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Validation of biological collections as a source of phenological data for use in climate change studies: a case study with the orchid *Ophrys sphegodes*

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Summary

1. The scarcity of reliable long-term phenological data has severely hindered the study of the responses of species to climate change. Biological collections in herbaria and museums are potential sources of long-term data for such study, but their use for this purpose needs independent validation. Here we report a rigorous test of the validity of using herbarium specimens for phenological studies, by comparing relationships between climate and time of peak flowering derived from herbarium records and from direct field-based observations, for the terrestrial orchid *Ophrys sphegodes*.

2. We examined herbarium specimens of *O. sphegodes* collected between 1848 and 1958, and recorded peak flowering time directly in one population of *O. sphegodes* between 1975 and 2006. The response of flowering time to variation in mean spring temperature (March–May) was virtually identical in both sets of data, even though they covered different periods of time which differ in extent of anthropogenic temperature change. In both cases flowering was advanced by *c.* 6 days per °C rise in average spring temperature.

3. The proportion of variation in flowering time explained by spring temperature was lower in the herbarium record than in direct field observations. It is likely that some of the additional variation was due to geographical variation in collection site, as flowering was significantly earlier at more westerly sites, which have had warmer springs, over their range of 3.44° of longitude.

4. Predictions of peak flowering time based on the herbarium data corresponded closely with observed peak flowering times in the field, indicating that flowering response to temperature had not altered between the two separate periods over which the herbarium and field data were collected.

5. *Synthesis*. These results provide the first direct validation of the use of herbarium collections to examine the relationships between phenology and climate when field-based observational data are not available.

Key-words: biological collections, climate change, flowering time, herbarium specimens, natural history collections, *Ophrys sphegodes,* Orchidaceae, phenology, spring, temperature

Introduction

Phenological events respond directly to climate. Recent climate change has undoubtedly affected the timing of development and seasonal events in many groups of organisms, including amphibians (Beebee 1995), birds (Crick *et al.* 1997), fungi (Kauserud *et al.* 2008) and plants (Sparks & Carey 1995; Fitter & Fitter 2002). Understanding the effects of recent climate change is a vital step towards predicting the consequences of future change. Moreover, only by elucidating the responses of individual species will we be able to predict the potentially disruptive effects of accelerating climate change on species interactions.

Detecting phenological trends in relation to long-term climate change is not straightforward. Because trends can be concealed by short-term inter-annual climate variation

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(Badeck *et al.* 2004), long datasets are needed. For most species, data collected specifically for the study of climate-induced phenological change are not available, or are difficult to find, reflecting the scarcity of long-term monitoring schemes (Sparks & Carey 1995). The choice of species for long-term studies of phenology has thus been dictated up to now by the availability of suitable field records. A further major obstacle is that most long-term data only record the beginning of phenological events in populations, such as dates of first flowering. Miller-Rushing, Inouye & Primack (2008) have shown that the use of such data to infer changes in phenology can be unreliable, and they advise that dates on which phenological stages reach their peak are preferable. However, long-term field-based records of the dates on which phenological events are at their peak are extremely rare.

Specimen-based records in biological collections are another potential source of data, verifiable in both space and time, for the study of climate-induced phenological change. Until recently, the potential of such records has been largely overlooked (Suarez & Tsutsui 2004), even though the only data available for studying phenological trends in many species are those held in natural history collections in museums or herbaria. Recent phenological studies have utilised less orthodox data sources, including historical archives (Aono & Kazui 2008), photographs (Miller-Rushing *et al.* 2006; Sparks, Huber & Croxton 2006; Crimmins & Crimmins 2008) and herbarium specimens (Primack *et al.* 2004; Bolmgren & Lönnberg 2005; Lavoie & Lachance 2006; Miller-Rushing *et al.* 2006; Bowers 2007; Kauserud *et al.* 2008; Gallagher, Hughes & Leishman 2009). Herbarium records are unique amongst these sources of information in that they capture an individual plant's phenological state at the time and location of collection, and therefore may represent a substitute for field observation. Herbarium specimens are also likely to have been collected when phenological stages such as flowering are near their peak, rather than at an early or late stage in such seasonal events. Recent studies suggest that herbarium collections may provide data that can be exploited in climate change studies, because findings have been broadly in line with trends reported in the phenological literature (Sparks 2007) and have supported the predictions of physiological models of phenological events such as flowering (Bowers 2007). Nevertheless, they depend on averaging-out the numerous possible influences and biases involved in a collection process that was not designed with the study of phenology in mind, within which the climatic signal-to-noise ratio might be low. Given the absence of long-term monitoring for most species, there is little direct evidence from which to evaluate the potential of averaged trends in events such as flowering time, derived from herbarium collections, as proxies for field data.

