Changes in the distribution and abundance of *Himantoglossum hircinum* (L.) Sprengel (Orchidaceae) over the last 100 years

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ABSTRACT

1. Species are likely to be most sensitive to climate change at the geographic limits of their distribution. The behaviour of such populations may therefore be a predictor of the response of the species to global change.
2. The northern limit of the Lizard Orchid, *Himantoglossum hircinum*, occurs in England, where 16 populations are currently known. British records over the past 100 years are particularly accurate for this species and it was one of the first for which changes in distribution were linked to an amelioration of climate (Good 1936).
3. Early records were checked to confirm the rise in population number in the early part of the century. Analysis of more recent data showed that this was followed by a sharp decline and numbers have only been rising again over the last decade. The range expanded with the earlier increase in population number, but did not contract as populations were lost.
4. Data collected between 1977 and 1998 in the largest population allowed flowering probability and seed production to be correlated with rainfall during the growing season. Analysis of the resulting model showed that both observed rises in population number followed periods during which the seasons for vegetative growth had been wet.
5. Populations have become both larger and more persistent due to an increased interest in conservation.
6. Changes in the abundance of *H. hircinum* are likely to depend on other factors, including patterns of human activity, as well as on climate change.

KEYWORDS: rainfall, life-cycle, range-limits, seed production, climate change.

INTRODUCTION

There is currently a great deal of research being undertaken to assess the effects of climate change on the distribution and abundance of individual species (e.g. Carey & Brown 1994; Sykes *et al.* 1996; Parmesan 1996). This research is based on the theory that ultimately the distribution of a species is limited by its physiological responses to climate. One of the earliest exponents of this theory was Ronald Good who in 1931 proposed his "Theory of Tolerance". He supported his theory with a paper on the distribution of the Lizard Orchid *Himantoglossum hircinum* (L.) Spreng. (Good 1936). In this paper he suggested that the increase in the distribution, and also the numbers of *H. hircinum* records, in the early part of this century were due to a climate change. Specifically, Good indicated that it had been "an amelioration of winter and spring temperatures and a slight increase in the preponderance of winter rain" that had made England similar to western France, which is at the heart of the species' range.

If Good was correct, we might expect that the distribution and abundance of *H. hircinum* in England would have increased further if the climate continued to be amenable. Furthermore, at least one climate scenario (Viner & Hulme 1994) suggests that England will become more like south-western France in the coming decades. Therefore, if *H. hircinum* does respond as Good suggested, we might expect the distribution and abundance of the species to increase (Carey & Brown 1994).

In this paper Good's theory is re-evaluated by re-analysing the early records of *H. hircinum* and also by adding records from the years 1934–1998.

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DATA AND METHODS

HISTORICAL DATA

The records used in this paper come from many sources. The Biological Records Centre (B.R.C.) at Monks Wood holds a historical database for species in Great Britain and has provided the majority of data. Within the B.R.C. file on *Himantoglossum hircinum* (L.) Sprengel is a large body of information collated by Mrs G. Crompton and L. Farrell to whom I am indebted. This information includes copies of correspondence between Good and various botanists within England and abroad as well as the notes he used to produce the 1936 paper. The record cards from the B.R.C. hold information on the date the species was seen, where it was seen and by whom. There are also sections for information on habitat and notes. The notes section often contains information on the number of flowers or plants seen.

Interpreting the records was not straightforward. It was not uncommon to have records from the same site in the same year given by different individuals who use different names for the location as well as different map references. Despite these inconsistencies it is almost always possible to determine which records are the same. I am fortunate that most of this work was done by others before me, by Good for the earlier records, and by G. Crompton and R. Fitzgerald for all records. I have added to their records by carefully re-reading the record cards, checking sources and correspondence on the species. The most modern records were supplied by M. Wigginton at the Joint Nature Conservation Committee and from personal observations.

The records suggest that two populations have arisen from garden escapes but there may be others. These two are included here. Several populations are due to "well-meaning naturalists" who transplanted whole plants to new sites and counties. The number of these "introductions" is impossible to estimate but any records that are known to have been due to introductions have been discounted from this analysis.

CONTINENTAL DISTRIBUTION

Himantoglossum hircinum is spread over much of southern Europe and a map of this distribution is published (Meusel *et al.* 1965) and also digitised on to an Atlas Flora Europaea grid (Carey *et al.* 1993). The species is especially common in the wine-growing regions of France where it is noted as a roadside weed growing on a wide range of neutral to basic substrates including broken concrete.

