

Long-term demographic fluctuations in an orchid species driven by weather: implications for conservation planning

MARION PFEIFER, KERSTIN WIEGAND, WOLFGANG HEINRICH
and GOTTFRIED JETSCHKE

Institute of Ecology, University of Jena, Dornburger Str. 159, 07743 Jena, Germany

Summary

1. Management decisions are increasingly based on matrix models intended to predict the long-term fate of endangered species. However, certain elements of these models, such as life-state transition probabilities (vital rates), are difficult to parameterize and their values may vary depending on external conditions such as weather. Details of how weather might influence population performance are rare, yet necessary to assess the effects of global climate change on a species' distribution.

2. Based on a 26-year data set of a population of *Himantoglossum hircinum* in a nature reserve in Germany, variations of life-history traits and vital rates were studied. Matrix analysis was used to identify the most important life-state transitions for population growth. Multiple linear regression was used to quantify the response of population traits and vital rates to changing weather conditions.

3. Population size increased exponentially and density effects could not be observed. Flowering plants and large plants had the highest and second highest reproductive value, respectively. The population's finite rate of increase fluctuated strongly among years; life-history traits varied strongly and were interlinked, thereby violating the assumptions of matrix modelling in a population viability analysis.

4. Some vital rates and the population growth rate showed a trend over the total period. A certain and sometimes large amount of that variability could be attributed to variability of weather conditions, with warmer winter conditions favouring population performance. Prediction of population size was fairly accurate within a time frame of 10 years, but size class structure was not.

5. *Synthesis and applications.* Matrix modelling proved to be unreliable for predicting long-term population dynamics, despite the long-term data set used for matrix construction. This can be explained by weather-dependent variability of vital rates driving population dynamics. A minimum study period of 4 years is necessary to produce relevant information for model development. Our study emphasizes the need for critical evaluation of management decisions based only on single short-term studies and for studies covering longer time intervals than 2–3 years.

Key-words: climate change, conservation, long-term predictions, protected species, PVA

Journal of Applied Ecology (2006) **43**, 313–324

doi: 10.1111/j.1365-2664.2006.01148.x

Introduction

For successful species conservation, one of the important tasks is to assess the current state of the population

and to understand how plant species respond to natural or management-induced habitat changes (Hegland, Leeuwen van & Oostermeijer 2001). However, plant population dynamics can be highly variable on a short time scale because of varying environmental conditions (e.g. habitat, climate and competitors). Thus, long-term observations are needed to obtain reliable information on life history and population dynamics (Waite & Hutchings 1991; Fieberg & Ellner 2001).

Management decisions are increasingly based on the predictions of matrix models regarding the future fate of a population at a field site. Matrix models are powerful tools for understanding the population dynamics of organisms of differing life forms and habitats (Enright, Franco & Silvertown 1995). Such models are used to determine the most important demographic parameters of the population (Hayward & McDonald 1997), to assess population performance under varying environmental conditions (Ehrlén *et al.* 2005), and to carry out a population viability analysis (PVA; Fieberg & Ellner 2001).

Since the 1990s, PVA has become a popular method for predicting extinction risks for populations of rare species (Boyce 1992; Brook *et al.* 2000; Morris *et al.* 2002). However, PVA is a modelling approach and its validity depends on the model structure and data quality (Beissinger & Westphal 1998; Ellner *et al.* 2002). The number of individuals sampled should be large to ensure accurate estimation of transition sets, and the number of transition rates sampled should be large enough to characterize the environment and its effect on the vital rates (Fieberg & Ellner 2001). It is suggested that predictions of a PVA will only be useful if it is known that the distributions of the population growth rate and vital rates, such as the transition from vegetative phase to reproductive phase, will not change in the future (Coulson *et al.* 2001) and that the timeframe chosen for the prediction is not longer than 10 or 20 years (Ellner *et al.* 2002).

The distribution of a population's vital rates may be profoundly affected by many factors, including habitat change, changes in the community structure and weather variability. Research is required to estimate how changes in these regulating factors influence the distribution of vital rates and population growth rates (Oostermeijer *et al.* 1996; Coulson *et al.* 2001; Ehrlén *et al.* 2005). We do know that changing climate has a profound influence on range expansion and contraction of many species (reviewed by Parmesan *et al.* 1999; McCarty 2001; Pearson & Dawson 2003), consequently weather should also have a strong influence on population performance. The general paucity of high-quality, long-term population data complicates the search and testing of hypotheses in the debate about the interaction between density-dependent and density-independent factors in the regulation of growth and dynamics of populations (Milne 1962; Andrewartha & Birch 1984; Turchin 1990). So far, there are only a few long-term studies, mainly on orchids, showing that weather may influence population development (Willems & Bik 1991; Tamm 1991; Wells *et al.* 1998; Carey 1999).

In this study, we attempted to quantify the influence of weather on population growth and variation in vital rates of *Himantoglossum hircinum* (L.) Sprengel (Orchidaceae). Our study was based on data of more than 13 000 plants, recorded within a population in a nature reserve in Germany from 1976 to 2001 (Heinrich & Voelckel 1999; Heinrich 2000). This long-

term data set provided us with a unique opportunity to investigate regulatory mechanisms in plant population ecology. We expected high variability in vital rates and population traits and tested whether there was a significant relationship between weather conditions in the current/previous years and population performance in terms of variability of vital rates as well as dormancy, mortality and recruitment pattern. Given that most field studies are temporally limited, we also attempted to find the minimum study period required to yield valuable information for the development of matrix models.

More specifically, this study addressed the following main questions. (i) How large is the variation in plant performance (e.g. life span) and population performance (e.g. structure, vital rates and growth)? (ii) How much of the variation in population traits can be attributed to weather variability? (iii) If the variation in population traits is great, how reliable are the predictions of transition matrices for future fate of populations? (iv) Can we recommend a minimum time required for data recording to be able to forecast population structure and growth over the next 10–20 years based on our results?

Methods

STUDY SPECIES

The lizard orchid *H. hircinum* is a conspicuous, long-lived terrestrial orchid that perennates via tubers. Leaves emerge from below-ground tubers in late autumn with the autumn rains, and most plants are apparent by November (Carey 1999). In late April, many of the larger plants start to develop inflorescences. Flowering usually takes place from May to June; vegetative reproduction is rare at our site and in populations in England (Carey 1999). After pollination, seeds take at least 4 weeks to ripen, the first fruits occurring in July. However, the number of flowers produced varies among plants, as does the number of capsules that are produced (Carey, Farrell & Stewart 2002; M. Pfeifer, unpublished data). In 1976, single new plants were observed in the study area.

Himantoglossum hircinum represents a suitable study system for several reasons. Its distribution is known in detail, and long-term data have been collected at our field site. The species is mainly distributed in southern Europe under mediterranean conditions and reaches its north-eastern range in Germany. Mediterranean orchids are known to be frost-sensitive. While temperatures below zero are believed to be a major limiting factor for their distribution, day length seems to be less important. An increase in population abundance and size has been observed in the last few decades in England and Germany (Carey 1996; Heinrich & Voelckel 1999). This northward range shift can probably be attributed to a change in climate as a result of global warming (Good 1936; Carey 1998).

