

Dormancy is associated with decreased adult survival in the burnt orchid, *Neotinea ustulata*

RICHARD P. SHEFFERSON and KADRI TALI*

Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba 305-8687 Japan, and *Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Riia 181, Tartu 51014, Estonia

Summary

1 Prolonged dormancy, a condition in which herbaceous perennial plants do not sprout for more than a year, has only been described to any great extent in long-lived clonal species, particularly in the family Orchidaceae. However, some short-lived, partly clonal or non-clonal perennials also experience dormancy, and their shorter life spans and reduced or absent clonality may change the life history costs and benefits of this phenomenon.

2 We explored the life history context of dormancy in one such plant, *Neotinea ustulata*. A total of 1013 plants were monitored in five populations across Estonia between 1993 and 2005. Cormack–Jolly–Seber (CJS) and multistate analyses, two statistical methods to estimate demographic parameters in open populations, were conducted to estimate the probabilities of survival, dormancy and state transition among flowering, vegetative and dormant states among the populations.

3 The best-fit CJS model suggested that dormancy varied among populations unpredictably, while survival varied in parallel among populations across time. Mean survival was 0.727 ± 0.115 (\pm SE) and mean dormancy was 0.543 ± 0.129 .

4 Multi-state analyses suggested that survival varied in parallel with life history state across all populations, with flowering plants surviving almost completely (0.999 ± 0.007) and dormant plants being the least likely to survive (0.684 ± 0.042). Vegetative plants were found to be intermediate (0.793 ± 0.051). All plants were likely to revert to a dormant state (range 0.451 ± 0.085 – 0.812 ± 0.053).

5 Dormancy appears to be maladaptive in *N. ustulata*, although we suggest that it may still be adaptive as a bet-hedging trait if it results in substantially lower variability in survival and fitness over the long term. We suggest that conservation measures aimed at preserving populations of dormancy-prone plants be linked to censuses focusing on detecting and estimating dormancy levels because high levels of dormancy indicate a low annual survival.

Key-words: adaptation, bet-hedging, clonal plants, maladaptive, mark–recapture, program MARK, short-lived perennial

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Introduction

Prolonged dormancy, also referred to as ‘adult whole-plant dormancy’ and hereafter referred to as ‘dormancy’, is a phenomenon in which a perennial herbaceous plant produces no above-ground tissue for one or more vegetation periods (Lesica & Steele 1994; Shefferson *et al.* 2005). This condition occurs in a wide range of

families in the plant kingdom (Lesica & Steele 1994), but is particularly common in the orchid family (Kull 2002). In fact, dormancy has been most frequently studied in the orchid genus *Cypripedium* (e.g. Kull 1987, 1995; Cochran & Ellner 1992; Shefferson *et al.* 2001, 2003, 2005; Brzosko 2002; Kéry & Gregg 2004) and the orchid species *Cleistes bifaria* (Gregg & Kéry 2006; Kéry & Gregg 2003; Kéry *et al.* 2005).

Most studies describing dormancy are observational assessments of population dynamics and viability (e.g. Rabotnov 1969; Willems 1982, 1989; Hutchings 1987a;

Mehrhoff 1989; Whigham & O'Neill 1991; Oostermeijer *et al.* 1994; Willems & Melsers 1998; Lesica 1999; Tali 2002). Only recently have the life history ramifications of dormancy been investigated. In one of the first studies describing experimental impacts on dormancy, Primack & Stacy (1998) noted increased fruiting success by manipulating pollination results in increased dormancy, and thus demonstrated the cost of reproduction to future sprouting. Shefferson *et al.* (2003) later noted that dormancy and survival appear to trade-off with one another in *Cypripedium parviflorum*, yielding a possible cost of dormancy, a trend also noted in *Cleistes bifaria* (Gregg & Kéry 2006). However, in a recent study, dormancy was induced in two unrelated orchid species, *Cypripedium calceolus* and *Cephalanthera longifolia*, without any associated reduction in survival (Shefferson *et al.* 2005). Ramet dynamics measured concurrently showed evidence of declining vigor in one experimentally stressed species (*Cypripedium calceolus*), but increased vigor in another species (*Cephalanthera longifolia*; Shefferson *et al.* 2006). This suggests that dormancy may act as an adaptive buffer against environmental stress rather than as a maladaptive trait, as it appears to decouple the negative effects of environmental variability from mortality.