DEMOGRAPHIC CHARACTERISTICS

"How long do *Himantoglossum hircinum* seeds take to germinate?" and "how long does the protocorm which develops remain underground before a leaf is produced?" are questions that, as yet, are not fully resolved. A recent study (P. Carey & H. Scott unpublished data) following the methodology of Rasmussen and Whigham (1993), has shown that 0–10% of seeds had signs of mycorrhizal infection (the first stages of germination) in the first autumn and winter after they were produced in 1996 whereas 10–40% of seeds produced in 1997 became infected almost immediately. The difference between the two autumns was that 1996 was dry and 1997 was wet. At the time of writing no seedlings have been noted from either 1996 or 1997 seeds. There is anecdotal evidence to suggest that seedlings appeared three years after an isolated plant flowered for the only time (Good 1936). A matrix of plant states (Table 1), calculated from data collected from two permanent plots at the largest population in England from 1985–1994 (P. Carey & N. Stewart in prep.) indicates the proportion (0·59) of plants remaining at this "seedling" stage from year to year is very high. The low death rate of large and medium plants in the transition matrix (Table 1) also indicates that *H. hircinum* can be a long-lived plant. Some individuals first censused in 1987 are still alive and flowering today (L. Farrell, pers. comm., N. Stewart, pers. comm.). Many of these plants flower in successive years but, more importantly for this study, many do not. One individual plant in Sussex flowered in 1984, then again in 1995 and 1996, but never in between. It is also not unusual for plants to remain underground as tubers during any one year (N. Stewart, pers. comm.; L. Farrell, pers. comm. and pers. obs.).

In this paper the growing season is defined as September to August. The plant is typically wintergreen, emerging with the autumn rains anywhere from late August to April (G. Crompton, pers. comm, L. Farrell, pers. comm.; N. Stewart, pers. comm. & pers. obs.). Most plants are

TABLE 1: TRANSITION MATRIX FOR MOVING FROM ONE LIFE STAGE TO ANOTHER FOR *HIMANTOGLOSSUM HIRCINUM*. TRANSITIONS ARE TAKEN AS THE MEAN TRANSITION PROBABILITIES FROM NINE YEARS OF DATA FROM TWO PERMANENT 10 × 10 M PLOTS AT THE LARGEST POPULATION IN ENGLAND.

			year t+1		
Plant size	seedling	small	medium	large	death
year t					
seedling	0·59	0·18	0·01	0·00	0·22
small	0·15	0·50	0·28	0·01	0·06
medium	0·03	0·10	0·47	0·38	0·02
large	0·01	0·07	0·18	0·71	0·03

apparent by November and only very small plants (seedling category in Table 1) emerge after this. The plants flower from late June to late July. Data collected from three permanent plots within the largest population in England between 1977 and 1994 (Carey & Stewart in prep.) were compared with climate data from the nearest weather station at Manston which is approximately 8 km north of the population. These data showed that the probability of a large plant flowering (Y) in growing season t is related (R^2 = 61·8, F = 25·29, p<0·001) to the precipitation (X) in the months September–April (the vegetative growth phase) in growing season t-1 (Equation 1). Therefore the flowering "initial" is likely to be determined by the size of the tuber set in the growing season before the growing season in which flowering takes place.

$Y_t = 0{\cdot}382 + 0{\cdot}0019X_{t-1}$ Equation 1

The production of seed pods was noted in the years 1988, 1989, 1991, 1992 and 1997. The number of pods produced per flowering spike (S) in growing season t was related (R^2 = 90·00, F = 26·89, p = 0·014) to the rainfall (X) in the growing season t (Equation 2).

$S_t = -10{\cdot}768 + 0{\cdot}0343X_t$ Equation 2

No relationship was found with temperature and flowering or seed pod production at this site.

The green leaves of this plant tend to brown either just before or during flowering. The plant then enters a brief dormant phase. Plants are maintained during the dormant phase by means of a tuber. If the plant is pollinated seeds take at least six weeks to ripen (L. Farrell, pers. comm.) and mature from late July to late August or even the beginning of September (pers. obs.). No relationships between climate and the seed ripening phase and dormant phase were found.

The seeds are approximately 130 × 30 × 30 µm and are assumed to fly long distances. However a large number of seeds remain lodged in many pods so that when the flowering stalk falls over the seeds drop near to the parent plant. This has led to swarms of seedlings around parent plants in the years 1987–1995 at the two largest populations (Carey & Stewart in prep; L. Farrell, pers. comm. and G. Crompton, pers. comm.).

