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Long-term monitoring of Green-winged Orchid (*Anacamptis morio*) at Upwood Meadows NNR, Huntingdonshire

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Abstract

The results of monitoring a population of *Anacamptis morio* over a 40-year period (1978-2017) in a permanent plot at Upwood Meadows NNR, Huntingdonshire, are presented. Flowering and vegetative plants were recorded each year, with individuals relocated using phenomarkers and triangulation. The majority of plants flowered for over half of their lifespan, the average lifespan of an individual plant was almost 10 years, and the known maximum lifespan above-ground for an individual was at least 36 years. The average age of the cohort became much younger over the course of the study, with potential reasons given including extreme old age, a lack of recruitment, and climate.

Key words: demography; fixed plot; recruitment; mortality; triangulation

Introduction

In 1962 Terry Wells became the Nature Conservancy's first grassland ecologist, based at Monks Wood, Huntingdonshire. In his first three years at the Research Station he set up a number of long-term monitoring projects, mainly across the chalk and limestone of southern England, designed to study the dynamics of British orchids and changes to associated vegetation. One of the first of these studies, set up in the early 1960s, followed the fate of a cohort of Autumn Lady's Tresses (*Spiranthes spiralis*) at Knocking Hoe in Bedfordshire. Now into its sixth decade, this survey is one of the longest running demographic plant studies in the world (Revels *et al.*, 2015). Such projects take on a life of their own, and become increasingly more valuable over time, often in ways not originally envisaged. To this day, repeat surveys of plots set up in the 1960s and '70s are providing a valuable insight into the changes that have taken place across the lowlands of England over the past fifty years and more (e.g. long-term changes to chalk grassland; Stroh *et al.*, 2017).

The discovery by Terry of an unimproved, species-rich meadow at Upwood, Huntingdonshire, presented an ideal opportunity to establish a study close to home, and in 1978 a similar experimental design to that at Knocking Hoe, albeit on a smaller scale, was set up at Great Bentley Meadow within Upwood Meadows NNR to investigate the flowering dynamics of Green-winged Orchid, *Anacamptis morio* (L.) Bateman, Pridgeon & Chase. Vegetation at the site overlies boulder clay and comprises a species-rich variant of NVC MG5 *Cynosurus cristatus-Centaurea nigra* grassland (Rodwell, 1992). Many locally uncommon species thrive in the meadows, including *A. morio*, *Genista tinctoria*, *Serratula tinctoria*, *Ophioglossum vulgatum* and, in poached ground near to cattle-troughs, the diminutive *Myosurus minimus* (Wells, 2003). The site topography precludes cutting (being ancient Ox-ploughed ridge & furrow, with numerous large ant hills), and so the meadows are grazed by cattle. The number of cattle present on site each year varies depending on weather and site conditions, and management ensures that the site is not under-grazed in any one year and that the majority of species are given the opportunity to flower and set seed. Numbers of livestock grazing the site each year (1978 to present) are noted by the site warden.

Anacamptis morio is a tuberous wintergreen perennial, flowering from mid-April to early June. It was included in the genus *Orchis* until phylogenic studies based on DNA sequences demonstrated a closer relationship to *Anacamptis* (Bateman *et al.,* 1997). Plants produce one inflorescence, which typically has 15-20 flowers, each with two pollinia. Flowers are self-compatible but rely on pollinator visits to set fruit (Nilsson, 1984). As the spur does not provide floral rewards, pollination depends upon deception. Each fruit contains many thousands of dust-like seeds that are wind dispersed, but only a small proportion of seeds will travel more than a metre from the parent plant (Jersakova & Malinova, 2007). Little is known about seed germination and seedling establishment in the wild, but *A. morio* does appear able to colonise new or recently disturbed grassland (e.g. Stroh, 2007). Ex-situ studies have found that propagation by seed requires a penetrative fungus that forms a mycorrhizal association with the developing seedling (Fay & Rankou, 2010). Mycorrhizal associates are known to include *Epulhoriza repens* and *Moniliopsis solani* (Lievens *et al.,* 2010). Each year, plants are capable of producing new tubers to replace the tubers that have been exhausted of food reserves during the flowering process.

