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12. The impact of climate change on biological phenology in the UK

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Executive summary

Phenology can be described as the study of the timing of recurring natural events. The UK has a long history of phenological recording, particularly of first and last dates, but systematic national recording schemes are able to provide information on the distributions of events. The majority of data concern spring phenology, autumn phenology is relatively under-recorded. The UK is not usually water-limited in spring and therefore the major driver of the timing of life cycles (phenology) in the UK is temperature [H]. Phenological responses to temperature vary between species [H] but climate change remains the major driver of changed phenology [M]. For some species, other factors may also be important, such as soil biota, nutrients and daylength [M].

Wherever data is collected the majority of evidence suggests that spring events have advanced [H]. Thus, data show advances in the timing of bird spring migration [H], short distance migrants responding more than long-distance migrants [H], of egg laying in birds [H], in the flowering and leafing of plants[H] (although annual species may be more responsive than perennial species [L]), in the emergence dates of various invertebrates (butterflies [H], moths [M], aphids [H], dragonflies [M], hoverflies [L], carabid beetles [M]), in the migration [M] and breeding [M] of amphibians, in the fruiting of spring fungi [M], in freshwater fish migration [L] and spawning [L], in freshwater plankton [M], in the breeding activity among ruminant mammals [L] and the questing behaviour of ticks [L]. There are fewer data from freshwater than terrestrial environments. Autumn event changes are more equivocal; although extended autumns are likely in the future [M]. Autumn flying moths have extended their flying period later into the autumn [M], potentially leading increased voltinism [L]; autumn fruiting of fungi have tended to show longer seasons [M], with both earlier start and later end to fruiting and questing behaviour of ticks is extending further into autumn [L]. Since fruit ripening of plants will also occur earlier there will be a longer interval between (wild and cultivated) fruit ripening and the end of season [M]. This may have impacts on those animal species needing to feed-up before the onset of winter [L].

A comprehensive study of UK phenological trends over a standardised time period (1976-2005) revealed that 84% of events had advanced and that there were considerable differences between trophic levels [H]; secondary consumers had not advanced as strongly as lower trophic levels [H]. Trends towards earliness were apparent in all environments [H] (Thackeray et al., 2010).

Spatial variation in response to climate change is widespread [H], with species altering their phenology in response to geographical differences in climate change [H]. Such changes can be due to large scale geographic factors, such as latitude or longitude or due to more local factors. There is some evidence for an urban heat island effect, with phenologies being more advanced than in the surrounding countryside [M]. Phylogenetic factors can be important, with closely related species having more similar phenological reposnses to climate change than more distantly related species [M].

Species exist in a complex network of predator/prey/host/symbiotic relationships. There is very strong evidence that changes in phenology are species-specific [H], and possibly even genotype-specific [M]. For example, the migration arrival of Sand Martin has advanced much more than that of Pied Flycatcher [M], and “common garden” experiments reveal phenological differences in leafing between different provenances of trees [M]. Consequently there are serious concerns that mistiming will cause future problems by altering food supply and hence the fitness of certain species [H]. In the UK, there is little direct evidence yet of phenological mis-match [M], although examples exist from other countries [M] (e.g. Pied Flycatcher in The Netherlands (Both et al., 2006)) and mismatch is also likely to be occur in the UK in the future [L] (e.g. Memmott et al., 2007). Currently, species that are able to adjust their phenologies to warmer climates do so through mainly through individual plasticity [H],

although in species with rapid generation time, microevolutionary responses have been demonstrated [M], and in some cases other mechanisms may be important [M] but we do not know if or how quickly species will be able to adapt genetically to new situations [L]. Species that do not adjust their phenology in response to climate change are more likely to show population declines [M]. Species which use environmental cues that are not directly related to climate (such as daylength), have a narrow ecological niche, rely on few species at a lower trophic level, have low mobility and low reproduction rates are those likely to be most at risk [L]. It is hard to identify which species these will be, since phenological data are available for relatively few species.

Definition

Phenology can be described as the study of the timing of recurring natural events. Some authorities replace “natural” with “biological” (Sparks & Menzel, 2002). In the UK this makes little difference since we don’t have much tradition of recording physical events such as lake freezing and thawing. In the UK, the recording of dates of biological events, such as first leafing or first arrival of migrant birds, goes back to the late 17th or early 18th centuries (Sparks & Collinson, 2008).

Types of phenological data

Most data concern the first or last dates of an event because these, particularly the former, are easiest to record. Data concerning percentile or mean dates are less common, and typically associated with monitoring schemes or with detailed scientific studies and Pearce-Higgins & Green (2014) show how these data provide valuable information about the underlying patterns of change. There has been some criticism of first dates as being non-representative, or sensitive to changes in population size and recorder effort (e.g. Clark & Thompson, 2011), but a number of studies have shown that these can be relatively robust (e.g. Sparks et al., 2001). There continues to be more data associated with spring events than with autumn or other seasons (Gallinat *et al*. 2015).

Sources of data

National phenological networks in the UK include those of the Royal Meteorological Society (RMS) (1875-1947), British Naturalists’ Association (1905-) and the UK Phenology Network/Nature’s Calendar (1998-) and all focus (or focussed) on first and last events (Sparks & Collinson, 2008). National biodiversity monitoring schemes in the UK that can determine phenology as a by-product include the Butterfly Monitoring Scheme (Roy & Sparks 2000), Rothamsted Insect Survey’s moth and aphid schemes (Woiwod 1997; Bell *et al.* 2015), the BTO’s bird monitoring schemes (see http://www.bto.org/birdtrends) and systematic records collected by coastal bird observatories (Croxton *et al.* 2006). In addition there are some long running site-specific schemes which are either institution-led or the work of individuals; these include the UK Environmental Change Network (e.g. Pozsgai & Littlewood, 2011), the Cumbrian Lakes monitoring (e.g. Thackeray *et al.* 2012) and the nest box scheme in Wytham Woods, Oxfordshire (e.g. McCleery & Perrins, 1998).

A new approach has been proposed by Bishop *et al.* (2013) for measuring flying period phenology of butterflies, which could be applied to other groups. This uses the timing of records obtained from distributional surveillance and they show that mean flight date for 22 of 30 species could be accurately measured in comparison to standardised population monitoring data. Flight period length could only be assessed accurately for seven species. Accuracy was largely determined by sample size, and they recommended a threshold of 6500 distributional records to provide accurate phenological estimates.

Analysis of phenological data

Although not increasing consistently each year, mean annual temperature has shown a significant warming trend since the mid-1980s in the UK, including 2014 which was the warmest year in the 350 year Central England Temperature series (Met Office 2015). Cold years, such as 2010, still occur, though less frequently. Consequently, any time series of phenological data that relate directly to temperature will also not have experienced a smooth trend. Thus, it is desirable to have longer time series in order to be able to detect any change in phenology statistically. A minimum of 20 years has been recommended (Sparks & Menzel, 2002; Luedeling & Gassner, 2012; see also Fig. 9.3 in Lehikoinen & Sparks, 2010) whilst recognising that this is not always available. If a phenological series coincides with a period of warming then any directional change will be correlated with temperature irrespective of whether it is the driver of change. Series that span periods of warming and cooling may thus provide a more realistic estimate of response to temperature (e.g. Crick & Sparks 1999), although some authors prefer to estimate partial effects having eliminated a linear trend through time (e.g. Estrella et al., 2007). The usual approach to detect phenological trend is to regress phenology on year, although other approaches are also used, such as a comparison of the mean date of recent years with a period in the past (e.g. Fitter & Fitter, 2002). The statistical significance of any changes assumes that years are independent i.e. that autocorrelation is not present in the data. Autocorrelation is probably only a minor issue in phenological series (Sparks & Tryjanowski, 2010).

It should be noted that many of the original analyses of phenological trends for different taxa based on long-terms recording schemes and datasets were undertaken in the late 1990s and early 2000s, and there is a need for re-analysis of such trends given the addition of an extra 10-15 years of data from the monitoring schemes upon which such analyses were based.

Literature review approach

Web of Science was searched on 28 June 2012 for the phrase "Phenolog*". This demonstrated the huge literature around phenology, generating 58,387 hits. A refinement to focus on UK related work as shown in Table 1 reduced the number by about 70%. Duplicates were then removed, and by reference to titles this list was reduced to about 800. Abstracts of papers were then examined to reduce the list further to c.125. Thus the focus here is on UK studies reported in peer-reviewed journals. A update was made on 12 February 2015 and the additional number of hits for "Phenolog*" in the year 2012-15 was 11,359 (which will include some duplicates from the first half of 2012). Further refinements were made as shown in Table 1. After removing duplicates, assessing titles for relevance and reviewing abstracts an additional 64 papers were assessed in detail.

Table 1. Search phrases and numbers of hits (total 17,418) from Web of Science on 28/6/2012, additional hits are for the years 2012-2015 searched on 12/2/2015.

	Phenolog* AND	Synchron* AND	Trends AND (Timing OR Time OR Date) AND
U.K.	15+6	32+10	166+24
UK	436+90	506+76	6179+733
United Kingdom	43+108	79+44	1101+433
England	319+89	507+75	4693+564
Wales	156+28	182+34	1495+272
Scotland	89+26	169+23	952+167
Northern Ireland	15+12	49+8	235+49

Types of papers

Papers can be broadly considered to cover one or more of the following topics; changes to phenology in experimental studies; studies of synchrony in species; studies reporting change to phenology; studies examining responsiveness of species to temperature, altitude, latitude or the North Atlantic Oscillation (NAO); studies examining locational or provenance differences.

The focus of this review is on the impacts of climate change on phenology, but including some examples that document temperature responsiveness of phenology, key synchrony links and experimental studies. For some events it has been shown that climate is just one driver of phenology (for example in lake plankton where nutrient status is also important: Elliott, 2012) but these other drivers are not covered in detail.

Birds

The two most common types of data are on timing of migration and on timing of egg laying. Data also exist for moult dates and dates of change in song (or commencement of song). Timing of migration has been recorded for many years by individual recorders, since the 1930s at British coastal bird observatories, in county bird reports (most post-WWII), by bird ringing schemes and more recently in the British Trust for Ornithology's Birdtrack scheme (http://blx1.bto.org/birdtrack/main/data-home.jsp). Data from observatories and from Birdtrack can supply percentiles, most other data only concern first and last records. These latter schemes may have difficulty maintaining recorder effort across the season and between seasons although some observatories use fixed time counts. Bird ringing schemes, such as the BTO's Constant Effort Sites Scheme (see http://www.bto.org/volunteer-surveys/ringing/surveys/ces), generally start too late to record the start of migration. The UK Phenology Network (UKPN - http://www.naturescalendar.org.uk/) has been collecting data on first arrivals since 1998 and in addition holds the RMS (1875-1947) records on its database. No systematic analysis of these bird migration data has yet been done.