We report a critical comparison of independent field- and herbarium-derived data as predictors of flowering time in a species (the terrestrial orchid *Ophrys sphegodes*) for which a unique long-term phenological record of peak flowering time was available (Hutchings 2010). As the flowering time of plants that flower in early summer is generally advanced after warmer springs, we examined relationships between the flowering date of *O. sphegodes* and climate in the 9 months prior to flowering. This corresponds with the period from the end of tuber dormancy to flowering in this species. Specific hypotheses were (i) that flowering date would be advanced by warmer springs, (ii) that the relationship between flowering date and mean spring temperature would be the same in data derived from herbarium records and annual field observations, and therefore (iii) that in a particular species for which this test is possible, herbarium records would be validated both as an effective proxy for long-term monitoring in climate change research and as a predictor of phenological responses to future climate change.

Materials and methods

STUDY SPECIES

Ophrys sphegodes (the early spider orchid) is a species of southern and central Europe, with a northern range limit that includes southern England. It is associated with ancient, species-rich grassland over calcareous soils. At present the species is rare in the UK, where it is largely confined to Dorset, West and East Sussex and Kent (Lang 1989; Harrap & Harrap 2005).

Although the length of the mycotrophic, subterranean phase of the life cycle of *O. sphegodes* is unclear, it is a short-lived species after its first appearance above ground, rarely flowering for more than three consecutive years. Few plants survive for more than 10 years after initial emergence (Hutchings 1987, 2010) and most survive for less than 3 years. In the UK, the leaves of *O. sphegodes* emerge above ground in September or October (Hutchings 1989). The flowering period is relatively short, commencing during late April or early May, and usually ending by late May (Lang 1989). In most populations in the UK inflorescences bear from one to six flowers (usually two or three), which open in succession from the bottom of the inflorescence. Pollination is followed by rapid withering of the flower. Sanger & Waite (1998) found that the number of inflorescences bearing ripening seed peaked at the end of June and that rapid dieback of the plant ensued; few plants remain above ground at the end of July. This relatively short reproductive period would be expected to conserve any climatically-induced phenological signal.

HERBARIUM DATA

We examined all 192 specimens of *O. sphegodes* held in herbaria at the Natural History Museum, London (BM, 133 specimens) and Royal Botanic Gardens, Kew (K, 59 specimens) to verify identification. All of the specimens originated from southern coastal counties of England (Dorset, Isle of Wight, Hampshire, East and West Sussex, and Kent), reflecting the limited historical distribution of *O. sphegodes* (Carey & Dines 2002). The geographical range of the sites from which specimens were collected was 3.44° (decimal) longitude and 0.76° (decimal) latitude. Specimens with incomplete data for site of collection and collection date were discarded. Because of the rarity of *O. sphegodes* in the UK, the dataset was comparatively small and therefore it was important to ensure that the records represented the peak flowering stage as closely as possible. For this reason only specimens with at least 60% of their flowers open were included in the study; normally most of the flowers are open at the same time in *O. sphegodes*. Some of the herbarium sheets consisted of multiple specimens mounted together. As the specimens in such cases had been collected by a single collector, on the same day and at the same location, they were treated as non-independent and the mean percentage of open flowers was derived. Individuals in fruit or with senescent flowers were excluded.

We rejected 53% of the 192 specimens: 2 were damaged, 9 had unclear or illegible records of collection date, 31 were not dated, 60 were imprecisely dated (only the month or year), 3 were in seed, and 1 presented fewer than 60% of flowers open. Nine specimens were duplicates (multiple specimens) and therefore mean results were used. The final data set comprised 77 specimens providing at least one data point for each of 57 years, spanning a 111-year period from 1848 to 1958.

