

## Demographic estimation methods for plants with unobservable life-states

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Demographic estimation of vital parameters in plants with an unobservable dormant state is complicated, because time of death is not known. Conventional methods assume that death occurs at a particular time after a plant has last been seen aboveground but the consequences of assuming a particular duration of dormancy have never been tested. Capture–recapture methods do not make assumptions about time of death; however, problems with parameter estimability have not yet been resolved. To date, a critical comparative assessment of these methods is lacking. We analysed data from a 10 year study of *Cleistes bifaria*, a terrestrial orchid with frequent dormancy, and compared demographic estimates obtained by five varieties of the conventional methods, and two capture–recapture methods. All conventional methods produced spurious unity survival estimates for some years or for some states, and estimates of demographic rates sensitive to the time of death assumption. In contrast, capture–recapture methods are more parsimonious in terms of assumptions, are based on well founded theory and did not produce spurious estimates. In *Cleistes*, dormant episodes lasted for 1–4 years (mean 1.4, SD 0.74). The capture–recapture models estimated ramet survival rate at 0.86 (SE ~0.01), ranging from 0.77–0.94 (SEs ≤0.1) in any one year. The average fraction dormant was estimated at 30% (SE 1.5), ranging 16–47% (SEs ≤5.1) in any one year. Multistate capture–recapture models showed that survival rates were positively related to precipitation in the current year, but transition rates were more strongly related to precipitation in the previous than in the current year, with more ramets going dormant following dry years. Not all capture–recapture models of interest have estimable parameters; for instance, without excavating plants in years when they do not appear aboveground, it is not possible to obtain independent time-specific survival estimates for dormant plants. We introduce rigorous computer algebra methods to identify the parameters that are estimable in principle. As life-states are a prominent feature in plant life cycles, multistate capture–recapture models are a natural framework for analysing population dynamics of plants with dormancy.

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Demographic analysis is central to ecological research and applications. For plants, which are by nature sessile, estimation of rates of survival and transitions between life-states, and of the numbers in these states, seems a straightforward task (Harper 1977). However, many

perennial plants have dormant states such as bulbs, corms, roots, or rhizomes that rest belowground for one or several growing seasons and are therefore not visible (Mehrhoff 1989, Light and MacConaill 1991, Waite and Hutchings 1991, Wells and Cox 1991, Lesica and Steele

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1994, Oostermeijer et al. 1996, Menges and Dolan 1998). Dormant plants cannot be distinguished from dead ones without digging them out, which may disturb the system or be impractical. Dormancy has been identified a major challenge to demographic modelling of plant populations such as in population viability analysis (Menges 2000); hence the interest in unbiased estimation of demographic rates in plants with an unobservable dormant state.

After an individual has last appeared aboveground during a study, there is typically a series of years when it is not seen and is thus either dormant or dead. Two methods for demographic estimation have previously been used in this situation: the conventional method, which comes in several versions, and capture–recapture methods. However, the application of either method to the problem of estimation in the presence of dormancy is not yet fully understood.

Several conventional methods employ strong assumptions about the duration of dormancy. They assume that either a plant dies immediately when it is not seen aboveground or that it survives for exactly a certain number of years dormant and then dies (Hutchings 1987, Gregg 1991, Oostermeijer et al. 1996, Hutchings et al. 1998, Primack and Stacy 1998, Wells et al. 1998, Lesica 1999). These assumptions have not been tested, and further, the consequences of making a particular selection among these assumptions have never been studied. In contrast, capture–recapture methods do not require assumptions about the fate of plants after they have last been seen. Shefferson et al. (2001) recognized that the Cormack–Jolly–Seber capture–recapture model may be used to estimate survival rates and the fraction of a population in the dormant state. The probabilistic nature of capture–recapture models avoids arbitrary decisions about a fixed and constant number of years of survival of dormant plants. In a follow-up paper, Shefferson et al. (2003) also applied multistate capture–recapture models to estimate rates of state transitions among different life-states. However, they were not able to resolve all issues regarding the identifiability of the model parameters. A proper understanding of parameter identifiability is essential for valid model selection and variance estimation.

Although any assumption about the fate of plants after they have been seen for the last time is unlikely to be exactly true, it is not clear how sensitive the estimates of survival and state transitions are to violations of these assumptions. If the assumptions are not met, and the kind of assumptions made have a strong influence on the demographic estimates, then many conclusions from previous studies about life-history of plants with dormant states may be somewhat flawed.