In Britain and Ireland *A. morio* is found across a wide edaphic gradient, from base-poor to base-rich soils and from short damp alluvial grassland to open dry lowland grassland. Core populations are scattered throughout southern England and the Welsh coastline and across a central belt in Ireland from west Galway to county Dublin, and south to Tipperary, with outliers in county Down in the north-east and west Cork in the far south-west. It has always been a rare species in Scotland, restricted to a handful of sites around Troax, Ayrshire, most of which are protected within the Bennane Head Grasslands SSSI.

Methods

From 1978 until 2017 data were collected at least once a year (and with one visit always in May) within a 5 x 4 metre quadrat, with the location of the quadrat made permanent in the first year of the survey by the use of phenomarkers anchored at two corners of the plot. Tape measures placed at these fixed points enable the surveyor to triangulate precisely an individual plant, and, by noting the co-ordinates, return to the same individual in future years (Figure 1). New plants are also searched for and recorded, following completion of the recording of known plant locations.

A number of attributes for each individual were recorded annually, including notes on whether the plant was present, in flower or vegetative, the number of flowers, the number of leaves, and the height of the inflorescence. Plants absent for more than three years were assumed to have died and were not searched for again. In addition, numbers of flowering spikes were recorded by volunteers each year within the NNR as a whole.

Figure 1. Terry Wells and Felicity Woodhead recording the Upwood Meadows permanent quadrat in 1978

Results from this study, using data collected from 1978 – 1995, were published by Wells *et al.* (1998). The results presented below use a more basic analytical approach to examine general population trends, but it seemed apposite to update and publish the main findings of this ongoing survey 40 years after its inception, and following the collation of an additional 22 years of quadrat data.

Results

Population dynamics 1978 – 2017

In total, 201 plants were recorded within the fixed quadrat over a 40-year survey period. Numbers were highest in the 1980s (mean 101 ±5), peaking at 118 plants in 1986 and 117 plants the following year (Figure 2). Numbers remained relatively stable from 1988 until 2010, with a range of between 54 and 92 individuals (mean 73 ±4), but in 2011 the population crashed from 83 individuals down to only 25, and numbers were lower still in 2012 (20 individuals). From 2013 until 2017 numbers recovered slightly, with a range of 30 – 40 individuals recorded (mean 32 ±2).

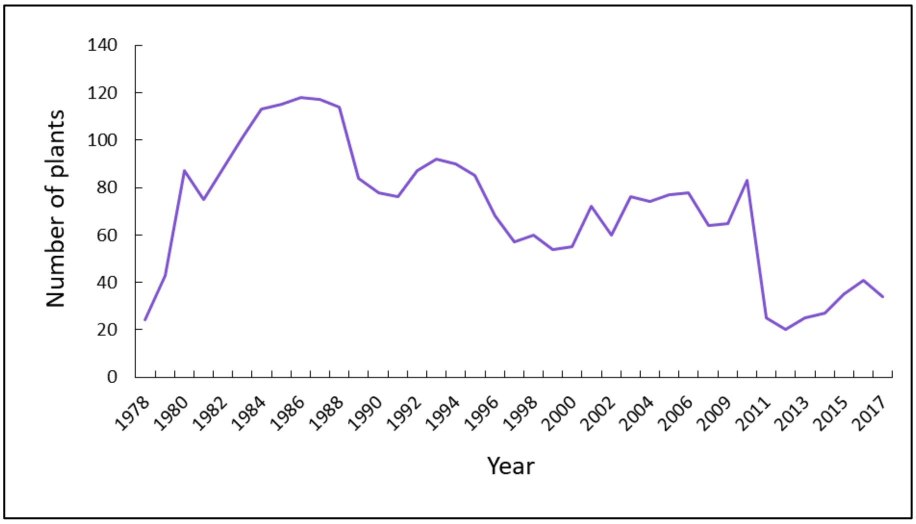

Figure 2. Total number of plants (flowering and vegetative) of *A. morio* within the permanent quadrat at Upwood Meadows, Huntingdonshire, 1978-2017