DATASET

A dataset was assembled which includes date of record, national grid reference, number of vegetative plants seen, number of flowering plants seen, habitat, and reason for disappearance (if appropriate). This dataset allowed the persistence of populations to be calculated. For many populations a record was not made in each year but it was often possible to make the assumption that the population persisted. In the case of two records at Box Hill in Surrey which are 106 years apart I, like Good (1936), have assumed that these are independent and demonstrate the recolonisation of a suitable site. There have been two populations at Burnham-on-Sea in Somerset but these are separated by approximately 8 km and 60 years and I have assumed that these records are not the same population. Unlike Good I have been more ready to accept that separate records at the same site are the same population. This is based on the demographic information gathered from seven populations, which indicates that there can be a long interval between generations and also that plants can remain in a less conspicuous state for many years. Both of these reasons would allow for the absence of records from a particular site.

Records before 1895 are very widely spaced in time and make interpretation, especially of figures, difficult. So for clarity in most of the Figures in this paper I have only analysed the period 1895–1998. Details of the earlier records are given by Good (1936).

Although many of the records are accurate to 1 km some are only accurate to 10 km and this, along with the need to keep the location of some sites secret, means that maps of the distribution of sites in England presented in this study are based on a 10 km grid.

If it takes three years for a seedling to appear (Good 1936), and another three years to become mature (P. Carey & N. Stewart in prep.) a time-lag of about six years would exist between the climatic conditions which lead to establishment and the date of first record for a population (although there may have been some delay between a plant first flowering and the first year in which it was seen).

In order to investigate the effect of climate on *H. hircinum* at the national level it was appropriate to use national weather statistics. Mean monthly rainfall data for England and Wales, supplied by P. Jones at the Climatic Research Unit at the University of East Anglia for the period 1895–1994, were available to compare with the records of *H. hircinum*. Equations 1 and 2 were applied to the rainfall data to give a probability of flowering and pod production for each growing season of the sequence. The product of these two equations gave a rough estimate (the standard error of this product based on the variance of Equations 1 and 2 was 0·54) of seed pod production per flowering plant in each year and, when multiplied by the number of populations recorded (assuming each population only had one flowering plant), an estimate of national seed pod production was obtained. The effect of severe droughts (more than 100 mm below the mean rainfall) on seeds was mimicked by reducing the seed pod production of year t, year t-1 and year t-2 in the model to zero. A six year time-lag was added to the date populations were recorded. Decadal smoothing was applied using LOWESS techniques (MINITAB 11) to both the data of the number of records and the estimate of seed production to mask some of the bias that is inevitable in the process of recording on a national scale.

RESULTS

Reassessment of the records has led to a few discrepancies between the data presented here and those in Good (1936). There are additional records of which Good was not aware and a number of records that Good considered as geographically separate which I consider were not. The population recorded in north-western England at Ingleborough Hill in 1810 (herb. G. B. Woodruff) seems the most unlikely of any that was not documented by Good and I ask the readers of this paper to look on it with scepticism.

The number of *Himantoglossum hircinum* populations in England varies dramatically with time (Fig. 1). There is a marked peak towards the end of the 1920s and early 1930s which is followed by a rapid decline and a remarkably constant number of populations from 1950–1990. Since 1990 there has been a rise in the number of populations.

There is a high turnover of populations with a high proportion of new records and a high proportion of populations disappearing from the records (Fig. 1) throughout the period 1895–1998.

Predictably, the mean age of populations declined as the number of populations increased (Fig. 2). Since 1940 the mean age of populations has increased steadily.

For 439 of the 750 records of *H. hircinum* it is possible to infer the number of flowering plants present in the population. This provides data from at least one year for 116 of the 201 populations. The total size of the population is known for 193 out of the 750 records which represents at least one year from 39 different populations. The mean size of *H. hircinum* populations has not increased over the last 100 years but since 1945 two populations have become much larger than any other recorded in England. One population on a golf links in Kent produced over 3000 flowers in 1991, although few of these produced any seed pods. This population was an order of magnitude larger than the other substantial population in Cambridgeshire, which was itself an order of magnitude larger than any other population.

The distribution of populations within England was mostly restricted to the south-eastern corner of England before 1910 with most of the populations being found around Dartford (Fig. 3a). During the next 30 years populations appeared in many of the counties of southern England (Fig. 3b). Despite the dramatic fall in the number of populations after 1940 the distribution of populations has not contracted (Fig. 3c) to the distribution that existed before 1910 (Fig. 3a).