In all studies in which some aspect of the life history context of dormancy has been assessed, there have been two common elements to the taxa under study: all are long-lived and all are clonal, with each potentially composed of several integrated ramets. Departures from these common characteristics may result in different relationships between dormancy and other life history traits. Life history theory predicts important differences between short- vs. long-lived organisms, where the former must emphasize high levels of reproduction in order to maintain or increase fitness, while the latter must emphasize high, adult survival rates (Murphy 1968; Charlesworth 1980; Stearns 1992). When long-lived organisms are also clonal, survival generally increases as genets grow more ramets (Morris & Doak 1998; Sackville Hamilton *et al.* 1987; Silvertown *et al.* 2001). Concurrently, growth of more ramets results in a reduction in year-to-year variation in adult survival, particularly in temporally heterogeneous environments (Sibly 1997). Thus, dormancy is now being considered as a means of buffering adult survival against environmental stochasticity in long-lived clonal plants (Shefferson *et al.* 2005).

How does dormancy affect plants that do not have long life spans and clonality? Here, we address this question through a long-term comparative study of five populations of one such species, the burnt orchid, *Neotinea ustulata*. We envisage a life span spectrum in which short-lived refers to plants with half-lives of approximately 3 years or less, given that 3 years is the absolute minimum number of years required in order to observe dormancy. *Neotinea ustulata* is a short-lived perennial with a half-life of 1–3 years, in contrast to *Cypripedium* species, some of which have recorded

half-lives as long as 24 years (Kull 2002; Tali 2002). Although capable of growing a secondary rhizome and clonally reproducing, *N. ustulata* rarely actually does (Tali *et al.* 2004). We estimated the probabilities of dormancy, survival and transition among major life history states in these populations using Cormack–Jolly–Seber (CJS) and multistate mark–recapture analyses (Hestbeck *et al.* 1991; Brownie *et al.* 1993; White & Burnham 1999).

Methods

STUDY SYSTEM AND FIELD METHODS

Neotinea ustulata Bateman, Pridgeon & Chase (formerly *Orchis ustulata* L.) is a tuberous, short-lived perennial herb noted for its relatively frequent dormancy and limited potential for clonal reproduction via buds and secondary rhizomes (Tali 2002; Tali *et al.* 2004). The plant has a 10–20-cm-long stem, 2–6 lanceolate leaves and a flower spike with flowers approximately 5 mm long (Tali *et al.* 2004). It generally grows in open, sunny meadows and prefers calcareous soils. It occurs in populations throughout Estonia, being most common on the west coast and western islands (Kull & Tuulik 2002).

We sampled and censused a total of 1013 individual plants in five populations, referred to as A, J, K, L and S, across Estonia from 1993 to 2005. Population A (Aljava, 58°33'22"N, 23°10'52"E, elevation 3–4 m) is a *Carici montanae*–*Seslerietum* meadow located on the seashore and has been ungrazed for the last 10 years. Population J (Jäneda, 59°15'19"N, 25°43'22"E, elevation 79 m) is a *Melampyre*–*Scorzoneretum* grassland (once a sports field) and is now overgrown with pines and spruce. Population K (Kapi, 58°37'42"N, 23°12'26"E, elevation 18–19 m) is a drier *Seslerio*–*Filipenduletum* grassland that was once the site for lime burning, and is now covered with a young pine forest. Population L (Lõetsa, 58°38'47"N, 23°19'13"E, elevation 10–12 m) is a *Seslerio*–*Filipenduletum* pasture less than 1 km from the Baltic Sea. Population S (Sillukse, 58°36'53"N, 23°34'5"E, elevation 11–12 m) is an overgrown *Seslerio*–*Filipenduletum* grassland on a working limestone quarry. Four of these populations are located within 30 km of each other, including three on the island of Muhu (populations A, K and L) and one on the western coast of the mainland (population S). The fifth population (population J) is located inland, 150 km away from the other populations. Three populations consist of the early-flowering variety of *N. ustulata* (*N. ustulata* ssp. *ustulata*, populations A, K and L), while the remaining two populations consist of the late-flowering variety (*N. ustulata* ssp. *aestivalis*, populations J and S; Tali 2002).