Age structure

The average age of individuals monitored within the fixed quadrat was 9.84 ±0.6 years (n = 201), with an age range from 1 to 36 years (Figure 3). Whilst just over 75% of all individuals lived for 13 years or less, 6.5% (13 plants) survived for 30 years or more. The cohort from the first year of the project (1978) lived, on average, the longest (17.1 ±2.5 years) (Figure 4). Given that the survey commenced when mature plants were already present in the quadrat, and so were of an indeterminate age at 'year 1', this figure must itself be an underestimate of longevity. Cohorts reached an average age of 10 years or more in all years up until 1989, but thereafter averaged only 6.4 ±0.5 years, with a maximum of 9.2 ±0.7 years in 2000.

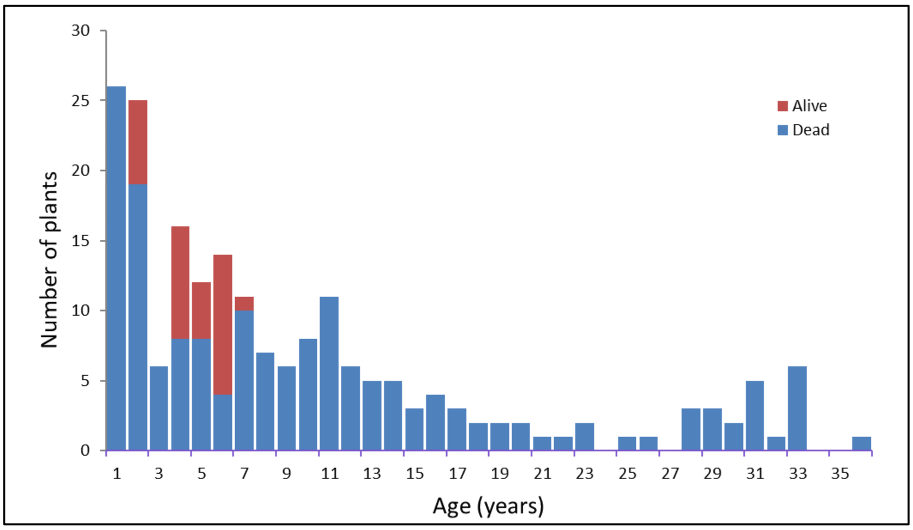

Figure 3. The age of *A. morio* plants monitored within the permanent quadrat at Upwood Meadows, Huntingdonshire. Plants that were still alive in 2017 are shown in red.

The average age of plants considered to have expired in any one cohort peaked at 17.6 ±1.9 years in 2011 (the year of the 'crash'; Figure 5). Note that cohorts from 2012 – 2017 were excluded from the analysis, as the majority of plants from these years were still living in 2017.

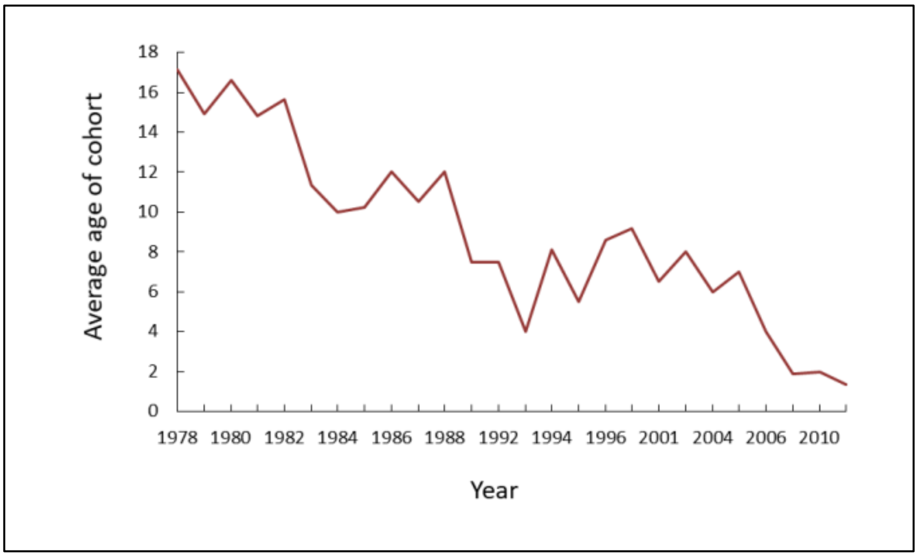

Figure 4. The average age reached by *A. morio* plants first found in each year at Upwood Meadows, Huntingdonshire, 1978 - 2011.