The aim of this paper is to make a comparison of different methods to estimate demographic rates in plants with a dormant state. First we review the methods used by plant ecologists to estimate survival and life state transitions rates and the fraction dormant. Then we emphasize the assumptions required for each method and assess parameter identifiability when applying the multistate capture–recapture model. We compare the methods in a numerical example by analysing the population dynamics of the terrestrial orchid *Cleistes bifaria*, estimating rates of survival and state transitions and the fraction of the population that is in the unobservable dormant state. We then use the most efficient and most parsimonious (in terms of assumptions) method, the multistate capture–recapture model, to test whether survival and state transition rates in this orchid are correlated with climate. Finally, we discuss the assumptions required for the different methods, give guidelines for their use and provide perspectives on the design and analysis of demographic studies of plants with dormant states.

## Methods

### Plant demographic data in encounter history format

The data arising from a plant demographic study may be written in an encounter history such as 0010111000 for each censused individual. In this row vector, columns represent years and entries are ones for years when the individual was recorded and zeroes when it was not. Often information is available about the life-state of the individual when seen aboveground, e.g. vegetative or flowering. Then the encounter history has entries such as F (flowering) or V (vegetative). A typical encounter history might be 00V0VFV000 for an individual that is first encountered in year 3 as vegetative, not seen in year 4, recorded in years 5–7 first as vegetative, then flowering and then vegetative again and not seen anymore in year 8 and thereafter. Zeroes are ambiguous with respect to state and fate and mean that an individual was either not detected aboveground, dormant, or dead. If every aboveground individual is seen with probability equal to 1, an interior zero (year 4) represents a dormant individual. In contrast, terminal zeroes (years 8–10) mean an individual can be either dead or dormant. Without excavation, there is no way of determining if or when an individual dies during years with terminal zeroes. Terminal zeroes in individual encounter histories are typical for many plant demographic studies. Note that the term individual can here denote either an entire genet, or plant parts such as ramets (=shoots), provided that the latter can be unambiguously identified over the years.

## Models to estimate demographic parameters

We distinguish between two classes of models to estimate demographic parameters in plants with dormant states; conventional and capture–recapture. Common to all are the following assumptions: 1) all individuals are independent. 2) No tags are lost or misread. 3) Probabilities of detection, survival, and state-transition are homogeneous within life-states (homogeneity of fate). 4) All aboveground individuals are detected with certainty, i.e. detection probability equals 1 for all plants except those in the dormant state. Further, specific assumptions for each model are described below.

### Conventional methods

Previously, plant ecologists used to make strong assumptions about when a zero in an observed encounter history represents a dormant rather than a dead individual. Specifically, the duration of dormancy was assumed to be known exactly and to be the same for all individuals. We describe five different versions of these methods by how they treat a plant with observed encounter history 00V0VVFV000.

Method 1 (Primack and Stacy 1998) recognizes that a plant must be dormant in years when there is an interior zero in its encounter history, but assumes that it dies in the first year of any number of terminal zeroes. In the above example, dormancy is assumed for year 4 and death to occur in the interval from year 7 to 8. Because dormancy is known to occur by the presence of internal zeroes, it is obvious that this method must underestimate survival rates and the fraction dormant.

Methods 2–4 recognize that a plant will not usually die immediately at the beginning of a series of terminal zeroes. They attempt to correct for the downward bias in method 1 by assuming that a plant is first dormant for one or several years during terminal zeroes (Gregg 1991, Wells et al. 1998, Lesica 1999). The maximum duration of survival of a dormant plant is estimated by the longest observed dormant episode (run of interior zeroes in an encounter history). This estimate is used as a yardstick to decide if and in what particular year a plant has died when it is not seen aboveground at the end of a study. In our numerical example with the orchid *Cleisthes bifaria* (below), runs of interior zeroes lasted up to 4 years. Conservatively, a plant might be declared dead if it fails to show up for three consecutive years. In our example encounter history, dormancy would be assumed for years 8 and 9 and death in the interval between years 9 and 10. The encounter history would be treated as 00VDVFVDD0. When we compared demographic estimates, we obtained similar results whether we assumed that a plant stayed dormant for 1, 2, 3, or 4 years before dying. Therefore we only present results for an assumed dormancy during terminal zeroes of 1, 2 or 3 years and refer to them as methods 2, 3 and 4.

Method 5 is an intermediate approach. Plants are assumed to have died in the interval right after their last appearance aboveground if they fail to show up for three consecutive years (Hutchings 1987, Hutchings et al. 1998). In our example, death would be assumed to occur between occasion 7 and 8. In contrast, had the plant been recorded aboveground in year 8 as well, the plant would have been designated as dormant in both years 9 and 10. Method 5 may thus underestimate mortality.

Based on these assumptions, conventional methods derive estimates of life-state- and year specific survival and transition rates by simply counting the number of transitions into the dead and other life-states, respectively, as well as of the fraction of plants in the dormant state. Standard errors can be estimated as  $SE = \sqrt{\hat{f} \times (1 - \hat{f}) / n}$  where  $\hat{f}$  is a survival or transition rate, or the fraction dormant and  $n$  is sample size.