Census recordings involved marking and mapping the location of each plant within 10 permanent 1 × 1 m plots per population in each growing season. Each plant's presence and life history state (i.e. flowering,

vegetative or absent) were recorded annually. Plots were checked multiple times during each growing season as sprouting and flowering times vary. We sampled 180, 137, 282, 282 and 132 plants in populations A, J, K, L and S, respectively, and each plant consisted of no more than one sprout per year.

ESTIMATION OF DEMOGRAPHIC PARAMETERS

We estimated demographic parameters per population via mark–recapture analysis, focusing on estimation of the probabilities of survival, dormancy and transitioning among above- and below-ground states. As a result of their microscopic seed size, rare germination events, the difficulty in determining parentage and in distinguishing new recruits from previously dormant individuals, we did not estimate recruitment in these populations. We estimated demographic parameters via CJS (Lebreton *et al.* 1992) and multi-state (Nichols *et al.* 1992) modelling in program MARK (White & Burnham 1999).

Cormack–Jolly–Seber modelling

Presence–absence data from all five populations were analysed via CJS modelling to estimate annual probabilities of dormancy (d), given as the complement to the probability of resighting (p , where $d = 1 - p$, Shefferson *et al.* 2001), and survival (S). Here, resighting (p) is the probability of observing an individual at time i that it is alive at time i , and was previously observed (Lebreton *et al.* 1992). Dormancy is its complement under the assumption of perfect detection of all previously seen individuals that are alive and above ground each year (Shefferson *et al.* 2001). We treat survival (S) as equal to apparent survival (ϕ), an unbiased estimator of survival corrected for dormancy and temporary emigration, owing to the inability of plants to emigrate. Factors tested for each parameter include population (abbreviated as ‘pop’), flowering variety (‘var’) and time (t), and the interactions and additive relationships among these factors. The global model, defined as the most fully parameterized, biologically relevant model analysed, included population–time interactions in both apparent survival and dormancy (model $S_{\text{popxt}} d_{\text{popxt}}$), from which further parameterizations were reduced until all possible models were tested. This resulted in a total of 64 models. Because flowering variety was a subset of population, we did not test for interactions between these two factors.

Model inference proceeded through the use of QAICc (quasi-Akaike Information Criterion corrected for small sample size) values (see Mark–recapture assumptions below), in which the model with lowest QAICc was considered the best-fit model and models with values ≤ 2.0 units greater were equally parsimonious with it. We further estimated Akaike weights, which estimate the probability that a model is the best model given that all relevant models have been parameterized (Burnham & Anderson 1998).

Multi-state modelling

For multistate mark–recapture analysis, life history state data from all five populations were used to estimate survival (S) and survival-conditional transitions (Ψ) among flowering (Flo), non-flowering vegetative (Veg) and dormant (Dor) states, under the assumption of perfect re-detection (p) of flowering and vegetative individuals (i.e. $p_{\text{Flo}} = 1$, $p_{\text{Veg}} = 1$ and $p_{\text{Dor}} = 0$; Kendall & Nichols 2002; Shefferson *et al.* 2003). Factors tested include state (sta), state transition (m), population (pop) and flowering variety (var, treated as a subset of population). We did not attempt to model annual survival or transition probabilities because of unidentifiable parameters under many multi-state models involving temporal variation (Kendall & Nichols 2002; Schaub *et al.* 2004; Kéry *et al.* 2005). The global model under this analysis involved a population–state interaction in survival, a population–transition interaction in state transitions, and resighting parameters fixed as previously mentioned (model $S_{\text{popsta}} p_{\text{fixed}} \Psi_{\text{popxm}}$). Further models were reduced from this parameterization.