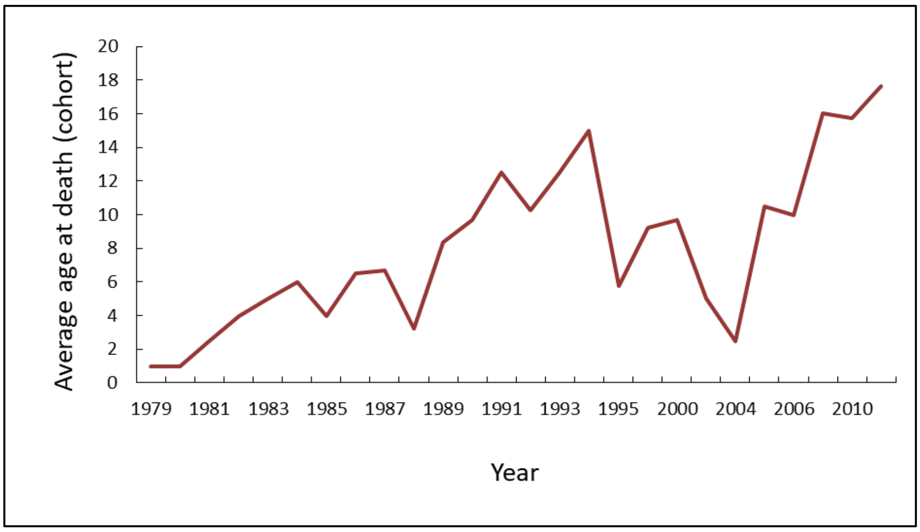

Figure 5. The average age reached by *A. morio* plants last found in each year at Upwood Meadows, Huntingdonshire, 1978 - 2011.

Flowering frequency

Flowering frequency varied considerably throughout the study, but in general terms tended to follow a fairly consistently even proportion of flowering vs vegetative plants, but with occasional sharp troughs (1988; 1997-98; 2002) when a far greater proportion of vegetative plants were recorded (Figure 6). In all but six years of the study the proportion of individuals flowering was above 40% per annum (Figure 7), and above 60% in 26 years out of 40, with maxima of 93% in 2004 and 96% 2011 (for the latter date, only one vegetative plant was found). The first year of survey (1978) is excluded from these results, as only flowering plants were counted. In subsequent years, flowering and vegetative plants were included in the census. In terms of flowering performance during the lifespan of an individual, all ages apart from those that survived for 1 year (84%) and 25 years (36%) flowered between 50 and 80% of years during their lifespan (Figure 8).

