) for

birds. Up-to-date summaries and visualization of all species-specific data housed in the NPDb can be accessed and viewed graphically on the USA-NPN website using the data dashboard or the phenology visualization tool (www.usanpn.org).

Application of *Nature's Notebook* and NPDb Data *Phenological Mismatch in Ruby-throated Hummingbirds*

As an example of potential data applications for the NPDb, we examined phenological synchrony and overlap between flowering and movements of a nectarivorous bird (Miller-Rushing et al.

2010). We compared spring temperatures in 2011 and 2012, flowering times of 10 plant species, and migration and arrival times of Ruby-throated Hummingbird (RTHU, *Archilochus colubris*) at registered Nature's Notebook sites in the northeastern extent of their US breeding range in Maine. Hummingbird species can be highly responsive to variation in climate and habitat resources (Russell et al. 1994, McKinney et al. 2012, Courter et al. 2013), and central and eastern portions of the United States experienced record-breaking early spring temperatures and flowering phenology in 2012 (Ellwood et al. 2013).

We assessed flowering of nine plant species; three species of milkweed (*Asclepias* spp.), red columbine (*Aquilegia canadensis*), jewelweed (*Impatiens capensis*), Japanese knotweed (*Polygonum cuspidatum*), tulip tree (*Liriodendron tulipifera*), common lilac (*Aquilegia canadensis*), and common dandelion (*Taraxacum officinale*; a species that is not likely to be used by hummingbirds, but that may provide an indication of small flowering forb phenology). We first calculated the proportion of sites that recorded hummingbird presence out of all sites that were actively monitoring this bird species in

Maine during eleven 10-day periods from 1 April through 18 June in 2011 and 2012. We also calculated the proportion of individual plants of these species that had flowers during the same 10-day periods. We used these 10-day increments because all sites were surveyed at least once during that interval. We assessed phenological synchrony as the difference in date of mean and peak phenology between birds and flowering within and between years. We calculated annual overlap of hummingbird and flowering as the definite integral of the area shared by these plotted phenological response curves (Miller-Rushing et al. 2010) using R 3.0.1 (R Core Team 2014).

Ruby-throated Hummingbirds were monitored at 80 total sites (38 in 2011, 61 in 2012), and flowering phenology was monitored at 116 individual plants (65 in 2011, 88 in 2012). We found that mean flowering date was over 7 days earlier in 2012 than in 2011, while peak flowering advanced by nearly a month (Figure 3.1). In contrast, mean date of RTHU detection was about 14 days later in 2012 and peak date was about 10 days later. Therefore, the time between both mean and peak RTHU migration and plant flowering was