We determined which candidate models to use in inference by testing the identifiability of parameters per model in Maple for Windows (Maplesoft Inc., Waterloo, Ontario, Canada) using the methods of Gimenez *et al.* (2003). We required the best-fit and equally parsimonious models to have all demographic parameters identifiable, as these models were used to provide parameter estimates, but allowed models with low support to have one unidentifiable parameter. Other models were eliminated from consideration. Parameter identifiability testing proceeded in this way down the list of top models, as ranked by AICc values, until we obtained a list of 10 candidate models. Model inference then proceeded through the use of AICc and Akaike weights.

We also asked which of the resulting survival and transition probabilities differed significantly from one another. We addressed this through the comparison of estimates from the best-fit model using program CONTRAST (Hines & Sauer 1989), which provides an approximate test of equality among proportions under a null hypothesis of no differences (Sauer & Williams 1989).

Mark-recapture assumptions

CJS models assume independence of fates and identity of rates among individuals (i.e. the ‘*iii* assumption’, Lebreton *et al.* 1992). We tested this assumption by bootstrapping 1000 iterations of the CJS global model from the dataset and ranking the deviance of the true global model against the bootstrapped deviances (White & Burnham 1999). In case of significant overdispersion, we estimated the overdispersion factor (\hat{c}), as the deviance of the true global model divided by the mean deviance from the 1000 bootstrapped models, and corrected AICc values to produce QAICc values for all models (Burnham & Anderson 1998).

Several types of variation in resighting probability may create significant overdispersion in the dataset, including variation by age, size and life history state. We could not test for variation by age and size because dormancy prevents us from knowing when each plant germinated and almost all plants maintained only one tuber in any given year. However, overdispersion may also result if previously sighted individuals are more or less likely to be re-seen depending on whether they were seen on the previous sampling occasion (Kendall *et al.* 1997), which could result if dormancy is a Markovian process (Schaub *et al.* 2004). We tested this using test 2.Ct of the overall goodness-of-fit test of the CJS model (Lebreton *et al.* 1992) in program U-CARE version 2.2 (Choquet *et al.* 2005), which estimated the trap-dependence statistic (N). Here, $N < 0$ or $N > 0$ if individuals seen in the previous year are more or less likely to be seen in the current year, respectively, and $N = 0$ under no such dependence. Multi-state modelling was used to estimate the probability of survival corrected for this dependence (Schaub *et al.* 2004).

No optimal methods exist to test the goodness-of-fit of the global model in multistate mark-recapture analysis. However, we conducted an overall goodness-of-fit analysis using U-CARE (Choquet *et al.* 2005) to test if the multistate data departed from the assumptions inherent in the Jolly-Move model, in which survival varies by previous state and time, and state transitions and resighting vary by previous state, current state and time (Brownie *et al.* 1993; Pradel *et al.* 2003).

Results

CJS MODELLING

The parametric bootstrap goodness-of-fit test indicated significant overdispersion in the global model (deviance = 1401.2, $P < 0.001$, $\hat{c} = 1.232$). On closer inspection, the overall goodness-of-fit test in test 2.Ct in U-CARE showed that individuals seen in year i were significantly more likely to be seen in year $i + 1$ than expected by chance,

significantly so in populations A, K and L (population A: $N = -0.97$, $\chi^2_4 = 11.1$, $P = 0.025$; J: $N = -1.9$, $\chi^2_8 = 12.2$, $P = 0.144$; K: $N = -6.1$, $\chi^2_8 = 74.9$, $P < 0.001$; L: $N = -4.8$, $\chi^2_{10} = 30.8$, $P < 0.001$; S: $N = -1.5$, $\chi^2_9 = 8.3$, $P = 0.507$). Thus, our tests of model assumptions suggested that dormancy is a Markovian process.