FIELD DATA

Records of the peak flowering time of *O. sphegodes* were made in 25 of the 32 years between 1975 and 2006 in a demographic study of a population consisting of many thousands of plants at Castle Hill National Nature Reserve, East Sussex, UK (Hutchings 2010). Peak flowering was based on assessment of the entire population to give a central tendency that would fit the flowering phenology of as many individual plants as closely as possible.

METEOROLOGICAL DATA

Mean monthly Central England Temperature (CET) records for the period 1848–2006 (Parker, Legg & Folland 1992) were obtained from the UK Meteorological Office (http://hadobs.metoffice.com/hadcet/cetml1659on.dat). This is the only complete climate record available for the years during which the herbarium records and field data were collected. However, data for Central England are strictly representative only for a roughly triangular area enclosed by Bristol, Preston and London (Parker, Legg & Folland 1992). This is to the north of the distribution range of *O. sphegodes*. Monthly mean temperatures were available from two Meteorological Office weather stations on the south coast, in locations corresponding with eastern and western centres of the distribution of *O. sphegodes*. Eastbourne, East Sussex UK, 21 km east of the Castle Hill field site, operated for the period during which the field records were collected. Monthly minimum and maximum temperature data were available for Southampton, to the west, for all but 5 of the 111 years of the collection period covered by the herbarium specimens. Data from both of these collection sites would be expected to represent the climate within the distribution range of *O. sphegodes* better than the climate records available from CET. The means of monthly minimum and maximum temperature were used for both stations. Historical temperature data were not available closer to any of the sites of collection of the individual specimens in the herbarium records.

ANALYSIS

The distribution of collection dates in the herbarium dataset for 1848–1958, expressed as number of days after 1 April, was checked for normality and presence of outliers. The peak flowering date for the Castle Hill population in the years 1975–2006 was similarly expressed as days after 1 April.

Both sets of flowering phenology data were examined for relationships with mean CET temperature data from the 9 months prior to the flowering season (i.e. the period of growth following breaking of tuber dormancy the previous summer). These data included mean monthly temperature and its averages over successive 3-month periods (September–November, December–February, and March–May). This was carried out to establish which temperature variables had the highest predictive power for flowering time in both sets of phenological data. Multiple regressions using mean temperatures for the individual months failed to produce a single model that could be applied to both of the datasets, because of collinearity between the variables, and the fact that the models included different individual months for the two data sets. However, the mean temperature for the 3 months from March to May had the highest individual correlation with peak flowering date in both sets of data in an analysis of single variables (Table 1). This was designated 'mean spring temperature' and was adopted as the single predictor variable in comparisons of the phenological responses in herbarium and field data. Models using mean spring temperature accounted for only marginally less variation than the best combinations of months in separate stepwise (forward) multiple regressions. In order to investigate whether distance from the weather station influenced the relationship, the phenological analysis was repeated using Eastbourne mean spring temperature data for the field phenological regressions and equivalent Southampton data for the herbarium phenological regressions.

Table 1. Comparison of correlations between flowering date and temperature for the herbarium records and the field data. Correlations are shown with mean temperatures for 3-monthly periods and individual months in the same year as flowering (January–May) or in the year previous to flowering (September–December). A negative correlation indicates that a higher mean temperature is associated with an earlier flowering date

Period of mean temperature	Herbarium data (1848–1958) $n = 77$	Field data (1975–2006) $n = 25$
Seasons:		
September–November	−0.004	−0.072
December–February	−0.065	−0.610**
March–May	−0.426**	−0.801**
Months:		
September	0.008	−0.273
October	0.108	0.226
November	−0.106	−0.171
December	0.047	−0.085
January	−0.003	−0.579**
February	−0.159	−0.549**
March	−0.396**	−0.609**
April	−0.153	−0.405*
May	−0.259*	−0.592**

**$P < 0.01$; *$P < 0.05$.

Variation in flowering time among the herbarium specimens was further investigated using a regression on (decimalised) longitude of origin. This sought to identify geographical sources of variation.

The linear regression model derived from the herbarium data and CET was used to predict peak flowering dates from mean spring temperature for the years between 1975 and 2006 for which field observations were available. Regression analyses were carried out with SPSS 16 (SPSS Inc., Chicago, IL, USA). Slopes and intercepts of regressions were compared using Graphpad Prism 5 (Graphpad software Inc., La Jolla, CA, USA). Predicted flowering dates were compared with observed flowering dates using principal axis regression (Sokal & Rohlf 1969).