Egg laying dates tend to originate from studies at particular localities, for example Wytham Woods, Oxfordshire (McCleery & Perrins, 1998) or from the BTO's Nest Record Scheme (NRS) (Crick & Sparks, 1999). The former type of scheme mostly concern only hole nesting birds where recording is simplified by placement of man-made bird boxes. The NRS may not maintain recorder effort throughout the season (Crick *et al*. 2003), but does involve a large number of species. Another source of material on egg-laying dates is from museum collections (Scharlemann, 2001). Museums may host large collections of eggs from the heyday of oology. However, since egg collection became largely illegal after the Protection of Birds Act 1954 there are fewer recent, legal, collections. Consequently they are less useful to demonstrate modern change in egg laying dates unless used in conjunction with current recording schemes to provide longer time series for examining historical trends. Collection date and location are typically included with the eggs and a laying date can be estimated from these, clutch size and the size of the blow hole. Much of this information is already in databases, reducing the need for inspection of each clutch.

Most records of bird migration, whether from county bird reports (e.g. Mason, 1995; Cotton, 2003) or bird observatories (e.g. Croxton et al., 2006) have shown a tendency for spring migrants to arrive earlier in recent years. Not all species show this advance (e.g. Browne & Aebischer, 2003), and not all are statistically significant. It has been shown that the advance has been greater for birds with shorter migration distances (intracontinental) than those originating in Africa (intercontinental), and greater for earlier arriving species than later arriving species (Lehikoinen & Sparks, 2010; Pearce-Higgins & Green, 2014), but exceptions occur in both respects. Pearce-Higgins & Green (2014) concluded that the advance in arrival of short and medium distance migrants is likely to have been caused by spring warming across the mid to high lattitudes in which the birds winter or migrate through. A few long term studies from individual recorders (e.g. Jenkins & Watson, 2000) have also been published, with similar results. Sparks et al. (2007) attempted a meta-analysis of county bird report data. They examined 145 spring arrival series and 67 departure series; half of the former showed significant trends towards earlier arrival and a third of the latter to later departure. Consistency in spring arrival trends for individual species across sites gives greater confidence in the validity of these first arrival data, for example Sand Martin advanced significantly at all sites while Spotted Flycatcher was not significant at all sites. Pearce-Higgins & Green (2014) collated trends of first arrival date from 1437 published time series across Europe and found that arrivals had advanced on average by 0.24 ± 0.04 d yr^{-1}. They also found that there was little evidence for trends in mean or last departure dates in the autumn, although short-distance migrants had delayed their departures by 0.26 d yr^{-1} compared with little change for medium and long-distance species.

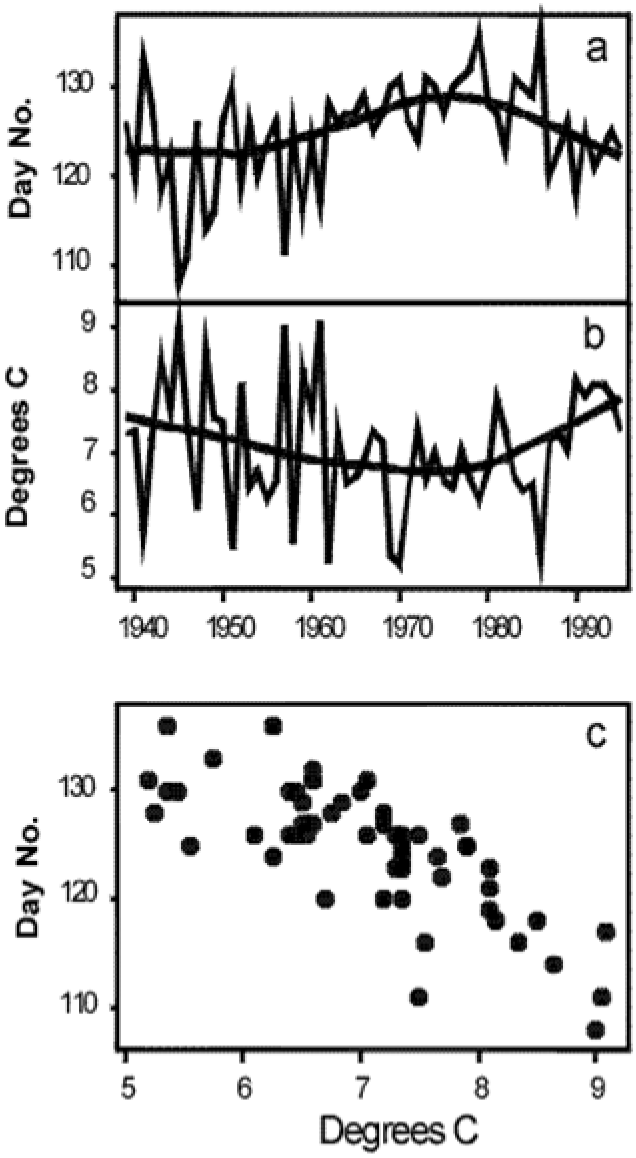
There can be some considerable differences between species, for example Sand Martin shows a much more rapid advance in phenology than does Swallow (Sparks & Tryjanowski, 2007). UK populations of Swallow that spend the non-breeding season in the Western cape of South Africa undertake a full primary moult that lasts c. 135d, close to the 140d residence time; this may be a factor that constrains their ability to start their return migration any earlier (Altwegg *et al.* 2012). Further analyses are beginning to suggest that those populations of bird which are failing to advance their migration timings in line with climate warming are more likely to show population declines compared with those that have advanced their spring arrival (see Moller *et al.* (2008) for 100 species in Western Europe, including the UK; and Salido *et al.* (2012) for 50 species in UK). Some studies do not include data from the most recent decade. For example, Cotton (2003) used data only up to 2000. A decadal update, where possible, as in the Jenkins & Sparks (2010) update of Jenkins & Watson (2000), is recommended. A combination of increased series length and responses to the recent warm decade would enhance chances of detecting statistically any trends in phenology.

Migration data concerning mean arrival dates are much less common. Sparks et al. (2005) examined *inter alia* first and mean arrival dates and showed that correlations between the two were all positive, but not necessarily significant. Furthermore they found that arrival distributions differed in skewness between locations and between years making modelling of combined distributions problematic. Lehikoinen & Sparks (2010) summarised more widespread arrival data than just to the UK and showed that 47% of 3,201 first arrival date series and 40% of 440 mean/median arrival series had become significantly earlier. Only 5% and 2% respectively had become significantly later. The mean trend in first arrival dates was 2.8 days earlier per decade and in median/mean arrival dates 1.8 days earlier per decade. Pearce-Higgins & Green (2014) collated trends of mean arrival date from 294 published time series across Europe and found that arrivals had advanced on average by 0.15 ± 0.02 d yr^{-1}, equivalent to an advance of 7 days between 1980 and 2010, however, they found no difference with respect to migration distance.

An advance in egg laying was apparent in long term series from the BTO NRS (Crick et al., 1997). When extended to more species and longer series (Crick & Sparks, 1999) the evidence for trends to earlier egg laying remained. The greater benefit of the longer series is that delayed egg laying could be shown in cooling periods and advanced laying in warming periods (Figure 1). Thackeray iet al. (2010) updated the trends in Crick *et al.* (1997) to show an average advance in mean laying date of 0.19 d yr^{-1} between 1976 and 2005. Studies from individual sites (e.g. McCleery & Perrins, 1998; Smith, 2007; Goodenough et al., 2011) tend to show advanced egg laying dates. While in most species, advances in average laying date are due to genuinely earlier laying (e.g. Crick & Sparks 1999), an unusual study of Long-tailed Tit (*Aegithalos* caudatus) has shown that average advancement occurred due to earlier termination of breeding, shortening the breeding season by 33% (Gullet *et al.* 2013). Thus there are differences between species in the magnitude of trends and not all trends are towards earliness (e.g. Chamberlain & Crick, 2003), although the majority are. For example, Goodenough *et al.* (2010), in a study of 6 woodland passerines at one site, suggested that while three resident species appeared to track changes in climate for earlier laying, the earliest nesting species (Coal Tit *Periparus ater*) did not, possibly to avoid the detrimental effects of later cold weather; and the two long-distance migrants did not, possibly because cues on their wintering grounds were not matched to the phenological changes on the breeding grounds. Pearce-Higgins & Green (2014) found that there was contradictory evidence from published studies comparing migration distance with changes in laying date, so they analysed 256 time series and found no overall difference between trend in mean laying date and migratory distance.

The ability to mark birds individually and to follow their breeding attempts allows the study of individual adaptability or plasticity in response to climate change. Individual plasticity can largely account for population responses to climate change (Przybylo et al. 2000, Reale et al. 2003, Bradshaw & Hozapfel 2006, Nussey et al. 2005, 2007; Charmantier *et al.* 2008; Gullet *et al.* 2013). For example, individual radiotagged female Red Grouse (*Lagopus lagopus*) followed in different years were able to adjust their lay dates according to Scottish spring temperatures, and showed roughly the same patterns as the population as a whole (Fletcher *et al.* 2012). However, it is interesting to note that a long term-study of migration phenology by Black-tailed Godwits (*Limosa limosa*) has found that individual birds returning to Iceland to breed in the spring were highly consistent in their timing, but the population as a whole had shifted towards earlier arrival (Gill *et al*. 2014). It is suggested that the population advance is not due to individual plasticity or micro-evolutionary shifts, but through the carry over effect of advanced breeding facilitating earlier migration due to the enhanced body condition of newly recruiting birds.

Figure 1. Relationship of temperature and laying date for Chaffinch showing changes in annual median laying date (a), changes in mean March-April Temperatures (b) and correlation between annual median laying date and temperature (c) (redrawn from Crick & Sparks, 1999).



Amphibians and reptiles

The UK only has a small number of these species but, because of its linkage with school-based nature studies in the past, frogspawning is still popularly recorded, for example in records collected by the UKPN. Most other studies concern single species at single sites. Available data include frog and toad spawning dates, migration dates of newts and Common Toads, and, less frequently, courtship or sloughing dates of Adder.

Reading (1998, 2003) showed temperature responses in the breeding of Common Toad in Dorset, although no trend towards earlier breeding. Sparks et al. (2007) revealed advanced migration of Common Toad in Huntingdonshire, despite a declining population. However, Arnfield *et al.* (2012) has found that 25 populations of Common Toad monitored in Derbyshire have tended to migrate progressively later over a recent 12 years and discuss how local factors appear to cause a variety of responses in different populations that have been studied by them and others. They concluded that it is difficult to generalise on the phenological response of this species to climate change.