The best-fit model in CJS analysis of general demographic data suggested strong differences among populations (Table 1). Intriguingly, as the data show, dormancy varied unpredictably among populations, while survival varied in concert. According to the best-fit CJS model, dormancy varied as an interaction between population and time (model 1, Table 1), suggesting that it varies unpredictably across space and time (Fig. 1). By contrast, survival varied in parallel across all populations over the 13-year period of the study (Fig. 1), even in population J, which was located considerably further inland from the other populations. When averaged among populations, survival for this species was 0.727 ± 0.115 (\pm SE), and on average, the probability of becoming dormant was 0.543 ± 0.129 , although high temporal and spatial variability led to high standard errors in both probabilities.

MULTI-STATE MODELLING

The overall goodness-of-fit test in U-CARE suggested that most of the data lacked significant overdispersion. However, two of the five populations significantly deviated from the JMV model (population A: $\chi^2_{46} = 34.8$, $P = 0.887$; J: $\chi^2_{27} = 13.0$, $P = 0.989$; K: $\chi^2_{111} = 166.9$, $P < 0.001$; L: $\chi^2_{86} = 121.6$, $P = 0.007$; S: $\chi^2_{66} = 55.4$, $P = 0.821$), suggesting extra binomial variation which we may have accounted for in the data analysis.

Multi-state modelling suggested that life history transitions varied among populations. The best-fit multi-state model suggested that survival varied across life history states similarly among populations, although mean survival varied at each population (state + population variation, model 11, Table 2). In addition, life history state transition probabilities varied among

Table 1 The best 10 models from Cormack-Jolly-Seber modelling of survival (S) and dormancy (d) probabilities for five populations of *Neotinea ustulata* in Estonia using program MARK (White & Burnham 1999). A total of 64 models were tested

Model	S	d	No. of parameters	QDeviance	ΔQAIC_c	w
1	pop + t	pop \times t	71	1185.25	0	0.999
2	pop	pop \times t	65	1219.23	21.19	< 0.001
3	var + t	pop \times t	68	1217.60	25.94	< 0.001
4	t	pop \times t	67	1225.66	31.87	< 0.001
5	var \times t	pop \times t	79	1205.26	37.16	< 0.001
6	var	pop \times t	62	1248.17	43.76	< 0.001
7	pop \times t	pop \times t	115	1137.71	48.47	< 0.001
8	c	pop \times t	61	1258.56	52.04	< 0.001
9	pop \times t	pop + t	71	1251.58	66.32	< 0.001
10	pop \times t	var \times t	79	1238.88	70.79	< 0.001

We estimated and set $\hat{c} = 1.2316$. ΔQAIC_c for the i th model is calculated as $\text{QAIC}_{c_i} - \min(\text{QAIC}_c)$. Akaike weight (w) indicates the level of support for a model on a scale of 0 (no support) to 1.0 (full support). Abbreviations: pop, population; var, flowering variety; t, time; c, invariant. The best-fit model is in bold type.