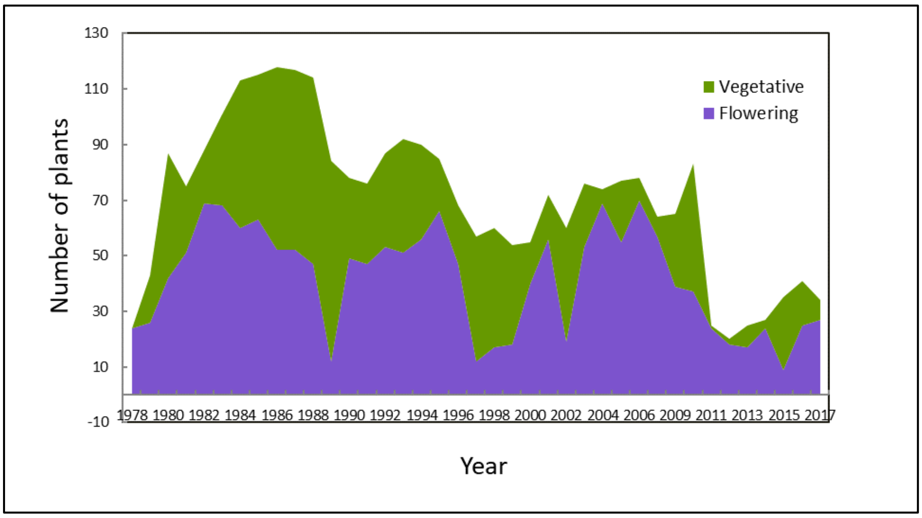

Figure 6. The population dynamics of *A. morio* within the permanent quadrat at Upwood Meadows, Huntingdonshire, 1978 - 2017, showing the total number of flowering (purple) and vegetative (green) individuals.

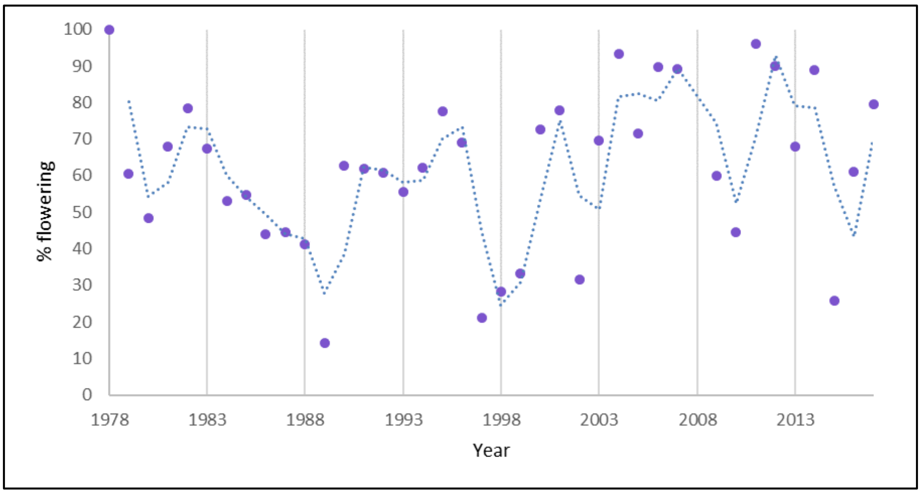

Figure 7. The percentage of individuals flowering within the permanent quadrat at Upwood Meadows, Huntingdonshire, 1978 - 2017. The dotted line illustrates the underlying trend.

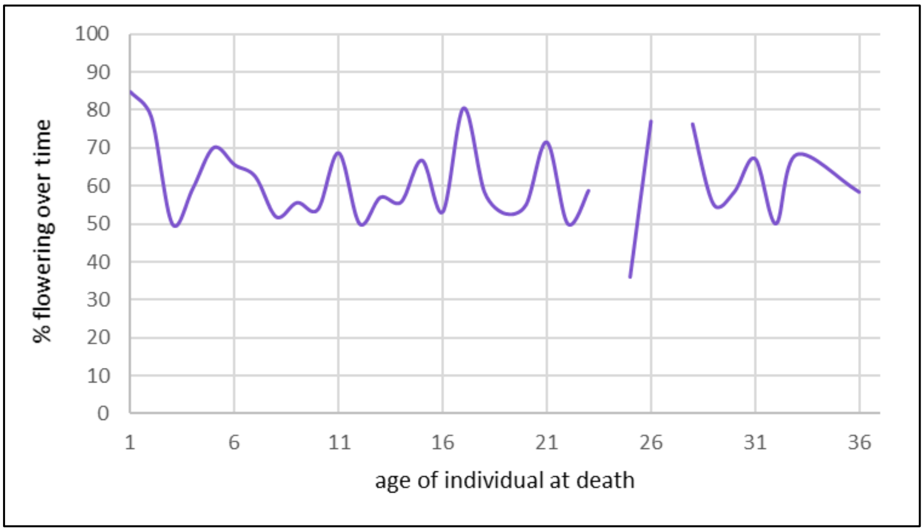

Figure 8. Flowering performance during the lifespan of an individual within the permanent quadrat at Upwood Meadows, Huntingdonshire, 1978 - 2017. Note that gaps in flowering percentage indicate a lack of plants that lived for the corresponding number of years.