STUDY SITE

Himantoglossum hircinum was studied in the Leutratl nature reserve near Jena (Germany, Thuringia, 50°56' 46" N, 11°35' 35" E), which is part of a landscape characterized by dry calcareous grasslands along the slopes formed by the Saale river. The climate is characterized by mild winters with few periods of frost (Kluge & Müller-Westermeier 2000). From 1961 to 1990, the average annual temperature and rainfall were 9.3 °C and 587 mm, respectively. Temperature as well as precipitation were relatively higher in the following 10 years (1991–2000; mean annual precipitation 612 mm, mean annual temperature 9.9 °C), especially in the winter months. A long-term monitoring site was established by the Institute of Ecology (University of Jena, Jena, Germany) in 1976 to study single plant species' responses to successional change in vegetation cover. The plot covers an area of 1.8 ha along a south-facing slope dominated by grassland communities. The plot has remained unmanaged since 1976, whereas the surrounding grassland has been mown or grazed by sheep annually. Grazing on the plot as a result of deer or other herbivores cannot be excluded but herbivore density is rather low in the area and scrub encroachment is obvious.

LONG-TERM DATA

Annually from 1976 to 2001, all plants of *H. hircinum* found at the monitoring site were labelled with wooden sticks (Heinrich 2000). A 'plant year' was defined as beginning in September of the previous calendar year and ending in August of the year of recording. One plant year was divided into four seasons, autumn (September–November), winter (December–February), spring (March–May), and summer (June–August). In early April, the permanent plot was carefully searched for *H. hircinum* plants and their leaf number counted. The number of sticks with 'missing' plants was recorded. After 2 years absence from the above-ground plant community ('dormancy'), plants were considered dead at the date of the disappearance. In early June, all flowering individuals were recorded and their leaves were individually tallied again because flowering individuals occasionally developed one or two additional leaves between April and June (Heinrich 2000).

INDIVIDUAL TRAITS

We assumed that plants remain below-ground for up to 2 years (dormancy) throughout their life. This problem, which is also well-known for several orchids and other perennial herbs, emphasizes the importance of the time frame of a study (Hutchings, Mendoza & Havers 1998). Because of the problem of dormancy, the complete life cycle is strictly known only for plants first observed in 1979 and last observed in 1998. Age of the individuals already existing in 1976–78 could not be

determined because they might have been alive in previous years. Additionally, it was impossible to know whether plants disappearing in 2000 or 2001 would re-emerge again in 2002. Hence, we calculated life span, meaning the actual length of life of the plants, and other life traits for all individuals known not to exist in 1976, 1977 and 1978, and we excluded those still existing in 1999 or later.

STATE VARIABLES AND MATRIX ANALYSIS

Several models can be constructed incorporating environmental stochasticity and genetic stochasticity. As our study population was neither small (effective population size $n_e \gg 100$) nor characterized by a low intrinsic population growth rate ($r = 0.19$, Pfeifer, Heinrich & Jetschke, 2006), inbreeding depression was believed to have no population-level effects (Mills & Smouse 1994) and genetic stochasticity could be ignored. Because of absence of periodicity in the time series of population size and percentage of flowering plants (tested by calculating the autocorrelation and partial autocorrelation function), density-dependence was ignored in the model. In summary, the application of a basic linear model with a projection matrix **A** was sufficient (Caswell 1982).

In demographic matrix models, the state vector is usually defined by the distribution of individuals among a set of categories (Caswell 1989; Guardia, Raventos & Caswell 2000). A size-based matrix model was constructed because size rather than age accounts for most of the variability in survivorship and reproduction in plant species (Werner 1975), and because individual flowering probability was strongly size-dependent after a threshold leaf size was exceeded (Pfeifer, Heinrich & Jetschke, 2006). We used leaf number as a measure of plant size because leaf number and plant size (summed leaf area) are strongly correlated ($R^2 = 0.87$, $P < 0.001$, $n = 50$). Based on the size and reproductive state of the plants, the orchid population recorded each year was divided into five states (Fig. 1): 1, seeds (*S*); 2, small individuals (one to four leaves) (*SI*); 3, large, sterile individuals (five to 15 leaves) (*LI*); 4, large, flowering individuals (five to 15 leaves) (*FI*); 5, dormant individuals (*D*). Seeds had to be included for methodological reasons, although the number of seeds in the soil could only be estimated.

Information on the seed and protocorm stage is sparse but demographic observations (Carey, pers. comm.) suggest that seed longevity is low in the soil. Seeds may be produced in large numbers (> 1 million in average years) but recruitment of plants is generally much lower. Drought killed whole populations in England but re-establishment from seed banks was not observed in the years thereafter (Carey, pers. comm.). Additionally, Carey & Farrell (2002) reported rotting of seeds because of wet conditions after 2 years.

From one year to the next, it was possible for plants to achieve any change of state between states 2–5. The transition to death was possible from all states but not incorporated into the figure (Fig. 1). From the

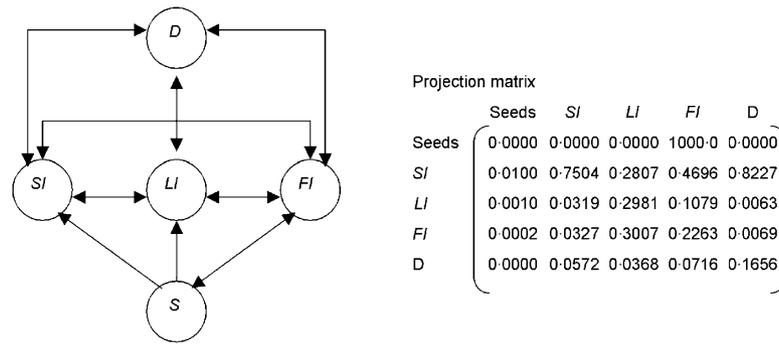


Fig. 1. Life-cycle graphs and projection matrix for *H. hircinum* illustrating the transitions between the size classes *S* (seeds), *SI* (small individuals), *LI* (large individuals), *FI* (flowering individuals) and *D* (dormant individuals). Transition probabilities from *S* to any other state could only be estimated. These estimates were based on literature data and observed fruiting success in 2003 and 2004. The other transition values were calculated and averaged. The first row in the projection matrix indicates the estimated number of seeds produced per average flowering plant (calculated from observed percentage of flowering plants fruiting and fruit set in 2002–04, and under the assumption of a mean number of 500 seeds capsule⁻¹). Transition to death was possible from all states but was not included for graphical reasons.

state-classified life table, a transition matrix was constructed. The values in the transition matrix were the probabilities of survival and transition between states from one year to the next. The probabilities of seed survival and transition from the protocorm stage (after germination of the seeds) to any of the other states could not be measured and were estimated based on suggestions on germination success of plant species. We set the probability to emerge as flowering or large plants from the below-ground protocorm stage as zero. The number of seeds produced per flowering individual was estimated from data in the literature (Carey & Farrell 2002) and the observed fruiting success of plants in 2003 and 2004.