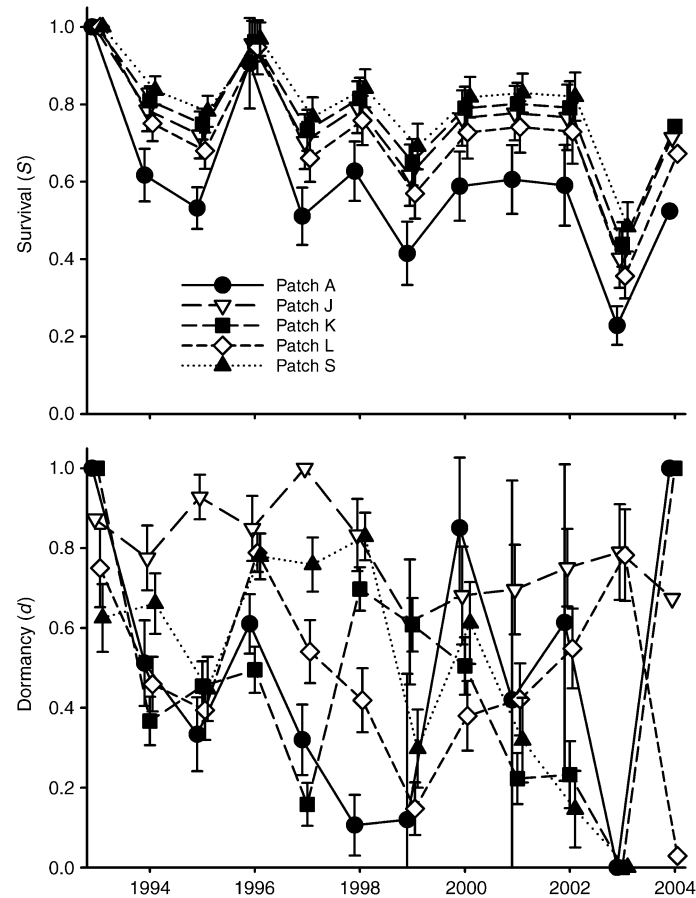


Fig. 1 Annual survival (S) and dormancy (d) probabilities among five Estonian populations of *Neotinea ustulata* sampled from 1993 to 2005, as estimated via Cormack–Jolly–Seber modelling in program MARK (White & Burnham 1999).

Table 2 The best 10 identifiable models tested using multistate modelling of state-based survival (S) and state transition (Ψ) probabilities for five populations of *Neotinea ustulata* in Estonia using program MARK (White & Burnham 1999)

Model	S	Ψ	No. of parameters	Deviance	ΔAIC_c	w
11	sta + pop	m \times pop	37	3254.3	0	1.000
12	pop	m \times pop	35	3283.6	25.17	< 0.001
13	sta + pop	m	36	3336.6	33.13	< 0.001
14	sta + var	m \times pop	34	3307.2	46.66	< 0.001
15	var	m \times pop	32	3321.9	57.27	< 0.001
16	c	m \times pop	31	3336.5	69.80	< 0.001
17	pop	m	11	3378.2	70.73	< 0.001
18	sta(Flo = Veg)	m \times pop	33	3343.4	78.79	< 0.001
19	sta \times var	m	12	3388.4	82.91	< 0.001
20	sta + var	m	10	3428.9	119.36	< 0.001

ΔAIC_c for the i th model is calculated as $AIC_c - \min(AIC_c)$. Akaike weight (w) indicates the level of support for a model on a scale of 0 (no support) to 1.0 (full support). Abbreviations: pop, population; sta, life history state; m, life history state transition; var, flowering variety. The best-fit model is in bold type. All models are fully identifiable with the exception of model 19, which has only 11 identifiable parameters.

populations, though unpredictably so (transition \times population interaction, model 11, Table 2). Overall survival estimated via multistate modelling for the species was 0.765 ± 0.030 , suggesting little bias in CJS survival estimates (Table 3).

Overall, dormant plants had significantly lower survival (0.684 ± 0.042) than vegetative (0.793 ± 0.051) and flowering plants (0.999 ± 0.007 ; program CON-

TRAST: $\chi^2_2 = 69.45$, $P < 0.001$; Table 3). In addition, all plants were most likely to transition to dormancy, although flowering and vegetative plants usually had a relatively high chance of re-flowering and remaining vegetative, respectively (Table 4). In population A, the probability of transitioning to dormancy was higher for flowering than for vegetative plants (Table 4), suggesting a possible cost of flowering to future sprouting.

Similarly, flowering and vegetative individuals in population J transitioned to dormancy more often than previously dormant individuals (Table 4), suggesting the possible cost of sprouting.

Discussion

IS DORMANCY ADAPTIVE?

Neotinea ustulata plants experience greater mortality when dormant than when above ground. Other species in which this has been noted include *Cypripedium parviflorum* (Shefferson *et al.* 2003), *Cleistes bifaria* (Gregg & Kéry 2006) and *Ophrys sphegodes* (Hutchings 1987b). These results confirm that decreased survival during dormancy appears to be common in the orchid family. Furthermore, our results cast doubt on an adaptive nature to dormancy.