Scott et al. (2008) detected advances in Common Frog spawning dates from Environmental Change Network sites. However, Beebee (1995) had earlier showed no significant change to

Common Frog spawning although activity in all three newt species, in Natterjack Toad and in Edible Frog had become significantly earlier. Likewise, migration of Palmate Newt and Smooth Newt had become earlier at a site in mid-Wales (Chadwick et al., 2006). Sparks et al. (2007) showed differences in timing of frogspawn with South Wales being considerably earlier than at a similar latitude in Huntingdonshire, suggesting locally adapted responses to ambient temperature (cold snaps after periods of warming are more likely in the east of England than in coastal South Wales). Spatial differences in frog spawning using national data were emphasized by Carroll et al. (2009) who further documented advance in frog spawning dates compared to a source from six decades previously. Phillimore et al. (2010) analysed >50,000 records of Common Frog spawning from UKPN data to show that while local populations showed some plasticity in response to temperature, local adaptation was a bigger factor. Using projections from UKCP09 for 2050-2070, the results suggested that plasticity would only be able to cope with c. 20% of the projected change required. Overall, the detection of change in amphibian phenology appears to be difficult since changes are modest and year-to-year variability is large.

Mammals

There are relatively few schemes in the UK from which mammal phenology data can be extracted. The Victorians were keen on recording first spring appearances of bats and sometimes of hedgehogs; but in recent years the hibernation phase has become more ephemeral and it is not clear if recording schemes for such events still exist.

The long term studies of Red Deer on Rum and Soay sheep on Hirta have shown advances in breeding activity and other aspects of life cycles (Forchammer et al., 2001; Clements et al., 2010; Moyes et al., 2011). The Wild White Cattle at Chillingham, Northumberland have been shown to have changed to earlier breeding with more winter births (Burthe et al., 2011). Interestingly, the advancement in birth date shown by the Red Deer population on Rum has not been associated with changes in offspring fitness, which had been expected (Moyes et al., 2005). This appear to be due to the antagonistic effects of different weather components on different aspects of Red Deer demography, combined with density dependent effects of population increases (Stopher et al., 2014).

Although not from UK, but in a comparable geographic location, a 27-year study of Roe Deer birth dates in northern France showed a lack of advancement in timing despite advances in vegetation phenology (Plard *et al.* 2014). This was suggested to be because timing was linked to day length in this species and the progressive mismatch was having negative impacts on calf survival and hence population fitness.

Fish

Schemes to monitor fish runs, e.g. of Salmon, can generate phenological data. In addition some schemes can provide spawning dates in freshwater fish, e.g. from the Cumbrian lakes project (Winfield et al., 2004). Kennedy & Crozier (2010) showed earlier migration of Atlantic Salmon in Northern Ireland. Conversely, in the River Dee in Wales there has been wholesale change in run timing of Atlantic Salmon from spring to summer (Aprahamian et al., 2008). Salmon reurning to Scottish rivers on the east coast are returning later now than in previous years, but this is linked to fish condition, itself linked to feeding conditions in the warmer seas during their marine phase (Todd *et al.* 2012). Salmon migration timing appears to have been affected by overexploitation, with fish now reaching sexual maturity at smaller sizes. Consequently, any temperature-related component to migration timing may be masked by other factors (e.g. Hard et al. 2008). However, spawning dates of other fish species may be also affected by temperature, for example, records of Perch spawning from Lake Windermere shows advancement in timing that appears related to warming over the last 30 years of a 50 year record (Winfield et al., 2004).

Terrestrial Invertebrates

This group contains some of the best monitored populations in the UK, having fixed effort schemes for monitoring butterflies (Butterfly Monitoring Scheme (BMS)), aphids (Rothamsted Insect Survey (RIS) suction traps) and moths (RIS light traps). Additional schemes generate data for dragonflies and hoverflies and it should be possible to monitor other groups through archived collections of the RIS suction traps.

Brakefield (1987) was one of the first to show the responsiveness of butterflies to temperature. Sparks & Yates (1997) combined historic data with data from the BMS to show phenological shifts in a limited number of species. Roy & Sparks (2000) then undertook a fuller examination of the BMS data including examination of both first appearance and peak dates. The majority of species demonstrated temperature sensitivity and advanced appearance dates. Both first and peak dates had advanced, but not necessarily to the same degree; advance being more pronounced in first dates. It should be noted that a small number of species analysed by Roy & Sparks (2000) showed some delay in emergence with warmer springs, possibly because the species requires some chilling stimulus to terminate dormancy (Bale & Hayward, 2010). Multivoltine species may be able to take advantage of longer warm seasons by increasing the number of generations in one year (e.g. Altermatt 2010), however, this could lead to a developmental trap if a species is stimulated into having an extra generation which has a low probability of survival. Van Dyck *et al.* (2015) suggests that this might be the case for wall brown butterflies *Lasiommata megera,* which has suffered population declines in some of the areas areas where they attempt three generations per year, but in which the season terminates before diapause can be initiated successfully.

Data on aphids have focussed on first capture dates, partly because the RIS scheme is designed as an early warning system for pest control. There can be huge year-to-year difference in first dates which appear to be very temperature responsive and have generally advanced (Zhou et al., 1995). Such work has been backed up by a Europe-wide analysis (Harrington et al., 2007). Recently a comprehensive spatio-temporal analysis of 50 years of aphid population data from the RIS has been undertaken (Bell *et al.* 2015). Fifty-five species were monitored and they have advanced their 1st flight date by 0.6 d yr^{-1} on average. Although 49% had advanced their last flight dates, the average change was relatively stationary; thus most species (85%) had lengthened their flight period by 0.34 d yr^{-1}. In terms of climate drivers, the accumulated day degrees above 16 °C was an increasingly strong predictor of 1st flight later in the year; but early in the year, when the first aphids were migrating, the effect of the winter North Atlantic Oscillation index was highly significant. Parthenogenetic species, and those that only used one host tended to show faster advances in 1st flights than those that were not.

Moths have also been shown to be emerging broadly earlier (Woiwod, 1997). This is despite research showing that approximately two thirds of moths are in population decline (Conrad et al., 2006), which would tend to generate later phenologies (Sparks *et al*. 2001, 2007). In a single trap in Scotland, two of four examined moth species had become significantly earlier by 8-10 days between 1968 and 2003 (Salama et al., 2007). There is an interesting contrast between spring/summer flying moths and autumn flying moths: while the former have tended to advance their median flying date in the RIS samples, the latter have shown trends towards later median flights, as might be expected with a lengthening of late season warmth (Woiwod & Gould 2008). Although not from the UK, studies from nearby Netherlands have shown rapid micro-evolutionary changes in egg hatching date of winter moth *Operophtera brumata* that has ensured the maintenance of synchrony with bud burst of its host, the oak *Quercus robur* (van Asch *et al.* 2012).

Records of the British Dragonfly Society have been analysed (Hassall et al., 2007) and reveal trends towards earlier records, on average by 6-8 days between 1960 and 2004 across the 25 species examined. Again, species differences are evident, for example with stronger trends for spring species than summer species. Hassall et al. (2007) only looked at data in decadal slices and it might be useful to re-analyse the data on an annual basis for greater precision.

Hoverfly phenology of 20 species has also been analysed from a single location in Peterborough for 1991-2007 (Graham-Taylor et al., 2009). Three of the species showed significant advances and responses to temperature were evident. The trend towards earliness across all species averaged 5.3 days/decade. This is possibly the only UK data on hoverfly phenology. The series is only 17 years long which is why detection of trends may be difficult.

Data from the Environmental Change Network (ECN) have shown an advance in first capture of the carabid beetle *Pterostichus madidus* (Pozsgai & Littlewood, 2011) and a more comprehensive analysis of 25 carabid species at two sites in Scotland showed that species that were less able to advance their timing were more likely to show population declines (Pozsgai & Littlewood 2014). Winter activity by the bumblebee *Bombus terrestris* have been observed in recent years on ECN sites (Stelzer et al., 2010). It is likely that other invertebrate monitoring schemes (e.g. of ladybirds) may generate phenological data and the UKPN also has a number of additional records (e.g. of queen wasp, 7-spot ladybird) that have not yet been analysed in detail.

Museum collections of insects are another potential source of information since location and date of collection are often provided on labels. However, these data are not computerised so considerable effort are needed to access them. Collections are focussed on the past with relatively little addition in recent years, but such data could be used to put modern dates into context. A recent analysis of 2630 specimens of four species of butterfly from 1876 to 1999 has shown how such data can provide useful long-term phenological trends (Brooks et al 2014). They showed that 10th percentile collections dates had advanced with warmer springs, but that the length of collection period was shorter as the season became earlier. They found that the data was consistent with observational data, suggesting that the data are reliable.

Since it has been shown that many invertebrate species respond to temperature, either between years or along altitudinal transects (e.g. Fielding et al., 2002), it is likely that many more phenological changes will be detected under projected future rapid warming. An example of potential importance for human and livestock health is the recent finding that ticks (*Ixodes ricinus*), a vector for diseases such as Lyme disease, show “questing” behaviour for potential hosts that advances with warmer spring temperatures (Gilbert *et* al 2014). They suggested that the questing season might actually lengthen by as much as a month at either end of the current seasonal range – increasing the potential exposure of hosts considerably with climate change. In addition to temperature effects the influence of the North Atlantic Oscillation (NAO) has been examined for Butterflies, with positive values of the index, associated with warmer wetter weather, leading to advances in flight periods (Westgarth-Smith et al., 2012) and for aphids, in which the NAO tended to help synchronise populations of green spruce aphid *Elatobium abietinum* across the UK (Saldana et al., 2007).

Freshwater invertebrates and phytoplankton

Malcolm Elliott recorded Alderfly emergence at Windermere (Elliott, 1996) between 1966 and 1995 and showed marked temperature responses but no advance in emergence. Further data are likely to exist on dates of caddisflies, stoneflies and mayflies but don’t appear to have been analysed with respect to phenological change. It is likely that angling societies, particularly fly-fishing clubs, may hold as-yet undiscovered data.

Plankton (both zoo- and phyto-) are recorded as part of the Cumbrian lakes monitoring studies and at Loch Leven. Studies have revealed sometimes notable advances associated with warming (e.g. George, 2012; Thackeray et al., 2012) and, as in other taxonomic groups, considerable differences between species (Feuchtmayr et al., 2012). In addition to temperature responses, responses to increased nutrients have been shown for some species which can confound the effects of temperature changes (Thackeray et al., 2008; Elliott, 2012).

Fungi

Dates of fungal fruiting have been recorded by individuals, by county groups, and in a national collection. Herbarium collections may provide another possible source of data. The UKPN records one fungal species, Fly Agaric, but no comprehensive analysis has yet been carried out.