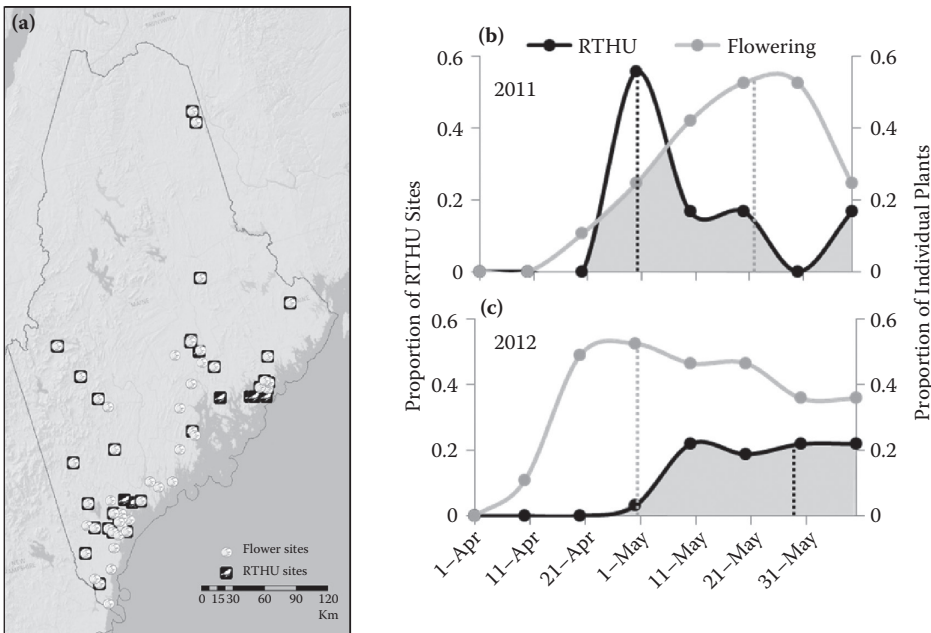


Figure 3.1. Map of registered USA National Phenology Network Nature's Notebook sites in (a) Maine, where the phenology of Ruby-throated Hummingbirds and relevant flowering plants was monitored in (b) 2011 and (c) 2012, and phenological synchrony and overlap of the proportion of sites with RTHU and proportion of individual nectar plants flowering per 10-day period from 1 April to 18 June, 2011–2012. Vertical dotted lines are the peak dates when the greatest proportion of sites reported hummingbirds (black) and the greatest proportion of individual plants were flowering (gray).

about 10 days later in 2012. Despite changes in synchrony, phenological overlap was almost two times greater in 2012 (1.74) than in 2011 (0.94), due to the earlier peak among hummingbirds in 2011. Analyses of long-term trends using historic records of the North American Bird Phenology Program for Ruby-throated Hummingbirds also showed the counterintuitive pattern of delayed phenology under early spring conditions of 2012. Courter et al. (2013) found that although Ruby-throated Hummingbirds have advanced their spring migration over the past 130 years, following warm winters their migration is delayed above 40° north following warm winters. Delays may be in response to the recent inability of plants to meet their winter chilling requirement in the southern United States, which in turn is reducing food resources, diminishing stopover habitat quality, and necessitating longer stopovers en route (Russell et al. 1994).

In contrast, our results suggest that phenological overlap actually increased despite drastic changes in synchrony. Overlap may be due to an even and prolonged, less concentrated or “peaky” distribution of bird migration and plant flowering. Nonetheless, it remains unclear whether there are fitness consequences to this interannual variation in phenology. Data on nesting and presence of fledglings and phenophases that also can be monitored through *Nature’s Notebook* would shed light on the potential impacts on population and evolutionary dynamics. Furthermore, to improve the accuracy of phenological estimates, sites should be monitored at least twice a week during periods of rapid phenological change. Infrequent monitoring rates are a limitation of the current size of the NPDb. We anticipate, however, that as the number and frequency of observations grow, analysis at finer temporal resolutions will be more robust.

Integrating Nature’s Notebook into Established Research and Monitoring Efforts

Ornithology enjoys a rich history of established, vetted, and standardized avian research and monitoring using methods such as point counts, area searches, nest monitoring, and mist-netting. These methods have been incorporated into national and international programs that have been collecting demographic and phenological data on bird

populations for decades, such as the monitoring avian productivity and survivorship (MAPS) program, and the North American breeding bird survey (BBS; Sauer et al. 1994, DeSante et al. 1995). Vegetation monitoring is a common component of many landbird research and monitoring programs; however, these methods and protocols are often far more variable throughout the discipline, and often do not include a plant phenology component. Furthermore, some avian researchers may be uncertain of exactly how to monitor plant phenology at new or already established study sites.

For nearly 50 years, Point Blue Conservation Science (Point Blue, founded as Point Reyes Bird Observatory) has studied bird populations at the Palomarin Field Station in Point Reyes National Seashore, Marin County, California (Porzig et al. 2011). Program efforts include year-round monitoring of resident and migrant landbirds through constant-effort mist-netting and nest-monitoring programs, studying habitat associations, weather and vegetation monitoring, and a rigorous intern-training program. Long before researchers ever considered that these long-term data would be used to understand the consequences of climate change (MacMynowski et al. 2007, Goodman et al. 2012), researchers at Palomarin were already studying the variation in timing of avian annual life cycles—such as when birds breed, molt, and migrate (DeSante and Baptista 1989, Howell and Gardali 2003, Elrod et al. 2011). However, despite interest in the resources that plants provide for birds, relatively little standardized information on plant phenology was previously collected at the station.