We cannot exclude the possibility that dormancy is a bet-hedging trait in *N. ustulata*, because traits that result in low fitness in the short term may result in high fitness over the long term, provided that variability is reduced. As we did not experimentally stress the plants in this study, we do not know whether they would respond to stress by increasing dormancy, mortality or both. As such, the more dormancy-prone plants may simply be less vigorous, perhaps due to being consistently annually stressed relative to less dormancy-prone plants (Shefferson *et al.* 2005). Stressful conditions may result from many factors, including low resource availability, high levels of competition and non-random variation in herbivory.

Demographic parameters in plant populations often vary with variation in resource availability and use (de Jong & van Noordwijk 1992). Size exacerbates this variation in clonal plants as the spread of ramets results

Table 3 Estimates of survival for plants of different life history states among five Estonian populations of *Neotinea ustulata* sampled and monitored from 1993 to 2005

Population	Life history state			Overall
	Flo	Veg	Dor	
A	0.999 ± 0.014	0.606 ± 0.070	0.455 ± 0.048	0.613 ± 0.026
J	0.999 ± 0.003	0.878 ± 0.051	0.796 ± 0.062	0.808 ± 0.053
K	0.999 ± 0.004	0.823 ± 0.043	0.716 ± 0.027	0.807 ± 0.012
L	0.999 ± 0.006	0.782 ± 0.049	0.660 ± 0.031	0.749 ± 0.020
S	0.999 ± 0.003	0.876 ± 0.034	0.793 ± 0.028	0.850 ± 0.019
Overall	0.999 ± 0.007	0.793 ± 0.051	0.684 ± 0.042	0.765 ± 0.030

Abbreviations: Flo, flowering; Veg, vegetative; Dor, dormant. Estimates and standard errors of population-specific survival for each state are from the best-fit model in multistate mark–recapture analysis (model 11, Table 2), and overall state estimates are means of these. Overall population estimates are from model 12 (Table 2), and overall species estimate is a mean of these. Populations A, K and L include only the early-flowering variety (ssp. *ustulata*), while J and S include only the late-flowering variety (ssp. *aestivalis*).

Table 4 Estimates of transitions among life history states in *Neotinea ustulata*, sampled and monitored in five Estonian populations from 1993 to 2005

Population	From State	Transition to		
		Flo	Veg	Dor
A	Flo	0.228 ± 0.026	0.127 ± 0.021	0.645 ± 0.030
	Veg	0.177 ± 0.053	0.372 ± 0.071	0.451 ± 0.085
	Dor	0.162 ± 0.044	0.205 ± 0.052	0.633 ± 0.048
J	Flo	0.087 ± 0.032	0.103 ± 0.028	0.810 ± 0.036
	Veg	0.068 ± 0.033	0.120 ± 0.044	0.812 ± 0.053
	Dor	0.146 ± 0.008	0.076 ± 0.024	0.778 ± 0.018
K	Flo	0.378 ± 0.022	0.179 ± 0.019	0.443 ± 0.025
	Veg	0.141 ± 0.022	0.346 ± 0.032	0.513 ± 0.040
	Dor	0.060 ± 0.013	0.209 ± 0.029	0.731 ± 0.022
L	Flo	0.280 ± 0.026	0.177 ± 0.022	0.543 ± 0.029
	Veg	0.086 ± 0.019	0.384 ± 0.034	0.530 ± 0.044
	Dor	0.084 ± 0.018	0.186 ± 0.030	0.730 ± 0.025
S	Flo	0.240 ± 0.034	0.167 ± 0.029	0.593 ± 0.039
	Veg	0.136 ± 0.031	0.255 ± 0.040	0.609 ± 0.047
	Dor	0.098 ± 0.020	0.211 ± 0.031	0.691 ± 0.026