Initially, we calculated mean transition probabilities for the period 1979–99 (Fig. 1). From the transition matrix, we derived the demographic parameters' finite rate of natural increase λ , the relative reproductive values (*RV*), the sensitivity of λ to absolute changes in elements of the projection matrix (Caswell 1982), and the elasticities for each matrix element as a relative measure of the contribution of the elements to λ (de Kroon *et al.* 1986).

To determine the minimum study period required for a reliable assessment of population growth, the temporal variation in λ was calculated for five time scenarios of hypothetical study durations, ranging from 2 to 6 years ($\lambda_1, \lambda_2, \lambda_3, \lambda_4, \lambda_5$). For example, for the 2-year scenario we derived λ from matrices based on transition probabilities between 2 years (λ_1 , 1979–80, 1980–81, and so on) and determined the variation of λ among all 2-year studies. Linear regression was applied to describe the positive trend in λ in all approaches. To correct for the trend in λ , we calculated the residuals as differences between the predicted and the observed values for each time step in the five approaches (λ_{corr1} to λ_{corr5}). We then calculated the variation of λ as the standard deviation of the corrected λ values. We hypothesized that the variation in the corrected values (λ_{corr1} to λ_{corr5}) within studies of the same duration should decrease with an

increase in length of time period chosen for the matrix construction.

To test for the predictive accuracy of the matrix models, we attempted to predict the current population size based on historical data (cf. Brook *et al.* 2000; Coulson *et al.* 2001; McCarthy, Anelman & Possingham 2003). Models parameterized for the period from 1979 to 1990 and for periods under the five scenarios were constructed. A future matrix projection of population stage structure and population size was carried out for the subsequent 20 years. Stage structure in 1990 was taken as the starting point. Predicted values were compared with observed values (between 1990 and 1999) for all models. All matrix analyses were carried out using Poptools version 2.5 (Hood 2004).

ABIOTIC CONTROL OF POPULATION CHARACTERISTICS

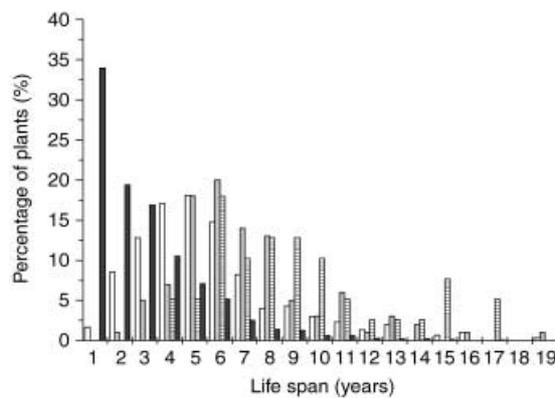
We applied multiple linear regression analyses to assess whether weather conditions have an influence on annual mortality (percentage of plants lost in year *t* relative to the population size in *t* – 1), recruitment (percentage of new plants in *t*), dormancy frequency (annual percentage of plants that stayed below-ground), vital rates and λ . From daily long-term weather data (1978–2001, weather station of Jena), we calculated several weather variables that were thought to be important with regard to the species' biology. Based on monthly, quarterly and annual time periods, we calculated mean temperature, summed precipitation, number of days with soil temperature below 0 °C (soil frost days) and number of days with air temperature below 0 °C for the plant year *t* and the previous plant year *t* – 1. The values of these weather variables were standardized. All regression analyses were carried out using SPSS 11.0. As multiple regression is often affected by collinear relationships (Mac Nally 2000), the resulting models were tested for collinearity among the predictor variables by calculating the variance inflation factor and the tolerance of the

Table 1. Life span calculated for flowering and dormant plants derived from the analysis of all plants observed from 1979 to 1998

	Flowering frequency			Frequency of dormancy events		
	1×	2×	> 2×	1×	2×	> 2×
Mean life span (year)	5.6 ± 3.0	7.1 ± 3.0	9.1 ± 3.4	5.7 ± 2.9	7.4 ± 3.1	10.9 ± 3.0
Number of plants	304	100	39	275	58	14

Table 2. Life span calculated for flowering plants with regard to their dormancy pattern derived from the analysis of all plants observed from 1979 to 1998. D, dormant; ND, not dormant throughout their life

	Flowering frequency					
	1×		2×		> 2×	
Dormancy	D	ND	D	ND	D	ND
Mean life span	9.0 ± 3.1	5.3 ± 2.8	9.9 ± 3.6	6.8 ± 2.7	13.7 ± 3.4	8.7 ± 3.2
Number of plants	23	281	10	90	3	36

**Fig. 2.** Life span of flowering and non-flowering plants. Bars of different colours indicate different flowering frequencies with plants flowering once (white bars), twice (grey bars), three times (hatched bars) and never flowering in their life (black bars). Distribution of life span among plants varied largely but mean life span increased significantly with flowering frequency.

independent predictor variables. Only those models that were not affected by multicollinearity were considered.

Results

PLASTICITY OF LIFE-HISTORY TRAITS

On average, plant size increased linearly with plant age up to an age of 6 years ($R^2 = 0.96$, $P < 0.001$) and size remained constant in later years. However, growth pattern differed strongly among plants (see Table S1 in the Supplementary material). Most plants did not reach the flowering stage (87%, $n = 2867$).

The life span of the plants varied and interacted with other life traits (Fig. 2). Many plants died in their first or second year above ground. The mean life span was 3.4 years, ranging from 1 year ($n = 979$) to 19 years ($n = 2$). The mean life span of flowering plants was longer than that of non-flowering plants, and the higher

the flowering frequency the longer the life ($R^2 = 0.40$, $P < 0.05$, Tables 1 and 2). Life span also increased with the number of dormancy events per plant (Table 1). Life span of flowering plants increased when they stayed below-ground for some time in their life (Table 2).

POPULATION TRAITS

The population started with 45 individuals in 1976 and increased exponentially in the following years (Fig. 3). Recruitment varied considerably among years, and the annual age class structure of the population was dominated by 1–3-year-old plants (Fig. 4).

Small plants (one to four leaves), which were not able to flower, largely dominated the size class structure of the population in any year (Fig. 5). The proportion of flowering and dormant plants showed no significant increase or decrease over the total period ($P > 0.05$) but varied strongly among years (Fig. 5).

TRANSITION PROBABILITIES AND MATRIX ANALYSIS

The population's finite rate of increase derived from the transition matrix for the total period added up to 1.23. The relative contribution of flowering plants and large plants to reproduction was $RV_{FI} = 68.1\%$ and $RV_{SI} = 21.7\%$, respectively. Elasticity values were highest for the transitions S to SI , SI to SI , SI to FI and LI to FI , in decreasing importance (Table 3).