### Capture–recapture methods

We considered two capture–recapture methods (single- and multistate capture–recapture models), depending on whether there is one or more than one aboveground state. These methods relax the strong assumption made by conventional methods about the duration of dormancy. The single state capture–recapture method is only a special case of the multistate model.

With one aboveground state, the Cormack–Jolly–Seber (CJS) capture–recapture model (Lebreton et al. 1992) is useful to estimate survival and the proportion of individuals dormant. It uses input data such as 001011100. Each encounter history can be written as a function of parameters for rates of survival,  $S_i$ , and of detection given survival,  $p_i$ . If it can be assumed that every marked plant aboveground is detected ('recaptured'), the complement of the detection rate,  $1 - p_i$ , reflects the fraction dormant (Shefferson et al. 2001). This model views dormancy as a form of random temporary emigration (Kendall et al. 1997). The conditional probability of the above encounter history, given a plant was first observed in year 3, is given by

Pr (0010111000 | first observed in year 3)

$$= S_3(1-p_4)S_4p_5S_5p_6S_6p_7 \\ \times [(1-S_7) + S_7(1-p_8)] \\ \times [(1-S_8) + S_8(1-p_9)][(1-S_9) + S_9(1-p_{10})]$$

where  $S_i$  is survival of a plant between year  $i$  and  $i+1$  and  $p_i$  is the probability that the plant is aboveground in year  $i$  given that it is alive. The part to the right of the first multiplication sign models the three terminal zeroes in the encounter history. Terminal zeroes mean that a plant has either died, or it survived and went/remained dormant. Terminal zeroes do contain information about survival and dormancy, and this information is used explicitly by capture–recapture models. Based on the number of plants with each encounter history, the

likelihood can be written as a product of multinomials and maximum likelihood estimates of parameters and their standard errors obtained numerically (Lebreton et al. 1992).

In our numerical example (below), we used program MARK (White and Burnham 1999) to estimate the average annual survival rate and the average fraction of dormant plants using model  $\{S_{const}, p_{const}\}$ , where survival  $S$  and the fraction of dormant plants  $1 - p$  was constant over years. Year-specific annual survival rates and fraction dormant were estimated using model  $\{S_{time}, p_{time}\}$ . As some individuals may not be independent from others, extramultinomial variation was likely to be found in the data. When not accounted for properly, such overdispersion leads to an underestimation of standard errors and to the selection of too highly parameterised models (Anderson et al. 1994). We estimated the degree of overdispersion in the data based on 1000 bootstrap repetitions of the respective CJS model and present adjusted standard errors.

When two aboveground states are distinguished, multistate capture–recapture models (Arnason 1973, Brownie et al. 1993) are useful to estimate rates of survival and transitions between states. Data for input look like 00V0V0V00. An important difference to the CJS model is that multistate models allow the transition between states between year  $i$  and  $i+1$  to depend on the state in year  $i$ . Hence, under this model, dormancy is a kind of Markovian temporary emigration (Kendall et al. 1997). Under the assumption that all aboveground plants are detected, the conditional probability of the full encounter history in our example can be written as

Pr (00V0V0V00 | first observed in year 3 as vegetative)

$$= S_3^V \psi_3^{VD} S_4^D \psi_4^{DV} S_5^V \psi_5^{VF} S_6^F \psi_6^{FV} \\ \times [(1 - S_7^V) \\ + S_7^V \psi_7^{VD} [(1 - S_8^D) + S_8^D \psi_8^{DD} [(1 - S_9^D) + S_9^D \psi_9^{DD}]]]$$

where  $S_i^r$  is survival of a plant in state  $r$  between year  $i$  and  $i+1$ ,  $\psi_i^{rs}$  is the transition probability of a plant in state  $r$  in year  $i$  to state  $s$  in year  $i+1$ , given that it survived to year  $i+1$ , and D, V, and F stand for the dormant, vegetative, and flowering states.

A product multinomial likelihood can again be written based on the number of plants with a certain encounter history, and maximum likelihood estimates are obtained numerically by such programs as MARK (White and Burnham 1999), or more recently M-SURGE (Choquet et al. 2003). In the numerical example (below), we fit multistate models in MARK by specifying three states (D, V, and F) and setting detection rate at 0 for the dormant state and at 1 for the two observable states, even though state D never actually occurs in the data set input to the program. This enabled rates of survival and of state-transitions among all three states to be obtained. To estimate a state specific, average annual survival and

state transition rate, we intended to use model  $\{S_{state}, \Psi_{state}\}$ . However, this was not possible, because the parameters in this model are not separately identifiable. Hence, we used model  $\{S_{const}, \Psi_{state}\}$ , which assumes that survival is the same for all states. Year specific annual survival rates were estimated under model  $\{S_{time}, \Psi_{state \times time}\}$ . To estimate the fraction of dormant plants under the multistate model, we calculated the normalized right eigenvector of the transition matrix.