Results

Data derived from herbarium specimens over the 111-year period from 1848 until 1958, and recorded in the field between

1975 and 2006, both confirmed the importance of spring temperature in determining flowering time. We found significant individual correlations between peak flowering date and several measures of mean temperature in the CET records in the preceding months (Table 1). For herbarium material, there were significant correlations with mean temperature in March and May of the year of flowering but the highest correlation was with mean temperature over the 3 month period from March–May. Results for the field data were similar, but with significant correlations for January, February, March, April and May. The strongest correlation was again with the mean for the period March–May.

As predicted, warmer years were associated with earlier flowering. The regression of flowering date obtained from the herbarium specimens on mean March–May (spring) temperature (Fig. 1a) accounted for 18% of the variation in flowering time. A 1 °C increase in mean temperature between March and May was associated with an advance in flowering of 6.5 days. Analysis of the field data yielded strikingly similar results. Linear regression of flowering date on mean spring temperature accounted for 64% of the variation in date of flowering (Fig. 1b) and a 1 °C increase in mean spring temperature was associated with an advance in flowering of 6.7 days. The regression models derived from the herbarium data and field data were statistically indistinguishable: neither the gradients ($F_{1,98}$ = 0.0035, P = 0.952) nor the intercepts ($F_{1,99}$ = 0.0908, P = 0.764) were significantly different, indicating that the phenological response to temperature was the same during the different periods over which the two sets of data were collected.

Applying the same analysis with less geographically distant temperature data for the field and herbarium records gave significant and strikingly similar results. Spring temperature at Southampton accounted for 13% of the phenological variation in herbarium data (Fig. 2a) and Eastbourne temperature accounted for 59% of that in the field data. In both cases flowering advanced by 5.7 days per 1 °C increase in spring temperature. The two regressions were again statistically indistinguishable (gradients, $F_{1,93}$ = 0.00007, P = 0.993; intercepts, $F_{1,94}$ = 0.854, P = 0.358). Furthermore, the gradients of the two regressions of field data on temperature recorded at Eastbourne and CET were not significantly different ($F_{1,46}$ = 0.481, P = 0.491), and neither were the gradients of the two regressions with herbarium data using Southampton and CET temperature records ($F_{1,145}$ = 0.130, P = 0.719); this indicates that the predicted flowering responses of the plants to temperature were consistent irrespective of the temperature records used. In both of these comparisons the intercepts were significantly different (field data, $F_{1,47}$ = 14.6, P = 0.004; herbarium data, $F_{1,146}$ = 10.3, P = 0.002),

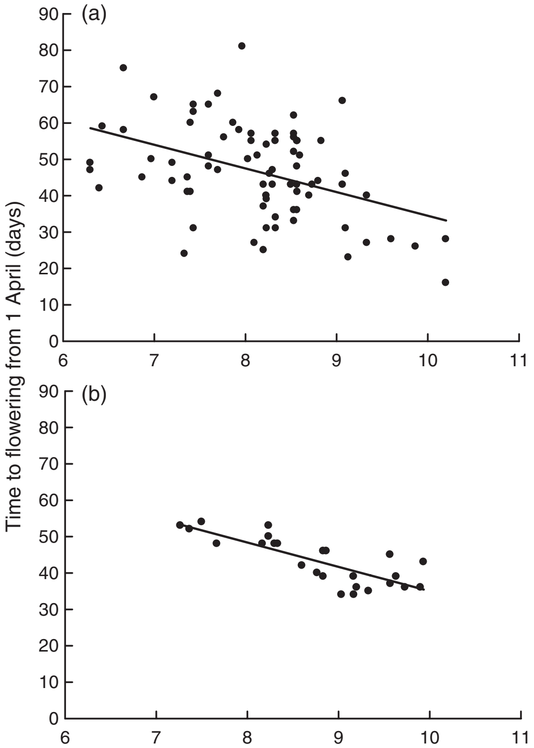

Fig. 1. Relationships between flowering date (expressed as days after 1 April) and mean spring temperature (March–May) in Central England derived from (a) herbarium records from 1848 to 1958 (y = 99.54–6.51x, r^2 = 0.182, P < 0.001, n = 77) and (b) field data between 1975 and 2006 (y = 101.88–6.69x, r^2 = 0.642, P < 0.0001, n = 25).