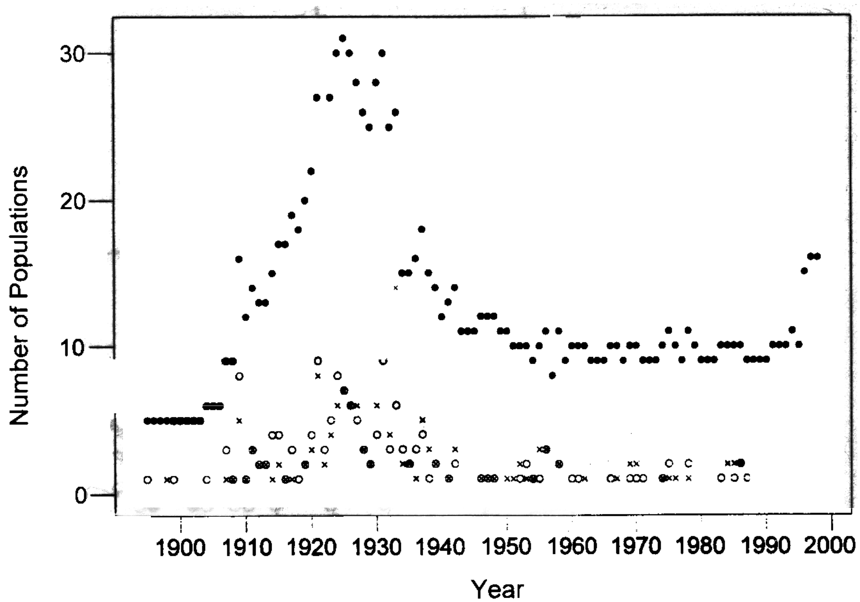


FIGURE 1: The number of populations of *Himantoglossum hircinum* present in England each year since 1895 (solid circles), the number of populations that are first records (open circles) and the number of populations with a last record in that year (crosses). For clarity, only years where there was at least one record of a new population are shown and also only years where there is at least one last record are shown.

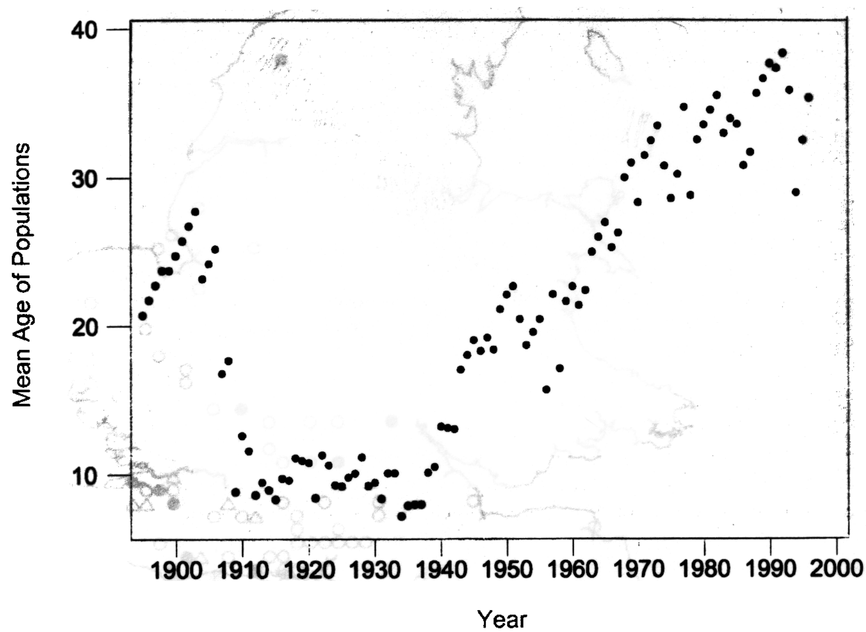
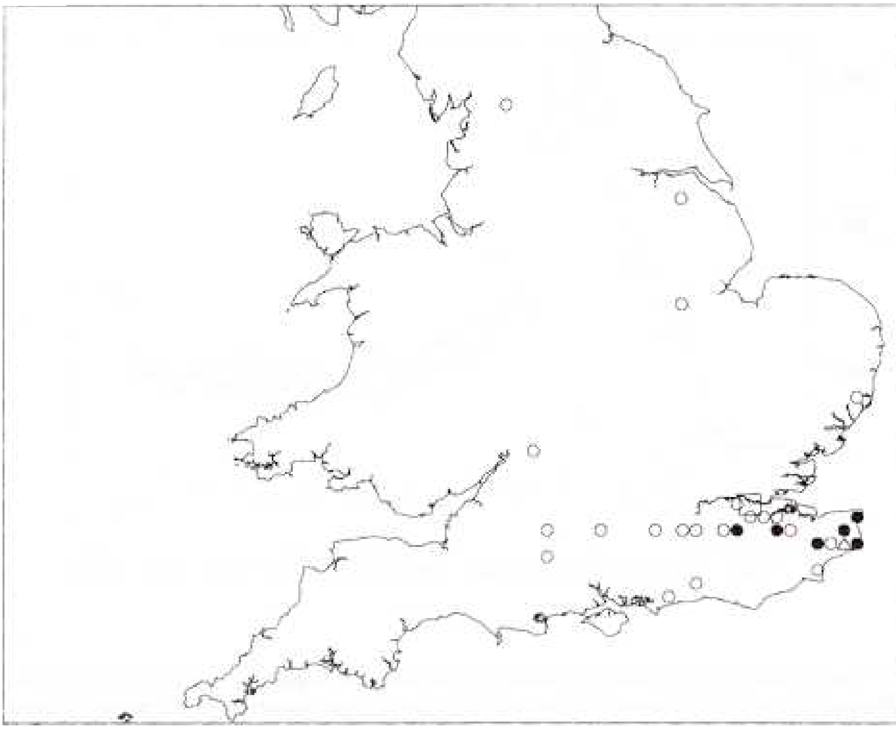
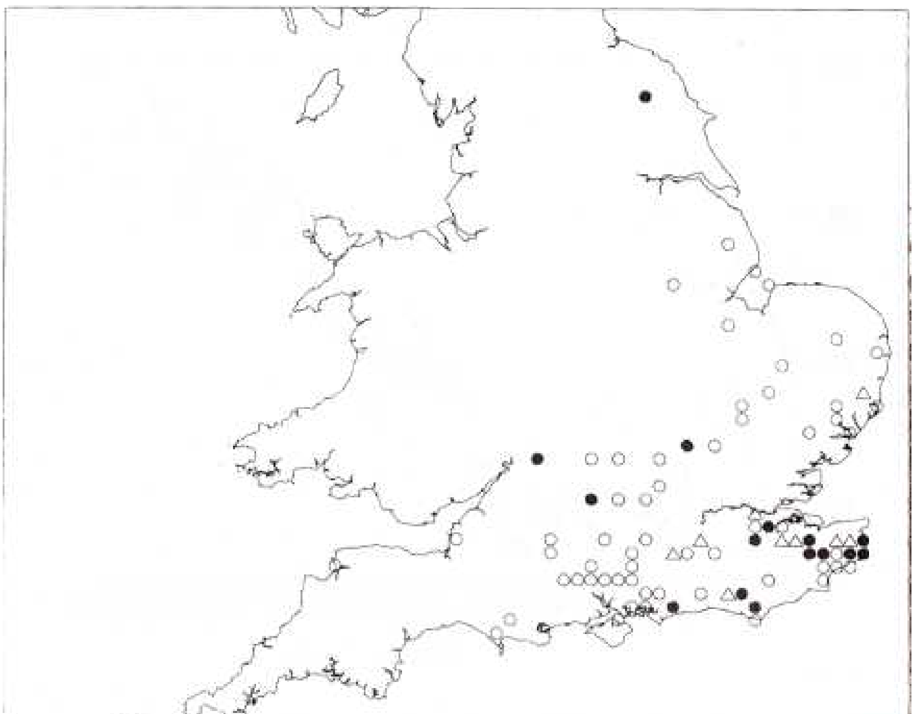