Vital rates varied considerably throughout the years (Fig. 6). Besides the high variation in lambda among years (Fig. 7), there was a significant overall positive increase in lambda that equated to the exponential increase in the population. The SD of the λ_{corr} values decreased from the 2-year approach ($\lambda_{\text{corr}1}$, $n = 20$, $SD = 0.180$) to the 3-year approach ($\lambda_{\text{corr}2}$, $n = 10$, $SD = 0.143$) and 4-year approach ($\lambda_{\text{corr}3}$, $n = 6$, $SD = 0.109$), indicating a decrease of uncertainty with increasing time period of measurements. However, the SD did not decrease

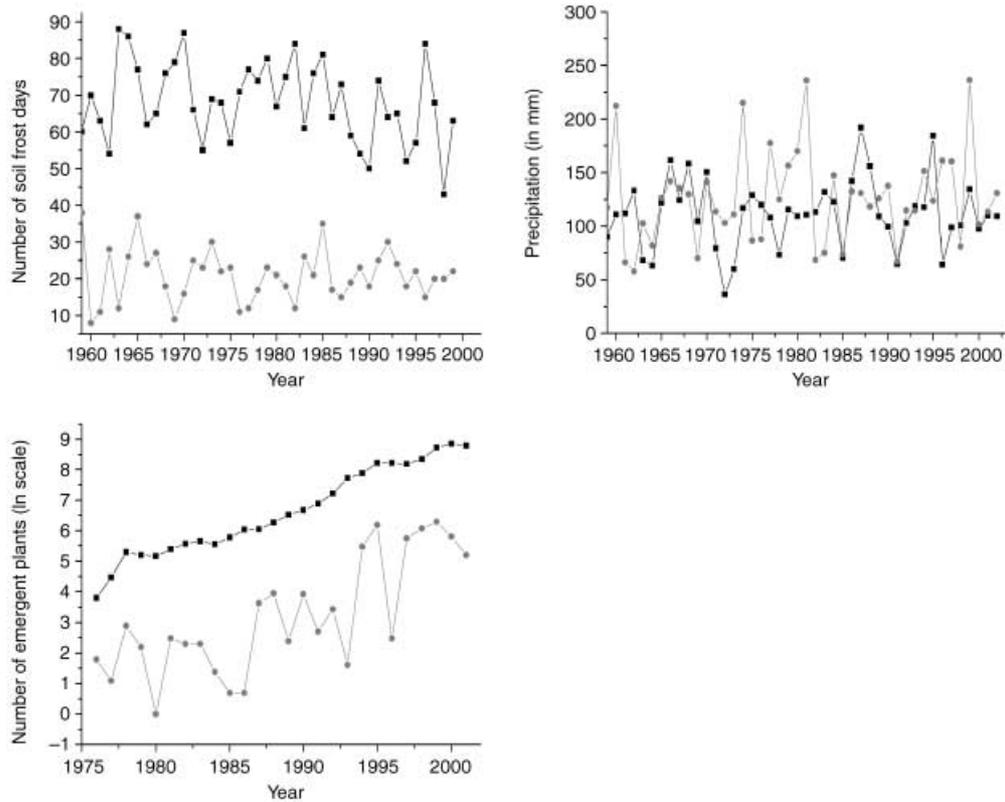


Fig. 3. Temporal development of key climatic variables (above) and population size (below). The figure shows the variation in the number of days with soil temperature below 0 °C (soil-frost days, SFD) in winter (squares) and autumn (circles). SFD in winter decreased significantly from 1990 to 2000. Precipitation in autumn (squares) and winter (circles) fluctuated strongly, with a rather wet winter from 1990 to 2001 (except in 1996). According to the increase in number of plants (squares), the number of plants flowering (circles) increased as well, although varying strongly.

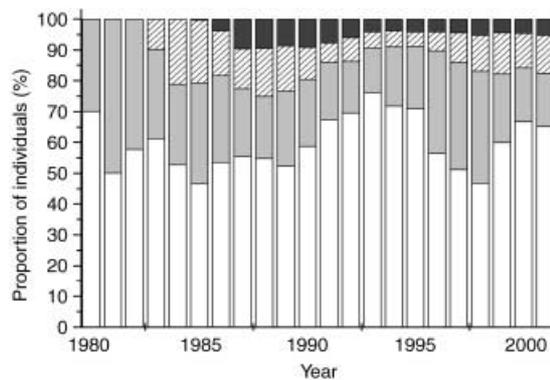


Fig. 4. Temporal development of age class structure of the population from 1979 to 1999. Plants were grouped into four age classes: age class 1, 1–3 years (white bars); 2, 4–7 years (grey bars); 3, 8–10 years (hatched bars); 4, > 10 years (black bars).

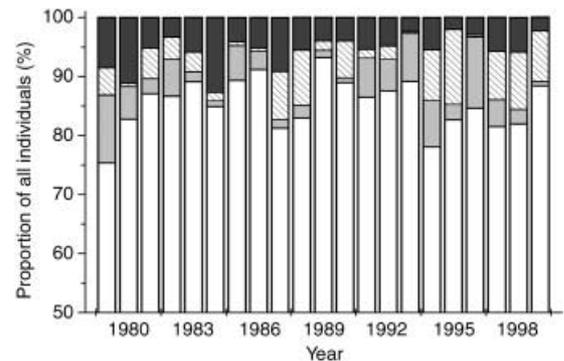


Fig. 5. Temporal development of size class structure of the population from 1979 to 1999. The scale of the y-axis starts at 50% for graphical reasons. Plants were classified into four size classes based on size and reproductive state of the plants: size class 1–*SI*, 1–4 leaves (white bars); 2–*LI*, 5–15 leaves not flowering (grey bars); 3–*FI*, 5–15 leaves flowering (hatched bars); 4–*D*, dormant (black bars).

further in the 5-year (λ_{corr4} , $n = 5$, $SD = 0.104$) and six-year (λ_{corr5} , $n = 4$, $SD = 0.107$) approaches.

The predicted total population size based on the matrix model (1979–90) was highly correlated with the observed population size between 1990 and 1999 (Table 4). However, the predicted and observed annual numbers of plants in the stages differed strongly (Table 4), for example the number of flowering or large plants

was either under- or overestimated by the projection model. Accuracy values indicated a high predictive quality of the model only for individuals in stage *SI* (Table 4). Model predictions for population size and structure based on the five hypothetical approaches were highly inaccurate (see Table S2 in the Supplementary material).

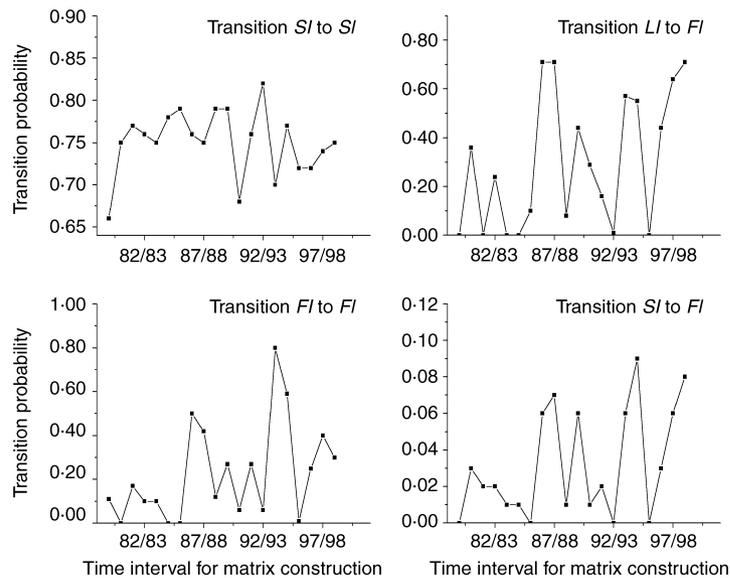


Fig. 6. Temporal development of selected vital rates. Annual transition probabilities from *SI* (small individuals, 1–4 leaves) to *SI*, *LI* (large individuals, 5–15 leaves, not flowering) to *FI* (flowering individuals, 5–15 leaves), *FI* to *FI*, and *SI* to *FI* are shown.