The most comprehensive analysis to date has been that of Gange et al. (2007) which showed widespread changes in autumn fungal phenology. Of 315 examined species 85 had significantly earlier first fruiting dates (by an average of 8.6 days/decade) and 105 had later last fruiting dates (by an average of 7.5 days/decade). Overall a longer fruiting season was evident but considerable species differences were also shown. More recently, Kauserud *et al.* (2012) analysed the autumn fruiting of 278 species in the UK and showed that saprotrophic species were extending their fruiting at the end of the season more than ectomycorrhizal (ECM) species, although advances at the beginning of the season were equivalent – they suggested that the ECM species are more constrained because they are dependent on the carbohydrate supply provided by their plant hosts, saprotrophs are less constrained and so can extend their seasons more. Early-autumn fruiters shifted their start dates considerably more than late autumn fruiters and they found that the trends in UK were more pronounced than in Norway, Switzerland and Austria, which they suggested was linked to the UK's maritime climate. Interestingly, Kauserud *et al.* (2012) also found that trends in phenology were more similar within genera than between genera, suggesting taxonomic constraints in fruiting phenology. Some species considered to be autumn fruiting are now fruiting in spring (Gange et al., 2011 but see Heilmann-Clausen & Læssøe, 2012). Advances in the timing of spring fruiting fungi have also been detected (Kauserud et al., 2010). The overall picture of fungal phenology is of widespread change, species differences, and differences between habitats, for example under coniferous or deciduous canopies. Some fungi appear to be changing their host affiliations.

Vascular Plants

The recording of plant phenology has a long history in the UK and there are some notable collections going back over the last three centuries. Changes have been evident over the last 250 years with current flowering dates earlier by 2-13 days than in any period since 1760 (Amano et al., 2010). The UKPN has been gathering phenological data since 1998 which can be used in conjunction with data collected by the Royal Meteorological Society (1875-1947). In addition there have been some notable long-term collectors who have provided a considerable resource for analysis. Foremost amongst these was Richard Fitter (Fitter & Fitter, 2002) who sadly finished recording in 2000 and died a few years afterwards. His data set has provided considerable detail on changes in the flowering dates of plants. Fitter & Fitter (2002) showed that the majority of species had become earlier but that there were considerable differences between species, and like some insects (see above), some species require chilling before leaf or flower emergence, and thus may have delayed phenologies in the presence of warmer winters and springs. They also noticed that changes had been more pronounced in insect pollinated and annual species. A recent review of plants and pollinator phenologies suggests that so far there is little evidence for mismatched timing occurring in response to climate change because most species have maintained their synchrony to date (Forrest 2015).

Earlier phenology in plants has been reported by many authors (e.g. Hepper, 2003), with early season species responding most (Sparks et al., 2000; Mazer *et al.* 2013) although Kirbyshire & Bigg (2010) showed that changes were also evident in summer flowering plants. Advances in pollen release in spring have also been reported (e.g. Emberlin et al., 2002; Emberlin et al., 2007). Mazer *et al.* (2013) showed that patterns of sensitivity to warming were also linked to phylogenetic relationships – species within early flowering families were more similar in responsiveness than species in different early flowering families. There is some evidence for spatial variation in phenological changes in relation to large scale and more local geographic factors. For example, and increase in urban landuse of 10% between 1934 and 2007 resulted in a change in advancement of flowering of blackthorn from 0.28 to 1.2 d yr^{-1}, of hawthorn from 0.16 to 0.57 d yr^{-1}, and of horse chestnut from 0.13 to 0.90 d yr^{-1}, possibly as a result of the urban heat island effect; the effects varying geographically, being strongest in the extreme south-west and in the north (Comber & Brunsden 2014). The urban heat island effect leading to earlier flowering than in the countryside appears to be a general phenomenon that has been found widely throughout the world (Jochner & Menzel 2015).

The links between the responsiveness of plants to spring warming and the likelihood of the species showing range shifts have been explored by Amano *et al.* (2014). Species that do not track warming by advancing their flowering were more likely to show range shifts northwards, thereby tracking climate change spatially to maintain their phenological climatic niche. They found that 38 perennial species showed neither spatial nor temporal tracking of climate change (for flowering time), whereas all but one annual species were able to do so. They suggest that selection on flowering times may be more critical for annual species and may allow more rapid adaptation because of their short generation times.

In general, most reported studies indicate an advance of spring events although changes in autumn are more equivocal. This has been emphasised on a Europe-wide scale by Menzel et al. (2006). It might be argued that some common trees are widely recognised and changes in their phenology may have more resonance with the public than if other taxonomic groups which they are less familiar with are used. A few studies on crops have also shown an advance, for example in White Clover (Williams & Abberton, 2004), in haymaking dates (Smith & Jones, 1991) and in general agricultural activity (Sparks et al., 2005). Other datasets, for example horticultural datasets on fruit and cut flowers exist, but appear not to have been formally analysed yet.

Genetic differences do occur in phenology and have been shown in common garden experiments (e.g. Jones et al., 2001; Salmela et al., 2011). In an experiment on Sessile Oak, budburst dates varied by more than 3 weeks between the 16 provenances examined with later provenances originating from high latitude and low altitude locations (Deans & Harvey, 1995). Likewise cultivar differences in phenology are clearly apparent. The phenology of budburst of Scots Pine *Pinus sylvestris* seedlings taken from 21 locations across Scotland showed that although there was some evidence for genetic adaptation to the different geographical locations, variability within sites was greater, linked to the variability of conditions within sites (Salmela *et al.* 2013).

Soil microbiota and soil chemistries can affect the phenological responses of vascular plants (Wagner *et al.* 2014) and so can influence the phenotypic plasticity shown by plants in different conditions. Thus it is possible that the impacts of climate change on the soil environment may influence vascular plant phenology in addition to the direct impacts on the plants themselves, but more work in this area is needed.

As for some other groups, museum collections or herbaria may be useful additional sources of data (e.g. Robbirt et al., 2011) and may be used to put an historical context to modern records. As in other groups, modern day herbarium collecting could be described as modest.

The Wildflower Society has been running a competition to record first spring week and last autumn week of flowering for many decades. They record which species are in flower on a particular date rather than what date a species flowers on; and this is another potential source of information on long-term changes. Likewise, photographs on fixed dates, such as on May Day or Remembrance Day, and the dates on which reserves open to the public for key plant species could also provide information on long-term changes (e.g. Sparks, 2007).

Satellite sensors can detect photosynthetic activity at landscape scales and have been used at a global scale to detect changes in the start and end of growing seasons as measured by the Normalised Difference Vegetation Index (NDVI) in spring and autumn respectively (e.g. Myneni et al., 1997). Within the UK the use of NDVI seems to have been restricted to spatial studies or short-term investigations. A continuing difficulty has been matching NDVI with ground-based observations. Since the latter tend to measure individual plants and the former measure landscapes this may not be easily resolvable.

Meta-analysis

Thackeray et al. (2010) undertook an assessment of terrestrial, freshwater and marine phenology for the UK over a standardised period 1976-2005. The use of the same period meant that comparisons between trophic levels and between environments were not affected by the years included in individual datasets. Approximately 84% of all trends were towards earliness and differences between trophic levels were apparent, with greater advancement at lower trophic levels. Trends towards earlier phenology were apparent in all environments. Moreover data were examined on a decadal basis to indicate that trends towards earliness have strengthened.

Conclusions from IPCC AR5

Since the previous LWEC report card, the IPCC has published it 5th Assessment Report and various conclusions concerning phenology were drawn that are relevant to this review. The chapter on terrestrial and freshwater ecosystems (Settele *et al.* 2014) concluded:

- The phenology of most organisms is sensitive to temperature, confounding effects are often small, and the response is rapid, leading to *high confidence* in detection and attribution of changes in phenology to warming
- There is *high confidence (much evidence, medium agreement)* that climate change-induced phenological shifts will continue to alter the interactions between species in regions with a marked seasonal cycle.
- The consequences for species interactions of differing phenological or movement-based responses to climate change are insufficiently known and may make projections based on individual species models unreliable.

Conclusions

The overall picture taken from the review is that there is an overwhelming body of evidence suggesting an advance in spring phenology associated with rising temperatures in a substantial proportion of species [H]. Other factors may also be important drivers of phenological change, for example nutrients for freshwater plankton or soil characteristics for vascular plants [M]. However, there is a potential for publication bias, with only those time series showing significant advance achieving publication while static series are essentially ignored. One way to deal with this is to focus just on those studies reporting on multiple series (e.g Parmesan & Yohe, 2003 which concluded a global advance in phenology). Another is to analyse all available data, irrespective of change, and to see how common that significant changes have been. Furthermore if this is keyed into a fixed time period it overcomes the problem that trends from different periods may not be comparable, for example because of the inclusion or exclusion of a particular cold or warm year. This was overcome at the European scale by Menzel et al. (2006) and within the UK by Thackeray et al. (2010). In both cases there is overwhelming evidence that the majority of events are advancing with time, but equally that changes are not uniform [H].

There continues to be criticism of differences in recorder effort, and the value of first event dates (Clark et al., 2011). However, such phenological data are remarkably robust [M]. Where comparison of first and population average dates has been possible (e.g. butterflies, birds) a correlation between first and mean/median/peak dates can usually be detected [M] (e.g. Sparks *et al.* 2001; Pearce-Higgins & Green 2014). However, advances in first dates can be greater than in mean dates. This may be explained by a change to the distributional shape of, for example, emergence phenology; with longer tails evident. That most events seem to be advancing while most population sizes are static or in decline confounds critics, since declining populations would likely lead to later dates. Unless merely an artefact of sampling because of changed population size, a change in a first event implies that there is a change in some aspect of the phenological distribution, and evidence of any change is important. Studies in birds and fish (e.g. Perrins 1970; Crick *et al.* 1993); Elliott & Hurley, 1998; Verhulst & Nilsson 2008) show that early breeders are those that are most productive and can therefore contribute more genetically to successive generations [M].

It is evident from this summary that changes in phenology are not uniform [H] (see also Thackeray et al., 2010) and the consequences for synchrony are major concerns for conservationists, agriculturalists and others. Will species be able to switch hosts if necessary (e.g. Nylin et al., 2009; Gange et al., 2011)? Enhanced food supply has been shown experimentally to advance breeding [M] (e.g. Harrison et al., 2010; Rufino *et al*. 2014) and, consequently, population declines attributed to mistiming with food supply [L] (e.g. of migrating birds: Ockendon et al., 2012) or hosts [L] (e.g. Cuckoo: Douglas et al., 2010) appear to be valid hypotheses. Changed pressures from parasitism [L] (Hicks et al., 2007), predation, or symbiotic relationships (e.g. with fungi) may all have important consequences if phenological mismatch worsens. Changes in phenology may also have knock-on effects on population size, distributional range and even CO2 storage [L] (e.g. Morecroft et al., 2003).