State-transitions are conditional upon survival, thus leading to estimates that sum to 1.00 across rows. Abbreviations: Flo, flowering; Veg, vegetative; Dor, dormant. Estimates are from the best-fit model in multistate mark–recapture analysis (model 11, Table 2). Populations A, K and L include only the early-flowering variety (ssp. *ustulata*), while J and S include only the late-flowering variety (ssp. *aestivalis*).

in greater access to resources. In clonal plants and other organisms, survival commonly increases with size (Prothero & Jürgens 1987; van Kleunen *et al.* 2000) and in dormancy-prone, long-lived clonal plants, survival increases and dormancy decreases with size or increasing numbers of ramets (Shefferson *et al.* 2005; Gregg & Kéry 2006; Shefferson 2006). Because size can be a measure of clonal vigour (Shefferson *et al.* 2006), dormancy may still be adaptive if it is more likely to occur in less vigorous individuals, and if survival during dormancy is higher than if the plant failed to become dormant. However, in the present system, size does not vary sufficiently to use as a proxy for vigour and we suggest further exploration of this matter.

SPATIAL AND TEMPORAL DEMOGRAPHIC PATTERNS

Adult survival and dormancy varied considerably among populations, supporting spatial differentiation in demographic trends in this species (Tali 2002; Tali *et al.* 2004). However, adult survival varied in concert across time while dormancy probability varied unpredictably, even in populations near one another. Although it is likely that we re-detected all above-ground individuals in the study, some of the variation that we observed might be due to annual variation in detection. Nonetheless, such patterns suggest that mortality in this species is strongly linked to large-scale climatic phenomena, whereas dormancy is more likely linked to local, microsite phenomena, possibly including biotic interactions such as differing kinds and levels of competition at each site. By contrast, in *Cypripedium parviflorum*, the probability of dormancy for plants in nearby patches varied in parallel across time, while adult survival stayed high and relatively steady, suggesting that dormancy was driven by climatic factors whereas adult survival may not have been (Shefferson *et al.* 2001). Although a comparison between *Cypripedium parviflorum* and *Neotinea ustulata* lacks the certainty that would be possible if they could have been sampled in sympatric populations, nonetheless these differences suggest that the cues governing dormancy and factors driving mortality are different in the two species.

Although we did not test for correlations between *Neotinea ustulata*'s demographic parameters and local climatic trends, other studies suggest some key variables that may be linked to dormancy in this species. In some species, including *Epipactis helleborine* and *Cypripedium parviflorum*, different measures of temperature and rainfall typically correlate well with dormancy (Shefferson *et al.* 2001; Light & MacConaill 2006), whereas in others, such as *Cypripedium reginae* and *Cleistes bifaria*, rainfall correlates well with survival (Kéry & Gregg 2004; Kéry *et al.* 2005). It may be fruitful to continue investigations into environmental influences on dormancy and survival in these species, particularly in light of the complex life history and

environmental relationships behind other synchronous phenomena, such as mast seeding (Kelly & Sork 2002; Buonaccorsi *et al.* 2003; Crone & Lesica 2004).

In conclusion, we have shown that dormancy is associated with decreased adult survival in a short-lived, minimally clonal orchid species, *N. ustulata*. In addition, we have found that demographic trends in dormancy vary unpredictably among populations and across time in this species, while survival varies synchronously among populations. We suggest that further research address the adaptive context of this condition, in particular by further examining relationships between dormancy and reproduction, as this would address key questions regarding trade-offs between vegetative growth and sexual reproduction, and how dormancy impacts these possible trade-offs. The fitness consequences of dormancy could best be addressed by determining whether dormancy is a genetically variable trait, and then by estimating both survival and fecundity in genotypes varying in dormancy levels. Selection experiments could then be carried out to determine whether dormancy is, indeed, adaptive or not. We further suggest a broad comparative study involving many dormancy-prone species to look further into the common elements of dormancy across life history variables such as life span and survivorship, and into how this trait has evolved from a phylogenetic standpoint.

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