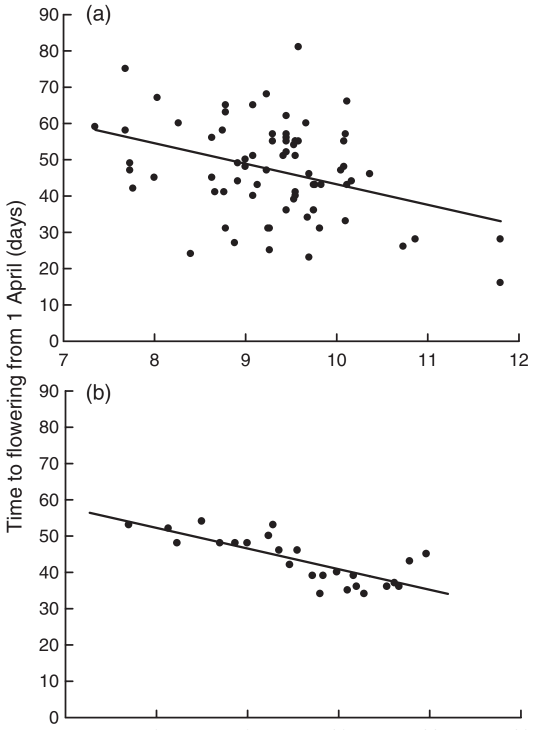

Fig. 2. Relationships between flowering date (expressed as days after 1 April) and mean spring temperature (March–May): (a) between herbarium records from 1855 to 1958 and temperature at Southampton (y = 99.8 –5.66x, r^2 = 0.134, P = 0.0016, n = 72); (b) between field data from 1975 to 2006 and temperature at Eastbourne (y = 97.7–5.68x, r^2 = 0.586, P < 0.0001, n = 25).

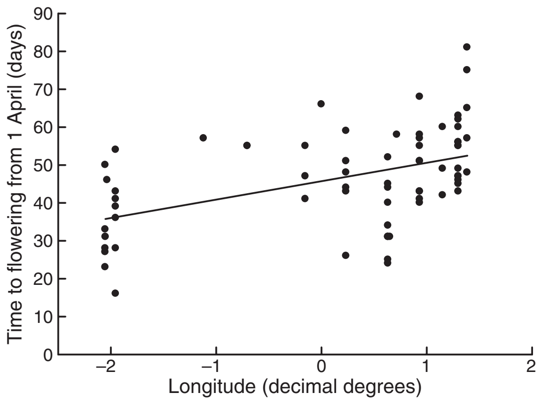

Fig. 3. Relationship between flowering date (expressed as days after 1 April) and longitude of collection site for the herbarium records. Negative values of decimalised longitude are westerly ($y = 45.74–4.86x, r^2 = 0.219, P = <0.001, n = 69$).

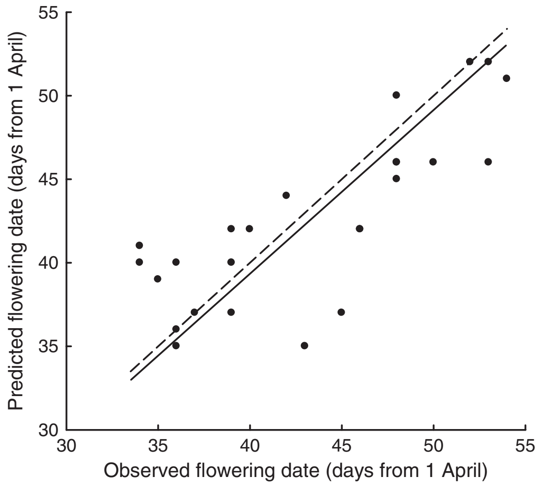

Fig. 4. Relationship between observed flowering date in the field (y_1) in 25 years between 1975 and 2006, and flowering date predicted from herbarium data for the same years (y_2). The principal axis regression (solid line) is $y_1 = -0.173 + 1.021y_2$, $r^2 = 0.63$, $P < 0.001$, $n = 25$. The dashed line would apply if there were exact correspondence between the observed flowering date and the predicted flowering date.

reflecting the differences between the temperature records used.