FIGURE 2: The mean age of populations of *Himantoglossum hircinum* in England from 1895 to the present.





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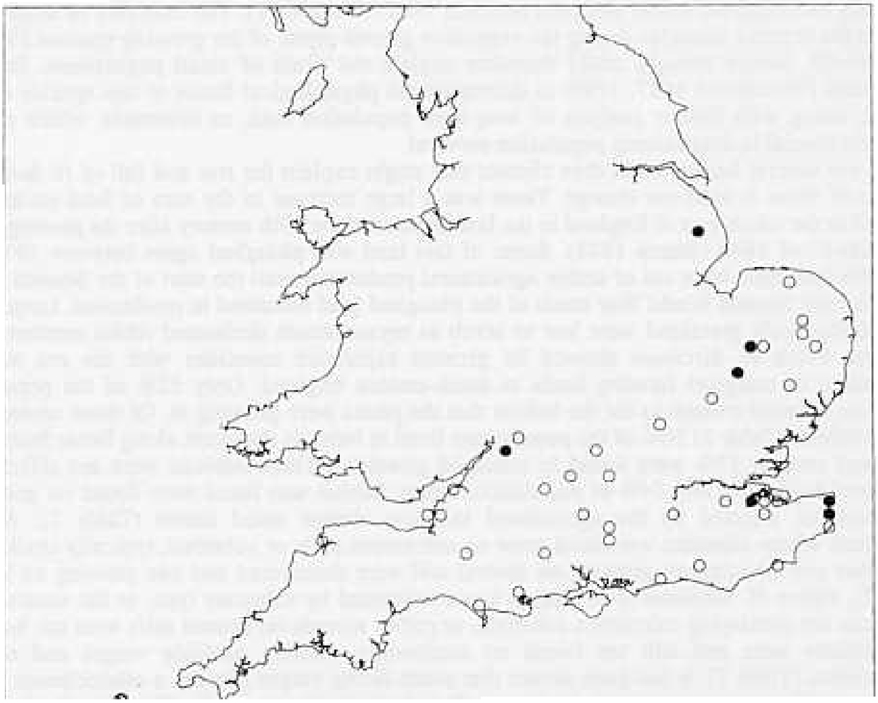

FIGURE 3: The distribution of *Himantoglossum hircinum* in England; a: all records from 1641–1910, b: 1911–1940, c: post 1940. Open circles denote one population, solid circles denote two populations, open triangles 3–5 populations. An open square represents the area around Dartford before 1910 which had 14 populations.