Births & deaths

The number of new plants (births) was highest in 1980 (23 individuals; and excluding the first year of the study), but thereafter the rate remained fairly constant throughout the 1980s, 1990s and 2000s, with numbers rarely exceeding more than five new plants in any one year (8 in 1994; 10 in 2009; 16 in 2011) (Figure 9). The number of deaths broadly tracked the number of births across much of the 40-year survey period. However, there were prominent spikes in 1989 (19 deaths), 2000 (10 deaths), 2010 (12 deaths) and the exceptional year of 2011 (44 deaths). Of these 44 individuals, 21 were more than 20 years old, and a further 7 were more than 10 years old. Additionally, 9 of the 44 were only two years old.

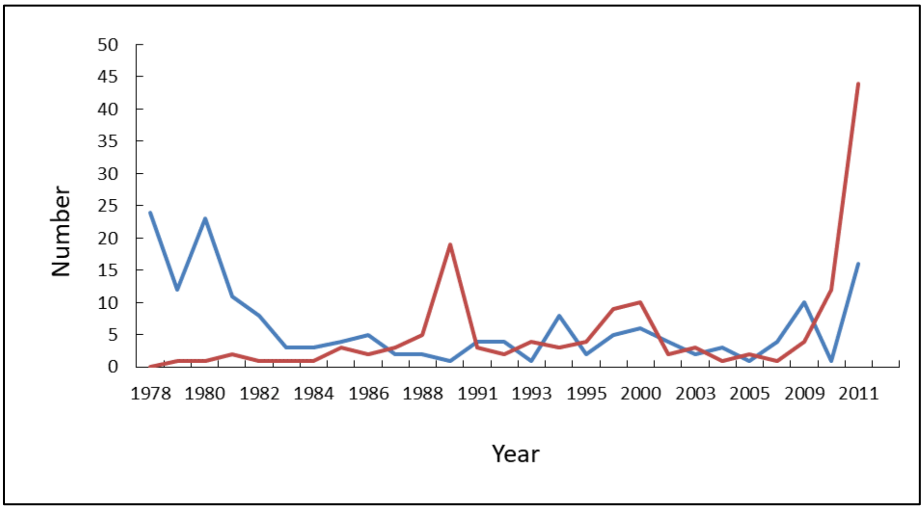

Figure 9. The number of births (plants first recorded/year) (red) and deaths (plants last recorded/year) (blue) of *A. morio* within the permanent quadrat at Upwood Meadows, Huntingdonshire. Note the exceptional number of deaths in 2011.

Discussion

The permanent plot at Upwood Meadows was established to investigate some of the factors influencing the flowering performance of *A. morio*. The method used to record each individual has led to a much greater understanding of the species' ecology and life-history, and also demonstrates the importance of a robust and easily-repeated monitoring design for use in long-term demographic studies. Counting the number of flowering spikes, but ignoring vegetative plants, will inevitably result in a skewed perspective of population dynamics. The combination of fine-scale fixed-point monitoring, alongside an annual count of flower spikes to monitor 'health' at the site-level, and noting of grazing pressure in each year as an extra variable, would seem ideal both in terms of scientific value and volunteer engagement, but as yet this system of monitoring is seldom replicated elsewhere.

When it comes to examining trends at Upwood Meadows, it is important to bear in mind the quadrat's small size and location; there are no replicates within the meadow, and the quadrat runs close to a boundary hedge and unmarked footpath, with the result that visitors sometimes trample vegetation within the plot. Consequently, changes at the small-scale may not necessarily mirror those at the larger site-scale. In addition, for long-lived perennials persisting within small areas, extinction risk is greater because populations recover more slowly (if at all) from a catastrophic event (such as an errant mole hill, which has been the cause of quite a few deaths within the permanent plot). There is, however, still much to be learnt from monitoring consistently within a permanent plot over such a lengthy time period. For example, Wells *et al.* (1998) showed that individual plants can be long-lived and are capable of flowering most years, contradicting previous assertions that an individual *A. morio* plant died after flowering i.e. that the species was monocarpic (Summerhayes, 1951). The results presented here, using an additional 22 years of data, have shown that the majority of plants flowered for over half of their lifespan, that the average lifespan of an individual plant was almost 10 years, and the known maximum lifespan above-ground for an individual was at least 36 years. Calculations for age exclude the juvenile phase of growth below ground, as well as non-detection above ground, but both factors are probably minor for this study, as the leaves of this species are visible one or two years after germination (Wells, 1981), and the (small) plot was thoroughly searched each year for new vegetative plants.