Because possible non independence of plants might have introduced extramultinomial variation, we estimated overdispersion for the most general multistate model  $\{S_{time}, \Psi_{state \times time}\}$  by a parametric bootstrap. We created a perfect data set without any overdispersion using the MLEs of the most general model as generating parameters, and calculated  $G$  as an omnibus goodness of fit criterion. This was repeated 1000 times. We estimated an overdispersion factor for our data set by dividing  $G$  for the actual data by the mean of  $G$  for the bootstrap resamples, and adjusted standard errors accordingly. This analysis was coded into program MSSURVIV (Hines 1994) by Jim Hines (pers. comm.), since there is currently no way to estimate the overdispersion in a multistate model in program MARK.

### Parameter identifiability in the multistate model

It is well known that in the fully time specific CJS model the last parameters for survival and recapture are not separately estimable (Lebreton et al. 1992). For the more complex multistate models with an unobservable state, it is not yet fully understood which parameters are separately estimable. We used the completely general approach of Catchpole, Morgan and Freeman (Catchpole et al. 1996, Catchpole and Morgan 1997) to assess intrinsic parameter identifiability in these multistate capture–recapture models. This requires the symbolic calculation of the rank of a matrix of first order derivatives of probabilities of survival and transitions, with respect to the parameters (Gimenez et al. 2003). If the rank is equal to the number of parameters in the model, the model is full rank and all parameters are intrinsically identifiable. If the rank is less than the number of parameters in the model, the model is parameter redundant. Hence, the likelihood of the model can be expressed as a function of fewer than the original number of parameters. In this case it is still possible that a subset of parameters are separately estimable and these can be identified also using this method. Using this approach, it is possible to determine for each parameter if it is separately identifiable or if it is only identifiable as a combination of other parameters. This is a general result that will apply to each non-sparse data set. For any particular data set at most these parameters are

identifiable. If the data are sparse, even fewer parameters may be estimable.

To test intrinsic parameter identifiability, we considered the most general multistate capture–recapture model  $\{S_{\text{state} \times \text{time}}, \Psi_{\text{state} \times \text{time}}\}$  along with 14 of its constrained versions. In these models, survival was either constant, time-dependent, state-dependent, or state- and time-dependent (both additive and interacting). The state transitions were constant over time, or time-dependent (where time-dependency was either the same in all states or not). These are the models that we believed to be particularly useful for plant ecologists. We used code for program MAPLE that was originally developed by Catchpole et al. (2002) and then adapted to multistate models by Gimenez et al. (2003).

### Numerical example

We compared all methods on a data set for the perennial orchid *Cleistes bifaria* (Gregg and Catling 2002), a species widely distributed in the SE United States (Luer 1975). Although self-compatible, *C. bifaria* (henceforward *Cleistes*) is naturally outcrossing and bee-pollinated (Gregg 1989). It occurs in a variety of acidic habitats: open oak–pine forests, meadows, and pine savannas, at elevations up to 1000 m. In West Virginia, *Cleistes* flowers in late June to early July. Reproduction is both sexual by seeds and asexual by root shoots; hence we use the ramet as demographic unit in this study and use the term interchangeably with ‘plant’. Considering ramets instead of genets avoids the need for arbitrarily assigning a state to a genet that consists of more than one ramet, when these ramets belong to different states (e.g. flowering and vegetative). Ramets are (i) vegetative with one, two or very occasionally three leaves, (ii) reproducing (with leaves and flowers/fruits), or (iii) they do not produce aboveground structures. Mean ramet heights measured in June 2002 were 18.7 cm (SD = 6.5 cm, n = 214) for vegetative and 37.5 cm (SD = 6.0 cm, n = 51) for flowering plants.

We conducted our study on a flat, seasonally wet, acidic, ca 9 ha meadow in West Virginia (39°16′45″N, 79°55′58″W), where the annual number of flowering plants ranged from some two dozen to several hundred throughout the study (K. B. Gregg, pers. obs.). The vegetation was dominated by grasses, with occasionally almost pure patches of willow sprouts (*Salix* sp.), bracken fern (*Pteridium aquilinum*), late low blueberry (*Vaccinium vacillans*), wild indigo (*Baptisia tinctoria*), scattered small saplings of red maple (*Acer rubrum*) and a groundcover of groundberry (*Rubus hispidus*) and numerous stems of sawbrier (*Smilax glauca*) (Gregg 1989). Here in 1980, a square 9.15 m plot (area 83.7 m<sup>2</sup>) was established.