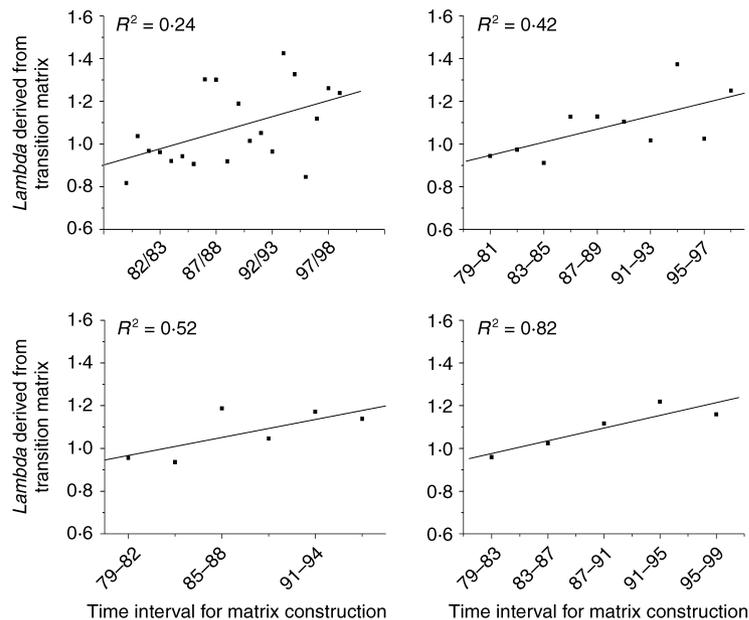


Fig. 7. Temporal variation in λ calculated for four scenarios of hypothetical study durations, ranging from 2 to 5 years (λ_1 , λ_2 , λ_3 , λ_4). There was a significant, positive trend in λ over the total period.

ABIOTIC CONTROL OF POPULATION TRENDS

Key climatic variables driving variability in vital rates were precipitation in winter and autumn as well as the number of soil frost days in winter and autumn (Table 5). Lambda was negatively influenced by low temperatures in winter of the present year and in autumn of the previous plant year. We found a weak correlation between precipitation in spring $t - 1$ and recruitment (Table 5). The low predictive quality of the model explaining annual mortality in t by precipitation

in $t - 1$ increased largely if the two strong outliers, 1979 and 1990, were ignored.

Alternative models were found in two cases. There was a significant positive correlation between precipitation in December $t - 1$ and the transition from *SI* to *FI* ($R^2 = 0.38$, $P < 0.01$). There was a negative significant correlation between soil frost days in winter t and the transition from *FI* to *FI* ($R^2 = 0.30$, $P < 0.05$). No significant correlation was detected between any other transition probabilities and any of the standardized monthly, quarterly and annual weather variables.

Table 3. Outcome of the (a) sensitivity analysis and (b) elasticity analysis based on the transition matrix (Fig. 1). Sensitivity measures the impact on λ of changing the absolute magnitude of a particular vital rate relative to changing other vital rates (Caswell 1982), while elasticity analysis calculates the proportional sensitivity of λ to changes in a vital rate (de Kroon *et al.* 1986). The higher the elasticity value of the vital rate is, the higher the relative contribution of that vital rate to the finite rate of increase of the population λ . Bold letters indicate life transitions that contribute most to λ .

	<i>S</i>	<i>SI</i>	<i>LI</i>	<i>FI</i>	<i>D</i>
(a)					
<i>S</i>	0.000	0.000	0.000	0.0003	0.000
<i>SI</i>	17.334	0.369	0.031	0.023	0.021
<i>LI</i>	67.516	1.437	0.121	0.089	0.081
<i>FI</i>	211.401	4.499	0.379	0.279	0.253
<i>D</i>	0.000	0.298	0.025	0.018	0.017
Σ	296.252	6.602	0.556	0.410	0.371
(b)					
<i>S</i>	0.000	0.000	0.000	0.215	0.000
<i>SI</i>	0.131	0.2010	0.007	0.008	0.013
<i>LI</i>	0.051	0.035	0.027	0.007	0.000
<i>FI</i>	0.032	0.111	0.086	0.048	0.001
<i>D</i>	0.000	0.013	0.001	0.001	0.002
Σ	0.215	0.369	0.121	0.279	0.017

Discussion

PLASTICITY OF THE PLANT'S LIFE HISTORY

Protocorms of *H. hircinum* plants grow below-ground for up to 3 (Carey & Farrell 2002) or even 5 (W. Heinrich, personal observation) years. The first stage of terrestrial orchid species is under-ground, complicating the analysis of the biology of the early life history (Rasmussen & Whigham 1998; Batty *et al.* 2001). Above-ground,

the typical plant increases in size in the first years of pre-maturity, until it flowers after 4 or 5 years of resource accumulation. However, we observed high variability in life-history traits of *H. hircinum*.

The average half-life of the cohorts was only 4.9 years, but some plants can live for up to 19 years and longer. Dormancy has been observed but was not common among the plants. Some plants re-emerge in the autumn after flowering. Many of them are much smaller then, probably because they have used up a considerable part of the resources stored in the tuber for the reproductive activity. Few of the largest plants flowered in a sequence of years. However, more than 80% of the plants did not reach the flowering stage. Most plants did not live longer than 2 (47%, $n = 3310$) or 3 (63%) years of above-ground emergence because of high juvenile mortality caused by extreme weather events or herbivore pressure.

The increase in life span with flowering frequency (Table 1) seems surprising, as we observed high reproductive effort in this species (M. Pfeifer, W. Heinrich & G. Jetschke, 2006). However, the number of plants flowering more than twice in their life was low. These plants might have experienced especially favourable microhabitat conditions. Some of the flowering plants increased their fitness by escaping temporally unfavourable conditions via dormancy, thereby causing part of the positive correlation between life expectancy and flowering frequency (Table 2).