Phenology has considerable resonance with the public and widescale changes in phenology are arguably the strongest message in demonstrating that climate change is already having an impact on UK wildlife. Studies are now considering how phenology may influence distributional range [L] (e.g. Buckley et al., 2011; Hulme 2011). Such stiudes will need to control for addiutional factors that affect phenology, for example nutrients are important for some phytoplankton [M] (see above) and, Hinsley et al. (1999) found that birds nested earlier in larger woods [L].

This review has identified a number of potential data sets that are not yet computerised, or that have not been fully evaluated. Furthermore a number of the reported studies are becoming “out-of-date” and it is recommended that the material is updated, reanalysed and re-reported; if only to confirm previous findings after a decade which included some exceptionally warm years.

References and further reading

Alberto, F., Bouffier, L., Louvet, J.-M., Lamy, J.-B., Delzon, S. & Kremer, A. (2011). Adaptive responses for seed and leaf phenology in natural populations of sessile oak along an altitudinal gradient. *Journal of Evolutionary Biology,* 24, 1442-1454.

Allan, E. & Pannell, J.R. (2009). Rapid divergence in physiological and life-history traits between northern and southern populations of the British introduced neo-species, *Senecio squalidus*. *Oikos*, 118, 1053-1061.

Altermatt, F. (2010). Tell me what you eat and I'll tell you when you fly: diet can predict phenological changes in response to climate change. *Ecology Letters,* 13, 1475–1484.

Altwegg, R., Broms, K., Erni, B., Barnard, P., Midgley, G.F. & Underhill, LG. (2012). Novel methods reveal shifts in migration pehnology of barn swallows in South Africa. *Proc. R. Soc. B,* 279, 1485-1490.

Amano, T., Freckleton, R.P., Queenborough, S.A., Doxford, S.W., Smithersm R.J., Sparks, T.H. & Sutherland, W.J. (2014). Links between plant species' spatial and temporal responses to a warming climate. *Proc. R. Soc. B,* 281, 20133017. http://dx.doi.org/10.1098/rspb.2013.3017

Amano, T., Smithers, R.J., Sparks, T.H. & Sutherland, W.J. (2010). A 250-year index of first flowering dates and its response to temperature changes. *Proceedings of the Royal Society B-Biological Sciences*, 277, 2451-2457.

Aprahamian, M.W., Davidson, I.C. & Cove, R.J. (2008). Life history changes in Atlantic salmon from the River Dee, Wales. *Hydrobiologia*, 602, 61-78.

Arnfield, H., Grant, R., Monk, C. & Uller, T. (2012) Factors influencing the timing of spring migration in common toads (*Bufo bufo*). *Journal of Zoology,* 288, 112-118.

Baines, D., Wilson, I.A. & Beeley, G. (1996). Timing of breeding in black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus* and distribution of insect food for the chicks. *Ibis*, 138, 181-187.

Bale, J.S. & Hayward, S.A.L. (2010). Insect overwintering in a changing climate. *Journal of Experimental Biology,* 213, 980-994.

Beebee , T.J.C. (1995). Amphibian breeding and climate. Nature, 374, 219–220.

Bell, J. R., Alderson, L., Izera, D., Kruger, T., Parker, S., Pickup, J., Shortall, C. R., Taylor, M. S., Verrier, P., Harrington, R. (2015). Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. *Journal of Animal Ecology,* 84, 21–34.

Bishop, T.R., Botham, M.S., Fox, R., Leather, S.R., Chapman, D.S. & Oliver, T.H. (2013) The utility of distribution data in predicting phenology. *Methods in Ecology and Evolution,* 4, 1024–1032.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441, 81-83.

Bradshaw, W.E. & Holzapfel, C.M. (2006) Evolutionary response to rapid climate change. *Science,* 312, 1477-1478.

Brakefield, P.M. (1987). Geographical variability in, and temperature effects on, the phenology of *Maniola jurtina* and *Pyronia tithonus* (Lepidoptera, Satyrinae) in England and Wales. *Ecological Entomology*, 12, 139-148.

Briers, R.A., Gee, J.H.R. & Geoghegan, R. (2004). Effects of the North Atlantic Oscillation on growth and phenology of stream insects. *Ecography*, 27, 811-817.

Brooks, S.J., Self, A., Toloni, F. & Sparks, T. (2014) Natural history museum collections provide information on phenological change in British butterflies since the late-nineteenth century. *International Journal of Biometeorology,* 58, 1749-1758.

Browne, S.J. & Aebischer, N.J. (2003). Temporal changes in the migration phenology of turtle doves *Streptopelia turtur* in Britain, based on sightings from coastal bird observatories. *Journal of Avian Biology*, 34, 65-71.

Buckley, L.B., Waaser, S.A., MacLean, H.J. & Fox, R. (2011). Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology*, 92, 2214-2221.

Burthe, S., Butler, A., Searle, K.R., Hall, S.J.G., Thackeray, S.J. & Wanless, S. (2011). Demographic consequences of increased winter births in a large aseasonally breeding mammal (*Bos taurus*) in response to climate change. *Journal of Animal Ecology*, 80, 1134-1144.

Buse, A., Dury, S.J., Woodburn, R.J.W., Perrins, C.M. & Good, J.E.G. (1999). Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology*, 13, 74-82.

Buse, A. & Good, J.E.G. (1996). Synchronization of larval emergence in winter moth (*Operophtera brumata* L) and budburst in pedunculate oak (*Quercus robur* L) under simulated climate change. *Ecological Entomology*, 21, 335-343.

Cannon, R.J.C. (1998). The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology*, 4, 785-796.

Carroll, E.A., Sparks, T.H., Collinson, N. & Beebee, T.J.C. (2009). Influence of temperature on the spatial distribution of first spawning dates of the common frog (*Rana temporaria*) in the UK. *Global Change Biology*, 15, 467-473.

Centritto, M., Lee, H.S.J. & Jarvis, P.G. (1999). Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). I. Plant growth, allocation and ontogeny. *Tree Physiology*, 19, 799-806.

Chadwick, E.A., Slater, F.M. & Ormerod, S.J. (2006). Inter- and intraspecific differences in climatically mediated phenological change in coexisting *Triturus* species. *Global Change Biology*, 12, 1069-1078.

Chamberlain, D.E. & Crick, H.Q.P. (2003). Temporal and spatial associations in aspects of reproductive performance of lapwings *Vanellus vanellus* in the United Kingdom, 1962-99. *Ardea*, 91, 183-196.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. & Sheldon, B.C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science,* 320, 800-803.

Clark, R.M. & Thompson, R. (2011). Sampling bias in the determination of first and last occurrences. *Plant Ecology & Diversity*, 4, 201-211.

Clements, M.N., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Kruuk, L.E.B. (2010). Getting the timing right: antler growth phenology and sexual selection in a wild red deer population. *Oecologia*, 164, 357-368.

Cocu, N., Harrington, R., Rounsevell, M.D.A., Worner, S.P. & Hulle, M. (2005). Geographical location, climate and land use influences on the phenology and numbers of the aphid, *Myzus persicae*, in Europe. *Journal of Biogeography*, 32, 615-632.

Comber, A. & Brunsden, C. (2014). A spatial analysis of plant phenophase changes and the impact of increases in urban land use. *Int. J. Climatol.* DOI: 10.1002/joc.4030.

Conrad, K.F., Warren, M.S., Fox, R. & Woiwod, I.P. (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132, 279-291.

Cotton, P.A. (2003). Avian migration phenology and global climate change. *PNAS*, 100, 12219-12222.

Crick, H.Q.P., Baillie, S.R. & Leech, D.I. (2003). The UK Nest Record Scheme: its value for science and conservation. *Bird Study,* 50, 254-270.

Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L. (1997). UK birds are laying eggs earlier. *Nature*, 388**,** 526.

Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. (1993) Seasonal variation in clutch size in British Birds. *Journal of Animal Ecology,* 62, 263-273.

Crick, H.Q.P. & Sparks, T.H. (1999). Climate change related to egg-laying trends. *Nature*, **399**, 423-424.

Croxton, P.J., Sparks, T.H., Cade, M., Loxton, R.G. (2006). Trends and temperature effects in the arrival of spring migrants in Portland (United Kingdom) 1959-2005. *Acta Ornithologica*, 41, 103-111.

Davis, C.C., Willis, C.G., Primack, R.B. & Miller-Rushing, A.J. (2010). The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 3201-3213.

Deans, J.D. & Harvey, F.J. (1995). Phenologies of 16 European provenances of sessile oak growing in Scotland. *Forestry*, 68, 265-273.

Deeming, D.C. & Du Feu, C.R. (2011). Long-term patterns in egg mortality during incubation and chick mortality during rearing in three species of tits in an English woodland. *Bird Study*, 58, 278-290.

Desrochers, A. & Magrath, R.D. (1993). Age-specific fecundity in European blackbirds (*Turdus merula*) - individual and population trends. *Auk*, 110, 255-263.

Diamond, S.E., Frame, A.M., Martin, R.A. & Buckley, L.B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology*, 92, 1005-1012.

Diegisser, T., Tritsch, C., Seitz, A. & Johannesen, J. (2009). Infestation of a novel host plant by *Tephritis conura* (Diptera: Tephritidae) in northern Britain: host-range expansion or host shift? *Genetica*, 137, 87-97.

Douglas, D.J.T., Newson, S.E., Leech, D.I., Noble, D.G. & Robinson, R.A. (2010). How important are climate-induced changes in host availability for population processes in an obligate brood parasite, the European cuckoo? *Oikos*, 119, 1834-1840.

Elliott, J.A. (2012). Predicting the impact of changing nutrient load and temperature on the phytoplankton of England's largest lake, Windermere. *Freshwater Biology*, 57, 400-413.

Elliott, J.M. (1996). Temperature-related fluctuations in the timing of emergence and pupation of Windermere alder-flies over 30 years. *Ecological Entomology*, 21, 241–247

Elliott, J.M. & Hurley, M.A. (1998). An individual-based model for predicting the emergence period of sea trout fry in a Lake District stream. *Journal of Fish Biology*, 53, 414-433.

Emberlin, J., Detandt, M., Gehrig, R., Jaeger, S., Nolard, N. & Rantio-Lehtimaki, A. (2002). Responses in the start of *Betula* (birch) pollen seasons to recent changes in spring temperatures across Europe. *International Journal of Biometeorology*, 46, 159-170.