Every year from 1990–1999, we searched the entire plot intensively at fruiting time (July–September) during 2–4 surveys to locate all *Cleistes* ramets, and to map their location within the plot. We marked each ramet with numbered plastic tags (approx. 4 × 0.75 cm) and recorded its fate and life-state (absent, vegetative, flowering). An attempt was made to locate all ramets ever marked previously, as well as to discover new ones. Plants that had been partly or mostly eaten by herbivores were recognizable and excluded from analysis if their state could not be assessed. The locations of all marked ramets not detected at the first survey were re-checked until almost every tag was found.

Detection probability (p) for marked ramets aboveground is the product of the probability to find a tag and the probability to detect an aboveground ramet, given that its tag had been found. We are confident that we found all marked ramets when aboveground next to their tag. Hence, we estimated p as the complement to the proportion of tags that had not been relocated. Over 10 years, among 3887 tag years, only 18 (0.5%) could not be relocated. Average detection probability p for marked ramets was thus >99.5% and ranged from >98.1–100% in any year. This enabled us to use methods which all assume that detection probability of individuals in the aboveground state equals 1.

### Climatic factors affecting survival and state transitions

We studied possible environmental factors affecting demographic rates in *Cleistes* using only the multistate capture–recapture model that requires the least restrictive assumptions of all methods compared. We considered total annual precipitation (June–May) during the current and the previous year, and mean spring temperature (March–May) and number of freezing days in spring (March–May) during the current year. We obtained these data for Elkins (West Virginia), 42 km from our study area. Total annual precipitation from 1990–1998 was 1303.5, 1129.0, 1117.1, 1034.5, 1329.7, 1046.0, 1083.3, 1478.8, and 1032.3 mm, mean spring temperature from 1991–1998 was 11.6, 8.9, 8.4, 9.3, 9.7, 8.7, 7.9, and 10.1°C and the number of spring frost days from 1991–1998 was 26, 34, 32, 39, 36, 39, 49, and 34. Weather covariates were correlated (range of correlation coefficients: 0.37–0.78), so we entered them into the analysis one at a time. Also, with 10 years of data, we did not entertain more complex covariate models, e.g. with quadratic or interaction terms.

Effects on survival were tested by comparison of model  $\{S_X, \Psi_{\text{state} \times \text{time}}\}$  with covariate X and model  $\{S_{\text{const}}, \Psi_{\text{state} \times \text{time}}\}$  with survival rate constant over time. Similarly, effects on transition rates were tested by comparison of models  $\{S_{\text{time}}, \Psi_{\text{state} \times X}\}$  and  $\{S_{\text{time}}, \Psi_{\text{state} \times X}\}$

and  $\{S_{\text{time}}, \Psi_{\text{state}}\}$ . Since the likelihood ratio test (LRT) is inflated when there is overdispersion, we conducted F tests (Lebreton et al. 1992, p. 106):  $F_{df, rdf} = \frac{L/df}{\hat{c}}$ , where L is the LRT statistic and df its associated degree of freedom. Rdf is the residual degrees of freedom and  $\hat{c}$  is an estimate of overdispersion. We expressed the amount of variation in  $\theta$  (i.e. survival or transition rate) explained by climatic covariate X as the reduction in deviance D due to fitting the covariate as  $(D\{\theta_{\text{const}}\} - D\{\theta_X\}) / (D\{\theta_{\text{const}}\} - D\{\theta_{\text{time}}\})$ . Here, const denotes a model without time variation, X a model with time-variation constrained to be a logit-linear function of X, and time a model with full time variation in parameter  $\theta$ . In capture–recapture modelling, it has become customary to use the Akaike information criterion (AIC) for selection of the best model among a set of competing candidates. Therefore, we also present Akaike weights (w), a standardized measure of relative support by the data for each model (Burnham and Anderson 1998).

## Results

### Parameter identifiability in the multistate capture–recapture model

Most multistate models likely useful to demographers had parameters that are identifiable (Table 1). Of particular interest is that this holds true even for some models with state specific survival rates, i.e. with one or more independent parameters for the survival of the dormant state. However, the parameters in the least complex model with state specific survival rates  $\{S_{\text{state}}, \Psi_{\text{state}}\}$  are not separately identifiable. It is the time-dependency of survival and state transition rates that enables separate survival estimates for the dormant state. Thus, if the underlying parameters for state-transitions are constant across time or nearly so, it is not possible to obtain unbiased estimates even under a time-dependent model that is intrinsically identifiable. Hence, it may be possible to obtain state-specific survival estimates with some data sets, but not with others.

### Prevalence of dormancy in *Cleistes bifaria*

We marked a total of 620 ramets of *C. bifaria* over the 10-year study period. Of these, 124 appeared for the first time in the last two cohorts, so dormancy could not be ascertained for them. Among the remaining 496 plants, 176 (35%) were dormant in at least one year. We observed a total of 225 dormant episodes with mean duration of 1.4 yr (1yr 71%, 2yr 19%, 3yr 7%, and 4yr 3%). Some plants had more than one dormant episode during the study.