The results of applying the seed pod production index to the rainfall data from 1895–1995 suggested that there was probably a rise in the seed production of *H. hircinum* during the years of the First World War (1914–18) (Fig. 4). This was followed by a second peak around 1930. Subseqently, there was a period of low seed production until the 1970s. Since then there have been three peaks in the seed production index favouring seed production, each peak being higher than the last.

DISCUSSION

Evidently the abundance (Fig. 1) and distribution of *Himantoglossum hircinum* (Fig. 3) increased markedly in the early decades of this century. The reasons why there was such an increase are not easy to determine. The amelioration in the climate proposed by Good is partly supported by the seed production model (Fig. 4). A period of conditions favouring seed production and survival in the second and third decades of this century coincides with the rise in the number of populations and the recent period of high rainfall, and therefore suitable conditions, has lead to the rise in the number of populations from a stable 10 or 11 between 1950 to 1990 to 16 by 1998. What the model does not explain is the decline in the number of populations. There is no obvious climatic cause for the death of populations, although it is possible that temperature could be a factor. However, as temperature could not be related to the performance of *H. hircinum* at the site in southern England between 1977 and 1997 no model could be proposed from those data. The lack of a relationship with temperature at the population in Kent may be because temperature only becomes a limiting factor further north. More detailed analysis of plants growing at the very northern edge of the distribution would be required to gain this information. In the last two years (pers. obs.) mortality has greatly exceeded the levels observed between 1987–94 (Table 1). The mortality of large plants followed the extreme droughts during the vegetative growth phase of the growing seasons 1995–96 and 1996–97. Severe drought could therefore explain the death of small populations. Detailed experiments (Woodward 1987, 1990) to determine the physiological limits of this species will be required, along with further analysis of long-term population data, to determine which climate factors are crucial in determining population survival.

There are several factors other than climate that might explain the rise and fall of *H. hircinum*. The first of these is land-use change. There was a large increase in the area of land set-aside to grassland in the south-east of England in the last decades of the 19th century after the passing of the "Corn Laws" of 1846 (Stamp 1948). Some of this land was ploughed again between 1914 and 1919. This land then went out of arable agricultural production until the start of the Second World War. After the Second World War much of the ploughed land remained in production. Large areas of remaining chalk grassland were lost to scrub as myxomatosis decimated rabbit numbers. The period in which *H. hircinum* showed its greatest expansion coincides with the era of least management of marginal farming lands in south-eastern England. Only 52% of the population records are detailed enough to list the habitat that the plants were growing in. Of those records that do list a habitat (Table 2) 50% of the populations lived in habitats that were along linear features or in pits and another 15% were found in managed grassland. These habitats were not affected by agricultural land-use. Only 14% of populations where habitat was listed were found on grassland that would be affected by the agricultural land-use change listed above (Table 2). All the populations where substrate was listed grew on calcareous soils or substrate, typically chalk, until 1996 when two populations growing on neutral soil were discovered and one growing on tarmac (Table 2). Either *H. hircinum* is becoming less constrained by substrate type, or the neutral soils and tarmac are overlaying calcareous substrate, or earlier records on neutral soils were not listed.

Populations were and still are found on earthworks, notably roadside verges and railway embankments (Table 2). It has been shown that south-facing slopes provide a microclimate that is analogous to flat areas many miles further south in latitude (Pigott 1968). This hypothesis would seem to be supported by the preference of *H. hircinum* for sloping embankments at the northern edge of its range. Unfortunately the theory fails at the large Cambridgeshire colony where most plants are found on the north-eastern facing slope of an earthwork where it is noticeably cooler than other parts of the site. I suggest that disturbance and/or a lack of a dense grass sward probably make earthworks a suitable habitat. The increase in building of roads and railways in the second half of the last century and the early years of this century would have led to a large increase in the available habitat for *H. hircinum* and could explain the increase in the number of populations. The subsequent decline of the species cannot be explained by a subsequent decline in the area of earthworks as road building has continued throughout this century and increased after the Second World War.