POPULATION PERFORMANCE

The population in the nature reserve Leutratal was characterized by high annual recruitment. Accordingly, the population was dominated by a large number of small plants. Nevertheless, we might have underestimated

Table 4. Predicted population size and population structure for the next nine time steps based on the matrix model using mean values from 1979 to 1990 compared with observed population size and structure between 1990 and 1999. The strength of correlation between observed and predicted numbers in each stage is indicated by the R^2 values, while the accuracy (Acc.) values were calculated for time step 5 (predicted) compared with 1994 (Acc. 1) and time step 9 (predicted) compared with 1999 (Acc. 2). Values close to zero indicate a high predictive quality of the model. R^2 (observed vs. predicted), accuracy = $(100 \times (\text{predicted} - \text{observed})/\text{observed})$

Time step	<i>SI</i>		<i>LI</i>		<i>FI</i>		<i>D</i>		Total	
	Predicted	Observed								
0	733	733	8	8	50	50	33	33	824	824
1	697	898	29	69	38	15	54	56	818	1038
2	1108	1251	75	78	47	31	57	69	1286	1429
3	1324	2059	83	190	69	5	86	55	1562	2309
4	1617	2189	101	222	84	240	106	153	1908	2804
5	2091	3168	134	103	105	486	130	76	2459	3833
6	2649	3258	170	466	134	12	167	113	3119	3849
7	3342	3122	213	177	170	313	211	219	3937	3831
8	4240	3699	271	114	215	434	267	267	4993	4514
9	5375	5598	344	49	273	540	338	145	6329	6332
10	6808		435		345		429		8017	
20	72632		4643		3684		4576		85536	
R^2	0.91		0.91		0.01*		0.6		0.57	
Acc. 1	-34.0		30.4		-78.5		70.7		-35.8	
Acc. 2	-4.0		601.5		-49.5*		133.41		-0.04	

*Not significant ($P > 0.05$).

Table 5. Models to predict variation in several population traits and transition probabilities between life states calculated using multiple linear regression analysis. *PR*, precipitation; *SFD*, number of days with soil temperature below 0 °C; *TE*, temperature; *SI*, small plants (1–4 leaves); *FI*, flowering plants; *l*, finite rate of increase; (+) positive coefficient; (–) negative coefficient

Target variable	Predictor variable(s)	R ² values	P
Recruitment	<i>PR</i> in spring $t - 1$ (–)	0.21	< 0.05
Mortality	<i>PR</i> in $t - 1$ (+)	0.23 (0.73*)	< 0.05 (< 0.001)
% dormant	<i>SFD</i> in October $t - 1$ (–) and <i>PR</i> in November t (–)	0.41	< 0.01
Transition <i>SI</i> to <i>FI</i>	<i>SFD</i> in winter t (–) and <i>PR</i> in autumn t (+)	0.45	< 0.01
Transition <i>LI</i> to <i>LI</i>	<i>SFD</i> in autumn t (+) and <i>PR</i> in winter t (–)	0.48	< 0.01
Transition <i>LI</i> to <i>FI</i>	<i>SFD</i> in winter t (–) and <i>SFD</i> in autumn t (–)	0.45	< 0.01
Transition <i>FI</i> to <i>FI</i>	<i>PR</i> in winter t (+) and <i>TE</i> in autumn $t - 1$ (–)	0.56	< 0.01
Rate of increase λ	<i>TE</i> in autumn $t - 1$ (+) and <i>SFD</i> in winter t (–)	0.51	< 0.01

*The years 1979 and 1990, which were indicated as outliers, and hence excluded in this model.

recruitment because the probability of missing small plants is high, especially in tall grass. Kéry & Gregg (2003) showed that the detectability of plants is life-state dependent, for example averaging only 82% for vegetative individuals, although it is much higher for flowering plants.

The annual proportions of flowering and dormant plants varied greatly. We are aware that an overestimation of dormancy frequency is likely. Most of the plants recorded as dormant in our study were marked ($n = 924$, 70.4%) and usually all sticks were found during the census. However, during extreme winter conditions leaves of particularly larger plants could have died back, consequently these plants would be recorded as absent during the annual census in April. This problem was also discussed by Wells & Cox (1991) in their 10-year study on *Ophrys apifera* and may explain part of the observed great variability in dormancy frequency between years.

Variation in flowering pattern has been observed for several orchid species, and has caused quite a debate about the factors responsible for it (Inghe 1990; Wells *et al.* 1998; Kindlmann & Balounova 1999). Flowering percentage of *H. hircinum* appears to depend largely on the weather of the present and previous years. This influence is mainly an indirect one via its effect on the size of the plants. However, weather appears also to affect directly the flower initial (Pfeifer, Heinrich & Jetschke, 2006), which is produced 1 year prior to flowering (Carey & Farrell 2002). Management actions attempting to increase flowering frequency might be less important in orchids because the large number of seeds produced by orchids can compensate for low flowering frequencies in unfavourable years. However, taking the matrix analysis results into account, it seems worthwhile to improve conditions for large and flowering plants by weeding out competing plants, which means scrub removal approximately every 5 years.

PLASTICITY OF VITAL RATES AND MATRIX ANALYSIS

Large plants and flowering plants contribute most to population growth. We do not know yet whether

offspring survival of large plants is greater than that of small plants. However, the size of the pods appears to be crucial (Carey & Farrell 2002) and, because larger plants produce larger pods, the seeds are also likely to be more vital (Carey, personal communication).

The observed fluctuations in population stage structure, vital rates related to reproduction, and consequently the fluctuations in annual λ values are probably caused by weather variability. A change in weather towards more favourable conditions at the range margin of *H. hircinum* is probably responsible for the overall positive increase in the population's finite rate on increase. Similar observations have been made for populations in England (Carey, personal communication). Less severe frost in winter and increased rainfall favoured population performance, confirming suggestions of other authors who attributed the range increase of *H. hircinum* in England to climate change (Good 1936; Carey 1999). Plants emerge with the autumn rains and thus drought and soil frosts in autumn may force the plants to stay below-ground during that season to increase their own fitness. We found that plants emerging early grew faster and reached a greater final size than late-emerging plants. Winter temperature has increased in the area during the last decade, probably permitting higher survival probability and especially larger photosynthetic activity of small and flowering plants. The latter enables the plant to store sufficient resources in below-ground structures, thereby increasing the plants' likelihood of flowering in the next year. However, early emerging plants also take a high risk. Orchid species are frost-sensitive. Soil frosts can damage roots, thereby negatively affecting resource uptake. Temperatures below 0 °C in autumn and winter can cause blackening and die-back of leaves, thereby preventing large plants from flowering. This is in line with our observation that high rainfall and warmer temperatures in winter coincide with an increased probability of flowering plants flowering again without a break, despite the high costs of reproduction in *H. hircinum*. The correlation between recruitment and spring precipitation was rather weak and an ecological explanation of that correlation is missing. The long time period

between germination of the seeds and emergence of the first leaves above-ground in combination with a lack of knowledge about seed bank dynamics of *H. hircinum* makes it difficult to find a direct and clear influence of weather on recruitment probability.

Weather has been repeatedly reported to influence size, flowering probability and survival of orchids (Inghe & Tamm 1988; Wells & Cox 1991; Wells *et al.* 1998; Carey & Farrell 2002). Density-independent factors are likely to be major drivers for population dynamics in plants at the range margin, although density-dependent regulation may occur (Wills *et al.* 1997; Gillman & Dodd 2000; Freckleton *et al.* 2003). Many researchers do not doubt that density dependence exists, but the importance of density dependence in determining population size might be rather low (Milne 1962). More long-term data sets need to be thoroughly checked using established time series techniques, for example autocorrelation and partial autocorrelation functions.