### Conventional estimates of demographic parameters in *Cleistes bifaria*

Estimates from conventional methods all suffered from a curious artefact: At least one of the state- or time-specific survival rates was estimated to be 1, hence plants could never die when in these groups (Table 2a, 3). The average (non state specific) survival rate estimates ranged from 0.851 to 0.937 (Table 2a). The fraction of dormant plants ranged from 0.15 to 0.40 (Table 2b), or, when averaging over annual estimates, from 0.22 to 0.42 (Table 4), depending on the specific method applied. Hence, estimates from conventional methods were sensitive to how terminal zeroes in the encounter history were treated.

### Capture–recapture estimates of demographic parameters in *Cleistes bifaria*

Very little overdispersion was detected in the data (CJS model:  $c = 1.199$ ; multistate model:  $c = 1.575$ ), however, to be conservative, we adjusted model selection

Table 1. Intrinsic identifiability of 15 multistate models useful for the estimation of survival and state-transition rates in plants with a dormant state when detectability is known, as determined by computer algebra methods (Catchpole and Morgan 1997, Gimenez et al. 2003). The table lists parameters that are separately identifiable, and the number of estimable quantities (i.e. parameters or combinations thereof), when data for k capture occasions are available. Parameters are denoted S (survival rate) and  $\Psi$  (state transition rate). Parameters may be constant over time and states (denoted as const), constant over time, but different among states (state), time-dependent and the same in all states (time), time-dependent in each state in an additive way (state+time), or time-dependent for each state separately (state  $\times$  time). Subscript m denotes the last parameter (referring to the interval between occasion k-1 and k).  $S_1^D$  denotes survival rate for the dormant state in the first period,  $\psi_1^{DY}$  the transition rate from the dormant state D to any other state Y for the first period, and  $\psi_m^{XY}$  the transition rate from any state X to any other state Y for the last time period.

Model	Identifiable parameters	Number of estimable quantities
1: $S_{\text{const}}, \Psi_{\text{state}}$	All	7
2: $S_{\text{state}}, \Psi_{\text{state}}$	None	8
3: $S_{\text{time}}, \Psi_{\text{state}}$	All	k + 5
4: $S_{\text{state} + \text{time}}, \Psi_{\text{state}}$	All	k + 7
5: $S_{\text{state} \times \text{time}}, \Psi_{\text{state}}$	None	3k + 1
6: $S_{\text{const}}, \Psi_{\text{state} + \text{time}}$	All	k + 5
7: $S_{\text{state}}, \Psi_{\text{state} + \text{time}}$	All	k + 7
8: $S_{\text{time}}, \Psi_{\text{state} + \text{time}}$	All	2k + 3
9: $S_{\text{state} + \text{time}}, \Psi_{\text{state} + \text{time}}$	All	2k + 5
10: $S_{\text{state} \times \text{time}}, \Psi_{\text{state} + \text{time}}$	All but $S_1^D$	4k
11: $S_{\text{const}}, \Psi_{\text{state} \times \text{time}}$	All but $\psi_1^{DY}$	6k – 7
12: $S_{\text{state}}, \Psi_{\text{state} \times \text{time}}$	All but $\psi_1^{DY}$	6k – 5
13: $S_{\text{time}}, \Psi_{\text{state} \times \text{time}}$	All but $S_m, \psi_1^{DY}$ and $\psi_m^{XY}$	7k – 10
14: $S_{\text{state} + \text{time}}, \Psi_{\text{state} \times \text{time}}$	All but $S_m, \psi_1^{DY}$ and $\psi_m^{XY}$	7k – 8
15: $S_{\text{state} \times \text{time}}, \Psi_{\text{state} \times \text{time}}$	None	9k – 18

Table 2. Comparison between estimation methods for state-specific survival rate (SE) and fraction dormant averaged across years in *Cleistes bifaria* from 1990–1999. Transition rate estimates from the multistate capture–recapture model are from a model with constant survival and time constant transition rates  $\{S_{\text{const}}, \Psi_{\text{state}}\}$ . Fraction dormant in a multistate model was calculated from the transition matrix with constant state specific values. Fraction dormant in the CJS model is calculated as 1 minus recapture rate in the model  $\{S_{\text{const}}, p_{\text{const}}\}$ . Standard errors for estimates under both multistate and CJS models are inflated to adjust for overdispersion (see text for details). For all conventional methods, fraction dormant is calculated as the observed proportion of plants in the dormant state. . . . – not estimable; <sup>a</sup>identical estimates are given for all states since state-dependent estimates could not be obtained for our data set.