Recent evidence of climate-change disruption to phenological relationships between birds and vegetation has highlighted the importance of incorporating phenological monitoring of plants into research and monitoring at Palomarin (Saino et al. 2011, Visser et al. 2012). With their primary expertise in avian ecology, station personnel looked to the broader scientific community for phenological monitoring methods. The broad scope, applications, and vetted and standardized plant phenology monitoring protocols of the USA-NPN and *Nature’s Notebook* provided the tools necessary for integration into the station’s long-term monitoring efforts. Furthermore, the USA-NPN’s ample offerings of webinars and in-person training workshops assured station researchers that data quality is a high programmatic priority.

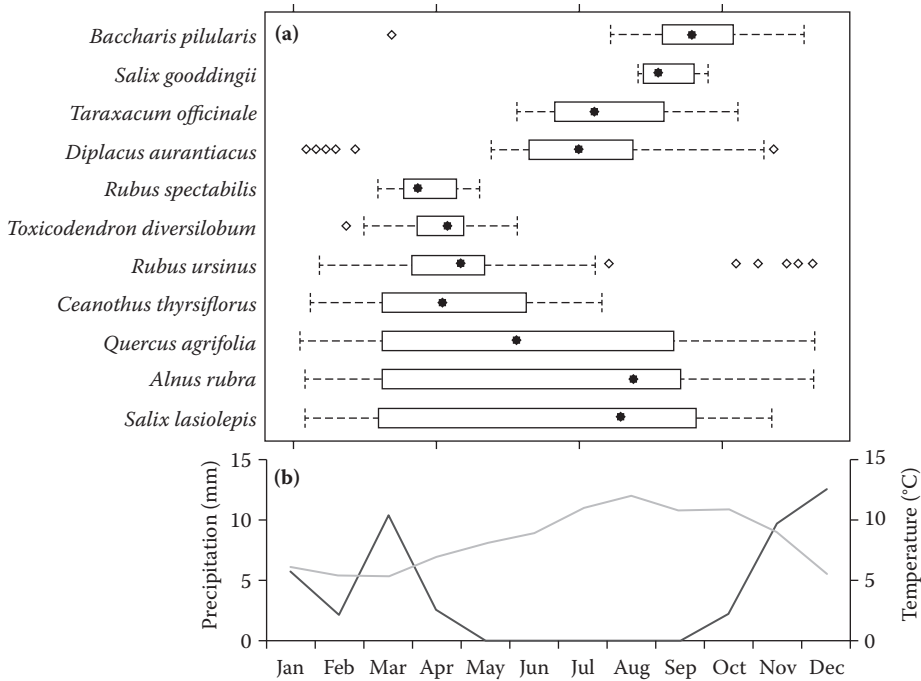


Figure 3.2. (a) The flowering phenology of plant species monitored at the Palomar Field Station, California; associated study sites in the Point Reyes area using the USA-NPN Nature’s Notebook program in 2012; and (b) mean daily precipitation (black line) and minimum temperature per month (gray line) for the Bolinas, California, region, 2012 (NOAA 2013). Box plots indicate median flowering date (black dot).

In 2012, Point Blue began collecting plant phenology data on 15 tree, shrub, and forb species at the Palomar Field Station and four additional associated long-term bird monitoring sites in the Point Reyes area (in Point Reyes National Seashore, Golden Gate National Recreation Area, and Marin County Open Space District; hereafter, Palomar study sites). The plant species selected are among the dominant species at the study sites that are ecologically important to the bird species studied. Plant phenology is monitored approximately every 7–10 days at some sites in conjunction with mist-netting visits, year-round except at two sites where no winter avian monitoring occurs. Although it requires a time commitment to conduct the phenology monitoring and ensure consistency among observers and proper data management, the efficiency of the protocols allows the plots to be monitored during normal mist-netting operational hours, given moderate bird capture rates.