A change in "recorder effort" might explain the pattern shown in Fig. 1. It may be no coincidence that the number of populations recorded plummeted just after Good wrote his paper. The recording of plants in England went through a depression during the late 1930s and 1940s but has been relatively consistent and accurate since the end of the Second World War. Therefore, the decline in the number of populations was not necessarily as sudden as that shown in Fig. 1 but may have declined more steadily. The number of populations recorded from about 1948 onwards can be considered reliable.

The pattern of increase in the number (Fig. 1) and distribution (Fig. 3) of populations and the subsequent decline in number but not distribution is similar to patterns described for infectious diseases (Mollison 1986). In the case of *H. hircinum* perhaps there was an "outbreak" caused by an increase in the number of susceptible sites, and the decline was caused by a reduction in the number of susceptible sites. Factors limiting the population biology of diseases can at times be relaxed and allow an outbreak. Similarly the limiting factors on the success of *H. hircinum* may have relaxed at the end of the 19th century. Amenable climatic conditions could have promoted the "outbreak" with a period of less favourable conditions at the end of the 1930s and 1940s detrimentally affecting the population parameters that would have allowed persistence (Mollison 1986). The seed production model provides an explanation for the "outbreak" during the first three decades of this century and a reason why populations did not increase further between 1935 and 1975. The model also suggests that we may be at the beginning of another "outbreak". Further research is required to identify the climatic conditions that might explain the decline in the number of populations.

TABLE 2: THE SUBSTRATE AND LAND-USE ON WHICH *HIMANTOGLOSSUM HIRCINUM* HAS BEEN RECORDED. THE PERCENTAGE OF RECORDS FROM THOSE WHERE SUBSTRATE AND/OR HABITAT WERE LISTED IS GIVEN AS IS THE PERCENTAGE OF THE TOTAL OF 201 SITES. LAND-USE IS SEPARATED INTO MAN-MADE LINEAR FEATURES, PITS, MANAGED GRASSLAND AND "UNMANAGED" GRASSLAND.

	Percentage of listed sites	Percentage of total
SUBSTRATE		
chalk	67·2	19·4
dunes/links	10·3	3·0
limestone	3·4	1·0
coraline oolite	3·4	1·0
glacial sand	1·7	0·5
sand and stones	1·7	0·5
gravel/clay	1·7	0·5
gravel	1·7	0·5
chalky gravel	1·7	0·5
tarmac	1·7	0·5
neutral soil	3·4	1·0
(unlisted 71.1%)		
LAND-USE		
Linear features		
roadside verge	16·7	7·0
path/trackside	3·8	1·5
green lane	7·1	3·0
railway cutting/embankment	7·1	3·0
tarmac	1·2	0·5
wall	1·2	0·5
earthwork	4·8	2·0
Pits		
chalk pit	7·1	3·0
gravel pit	1·2	0·5
Managed grassland		
golf course	8·0	3·5
garden	3·8	1·5
parkland	2·4	1·0
churchyard	1·2	0·5
Unmanaged grassland		
edge of wood	8·0	3·5
edge of scrub/hedgerow	4·8	2·0
grassland	13·7	5·5
common	1·1	0·5
dune slacks	1·1	0·5
beach	1·2	0·5
riverbank	1·2	0·5
heath	1·2	0·5
pasture	1·2	0·5
uncultivated land	1·2	0·5
(unlisted 58.2%)		

The large and rapid increase of *H. hircinum* in England in the early part of this century could also have been due to an increase in the number of seeds arriving from France if the species became much more abundant in France. This theory may be testable but the abundance of *H. hircinum* in France before 1978 is unknown to the author. Changes in the weather of northern France are highly correlated with those of southern England and it is reasonable to assume that seed production in northern France is high in years when it is high in England. If France was the source of the seeds it could be instructive to think of a large core-population in that country with mostly satellite populations in England (Gotelli & Simberloff 1987). Satellite populations seldom reach an adequate size to maintain themselves without further input of individuals.

There is one other seed vector responsible for at least some populations. Many plants were collected, especially from France, and planted in gardens especially in the 19th century; to a lesser extent this is still occurring today. Potential escapes from these introduced plants, and introductions into the wild, make any proposed study of metapopulation dynamics awkward but not impossible. Of course, there were many more movements of people between France and England during the peak seed producing years 1913–1917 than is normal because of military activity. The adhesive properties of the seeds (pers. obs.) may have led to accidental transport of seeds from France during this period.