Whilst it is clear that *A. morio* has the potential to be very long-lived, a lack of recruitment that fails to buffer for loss over time, or sudden damaging events, leaves a population vulnerable to a rapid crash in numbers. Within the monitored plot, the number of births was generally low each year, apart from the exceptional year of 1980, and broadly tracked the number of deaths. This would suggest stability. However, there were spikes in the number of deaths roughly every ten years, and the average age of the cohort became much younger over the course of the study. Although speculative at the present time, the dramatic fall in numbers recorded in 2011 may be due to three main factors; lack of recruitment, extreme old age - the average age of the plants that died in 2011 was almost 18 years, with half of all individuals over 20 years old – and climate.

Wells *et al.*, (1998) found that the leaves of *A. morio* are susceptible to frost-damage, perhaps not surprisingly for a temperate species, with below-freezing temperatures in autumn and winter causing blackening and die-back of leaves, which can then prevent flowering in the subsequent spring. In addition, soil frosts can damage the tubers that are formed annually during the flowering period and act as food reserves fuelling growth the following year, thereby negatively affecting resource uptake. Climate data available from the Met Office website show the mean temperature in Huntingdonshire for December 2009 was -1.5 ^{0}C colder than the long-term average, up to -3.5 ^{0}C colder than average in January 2010 and -1.5 ^{0}C colder than average in February 2010. The following winter was colder still, with temperatures in December 2010 dropping more than -3.5 ^{0}C below the average, and falling below minus double figures (with a low of -17 ^{0}C) for multiple days. Such unusually cold temperatures may not in themselves have directly resulted in the high number of deaths recorded in the spring of 2011, but they might well have been a contributing factor in further weakening the tubers of extant plants, many of which were ten or more years older than the average age.

There would also appear to be a weak correlation at the site-scale, with 2011 producing the lowest count of flowering spikes across the meadow since 1998, and at least 2,000 fewer spikes than 2010, when the count stood at just over 4,000 (Sheila Wells, pers. comm.). It may be that the very cold winter of 2010/11 substantially restricted the number of plants with sufficient reserves to flower in 2011, but milder temperatures in the winter of 2011/12 meant that plants that remained vegetative in 2011 (but were not counted at the site-scale) flowered again in 2012. This would add weight to the findings by Wells *et al.* (1998) about leaf-blackening, but would not necessarily corroborate the speculative link presented here between extreme cold and the death of individuals. However, the suspicion remains that prolonged abnormally low temperatures in winter, coupled with old age, resulted in higher mortality rates.

Standing water for prolonged periods of time may have some influence over flowering, birth or mortality of *A. morio*, but water levels have not, due to past damage to dip-wells, been recorded at Upwood Meadows throughout the entirety of the study period and so could not be included as an additional factor for investigating change over time. However, cattle numbers are noted each year and grazing has been of a consistently sufficient intensity and timing to maintain species-rich vegetation across the site. Certainly, all of the key indicator species for which the site was notified are still present, some in large numbers, and the *A. morio* count for the SSSI in 2017 produced by far the largest number of flowering spikes ever recorded. In recent years, the number of births within the fixed quadrat have slowly risen following the sharp fall in numbers in 2011, and it will be interesting to see if in future years numbers rival levels recorded in the 1980s. Often, we are only able to construct a true picture of a species demography, and its fate at a particular locality, by long-term repeat monitoring over decades. There is still much to analyse from the current dataset, and much to learn about the life-cycle of *A. morio*, including the main factors responsible for recruitment and mortality. It is hoped that this short paper will inspire others to replicate Wells' monitoring design at other sites, so that comparable data can be collected and analysed.

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