We compared timing and duration of flowering among 11 plant species at Palomar study sites using box plots generated in R 3.1.0 (R Core Team 2014). We found a wide range of plant

phenological strategies from long to short durations (Figure 3.2). Additionally, while some species appear to respond to winter precipitation, flowering in the spring, others may respond to increasing temperatures, flowering in the late summer (Figure 3.2). These phenological patterns, along with other plant phenophases including leaf-out and fruiting, can now be compared with annual patterns of migratory bird phenophases including arrival, departure, passage, breeding, and molt. Furthermore, long-term monitoring could reveal the normal range of variation in plant and avian phenology, trends, and extreme events, as well as how these phenological patterns respond to climate variation and climate change (Gordo and Sanz 2010, Ellwood et al. 2013).

In addition to increased understanding of the ecological communities at these long-term study sites resulting from implementation of Nature’s Notebook, incorporating phenology monitoring efforts at Palomar has enhanced the intern training experience by broadening awareness and expertise to other ecological components of the systems they are studying and providing a better understanding of how ecological informatics,

including citizen science projects like *Nature's Notebook*, are changing ecological research (Jeong et al. 2011, Hurlbert and Liang 2012, Miller-Rushing et al. 2012). Additionally, it has the potential to engage the visiting public and contributes to local, regional, and national efforts to track the influences of climate change.

DISCUSSION

Interannual and seasonal changes in habitat resources are central to understanding avian spatial and temporal distribution patterns, habitat ecology, reproductive success, and adaptive evolution in light of phenological synchrony across trophic levels (Both et al. 2009). Including vegetation phenology monitoring within bird monitoring programs can provide important insights into these dynamics. By moving beyond assessment of vegetation structure and composition alone, which may experience minimal change within and among years, phenology data provide information relevant to habitat quality that can change over short time periods of days to weeks. Furthermore, because phenology is highly sensitive to climate, phenology data can help develop a more mechanistic understanding of migratory bird habitat selection (Smith et al. 2007, McGrath et al. 2009, Carlisle et al. 2012).

Although a number of successful national scale bird monitoring programs involving both professional and citizen scientists exist, no contemporary programs for monitoring plant phenology have been implemented with comparable spatial scale and ecological complexity with equivalent success. The USA-NPN *Nature's Notebook* program is providing a unique range of data products and tools that can be directly applied, implemented, and integrated into bird monitoring and research programs for a wide group of users, including state and federal natural resource management agencies (Enquist et al. 2014) and nongovernmental conservation organizations, academic researchers, and citizen science and public education programs. Furthermore, despite the diversity of objectives, goals, and objectives represented by this wide range of stakeholders, the use of standardized data collection protocols and a shared database (NPDb) allows data to be integrated, comparable, and applicable to novel questions at both fine and coarse geographic scales.

Currently, *Nature's Notebook* is being applied by the Inventory and Monitoring Program of the US National Park Service through the California Phenology Project (www.usanpn.org/cpp/) and the Northeast Temperate Network (science.nature.nps.gov/im/units/netn/) to understand ecosystem responses to climate variability and climate change, inform natural resource management and decision making, and engage and educate the public. Existing efforts have produced extensive protocols and recommendations for implementing phenology monitoring using *Nature's Notebook* and these are freely available online through their websites. Building upon these early successes, the National Wildlife Refuge System of the US Fish and Wildlife Service is now implementing phenology via *Nature's Notebook* in its inventory and monitoring efforts. Detailed information about these programs and how to initiate an observation program is available through the USA-NPN website (www.usanpn.org).

Recommendations for Implementing Phenology Monitoring

Organizations should consider several factors when implementing or integrating *Nature's Notebook* into new or existing avian research and monitoring programs for migratory as well as resident birds. These include (1) selection of focal vegetation species for monitoring, (2) determining the number of sites to monitor and the number of individual plants of each species at each site, (3) the frequency of monitoring visits to each site, and (4) the phenological metrics of interest (e.g., onset, peak, duration) and methods for calculation.

Selecting focal plant species will depend on the objectives of the study, the bird species of interest, and the composition and diversity of vegetation communities at sites. Focal plant species should be relevant to bird species of interest, such as use as a foraging substrate or as a food resource; be sufficiently abundant to monitor multiple individuals at multiple sites; and capture flowering or other key phenophases throughout the study season (Figure 3.2).