Populations die out for several reasons. Individuals can apparently be killed by drought. They can be dug-up or picked (Table 3), their habitat can be destroyed or there can be a slow change in the plant community e.g. a grassland may become covered in scrub. Of the 201 populations recorded the fate of 73 can at least partly be deduced from details in the record. Sixteen populations can be considered extant, 40 populations or large parts of populations were picked or dug-up by collectors, six populations died out because of disturbance to the habitat, e.g. ploughing, four were built upon, three became overgrown, two were mown and one was trampled and/or grazed by horses. Curiously, the earliest population recorded was lost in 1641 due to the road becoming wider (Pearsall & Hall 1933). This surely must be the first recorded damage caused to rare wildlife by road improvement.

The two largest populations in England may now be large enough to sustain themselves and act as core-populations unless the habitat in which they live is totally destroyed. As both populations are spread over an area greater than 500 m^2 it would have to be a considerable disturbance event to remove the habitat completely. As both of the sites are managed for the protection of the species, land-use change is also unlikely to cause their demise. In the last three years three new populations have been recorded several kilometres to the north-east of the largest population in Kent and are likely to have originated from seed being carried by the prevailing south-westerly winds from the largest population.

In addition to the three new sites listed above, seven other new populations have been recorded and these are widely scattered over southern England. It is difficult to predict such a distribution from wind dispersal alone as typically most seeds are only predicted to be dispersed up to a few hundred metres (Carey 1998). Three of these populations are on golf courses, one is on a road-side verge, two more populations are on chalk grassland and the last population is growing on broken

TABLE 3: NUMBER OF POPULATIONS PICKED OR DUG-UP IN ENGLAND.

Period	Number of populations	% of populations
	14	
	3	
	8	
	11	

The last population eradicated by this method was in 1952.

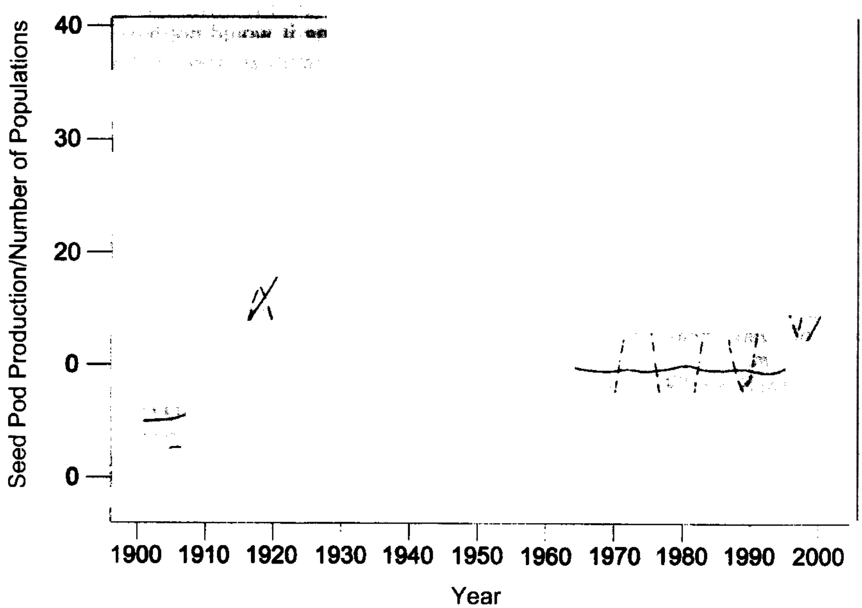

FIGURE 4: The number of populations of *Himantoglossum hircinum* (solid line) compared with the modelled annual seed pod production (advanced by six years) of *H. hircinum* in England (dashed line). Both lines have undergone decadal smoothing.

tarmac. Of the 16 extant populations six are on golf courses. This may indicate that golf courses (especially golf links) provide large areas of suitable habitat for *H. hircinum*. It is certainly possible that golfers provide a vector for the adhesive seeds that are subsequently deposited on other courses.

The protection of this species under law and a change in attitude to the collection of wild plants probably explains the increase in the persistence of populations since the Second World War (Fig. 2). The high percentage of populations picked or dug-up before 1901 (Table 3) is partly related to the fact that the records from this period largely come from herbaria and must have been picked to be placed in the herbaria. At least 19% of all the populations recorded in the 1930s were picked or dug-up (Table 3) which helps to explain why there was such a rapid decline in the number of populations in the late 1930s.

CONCLUSION

It seems that Good (1936) had good reason to believe that it was an amelioration in the climate that lead to the increase in the number of populations of *H. hircinum* in the early part of this century (Fig. 4) although the critical factor was increased rainfall and not temperature. The model created from demographic data collected in southern England showed that two successive wet growing seasons that were not followed by a severe drought were required to produce viable seeds. When the model was extrapolated to the rainfall data for England from 1895–1995, favourable conditions for establishment existed between 1910–1930 and post 1975. These conditions coincide with the peaks in the number of populations recorded in England.

ACKNOWLEDGMENTS

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