Waite & Hutchings (1991) emphasized the importance of long-term observations for obtaining reliable results in a matrix analysis to predict long-term population size. Long-term studies encompassing a broad range of weather conditions and spatial variability enhance the validity of the estimates of demographic parameters and consequently of the population projections (Hunt 2001). We showed that λ fluctuated strongly among years (Fig. 7) and that, depending on the years one chooses for matrix construction, one could predict extinction ($\lambda < 1$) or growth ($\lambda > 1$) of the population. Based on data covering 11 years, we were able to project correctly the population size into the next 9 years. However, model predictions were highly inaccurate for population structure, especially for the estimated numbers of plants in the stages *FI* and *LI*. Based on our results, we suggest that, given a large sampled area, a minimum time period of 4 years is needed to parameterize a PVA model (Fieberg & Ellner 2001). While λ was predicted fairly well using transition matrices for short time intervals, simulated projection of population size and structure into the future significantly differed from real observations.

CONCLUSIONS

To our knowledge, this is one of the first papers that show the large extent to which λ and vital rates fluctuate because of weather variability. These results might be general for other orchids. We found great variability in the vital rates of *H. hircinum* and were able to explain a considerable part of this variation in weather variability. It is important to realize that the population studied was a peripheral one, and information on variation in dynamics of central populations is not yet available. Several studies have considered weather as a major factor influencing population traits of orchids (Wells & Cox 1991; Wells *et al.* 1998; Carey 1999; Carey, Farrell & Stewart 2002). This seems an important

point if management of an endangered species is to be attempted. A field survey covering only 2 or 3 unfavourable years in terms of weather might lead to completely wrong conclusions about the species' future fate at a site. The influence of weather might also mask the outcome of comparisons among various management strategies. If weather drives the vital rates of a species, estimates of the future fate of this species require long-term field surveys that cover years differing in their weather conditions (Hunt 2001). Even then, prediction of size class distributions are difficult at any temporal scale. As suggested by other authors, using PVA to predict absolutely long-term risk of a population is not very useful, whether stochasticity is incorporated into the models or not (Fieberg & Ellner 2001). Risk estimates for longer time intervals (> 50 years) are increasingly imprecise because the predicted long-term risk is extremely sensitive to the estimated mean growth rate (Fieberg & Ellner 2001; Ellner *et al.* 2002), which may vary greatly among years, as shown in this study. However, if short-term predictions are made, model accuracy might be sufficient (Brook *et al.* 2000), as long as data quality is high. While the temporal predictive power of matrix modelling can be doubted (Beissinger & Westphal 1998), transition matrix analysis remains an important tool for comparative analyses studying the influence of local habitat characteristics on species performance (Grigulis *et al.* 2001; Hegland, Leeuwen van & Oostermeijer 2001), ranking the importance of several management regimes for population dynamics (Lindenmayer & Possingham 1996; Grigulis *et al.* 2001; McCarthy, Andelman & Possingham 2003; Brys *et al.* 2004; Ehrlén *et al.* 2005) and determining life-history variation in response to successional change in vegetation cover (Valverde & Silvertown 1998).

Acknowledgements

We acknowledge the help in the field by many people too numerous to list. We thank Gerhard Kluge and Gerhard Daut for the provision of the weather data used in the regression analysis. We acknowledge Jens Schumacher for statistical advice, and we thank Markus Wagner, Katrin Meyer, Vicky Temperton, Andrew Davis, Pete Carey, the editorial team of the *Journal of Applied Ecology*, and three anonymous referees for helpful comments on the manuscript. The long-term monitoring was started by the Institute of Ecology (University of Jena) and was partly funded by the Thüringer Landesanstalt für Umwelt und Geologie and the Arbeitskreis Heimische Orchideen Thüringen. The work was part of a PhD project funded by a studentship of the federal state Thuringia.

References

- Andrewartha, H.G. & Birch, L.C. (1984) *The Ecological Web*. University of Chicago Press, Chicago IL.
- Batty, A.L., Dixon, K.W., Brundrett, M. & Sivasitharnpararn, K. (2001) Constraints to symbiotic germination of terrestrial