Nature's Notebook is relatively easy to implement, but the amount of time required for observer training, data collection, data entry and management, and analysis should be carefully considered. As such, the number of sites and individual plants

monitored will greatly depend on monetary and personnel resources for the study and the size and complexity of the study area. The greater the size or ecological complexity of a study area, the more sites or individual plants may be necessary to capture the phenological variation of the area. Similarly, the frequency of observations should also take into account the variation in plant phenology over time and space. During peak periods of change, such as spring leaf-out or flowering, one or two visits per week are preferable for capture of phase transitions, while during periods of less change, such as winter in northeastern temperate regions, one visit per month or less may be acceptable. For integration into established programs, phenology monitoring can be concurrent with other efforts, such as avian point counts, nest searching, or mist-netting, as at the Palomarin field station and associated study sites.

A wide variety of phenological metrics can be calculated from data collected using *Nature's Notebook* and available in the NPDb (Gerst et al., unpubl. ms). The onset, peak, and duration of phenophases within individuals or at sites are all common metrics. Each metric has important considerations related to sampling, analysis, and confounding factors. For example, estimates of onset may be sensitive to changes in population size and sampling frequency (Miller-Rushing et al. 2008, 2010). Therefore, desired metrics and expected analytical techniques should be considered before implementation of monitoring and data collection. Accordingly, the USA-NPN can provide an array of resources and support to facilitate project design, research, development, and implementation.

CONCLUSIONS

To understand long-term ecological responses to climate change that are critical for adaptive management and conservation of natural resources, we need multitaxa phenology monitoring across broad biogeographic regions (Parmesan 2007, Lawler 2009, Richardson et al. 2013, Enquist et al. 2014). As we have shown, the professional and amateur science communities have implemented and participated in a number of large bird-monitoring campaigns. These programs have primarily focused on landbirds and terrestrial systems; increased monitoring of freshwater and marine birds and habitats will provide additional

insight into broader avian phenology dynamics. Unequivocally, colocated data on phenology of bird habitat and food resources will help us unravel the complexities of trophic cascades, phenological mismatch, and phenotypic plasticity and aid in assessing species vulnerability to environmental disturbance and change at spatiotemporal scales and ecological resolutions relevant to the interannual and seasonal ranges of migratory bird species across the globe.

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LITERATURE CITED

- Aborn, D. A., and F. R. Moore. 1997. Pattern of movement by Summer Tanagers (*Piranga rubra*) during migratory stopover: A telemetry study. *Behaviour* 134:1077–1100.
- Ahas, R., A. Aasa, A. Menzel, V. G. Fedotova, and H. Scheifinger. 2002. Changes in European spring phenology. *International Journal of Climatology* 22:1727–1738.
- Baker, A. J., P. M. Gonzalez, T. Piersma, L. J. Niles, I. de Lima Serrano do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in Red Knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London B* 271:875–882.
- Balbontin, J., A. P. Møller, I. G. Hermosell, A. Marzal, M. Reviriego, and F. de Lope. 2009. Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. *Journal of Animal Ecology* 78:981–989.

- Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, J. E. G. Good, R. Harrington, S. Hartley, T. H. Jones, R. L. Lindroth, M. C. Press, I. Symrnioudis, A. D. Watt, and J. B. Whittaker. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1–16.
- Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Current Biology* 20:243–248.
- Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83.
- Both, C., M. van Asch, R. G. Bijlsma, A. B. van den Burg, and M. E. Visser. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology* 78:73–83.
- Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences of the USA* 96:9701–9704.
- Buler, J. J., F. R. Moore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. *Ecology* 88:1789–1802.
- Carlisle, J. D., K. L. Olmstead, C. H. Richart, and D. L. Swanson. 2012. Food availability, foraging behavior, and diet of autumn migrant landbirds in the Boise foothills of southwestern Idaho. *Condor* 114:449–461.
- Chernetsov, N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. *Journal of Ornithology* 147:185–191.
- Chuine, I. 2010. Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B* 365:3149–3160.
- Chuine, I., P. Yiou, N. Viovy, B. Seguin, V. Daux, and E. L. R. Ladurie. 2004. Historical phenology: grape ripening as a past climate indicator. *Nature* 432:289–290.
- Coppack, T., and C. Both. 2002. Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90:369–378.
- Cotton, P. A. 2003. Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the USA* 100:12219–12222.
- Courter, J. R., R. J. Johnson, W. C. Bridges, and K. G. Hubbard. 2013. Assessing migration of Ruby-throated Hummingbirds (*Archilochus colubris*) at broad spatial and temporal scales. *Auk* 130:107–117.
- Denny, E. G., K. L. Gerst, A. J. Miller-Rushing, G. L. Tierney, T. M. Crimmins, C. A. F. Enquist, P. Guertin, A. H. Rosemartin, M. D. Schwartz, K. A. Thomas, and J. F. Weltzin. 2014. Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *International Journal of Biometeorology* 58:591–601.
- Desante, D. F., and L. F. Baptista. 1989. Factors affecting the termination of breeding in Nuttall's White-crowned Sparrows. *Wilson Bulletin* 101:120–124.
- Desante, D. F., K. M. Burton, J. F. Saracco, and B. L. Walker. 1995. Productivity indices and survival rate estimates from MAPS, a continent-wide programme of constant-effort mist-netting in North America. *Journal of Applied Statistics* 22:935–947.
- Dickinson, J. L., B. Zuckerberg, and D. N. Bonter. 2010. Citizen science as an ecological research tool: challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics* 41:149–172.
- Ellwood, E. R., S. A. Temple, R. B. Primack, N. L. Bradley, and C. C. Davis. 2013. Record-breaking early flowering in the eastern United States. *PLoS One* 8:e53788.
- Elrod, M. L., N. E. Seavy, R. L. Cormier, and T. Gardali. 2011. Incidence of eccentric molt in first-year Wrentits increases with fledge date. *Journal of Field Ornithology* 82:325–332.
- Enquist, C. A., J. L. Kellermann, K. L. Gerst, and A. J. Miller-Rushing. 2014. Phenology research for natural resource management in the United States. *International Journal of Biometeorology* 58:579–589.
- Fink, D., W. M. Hochachka, B. Zuckerberg, D. W. Winkler, B. Shaby, M. A. Munson, G. Hooker, M. Riedewald, D. Sheldon, and S. Kelling. 2010. Spatiotemporal exploratory models for broad-scale survey data. *Ecological Applications* 20:2131–2147.
- Forrest, J., and A. J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B* 365:3101–3112.
- Freeman, S. N., D. G. Noble, S. E. Newson, and S. R. Baillie. 2007. Modeling population changes using data from different surveys: the common birds census and the breeding bird survey. *Bird Study* 54:61–72.
- Gillies, C. S., and C. C. St Clair. 2010. Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology* 47:182–190.