Emberlin, J., Laaidi, M., Detandt, M., Gehrig, R., Jaeger, S., Myszkowska, D., Nolard, N., Rantio-Letitimaeki, A. & Stach, A. (2007). Climate change and evolution of the pollen content of the air in seven European countries: The example of birch. *Revue Francaise d'Allergologie et d'Immunologie Clinique*, 47, 57-63.

Emberlin, J., Mullins, J., Corden, J., Jones, S., Millington, W., Brooke, M. & Savage, M. (1999). Regional variations in grass pollen seasons in the UK, long-term trends and forecast models. *Clinical and Experimental Allergy*, 29, 347-356.

Emberlin, J., Smith, M., Close, R. & Adams-Groom, B. (2007). Changes in the pollen seasons of the early flowering trees *Alnus* spp. and *Corylus* spp. in Worcester, United Kingdom, 1996-2005. *International Journal of Biometeorology*, 51, 181-191.

Erenler, H.E. & Gillman, M.P. (2010). Synchronisation of adult activity of the archaic moth, *Micropterix calthella* L. (Lepidoptera, Micropterigidae), with anthesis of sedges (*Carex* spp., Cyperaceae) in an ancient wood. *Arthropod-Plant Interactions*, 4, 117-128.

Estrella, N., Sparks, T.H. & Menzel, A. (2007). Trends and temperature response in the phenology of crops in Germany. *Global Change Biology*, 13, 1737-1747.

Feuchtmayr, H., Thackeray, S.J., Jones, I.D., De Ville, M., Fletcher, J., James, B. & Kelly, J. (2012). Spring phytoplankton phenology - are patterns and drivers of change consistent among lakes in the same climatological region? *Freshwater Biology*, 57, 331-344.

Fielding, C.A., Whittaker, J.B., Butterfield, J.E.L. & Coulson, J.C. (1999). Predicting responses to climate change: the effect of altitude and latitude on the phenology of the Spittlebug *Neophilaenus lineatus*. *Functional Ecology*, 13, 65-73.

Fitter, A.H. & Fitter, R.S.R. (2002). Rapid changes in flowering time in British plants. *Science*, 296, 1689-1691.

Fitter, A.H., Fitter, R.S.R., Harris, I.T.B. & Williamson, M.H. (1995). Relationships between first flowering date and temperature in the flora of a locality in central England. *Functional Ecology*, 9, 55-60.

Fletcher, K., Howarth, D., Kirby, A., Dunn, R. & Smith, A. (2013). Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis,* 155, 456-463.

Forchhammer, M.C., Clutton-Brock, T.H., Lindström, J. & Albon, S.D. (2001). Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology ,*70, 721–729.

Forrest, J.R.K. (2015) Plant – pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? *Oikos,* 124, 4-13.

Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015) Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution,* 30, 169-176.

Gange, A.C., Gange, E.G., Mohammad, A.B. & Boddy, L. (2011). Host shifts in fungi caused by climate change? *Fungal Ecology*, 4, 184-190.

Gange, A.C., Gange, E.G., Sparks, T.H. & Boddy, L. (2007). Rapid and recent changes in fungal fruiting patterns. *Science*, 316, 71.

George, D. G. (2012). The effect of nutrient enrichment and changes in the weather on the abundance of *Daphnia* in Esthwaite Water, Cumbria. *Freshwater Biology*, 57, 360-372.

Gilbert, L., Aungier, J. & Tomkins, J.L. (2014). Climate of origin affects tick (*Ixodes ricinus*) host-seeking behavior in response to temperature: implications for resilience to climate change? *Ecology and Evolution,* 4, 1186–1198.

Gill, J.A., Alves, J.A., Sutherland, W.J., Appleton, G.F., Potts, P.M., Gunnarsson, T.G. (2014). Why is timing of bird migration advancing when individuals are not? *Proc. R. Soc. B,* 281, 20132161. http://dx.doi.org/10.1098/rspb.2013.2161

Goodenough, A.E., Hart, A.G. & Elliot, S.L. (2011). What prevents phenological adjustment to climate change in migrant bird species? Evidence against the "arrival constraint" hypothesis. *International Journal of Biometeorology*, 55, 97-102.

Goodenough, A.E., Hart, A.G. & Stafford, R. (2010). Is adjustment of breeding phenology keeping pace with the need for change? Linking observed response in woodland birds to changes in temperature and selection pressure. *Climatic Change,* 102, 687–697.

Graham-Taylor, L.G., Stubbs, A.E. & Brooke, M. de L. (2009). Changes in phenology of hoverflies in a central England garden. *Insect Conservation and Diversity*, 2, 29-35.

Greenwood, J.G. (2007). Earlier laying by Black Guillemots *Cepphus grylle* in Northern Ireland in response to increasing sea-surface temperature. *Bird Study*, 54, 378-379.

Gullett, P., Hatchwell, B.J., Robinson, R.A. & Evans, K.L. (2013) Phenological indices of avian reproduction: cryptic shifts and prediction across large spatial and temporal scales. *Ecology and Evolution,* 3, 1864–1877.

Handley, R.J. & Davy, A.J. (2005). Temperature effects on seed maturity and dormancy cycles in an aquatic annual, *Najas marina*, at the edge of its range. *Journal of Ecology*, 93, 1185-1193.

Hard, J.J., Gross, M.R., Heino, M., Hilborn, R., Kope, R.G., Law, R. & Reynolds, J.D. (2008). Evolutionary consequences of fishing and their implications for salmon. *Evolutionary Applications*, 1, 388-408.

Harrington, R., Clark, S.J., Welham, S.J., Verrier, P.J., Denholm, C.H., Hullé, M., Maurice, D., Rounsevell, M.D., Cocu, N. & European Union Examine Consortium (2007). Environmental change and the phenology of European aphids. *Global Change Biology*, 13, 1550–1564.

Harrison, T.J.E., Smith, J.A., Martin, G.R., Chamberlain, D.E., Bearhop, S., Robb, G.N. & Reynolds, S.J. (2010). Does food supplementation really enhance productivity of breeding birds? *Oecologia*, 164, 311-320.

Hassall,C., Thompson D.J., French G.C. & Harvey I.F. (2007). Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology*, 13, 933–941.

Hastie, L.C. & Young, M.R. (2003). Timing of spawning and glochidial release in Scottish freshwater pearl mussel (*Margaritifera margaritifera*) populations. *Freshwater Biology*, 48, 2107-2117.

Heilmann-Clausen, J. & Læssøe, T. (2012) On species richness estimates, climate change and host shifts in wood-inhabiting fungi. *Fungal Ecology,* 5, 641-646.

Hepper, F.N. (2003). Phenological records of English garden plants in Leeds (Yorkshire) and Richmond (Surrey) from 1946 to 2002. An analysis relating to global warming. *Biodiversity and Conservation*, 12, 2503-2520.

Hicks, B.J., Aegerter, J.N., Leather, S.R. & Watt, A.D. (2007). Asynchrony in larval development of the pine beauty moth, *Panolis flammea*, on an introduced host plant may affect parasitoid efficacy. *Arthropod-Plant Interactions*, 1, 213-220.

Hinsley, S.A., Rothery, P. & Bellamy, P.E. (1999). Influence of woodland area on breeding success in Great Tits *Parus major* and Blue Tits *Parus caeruleus*. *Journal of Avian Biology*, 30, 271-281.

Hodgson, J.A., Thomas, C.D., Oliver, T.H., Anderson, B.J., Brereton, T.M. & Crone, E.E. (2011). Predicting insect phenology across space and time. *Global Change Biology*, 17, 1289-1300.

Huin, N. & Sparks, T.H. (1998). Arrival and progression of the Swallow *Hirundo rustica* through Britain. *Bird Study*, 45, 361-370.

Hulme, P.E. (2011). Consistent flowering response to global warming by European plants introduced into North America. *Functional Ecology*, 25, 1189-1196.

Hulme, P.E. (2011). Contrasting impacts of climate-driven flowering phenology on changes in alien and native plant species distributions. *New Phytologist*, 189, 272-281.

Huntington, T.G. (2004). Climate change, growing season length, and transpiration: Plant response could alter hydrologic regime. *Plant Biology*, 6, 651-653.

Jenkins, D. & Sparks, T.H. (2010). The changing bird phenology of Mid Deeside, Scotland 1974-2010. *Bird Study*, 57, 407-414.

Jenkins, D. & Watson, A. (2000). Dates of first arrival and song of birds during 1974-99 in mid-Deeside, Scotland. *Bird Study*, 47, 249-251.

Jochner, S. & Menzel, A. (2015). Urban phenological studies – Past, present, future. *Environ. Poll.* http://dx.doi.org/10.1016/j.envpol.2015.01.003

Jones, A.T., Hayes, M.J. & Hamilton, N.R.S. (2001). The effect of provenance on the performance of *Crataegus monogyna* in hedges. *Journal of Applied Ecology*, 38, 952-962.

Kauserud,H., Heegaard, E., Büntgen, U., Halvorsen, R., Egli, S., Senn-Irlet, B., Krisai-Greilhuber, I., Dämon, W., Sparks, T., Nordén, J., Høiland, K., Kirk, P., Semenov, M., Boddy, L. & Stenseth, N.C. (2012). Warming-induced shift in European mushroom fruiting phenology. *Proc. Natl Acad. Sci. USA*, 109, 14488–14493.

Kauserud, H., Heegaard, E., Semenov, M.A., Boddy, L., Halvorsen, R., Stige, L.C., Sparks, T.H., Gange, A.C. & Stenseth, N.C. (2010). Climate change and spring-fruiting fungi. *Proceedings of the Royal Society B-Biological Sciences*, 277, 1169-1177.

Kelly, N. (2010). Accounting for correlated error structure within phenological data: a case study of trend analysis of snowdrop flowering. In Hudson , I.L. & Keatley, M.R. (Eds.) *Phenological Research: Methods for Environmental and Climate Change Analysis*. Springer, Dordecht, pp. 271-298.

Kennedy, R.J. & Crozier, W.W. (2010). Evidence of changing migratory patterns of wild Atlantic salmon *Salmo salar* smolts in the River Bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology*, 76, 1786-1805.

Kerlin, D.H., Thirgood, S.J., Miller, D.R., Aebischer, N.J., Smith, A.A. & Haydon, D.T. (2011). State-dependent dynamics of cycles in red grouse abundance. *Ecography*, 34, 39-48.

Kerslake, J.E. & Hartley, S.E. (1997). Phenology of winter moth feeding on common heather: Effects of source population and experimental manipulation of hatch dates. *Journal of Animal Ecology*, 66, 375-385.

Kirbyshire, A.L. & Bigg, G.R. (2010). Is the onset of the English summer advancing? *Climatic Change*, 100, 419-431.