- orchid seed in a mediterranean bushland. *New Phytologist*, **152**, 511–520.
- Beissinger, S.R. & Westphal, M.I. (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, **62**, 821–841.
- Boyce, M. (1992) Population viability analysis. *Annual Review of Ecology and Systematics*, **23**, 481–506.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akcakaya, H.R. & Frankham, R. (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature*, **404**, 385–387.
- Brys, R., Jacquemyn, H., Endels, P., de Blust, G. & Hermy, M. (2004) The effects of grassland management on plant performance and demography in the perennial herb *Primula veris*. *Journal of Applied Ecology*, **41**, 1080–1091.
- Carey, P.D. (1996) DISPERSE: A cellular automaton for predicting the distribution of species in a changed climate. *Global Ecology and Biogeography Letters*, **5**, 217–226.
- Carey, P.D. (1998) Modelling the spread of *Himantoglossum hircinum* (L.) Spreng. at a site in the south of England. *Botanical Journal of the Linnean Society*, **126**, 159–172.
- Carey, P.D. (1999) Changes in the distribution and abundance of *Himantoglossum hircinum* (L.) Sprengel (Orchidaceae) over the last 100 years. *Watsonia*, **22**, 353–364.
- Carey, P.D. & Farrell, L. (2002) *Himantoglossum hircinum* (L.) Sprengel. *Journal of Ecology*, **90**, 206–218.
- Carey, P.D., Farrell, L. & Stewart, N.F. (2002) The sudden increase in the abundance of *Himantoglossum hircinum* in England in the past decade and what has caused it. *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations* (eds P. Kindlmann, J.H. Willems & D. Whigham), pp. 187–208. Backhuys, Leiden, the Netherlands.
- Caswell, H. (1982) Stable population structure and reproductive value for populations with complex life cycles. *Ecology*, **63**, 1223–1231.
- Caswell, H. (1989) *Matrix Population Models*. Sinauer, Sunderland, MA.
- Coulson, T., Mace, G.M., Hudson, E. & Possingham, H. (2001) The use and abuse of population viability analysis. *Trends in Ecology and Evolution*, **16**, 219–221.
- Ehrlén, J., Stryjänen, K., Leimu, R., Garcia, M.B. & Lehtilä, K. (2005) Land use and population growth of *Primula veris*: an experimental demographic approach. *Journal of Applied Ecology*, **42**, 317–326.
- Ellner, S.P., Fieberg, J., Ludwig, D. & Wilcox, C. (2002) Precision of population viability analysis. *Conservation Biology*, **16**, 258–261.
- Enright, N.J., Franco, M. & Silvertown, J. (1995) Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. *Oecologia*, **104**, 79–84.
- Fieberg, J. & Ellner, S.P. (2001) Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters*, **4**, 244–266.
- Freckleton, R.P., Silva Matos, D.M., Bovi, M.L.A. & Watkinson, A.R. (2003) Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvesting for a tropical palm tree. *Journal of Applied Ecology*, **40**, 846–858.
- Gillman, M.P. & Dodd, M. (2000) Detection of delayed density dependence in an orchid population. *Journal of Ecology*, **88**, 204–212.
- Good, R. (1936) On the distribution of lizard orchid (*Himantoglossum hircinum* Koch). *New Phytologist*, **35**, 142–170.
- Grigulis, K., Sheppard, A.W., Ash, J.E. & Groves, R.H. (2001) The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology*, **38**, 281–290.
- Guardia, R., Raventos, J. & Caswell, H. (2000) Spatial growth and population dynamics of a perennial tussock grass (*Achnatherum calamagrostis*) in a badland area. *Journal of Ecology*, **88**, 950–963.
- Hayward, G.D. & McDonald, D.B. (1997) Matrix population models as a tool in development of habitat models. *Biology and Conservation of Owls of the Northern Hemisphere* (eds J.R. Duncan, D.H. Johnson, T.H. Nicholls), pp. 205–212. General Technical Report NC-190. US Forest Service, Winnipeg, Manitoba, Canada.
- Hegland, S.J., van Leeuwen, M. & Oostermeijer, J.G.B. (2001) Population structure of *Salvia pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. *Journal of Applied Ecology*, **38**, 1277–1289.
- Heinrich, W. (2000) Die Bocks-Riemenzunge (*Himantoglossum hircinum*) – Langzeitbeobachtungen auf markierten Dauerflächen. Heimische Orchideen. *Artenmonitoring und Langzeitbeobachtung, Populationsdynamik und Artenschutz* (ed. Arbeitskreis Heimische Orchideen), pp. 36–48. Uhlstädt, Germany.
- Heinrich, W. & Voelckel, H. (1999) Die Bocks-Riemenzunge [*Himantoglossum hircinum* (L.) Spreng.] – Orchidee des Jahres 1999. *Berichte Aus den Arbeitskreisen für Heimische Orchideen*, **16**, 83–123.
- Hood, G. (2004) *Poptools*, Version 2-6-2. <http://www.cse.csiro.au/poptools>, Accessed 2 April 2004. CSIRO, Canberra, Australia.
- Hunt, L.P. (2001) Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology*, **38**, 238–252.
- Hutchings, M.J., Mendoza, A. & Havers, W. (1998) Demographic properties of an outlier population of *Orchis militaris* L. (Orchidaceae) in England. *Botanical Journal of the Linnean Society*, **126**, 95–107.
- Inghe, O. (1990) Computer simulations of flowering rhythms in perennials: is there a new area to explore in the quests for chaos? *Journal of Theoretical Biology*, **14**, 449–469.
- Inghe, O. & Tamm, C.O. (1988) Survival and flowering of perennial herbs. V. Patterns of flowering. *Oikos*, **51**, 203–219.
- Kéry, M. & Gregg, K.B. (2003) Effects of life-state on detectability in a demographic study of the terrestrial orchid *Cleistes bifaria*. *Journal of Ecology*, **91**, 265–273.
- Kindlmann, P. & Balounova, Z. (1999) Flowering regimes of terrestrial orchids: unpredictability or regularity? *Journal of Vegetation Science*, **10**, 269–273.
- Kluge, G. & Müller-Westermeier, G. (2000) *Das Klima ausgewählter Orte der Bundesrepublik Deutschland: Jena*. Berichte des Deutschen Wetterdienstes No. 213. Deutscher Wetterdienst, Offenbach, Germany.
- de Kroon, H., Plaiser, A. & van Groenendael, J. Caswell, H. (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology*, **67**, 1427–1431.
- Lindenmayer, D.B. & Possingham, H.P. (1996) Ranking conservation and timber management options for Leadbeater's possum in southeastern Australia using population viability analysis. *Conservation Biology*, **10**, 235–251.
- Mac Nally, R. (2000) Regression and model-building in conservation biology, biogeography and ecology: the distinction between and reconciliation of 'redictive' and 'explanatory' models. *Biodiversity and Conservation*, **9**, 655–671.
- McCarthy, M.A., Andelman, S.J. & Possingham, H.P. (2003) Reliability of relative predictions in population viability analysis. *Conservation Biology*, **17**, 982–989.
- McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology*, **15**, 320–331.
- Mills, L.S. & Smouse, P.E. (1994) Demographic consequences of inbreeding in remnant populations. *American Naturalist*, **144**, 412–431.
- Milne, A. (1962) On the theory of natural control of insect population. *Journal of Theoretical Biology*, **3**, 19–50.
- Morris, W.F., Bloch, P.L., Hudgens, B.R., Moyle, L.C. & Stinchcombe, J.R. (2002) Population viability analysis in

- endangered species recovery plans: past use and future improvements. *Ecological Applications*, **12**, 708–712.
- Oostermeijer, J.G.B., Brugman, M.L., den Boer, E.R. & den Nijs, H.C.M. (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology*, **84**, 153–166.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Killberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Pfeifer, M., Heinrich, W. & Jetschke, G. (2006) Climate, size, and flowering history determine flowering pattern of an orchid. *Botanical Journal of the Linnean Society*, 2006.
- Rasmussen, H.N. & Whigham, D. (1998) The underground phase: a special challenge in studies of terrestrial orchid populations. *Botanical Journal of the Linnean Society*, **126**, 49–64.
- Tamm, C.O. (1991) Behaviour of some orchid populations in a changing environment. Observations on permanent plots, 1943–90. *Population Ecology of Terrestrial Orchids* (eds T.C.E. Wells, J.H. Willems), pp. 1–14. SPB Publishing, The Hague, the Netherlands.
- Turchin, P. (1990) Rarity of density dependence or population regulation with lags. *Nature*, **344**, 660–662.
- Valverde, T. & Silvertown, J. (1998) Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle. projection matrix analysis. *Journal of Ecology*, **86**, 545–562.
- Waite, S. & Hutchings, M.J. (1991) The effects of different management regimes on the population dynamics of *Ophrys sphegodes*: analysis and description using matrix models. *Population Ecology of Terrestrial Orchids* (eds T.C.E. Wells, J. H. Willems), pp. 161–175. SPB Publishing, The Hague, the Netherlands.
- Wells, T.C.E. & Cox, R. (1991) Demographic and biological studies on *Ophrys apifera*: some results from a 10 years study. *Population Ecology of Terrestrial Orchids* (eds T.C.E. Wells, J.H. Willems), pp. 47–62. SPB Publishing, The Hague, the Netherlands.
- Wells, T.C.E., Rothey, P., Cox, R. & Bamford, S. (1998) Flowering dynamics of *Orchis morio* L. and *Herminium monorchis* (L.) R.Br. at two sites in eastern England. *Botanical Journal of the Linnean Society*, **126**, 39–48.
- Werner, P.A. (1975) Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia*, **20**, 197–201.
- Willems, J.H. & Bik, L. (1991) Long-term dynamics in a population of *Orchis simia* in the Netherlands. *Population Ecology of Terrestrial Orchids* (eds T.C.E. Wells, J.H. Willems), pp. 33–45. SPB Publishing, The Hague, the Netherlands.
- Wills, C., Condit, R., Foster, R.B. & Hubbell, S.P. (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Science USA*, **94**, 1252–1257.

Received 7 July 2005; final copy received 24 November 2005

Editor: Phil Hulme

Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Table S1. Variation in the growth pattern of flowering ($N = 443$) and non-flowering ($N = 2867$) plants from 1979 to 1998.

Table S2. Model predictions for population size a structure based on the five hypothetical approaches.