- Goodman, R. E., G. Lebuhn, N. E. Seavy, T. Gardali, and J. D. Bluso-Demers. 2012. Avian body size changes and climate change: warming or increasing variability? *Global Change Biology* 18:63–73.
- Gordo, O., and H. Doi. 2012. Spring phenology delays in an insular subtropical songbird: is response to climate change constrained by population size? *Journal of Ornithology* 153:355–366.
- Gordo, O., and J. J. Sanz. 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. *Global Change Biology* 16:1082–1106.
- Greenberg, R., A. Kozlenko, M. Ettersson, and T. Dietsch. 2008. Patterns of density, diversity, and the distribution of migratory strategies in the Russian boreal forest avifauna. *Journal of Biogeography* 35:2049–2060.
- Howell, S. N. G., and T. Gardali. 2003. Phenology, sex ratios, and population trends of *Selasphorus* hummingbirds in central coastal California. *Journal of Field Ornithology* 74:17–25.
- Hurlbert, A. H., and Z. F. Liang. 2012. Spatiotemporal variation in avian migration phenology: citizen science reveals effects of climate change. *PloS One* 7:e31662.
- Jenni, L., and M. Kery. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London B* 270:1467–1471.
- Jeong, S. J., C. H. Ho, H. J. Gim, and M. E. Brown. 2011. Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982–2008. *Global Change Biology* 17:2385–2399.
- Jones, T., and W. Cresswell. 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology* 79:98–108.
- Kaheil, Y. H., M. K. Gill, M. McKee, L. A. Bastidas, and E. Rosero. 2008. Downscaling and assimilation of surface soil moisture using ground truth measurements. *IEEE Transactions on Geoscience and Remote Sensing* 46:1375–1384.
- Kang, S. Y., S. W. Running, J. H. Lim, M. S. Zhao, C. R. Park, and R. Loehman. 2003. A regional phenology model for detecting onset of greenness in temperate mixed forests, Korea: an application of MODIS leaf area index. *Remote Sensing of Environment* 86:232–242.
- Kelly, J. F., and R. L. Hutto. 2005. An east–west comparison of migration in North American wood warblers. *Condor* 107:197–211.
- Lawler, J. J. 2009. Climate change adaptation strategies for resource management and conservation planning. *Year in Ecology and Conservation Biology* 2009 1162:79–98.
- MacMynowski, D. P., and T. L. Root. 2007. Climate and the complexity of migratory phenology: sexes, migratory distance, and arrival distributions. *International Journal of Biometeorology* 51:361–373.
- MacMynowski, D. P., T. L. Root, G. Ballard, and G. R. Geupel. 2007. Changes in spring arrival of Nearctic–Neotropical migrants attributed to multiscalar climate. *Global Change Biology* 13:2239–2251.
- Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142:307–315.
- Marra, P. P., and R. L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116:284–292.
- McGrath, L. J., C. van Riper, and J. J. Fontaine. 2009. Flower power: tree flowering phenology as a settlement cue for migrating birds. *Journal of Animal Ecology* 78:22–30.
- McKellar, A. E., P. P. Marra, S. J. Hannon, C. E. Studds, and L. M. Ratcliffe. 2013. Winter rainfall predicts phenology in widely separated populations of a migrant songbird. *Oecologia* 172:595–605.
- McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology* 93:1987–1993.
- McWilliams, S. R., and W. H. Karasov. 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. *Comparative Biochemistry and Physiology A* 128:579–593.
- Menzel, A. 2005. A 500 year pheno-climatological view on the 2003 heatwave in Europe assessed by grape harvest dates. *Meteorologische Zeitschrift* 14:75–77.
- Menzel, A., T. H. Sparks, N. Estrella, E. Koch, A. Aasa, R. Ahas, and A. N. A. Zust. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology* 12:1969–1976.
- Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B* 365:3177–3186.