Klapwijk, M.J., Groebler, B.C., Ward, K., Wheeler, D. & Lewis, O.T. (2010). Influence of experimental warming and shading on host-parasitoid synchrony. *Global Change Biology*, 16, 102-112.

Lawn, M.R. (1998). Arrival patterns of male Willow Warblers *Phylloscopus trochilus* in relation to age, territory density and pairing success. *Ringing and Migration*, 19, 31-38.

Lawrence, A.J. & Soame, J.M. (2004). The effects of climate change on the reproduction of coastal invertebrates. *Ibis*, 146, 29-39.

Lehikoinen, E. & Sparks, T.H. (2010). Changes in migration. pp. 89-112 in: Moller, A.P. Fiedler, W. & Berthold, P. (Eds). *Effects of climate change on birds*. Oxford University Press, Oxford.

Luedeling, E. & Gassner, A. (2012). Partial Least Squares Regression for analyzing walnut phenology in California. *Agricultural and Forest Meteorology*, 158, 43-52.

Mason, C.F. (1995). Long-term trends in the arrival dates of spring migrants. Bird *Study*, 42, 182-189.

Mazer, S.J., Travers, S.E., Cook, B.I., Davies, T.J., Bolmgren, K., Kraft, N.J.B., Salamin, N. & Inouye, D.W. (2013). Flowering date of taxonomic families predicts phenological sensitivity to temperature: implications for forecasting the effects of climate change on unstudied taxa. *American Journal of Botany,* 100, 1381-1397.

McCleery, R.H. & Perrins, C.M. (1998). Temperature and egg-laying trends. *Nature*, 391, 30–31.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, 10, 710-717.

Menzel, A., Sparks, T.H., Estrella, N. & Roy, D.B. (2006). Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography*, 15, 498-504.

Met Office (2015) 2014 confirmed as UK's warmest year on record. http://www.metoffice.gov.uk/news/releases/archive/2015/Record-UK-temps-2014 (Accessed 01/03/2015).

Miles, J.E., Bale, J.S. & Hodkinson, I.D. (1997). Effects of temperature elevation on the population dynamics of the upland heather psyllid *Strophingia ericae* (Curtis) (Homoptera: Psylloidea). *Global Change Biology*, 3, 291-297.

Moller, A.P., Rubolini, D. & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Natl Acad. Sci. USA,* 105, 16195 – 16200.

Morecroft, M.D., Stokes, V.J. & Morison, J.I.L. (2003). Seasonal changes in the photosynthetic capacity of canopy oak (*Quercus robur*) leaves: the impact of slow development on annual carbon uptake. *International Journal of Biometeorology*, 47, 221-226.

Morgan, D. & Solomon, M.G. (1993). PEST-MAN: A forecasting system for apple and pear pests. *Bulletin Oepp (Organisation Europeenne et Mediterraneenne pour la Protection des Plantes)*, 23, 601-605.

Moser, B., Fridley, J.D., Askew, A.P. & Grime, J.P. (2011). Simulated migration in a long-term climate change experiment: invasions impeded by dispersal limitation, not biotic resistance. *Journal of Ecology*, 99, 1229-1236.

Moyes, K., Nussey, D.H., Clements, M.N., Guinness, F.E., Morris, A., Morris, S., Pemberton, J.M., Kruuk, L.E.B. & Clutton-Brock, T.H. (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology*, 17, 2455-2469.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, 386, 698-702.

Nunn, A.D., Frear, P.A., Lee, M. & Cowx, I.G. (2010). Is there evidence for a shift in fish growth and recruitment success linked to climate change? *Journal of Fish Biology*, 77, 1780-1792.

Nussey, D.H., Clutton-Brock, T.H., Elston, D.A., Albon, S.D. & Kruuk, L.E.B. (2005). Phenotypic plasticity in a maternal trait in red deer. *Journal of Animal Ecology,* 74, 387-396.

Nussey, D.H., Wilson, A.J. & Brommer, J.E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol*., 20, 831–844.

Nylin, S., Nygren, G.H., Soderlind, L. & Stefanescu, C. (2009). Geographical variation in host plant utilization in the comma butterfly: the roles of time constraints and plant phenology. *Evolutionary Ecology*, 23, 807-825.

Ockendon, N., Hewson, C.M., Johnston, A. & Atkinson, P.W. (2012). Declines in British-breeding populations of Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone in Africa, possibly via constraints on arrival time advancement. *Bird Study*, 59, 111-125.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.

Peach, W.J., Siriwardena, G.M. & Gregory, R.D. (1999). Long-term changes in over-winter survival rates explain the decline of reed buntings *Emberiza schoeniclus* in Britain. *Journal of Applied Ecology*, 36, 798-811.

Pearce-Higgins, J.W. & Green, R.E. (2014) *Birds and Climate Change.* Cambridge University Press, Cambridge.

Pearce-Higgins, J.W. & Yalden, D.W. (2003). Variation in the use of pasture by breeding European Golden Plovers *Pluvialis apricaria* in relation to prey availability. *Ibis*, 145, 365-381.

Perrins, C.M. (1970) The timing of birds' breeding seasons. *Ibis*, 112, 242–255

Phelps, A. (2008). Changes in the phenology of the Adder, *Vipera berus*, over four decades: a comparison with Prestt (1971). *Herpetological Bulletin*, 103, 32-36.

Phillimore, A.B., Hadfield, J.D., Jones, O.R. & Smithers, R.J. (2010). Differences in spawning date between local populations of common frog reveal local adaptation. *Proc. Natl Acad. Sci. USA,* 107, 8282-8297.

Plard F, Gaillard J-M, Coulson T, Hewison AJM, Delorme D, et al. (2014) Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe Deer. *PLoS Biol,* 12(4), e1001828. doi:10.1371/journal.pbio.1001828

Power, S.A., Green, E.R., Barker, C.G., Bell, J.N.B. & Ashmore, M.R. (2006). Ecosystem recovery: heathland response to a reduction in nitrogen deposition. *Global Change Biology*, 12, 1241-1252.

Pozsgai, G. & Littlewood, N.A. (2011). Changes in the phenology of the ground beetle *Pterostichus madidus*. *Insect Science*, 18, 462-472.

Pozsgai, G. & Littlewood, N.A. (2014) Ground beetle (Coleoptera: Carabidae) population declines and phenological changes: Is there a connection? *Ecological Indicators*, 41, 15-24.

Prieto, P., Penuelas, J., Niinemets, U., Ogaya, R., Schmidt, I.K., Beier, C., Tietema, A., Sowerby, A., Emmett, B.A., Lang, E.K., Kroel-Dulay, G., Lhotsky, B., Cesaraccio, C., Pellizzaro, G., de Dato, G., Sirca, C. & Estiarte, M. (2009). Changes in the onset of spring growth in shrubland species in response to experimental warming along a north-south gradient in Europe. *Global Ecology and Biogeography*, 18, 473-484.

Przybylo, R., Sheldon, B.C. & Merila, J. (2000). Climatic effects in breeding and morphology: evidence for phenotypic plasticity. *J. Anim. Ecol.*, 69, 395–403.

Ransome, R.D. & Mcowat, T.P. (1994). Birth timing and population-changes in greater horseshoe bat colonies (*Rhinolophus ferrumequinum*) are synchronized by climatic temperature. *Zoological Journal of the Linnean Society*, 112, 337-351.

Reading, C.J. (1998). The effect of winter temperatures on the timing of breeding activity in the common toad *Bufo bufo*. *Oecologia*, 117, 469-475.

Reading, C.J. (2003). The effects of variation in climatic temperature (1980-2001) on breeding activity and tadpole stage duration in the common toad, *Bufo bufo*. *Science of the Total Environment*, 310, 231-236.

Reale, D., McAdam, A.G., Boutin, S. & Berteaux, D. (2003). Genetic and plastic responses of a northern mammal to climate change. *Proc. R. Soc. Lond. B,* 270, 591–596.

Robbirt, K. M., Davy, A.J., Hutchings, M.J. & Roberts, D.L. (2011). Validation of biological collections as a source of phenological data for use in climate change studies: a case study with the orchid *Ophrys sphegodes*. *Journal of Ecology*, 99, 235-241.

Roy, D.B. & Sparks, T.H. (2000). Phenology of British butterflies and climate change. *Global Change Biology*, 6, 407-416.

Ruffino, L., Salo, P., Koivisto, E., Banks, P.B. & Korpimäki, E. (2014) Reproductive responses of birds to experimental food supplementation: a meta-analysis. *Frontiers in Zoology,* 11, 80. doi:10.1186/s12983-014-0080-y.

Rutishauser, T., Schleip, C., Sparks, T.H., Nordli, O., Menzel, A., Wanner, H., Jeanneret, F., Luterbacher, J. (2009). Temperature sensitivity of Swiss and British plant phenology from 1753 to 1958. *Climate Research*, 39, 179-190.

Saether, B.-E., Grotan, V., Engen, S., Noble, D.G. & Freckleton, R.P. (2011). Rarity, life history and scaling of the dynamics in time and space of British birds. *Journal of Animal Ecology*, 80, 215-224.

Salama, N.K.G., Knowler, J.T. & Adams, C.E. (2007). Increasing abundance and diversity in the moth assemblage of east Loch Lomondside, Scotland over a 35 year period. *Journal of Insect Conservation*, 11, 151-156.

Saldana, S., Lima, M. & Estay, S. (2007). Northern Atlantic Oscillation effects on the temporal and spatial dynamics of green spruce aphid populations in the UK. *Journal of Animal Ecology*, 76, 782-789.

Salido, L., Purse, B. V., Marrs, R., Chamberlain, D. E. & Shultz, S. (2012). Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. *Ecography,* 35, 604–613.

Salmela, M.J., Cavers, S., Cottrell, J.E., Iason, G.R. & Ennos, R.A. (2011). Seasonal patterns of photochemical capacity and spring phenology reveal genetic differentiation among native Scots pine (*Pinus sylvestris* L.) populations in Scotland. *Forest Ecology and Management*, 262, 1020-1029.

Salmela, M.J., Cavers, S., Cottrell, J.E., Iason, G.R. & Ennos, R.A. (2013). Spring phenology shows genetic variation among and within populations in seedlings of Scots pine (*Pinus sylvestris* L.) in the Scottish Highlands. *Plant Ecology & Diversity,* 6, 523-536.

Scharlemann, J.P. (2001). Museum egg collections as stores of long-term phenological data. *International Journal of Biometeorology*, 45, 208-211.

Scott, W.A., Pithart, D. & Adamson, J.K. (2008). Long-term United Kingdom trends in the breeding phenology of the Common Frog, *Rana temporaria*. *Journal of Herpetology*, 42, 89-96.

Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T. & Taboada, M.A. (2014) Terrestrial and inland water systems. pp. 271-359 in: Ed. by Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R. & White, L.L. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Serra, L., Clark, N.A. & Clark, J.A. (2006). Primary moult, body mass and migration of Grey Plovers *Pluvialis squatarola* in Britain. *Ibis*, 148, 292-301.

Shortall, C.R. & Timmis, G.L.S. (2011). Long-term changes in the abundance and phenology of *Hoplia philanthus* (Fuessly) Col: Scarabaeidae at Silwood Park. *Entomologist's Record and Journal of Variation*, 123, 195-198.

Smith, K.W. (2006). The implications of nest site competition from starlings *Sturnus vulgaris* and the effect of spring temperatures on the timing and breeding performance of great spotted woodpeckers *Dendrocopos major* in southern England. *Annales Zoologici Fennici*, 43, 177-185.

Smith, R.S. & Jones, L. (1991). The phenology of mesotrophic grassland in the Pennine dales, northern England - historic hay cutting dates, vegetation variation and plant-species phenologies. *Journal of Applied Ecology*, 28, 42-59.

Sparks, T.H. (2007). Lateral thinking on data to identify climate impacts. *Trends in Ecology and Evolution*, 22, 169-171.

Sparks, T.H., Bairlein, F., Bojarinova, J.G., Hüppop, O., Lehikoinen, E.A., Rainio, K., Sokolov, L.V., Walker, D. (2005). Examining the total arrival distribution of migratory birds. *Global Change Biology*, 11, 22-30.

Sparks, T.H., Carey, P.D.. (1995). The responses of species to climate over two centuries - an analysis of the Marsham phenological record, 1736-1947. *Journal of Ecology*, 83, 321-329.

Sparks, T.H., Carey, P.D. & Combes, J. (1997). First leafing dates of trees in Surrey between 1947 and 1996. *London Naturalist*, 76, 15-20.

Sparks, T. & Collinson, N. (2008). The history and current status of phenological recording in the UK. pp. 170-173 in: Nekovar, J., Koch, E., Kubin, E., Nejedlik, P., Sparks, T., Wielgolaski, F.-E. (Eds). *The history and current status of plant phenology in Europe. COST Action 725.* COST, Brussels.

Sparks, T. & Crick, H. (1999). Opinion - The times they are a-changing? *Bird Conservation International*, 9, 1-7.

Sparks, T.H., Croxton, P.J., Collinson, N. & Taylor, P.W. (2005). Examples of phenological change, past and present, in UK farming. *Annals of Applied Biology*, 146, 531-537.

Sparks, T.H., Huber, K., Bland, R.L., Crick, H.Q.P., Croxton, P.J., Flood, J., Loxton, R.G., Mason, C.F., Newnham, J.A. & Tryjanowski, P. (2007). How consistent are trends in arrival (and departure) dates of migrant birds in the UK? *Journal of Ornithology*, 148, 503-511.

Sparks, T.H., Huber, K. & Tryjanowski, P. (2008). Something for the weekend? Examining the bias in avian phenological recording. *International Journal of Biometeorology*, 52, 505-510.

Sparks, T.H., Jaroszewicz, B., Krawczyk, M. & Tryjanowski, P. (2009). Advancing phenology in Europe's last lowland primeval forest: non-linear temperature response. *Climate Research*, 39, 221-226.

Sparks, T.H., Jeffree, E.P. & Jeffree, C.E. (2000). An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology*, 44, 82-87.

Sparks, T.H. & Mason, C.F. (2004). Can we detect change in the phenology of winter migrant birds in the UK? *Ibis*, 146, 57-60.

Sparks, T.H. & Menzel, A. (2002). Observed changes in seasons: an overview. *International Journal of Climatology*, 22, 1715-1725.

Sparks, T.H., Roberts, D.R. & Crick, H.Q.P. (2001). What is the value of first arrival dates of spring migrants in phenology? *Avian Ecology & Behaviour*, 7. 75-86.

Sparks, T. & Tryjanowski, P. (2007). Patterns of spring arrival dates differ in two hirundines. *Climate Research*, 35, 159-164.

Sparks, T & Tryjanowski, P. (2010). Regression and causality. In Hudson , I.L. & Keatley, M.R. (Eds.) *Phenological research. Methods for environmental and climate change analysis*. Springer, Dordecht, pp. 123-145.

Sparks, T., Tryjanowski, P., Cooke, A., Crick, H. & Kuzniak, S. (2007). Vertebrate phenology at similar latitudes: temperature responses differ between Poland and the United Kingdom. *Climate Research*, 34, 93-98.

Sparks, T.H. & Yates, T.J. (1997). The effect of spring temperature on the appearance dates of British butterflies 1883-1993. *Ecography*, 20, 368-374.

Stelzer, R.J., Chittka, L., Carlton, M. & Ings, T.C. (2010). Winter active bumblebees (*Bombus terrestris*) achieve high foraging rates in urban Britain. *PLoS One*, 5, e9559.

Stinchcombe, J.R. & Schmitt, J. (2006). Ecosystem engineers as selective agents: the effects of leaf litter on emergence time and early growth in *Impatiens capensis*. *Ecology Letters*, 9, 258-70.

Stopher, K.V., Bento, A.I., Clutton-Brock, T.H., Pemberton, J.M. & Kruuk, L.E.B. (2014). Multiple pathways mediate the effects of climate change on maternal reproductive traits in a red deer population. *Ecology,* 95, 3124-3138.

Strati, S., Patino, S., Slidders, C., Cundall, E.P. & Mencuccini, M. (2003). Development and recovery from winter embolism in silver birch: seasonal patterns and relationships with the phenological cycle in oceanic Scotland. *Tree Physiology*, 23, 663-673.

Summers, D.W. (1995). Long-term changes in the sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish rivers. *Fisheries Management and Ecology*, 2, 147-156.

Summers, R.W., Underhill, L.G., Howells, R.J., Vickery, J.A. & Prys Jones, R.P. (1996). Phenology of migration and use of wintering sites by the increasing population of dark-bellied brent geese *Branta bernicla bernicla*. *Journal of Zoology*, 239, 197-208.

Sunley, R.J., Atkinson, C.J. & Jones, H.G. (2006). Chill unit models and recent changes in the occurrence of Winter chill and Spring frost in the United Kingdom. *Journal of Horticultural Science & Biotechnology*, 81, 949-958.

Thackeray, S.J., Henrys, P.A., Jones, I.D. & Feuchtmayr, H. (2012). Eight decades of phenological change for a freshwater cladoceran: what are the consequences of our definition of seasonal timing? *Freshwater Biology*, 57, 345-359.

Thackeray, S.J., Jones, I.D. & Maberly, S.C. (2008). Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. *Journal of Ecology*, 96, 523-535.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M. S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W. A., Smith, M., Smithers, R.J., Winfield, I.J. & Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16, 3304-3313.

Thompson, R. & Clark, R.M. (2008). Is spring starting earlier? Holocene, 18, 95-104.

Tikkanen, O.P., Woodcock, B., Watt, A. & Lock, K. (2006). Are polyphagous geometrid moths with flightless females adapted to budburst phenology of local host species? *Oikos*, 112, 83-90.

Todd, C.D., Friedland, K.D., MacLean, J.C., Whyte, B.D., Russell, I.C., Lonergan, M.E. & Morrissey, M.B. (2012). Phenological and phenotypic changes in Atlantic salmon populations in response to a changing climate. *Ices Journal of Marine Science,* 69, 1686-1698.

Tryjanowski, P., Panek, M. & Sparks, T. (2006). Phenological response of plants to temperature varies at the same latitude: case study of dog violet and horse chestnut in England and Poland. *Climate Research*, 32, 89-93.

Van Asch, M., Salis, L., Holleman, L.J.M., van Lith, B. & Visser, M.E. (2012) Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change,* 3, 244-248.

Van Dyck, H., Bonte, D., Puls, R., Gotthard, K. & Maes, D. (2015). The lost generation hypothesis: could climate change drive ectotherms into a developmental trap? *Oikos,* 124, 54–61.

Verhulst, S. & Nilsson, J.-A. (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Phil. Trans. R. Soc. B,* 363, 399–410.

Visser, M.E., Adriaensen, F., van Balen, J.H., Blondel, J., Dhondt, A.A., van Dongen, S., du Feu, C., Ivankina, E.V., Kerimov, A.B., de Laet, J., Matthysen, E., McCleery, R., Orell, M. & Thomson, D.L. (2003). Variable responses to large-scale climate change in European *Parus* populations. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 367-372.

Wagner, M.R., Lundberg, D.S., Coleman-Derr, D., Tringe, S.G., Dangl, J.L., & Mitchell-Olds, T. (2014). Natural soil microbes alter flowering phenology and the intensity of selection on flowering time in a wild Arabidopsis relative. *Ecology Letters,* 17, 717–726.

Westgarth-Smith, A.R., Roy, D.B., Scholze, M., Tucker, A. & Sumpter, J.P. (2012). The role of the North Atlantic Oscillation in controlling UK butterfly population size and phenology. *Ecological Entomology*, 37, 221-232.

Wilkinson, N.I. & Wilson, J.D. (2010). Breeding ecology of Twite *Carduelis flavirostris* in a crofting landscape. *Bird Study*, 57, 142-155.

Williams, T.A. & Abberton, M.T. (2004). Earlier flowering between 1962-2002 in agricultural varieties of white clover. *Oecologia*, 138, 122-126.

Winfield, I.J,. Fletcher, J.M., Hewitt, D.P. & James, J.B. (2004). Long-term trends in the timing of the spawning season of Eurasian perch (*Perca fluviatilis*) in the north basin of Windermere, U.K.. In: Barry, T.P. & Malison, J.A. (Eds.) *Proceedings of PERCIS III, the Third International Percid Fish Symposium.* pp. 95-96

Woiwod, I.P. (1997). Detecting the effects of climate change on Lepidoptera. *Journal of Insect Conservation*, 1, 149-158

Woiwod, I. P., & Gould, P. J. L. (2008). Long-term moth studies at Rothamsted. *The moths of Hertfordshire*, 31-44.

Worner, S.P., Tatchell, G.M. & Woiwod, I.P. (1995). Predicting spring migration of the damson-hop aphid *Phorodon humuli* (Homoptera, Aphididae) from historical records of host-plant flowering phenology and weather. *Journal of Applied Ecology*, 32, 17-28.

Zhou, X.L., Harrington, R., Woiwod, I.P., Perry, J.N., Bale, J.S. & Clark, S.J. (1995). Effects of temperature on aphid phenology. *Global Change Biology*, 1, 303-313.