Method/life-state/ transition	MS capture– recapture model	CJS capture– recapture model	Method 1 1st terminal 0 = death	Method 2 1st terminal 0 = dormant	Method 3 1st–2nd terminal 0 = dormant	Method 4 1st–3rd terminal 0 = dormant	Method 5 Intermediate approach
a) State specific survival rate estimates							
Dormant	0.860 (0.009) <sup>a</sup>	0.861 (0.010)	1.00 (0.00)	0.556 (0.021)	0.733 (0.016)	0.810 (0.013)	1.00 (0.00)
Vegetative	0.860 (0.009) <sup>a</sup>	0.861 (0.010)	0.735 (0.012)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.883 (0.009)
Flowering	0.860 (0.009) <sup>a</sup>	0.861 (0.010)	0.817 (0.024)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.904 (0.019)
Mean	0.860	0.861	0.851	0.852	0.911	0.937	0.929
b) Fraction of population dormant							
Mean	0.326	0.291 (0.015)	0.150 (0.008)	0.287 (0.009)	0.352 (0.009)	0.398 (0.009)	0.262 (0.009)
c) State-specific transition rate estimates							
Dor to dor	0.402 (0.033)	...	0.298 (0.026)	0.298 (0.026)	0.610 (0.020)	0.714 (0.016)	0.462 (0.024)
Dor to veg	0.559 (0.032)	...	0.655 (0.027)	0.655 (0.027)	0.364 (0.020)	0.267 (0.016)	0.502 (0.024)
Dor to flo	0.040 (0.010)	...	0.047 (0.012)	0.047 (0.012)	0.026 (0.007)	0.019 (0.005)	0.036 (0.009)
Veg to dor	0.308 (0.015)	...	0.193 (0.009)	0.407 (0.013)	0.407 (0.013)	0.407 (0.013)	0.328 (0.013)
Veg to veg	0.592 (0.016)	...	0.691 (0.014)	0.508 (0.014)	0.508 (0.014)	0.508 (0.014)	0.575 (0.014)
Veg to flo	0.100 (0.009)	...	0.116 (0.008)	0.086 (0.008)	0.086 (0.008)	0.086 (0.008)	0.097 (0.008)
Flo to dor	0.203 (0.030)	...	0.151 (0.025)	0.307 (0.029)	0.307 (0.029)	0.307 (0.029)	0.233 (0.028)
Flo to veg	0.385 (0.033)	...	0.410 (0.034)	0.335 (0.030)	0.335 (0.030)	0.335 (0.030)	0.370 (0.032)
Flo to flo	0.412 (0.034)	...	0.439 (0.035)	0.359 (0.030)	0.359 (0.030)	0.359 (0.030)	0.396 (0.032)

and variance estimation. Both models estimated average annual (non state-specific) survival rate at 0.86 (Table 2a). Year specific survival rate estimates under a multistate model ranged from 0.77–0.94 (Table 3) and were very similar under the CJS model. Surviving plants in the dormant state moved to the vegetative state most often, while those in the vegetative and flowering states remained in their respective states most often (Table 2c). Only 4% of surviving dormant plants ever became a flowering plant directly after being dormant. The average fraction of the population that was in the dormant state was very similar under either model and estimated at around 0.30 in *Cleistes* (Table 2b). However, there were large annual fluctuations (0.16–0.47; Table 4). Both capture–recapture models thus yielded very similar results for the key demographic parameters.

### Comparison between conventional and capture–recapture methods for demographic analysis

As expected, conventional model 1 underestimated dormancy at only 15% of the population vs 33% and 29% for the capture–recapture models, respectively; on the other hand, survival rate was estimated only slightly lower at 85% rather than 86% (Table 2a,b). Conventional model 5 overestimated survival at 93%, and results from conventional models 2–4 were variable (Table 2a,b). Certain life-state transition rates were strikingly different among the models. For example, the MS capture–recapture model produced transition rates from dormant to dormant and from dormant to vegetative of 40% and 56%, respectively (Table 2c). In contrast, for the same two transitions, the conventional models presented these respective percentages: 30% and 66% (models 1, 2), 61% and 36% (model 3), 71% and 27% (model 4), and 46% and 50% (model 5; Table 2c). That is, two of the conventional models strongly reversed the dynamics with regard to transitions from the dormant state. When estimated with the two capture–recapture models, the annual fraction of dormant plants was very similar (0.29 and 0.33), whereas the estimates varied from 0.15 to 0.40 when using conventional methods (Table 2b). The variable results from conventional methods show that parameter estimates are very sensitive to the additional assumptions made by conventional methods.

### Factors affecting survival and state transition rates

Using multistate capture–recapture models, we found evidence for climatic effects on both survival and transition rates in *Cleistes*. Survival was higher in years with greater total precipitation ( $F_{1,568} = 4.20$ ,  $p = 0.04$ ); 29% of the temporal variation in survival was accounted for by this relationship (Table 5a). In contrast, there was no evidence for an effect on survival of spring frost days

( $F_{1,568} = 2.64$ ,  $p = 0.10$ ) or mean spring temperatures ( $F_{1,568} = 0.44$ ,  $p = 0.51$ ). Comparison of these models by AIC weights indicated that there was considerable annual variation that was not explained by these covariates (Table 5a).