The effect of longitude of origin on the flowering time of herbarium specimens was significant (Fig. 3). Flowering was earlier at more westerly collection sites by an average of 4.86 days per degree longitude.

The regression model derived from herbarium specimens (1848–1958) and CET was used to predict flowering dates for each of the 25 years between 1975 and 2006 for which there were field records of time of flowering. These predictions were highly correlated with the observed peak flowering dates ($P < 0.01$); the principal axis regression between observed and predicted dates had a coefficient close to unity (1.021) and accounted for 63% of the variation (Fig. 4).

Discussion

Although biological collections can potentially provide valuable evidence of the impacts of climate change on the phenology of plant and animal species (Sparks 2007), their value as a proxy for field data has not previously been tested independently for any species. Miller-Rushing *et al.* (2006) compared flowering dates in recent benchmark years with those derived from historical photographs and herbarium specimens (1900–1921) for a range of species and found that not only were the deviations highly correlated with the corresponding differences in spring temperature but they yielded a trend that was very similar to that observed in independent field data of first flowering dates for the years 1887–1903. Bolmgren & Lönnberg (2005) established correspondence between flowering times derived from herbarium records and phenological observations, but did not investigate the underlying climatic drivers. The power of historical collection data to predict the consequences of future climate change needs to be tested directly. The availability of field data for the rare terrestrial orchid *Ophrys sphegodes*, recorded at a single site in the UK over a 32-year period, provided a unique opportunity to seek validation of the relationship between flowering date and mean spring temperature that was apparent from analysis of data from herbarium specimens collected over a much longer, and different, period of years. The comparison is greatly strengthened by the fact that peak flowering time was recorded in the field, rather than date of first flowering, which is more common in long-term phenological records. It is now clear that first flowering dates may not be ideal measures of plant responses to climate change, because the extremes of flowering distributions are more susceptible to confounding effects than central values (Miller-Rushing, Inouye & Primack 2008). Herbarium collections also tend to reflect peak flowering, as collectors generally aim to obtain prime specimens in full flower, as testified by the fact that we had to discard only one specimen in which too few flowers were open to satisfy our sampling criterion.

Both historical and contemporary data showed that the peak flowering date of *O. sphegodes* was earlier in years with warmer springs, as expected (see also Hutchings 2010). This was the case both when the two phenological records were related to a common temperature record (CET) and when field and herbarium records were related to different but more geographically proximate temperature records (Eastbourne and Southampton respectively). The close correspondence between field and herbarium regressions, irrespective of the geographical locations of the temperature records tested, argues for the robustness of the relationships. Furthermore, using geographically different temperature records did not significantly alter the results for either contemporary or historical sources of data. Previous phenological studies have found similar correlations between flowering date and measures of spring temperature in spring- and summer-flowering species. The estimated advance in peak flowering date of 5.7–6.7 days per 1 °C rise in temperature in *O. sphegodes* is within the range reported for advance in first flowering date in other species in the UK. Fitter *et al.* (1995) reported a mean advance of first flowering date of 4.4 days per 1 °C for 243 species at a single locality but with considerable differences between species; similarly, first flowering dates of 24 species, averaged across the UK, advanced between 2 and 10 days per 1 °C increase in temperature (Sparks, Jeffree & Jeffree 2000).

The relationships between peak flowering date and spring temperature derived from contemporary and historical data for *O. sphegodes* were nearly identical, indicating a common response to spring temperature, notwithstanding that the historical collection and field observation periods were dissimilar in length, separated in time and different in geographical extent. This consistent response is important, as the pace of climate change has accelerated since 1975 when the field studies were initiated (IPCC 2007). None of the herbarium specimens was collected after 1958 and they therefore largely pre-date the period of fastest anthropogenic climate change. Because the field and herbarium data were independent, it was possible also to test the power of the earlier herbarium records to predict the effects of subsequent climatic warming. Importantly, although there was some variation between years in the accuracy of predictions, the overall predictive power was extremely good, with the principal axis regression line for predicted and observed values lying close to the ideal 1 : 1 relationship.