- Miller-Rushing, A. J., T. L. Lloyd-Evans, R. B. Primack, R. B. and P. Satzinger. 2008. Bird migration times, climate change, and changing population sizes. *Global Change Biology* 14:1959–1972.
- Miller-Rushing, A. J., and R. B. Primack. 2008. Global warming and flowering times in Thoreau's concord: A community perspective. *Ecology* 89:332–341.
- Miller-Rushing, A., R. Primack, and R. Bonney. 2012. The history of public participation in ecological research. *Frontiers in Ecology and the Environment* 10:285–290.
- Møller, A. P. 2001. Heritability of arrival date in a migratory bird. *Proceedings of the Royal Society of London B* 268:203–206.
- Møller A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the USA* 105:16195–16200.
- Nemeth, Z., and F. R. Moore. 2007. Unfamiliar stopover sites and the value of social information during migration. *Journal of Ornithology* 148:S369–S376.
- Norris, D. R., and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* 109:535–547.
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13:1860–1872.
- Pau, S., E. M. Wolkovich, B. I. Cook, T. J. Davies, N. J. B. Kraft, K. Bolmgren, J. L. Betancourt, and E. E. Cleland. 2011. Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology* 17:3633–3643.
- Paxton, K. L., C. Van Riper, and C. O'Brien. 2008. Movement patterns and stopover ecology of Wilson's Warblers during spring migration of the lower Colorado River in southwestern Arizona. *Condor* 110:672–681.
- Porzig, E. L., K. E. Dybala, T. Gardali, G. Ballard, G. R. Geupel, and J. A. Wiens. 2011. Forty-five years and counting: Reflections from the Palomarin Field Station on the contribution of long-term monitoring and recommendation for the future. *Condor* 113:713–723.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag, and M. Toomey. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169:156–173.
- Rosemartin, A. H., T. M. Crimmins, C. A. Enquist, K. L. Gerst, J. L. Kellermann, E. E. Posthumus, P. Guertin, and J. F. Weltzin. 2013. Organizing phenological data resources to inform natural resource conservation. *Biological Conservation* 173:90–97.
- Russell, R. W., F. L. Carpenter, M. A. Hixon, and D. C. Paton. 1994. The impact of variation in stopover habitat quality on migrant Rufous Hummingbirds. *Conservation Biology* 8:483–490.
- Saino, N., R. Ambrosini, D. Rubolini, J. von Hardenberg, A. Provenzale, K. Huppopp, O. Huppopp, A. Lehikoinen, E. Lehikoinen, K. Rainio, M. Romano, and L. Sokolov. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society of London B* 278:835–842.
- Sandberg, R., and F. R. Moore. 1996. Fat stores and arrival on the breeding grounds: Reproductive consequences for passerine migrants. *Oikos* 77:577–581.
- Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer difference in the North American breeding bird survey. *Auk* 111:50–62.
- Schwartz, M. D. 1994. Monitoring global change with phenology: the case of the spring green wave. *International Journal of Biometeorology* 38:18–22.
- Schwartz, M. D. 1999. Advancing to full bloom: planning phenological research for the 21st century. *International Journal of Biometeorology* 42:113–118.
- Schwartz, M. D., J. L. Betancourt, and J. F. Weltzin. 2012. From Caprio's lilacs to the USA National Phenology Network. *Frontiers in Ecology and the Environment* 10:324–327.
- Seewagen, C. L., C. G. Guglielmo, and Y. E. Morbey. 2013. Stopover refueling rate underlies protandry and seasonal variation in migration timing of songbirds. *Behavioral Ecology* 24:634–642.
- Sherry, T. W. and R. T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of Neotropical–Nearctic migrant birds. *Ecology* 77:36–48.
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Silvertown, J. 2009. A new dawn for citizen science. *Trends in Ecology and Evolution* 24:467–471.
- Singer, M. C., and C. Parmesan. 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B* 365:3161–3176.

- Smith, R. J., and F. R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology* 57:231–239.
- Smith, S. B., K. H. McPherson, J. M. Backer, B. J. Pierce, D. W. Podlesak, and S. R. McWilliams. 2007. Fruit quality and consumption by songbirds during autumn migration. *Wilson Journal of Ornithology* 119:419–428.
- Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* 142:2282–2292.
- Taylor, P. D., S. A. Mackenzie, B. G. Thurber, A. M. Calvert, A. M. Mills, L. P. McGuire, and C. G. Guglielmo. 2011. Landscape movements of migratory birds and bats reveal an expanded scale of stopover. *PloS One* 6:e27054.
- Tøttrup, A. P., K. Rainio, T. Coppack, E. Lehikoinen, C. Rahbek, and K. Thorup. 2010. Local temperature fine-tunes the timing of spring migration in birds. *Integrative and Comparative Biology* 50:293–304.
- van Asch, M., and M. E. Visser. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology* 52:37–55.
- Vegvari, Z., V. Bokony, Z. Barta, and G. Kovacs. 2010. Life history predicts advancement of avian spring migration in response to climate change. *Global Change Biology* 16:1–11.
- Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B* 272:2561–2569.
- Visser, M. E., L. te Marvelde, and M. E. Lof. 2012. Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* 153:S75–S84.
- Walther, G. R. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B* 365:2019–2024.
- White, M. A., K. M. de Beurs, K. Didan, D. W. Inouye, A. D. Richardson, O. P. Jensen, J. O’Keefe, G. Zhang, R. R. Nemani, W. J. D. van Leeuwen, J. F. Brown, A. de Wit, M. Schaepman, X. M. Lin, M. Dettinger, A. S. Bailey, J. Kimball, M., D. Schwartz, D. D. Baldocchi, J. T. Lee, and W. K. Lauenroth. 2009. Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982–2006. *Global Change Biology* 15:2335–2359.
- Wilson, S., S. L. LaDeau, A. P. Tøttrup, and P. P. Marra. 2011. Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. *Ecology* 92:1789–1798.
- Yang, L. H., and V. H. W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters* 13:1–10.