Rigorous validation of the type presented here, although only based on data for a single species to date, serves to increase confidence in the use of biological collections for predicting future phenological responses to climate change. Despite the strong underlying mean temperature signal, variation in flowering time may be influenced by a myriad of factors, and there are likely to be more confounding factors in the herbarium record than in the field data, because it includes specimens taken from a wider range of geographical locations and microhabitats. Predictions based solely on mean spring temperature in Central England accounted for 18% of the variation in flowering date seen in herbarium specimens, but 64% of variation in flowering date in the field records from a single site. Use of more local temperature records in fact accounted for slightly (but not significantly) less variation in both cases, possibly because of the use of minimum and maximum temperatures averaged on a monthly rather than daily basis. Another important explainable source of variation in flowering time in the herbarium record was the geographical range of collection sites, as seen in the significant regression on longitude. This was the major gradient in distribution, and earlier flowering at westerly sites is consistent with a climatic trend to warmer springs in the west. This suggests that, had local temperature records been available for each collection site, even more of the variation in flowering time would have been accounted for by spring temperature. Despite the lower signal-to-noise ratio in the herbarium record, the signal was the same as in the field data and it was applicable over a much longer period. Bowers (2007) used physiological models based on previously determined flowering requirements (trigger dates and heat sums above a 10 °C threshold) to predict, retrospectively, advancing flowering dates of shrubs in the Sonoran desert through the 20th century. A correlated tendency towards earlier collection dates in herbarium material over the same period supported the hypothesis that there had been a genuine response to changing climate, especially as there was no evidence that collector behaviour had changed over the period of study. However, the use of herbarium specimens assumes that they are representative samples of the population from which they are drawn. The potential for bias resulting from variation in collection effort has been voiced as a concern by previous authors (Case *et al.* 2007). Our study demonstrates both that collector bias is not a problem when the herbarium data accepted for use in scientific studies are subjected to carefully controlled selection criteria, and that it is not necessary to have hundreds of specimens in order to extract useful information about the relationships between climate and time of flowering. Although further validation using additional species with different phenologies is desirable, the extreme scarcity of suitable field observations limits opportunities for this to be achieved at the present time. As a spring-flowering plant, *O. sphegodes* falls into a group identified as having flowering phenologies that are likely to be particularly sensitive to temperatures early in the year (Fitter *et al.* 1995), although both the scale and direction of changes in phenology can be idiosyncratic and potentially influenced by additional climatic drivers (Crimmins, Crimmins & Bertelsen 2010). Species that flower later in the summer may be less sensitive to warmer temperatures, and species that reproduce in the autumn may be sensitive in the opposite direction; analysis of 34 500 dated herbarium records of autumn-fruiting of mushrooms in Scandinavia has revealed an average delay of 12.9 days since 1980, as the growing season has been extended by warming (Kauserud *et al.* 2008).

For most species of plants and animals, biological collections are the only source of long-term phenological data. It is estimated that some 2.5 billion specimens of flora and fauna are held in biological collections worldwide (Graham *et al.* 2004). The current drive toward digitisation of collections is facilitating the dissemination of the information they contain. An estimated 60 million records are already available for a wide range of taxa *via* internet information networks such as the Global Biodiversity Information Facility and HerpNET (Graham *et al.* 2004). With appropriate validation, the exploitation of this resource will have increasing relevance and value (Prather *et al.* 2004) as we seek to understand and predict the consequences of continuing climate change.

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References

Aono, Y. & Kazui, K. (2008) Phenological data series of cherry tree flowering in Kyoto, Japan, and its application to reconstruction of springtime temperatures since the 9th century. *International Journal of Climatology*, **28**, 905–914.

Badeck, F.W., Bondeau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J. & Sitch, S. (2004) Responses of spring phenology to climate change. *New Phytologist*, **162**, 295–309.

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

Bolmgren, K. & Lönnberg, K. (2005) Herbarium data reveal an association between fleshy fruit type and earlier flowering time. *International Journal of Plant Science*, **166**, 663–670.

Bowers, J.E. (2007) Has climatic warming altered spring flowering date of Sonoran Desert shrubs? *The Southwestern Naturalist*, **52**, 347–355.

Carey, P.D. & Dines, T.D. (2002) Ophrys sphegodes. *New Atlas of the British Flora* (eds C.D. Preston, D.A. Pearman & T.D. Dines), p. 865. Oxford University Press, Oxford, UK.

Case, M.A., Flinn, K.M., Jancaitis, J., Alley, A. & Paxton, A. (2007) Declining abundance of American ginseng (*Panax quinquefolius* L.) documented by herbarium specimens. *Biological Conservation*, **134**, 22–30.

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

Crimmins, M.A. & Crimmins, T.M. (2008) Monitoring plant phenology using digital repeat photography. *Environmental Management*, **41**, 949–958.

Crimmins, T.M., Crimmins, M.A. & Bertelsen, C.D. (2010) Complex responses to climate drivers in onset of spring flowering across a semi-arid elevation gradient. *Journal of Ecology*, **98**, 1042–1051.

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.

Gallagher, R.V., Hughes, L. & Leishman, M.R. (2009) Phenological trends among Australian alpine species: using herbarium records to identify climate-change indicators. *Australian Journal of Botany*, **57**, 1–9.

Graham, C.H., Ferrier, S., Huettman, F., Moritz, C. & Peterson, A.T. (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution*, **19**, 497–503.

Harrap, A. & Harrap, S.. (2005) *Orchids of Britain and Ireland*. A & C Black Publishers Ltd, London.

Hutchings, M.J. (1987) The population biology of the early spider orchid, *Ophrys sphegodes* Mill I. A demographic study from 1975 to 1984. *Journal of Ecology*, **75**, 711–727.

Hutchings, M.J. (1989) Population biology and conservation of *Ophrys sphegodes*. *Modern Methods in Orchid Conservation: The Role of Physiology, Ecology and Management* (ed. H.W. Pritchard), pp. 101–115. Cambridge University Press, Cambridge, UK.

Hutchings, M.J. (2010) The population biology of the early spider orchid, *Ophrys sphegodes* Mill III. Demography across three decades. *Journal of Ecology*, **98**, 867–878.

IPCC (2007) *Intergovernmental Panel on Climate Change: Climate Change 2007: Impacts, Adaptation and Vulnerability*. *Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Kauserud, H., Stige, L.C., Vik, J.O., Økland, R.H., Høiland, K. & Stenseth, N.C. (2008) Mushroom fruiting and climate change. *Proceedings of the National Academy of Sciences*, **105**, 3811–3814.

Lang, D.. (1989) *A Guide to the Wild Orchids of Great Britain and Ireland*. Oxford University Press, Oxford, UK.

Lavoie, C. & Lachance, D. (2006) A new herbarium-based method for reconstructing the phenology of plant species across large areas. *American Journal of Botany*, **93**, 512–516.

Miller-Rushing, A.J., Inouye, D.W. & Primack, R.B. (2008) How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency *Journal of Ecology*, **96**, 1289–1296.

Miller-Rushing, A.J., Primack, R.B., Primack, D. & Mukunda, S. (2006) Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *American Journal of Botany*, **93**, 1667–1674.

Parker, D.E., Legg, T.P. & Folland, C.K. (1992) A new daily central England temperature series, 1772-1991. *International Journal of Climatology*, **12**, 317–342.

Prather, L.A., Alvarez-Fuentes, O., Mayfield, M.H. & Ferguson, C.J. (2004) The decline of plant collecting in the United States: a threat to the infrastructure of biodiversity studies. *Systematic Botany*, **29**, 15–28.

Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J. & Del Tredici, P. (2004) Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany*, **91**, 1260–1264.

Sanger, N.P. & Waite, S. (1998) The phenology of *Ophrys sphegodes* (the early spider orchid): what annual censuses can miss. *Botanical Journal of the Linnean Society*, **126**, 75–81.

Sokal, R.R. & Rohlf, F.J. (1969) *Biometry*. W.H.Freeman, New York, USA.

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

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., Huber, K. & Croxton, P.J. (2006) Plant development scores from fixed-date photographs: the influence of weather variables and recorder experience. *International Journal of Biometeorology*, **50**, 275–279.

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.

Suarez, A.V. & Tsutsui, N.D. (2004) The value of museum collections for research and society. *BioScience*, **54**, 66–74.

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