Total precipitation in year  $i-1$  was significantly correlated with state-transition rates in year  $i$  ( $F_{1,568} = 5.23$ ,  $p < 0.001$ ). This relationship accounted for 25% of the temporal variation in transition rates (Table 5b). Interestingly, total precipitation in year  $i-1$  was a much better predictor of transition rates than was total precipitation in year  $i$ , which had no better fit than a constant model ( $F_{6,584} = 1.00$ ,  $p = 0.42$ ). For all three life-states, plants were more likely to produce above-ground shoots between years  $i$  and  $i+1$  when the period between year  $i-1$  and  $i$  was wet (Fig. 1). Transition rates of dormant plants were more similar to those of vegetative than those of flowering plants (Fig. 1a–c). In addition, more frequent transitions to the dormant state were observed with lower mean spring temperature ( $F_{6,584} = 4.44$ ,  $p < 0.001$ ), but there was no evidence for an effect of the number of spring frost days ( $F_{6,584} = 1.52$ ,  $p = 0.17$ ). Again, comparing these models by AIC weights indicated the presence of much unexplained annual variation in transition rates (Table 5b).

## Discussion

### Comparison of conventional and capture–recapture methods

The main difference between conventional and capture–recapture methods is that conventional methods do not use the information contained in terminal zeroes in the encounter histories. Instead, they make assumptions about the fate of individuals that are not seen at the end of an encounter history. In contrast, capture–recapture methods do not make such assumptions but instead use the information about survival and dormancy contained in the terminal zeroes of encounter histories. Capture–recapture methods are therefore both more parsimonious in terms of assumptions and more efficient in terms of making use of all available information.

It is clear from Tables 2–4 that a relatively wide range of values can be obtained for estimates of survival and transition rates depending on which assumption one makes about the duration of dormancy and the timing of death. Such results complicate comparisons across studies, especially since our conventional methods 1–5 are not the only conceivable ad hoc methods. Further, particularly striking differences emerged among the conventional models for transitions from the dormant state, such that under some models the trends were essentially reversed from those in others (Table 2c). In



Table 3. Comparison between estimation methods for annual survival rate (SE) in *Cleistes bifaria* from 1990–1999. Survival rate estimates were obtained from two capture–recapture methods and five conventional methods (see text). Survival refers to the interval from year  $i$  to year  $i+1$ , so no estimates are available for 1999 for any method. Estimates from capture–recapture models are based on multistate model  $\{S_{\text{time}}, \Psi_{\text{state} \times \text{time}}\}$  and on CJS model  $\{S_{\text{time}}, \Psi_{\text{time}}\}$ . Standard errors for estimates under both multistate and CJS model are inflated to adjust for overdispersion (see text for details). . . . – not estimable.

Method/year $i$	MS capture–recapture model	CJS capture–recapture model	Method 1 1st terminal 0 = death	Method 2 1st terminal 0 = dormant	Method 3 1st–2nd terminal 0 = dormant	Method 4 1st–3rd terminal 0 = dormant	Method 5 Intermediate approach
1990	0.855 (0.037)	0.831 (0.038)	0.787 (0.030)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	0.787 (0.030)
1991	0.772 (0.044)	0.785 (0.050)	0.742 (0.033)	0.820 (0.026)	1.00 (0.00)	1.00 (0.00)	0.742 (0.032)
1992	0.868 (0.051)	0.865 (0.055)	0.863 (0.028)	0.765 (0.030)	0.833 (0.024)	1.00 (0.00)	0.863 (0.028)
1993	0.867 (0.043)	0.869 (0.049)	0.887 (0.026)	0.878 (0.025)	0.785 (0.028)	0.846 (0.022)	0.887 (0.026)
1994	0.905 (0.033)	0.907 (0.036)	0.917 (0.021)	0.908 (0.021)	0.898 (0.021)	0.814 (0.024)	0.917 (0.021)
1995	0.825 (0.027)	0.824 (0.030)	0.822 (0.024)	0.949 (0.013)	0.941 (0.014)	0.932 (0.014)	0.822 (0.024)
1996	0.939 (0.027)	0.941 (0.030)	0.893 (0.020)	0.841 (0.021)	0.954 (0.012)	0.947 (0.012)	1.00 (0.00)
1997	0.812 (0.099)	0.866 (0.039)	0.830 (0.023)	0.912 (0.016)	0.865 (0.018)	0.961 (0.010)	1.00 (0.00)
1998	. . . .	. . . .	0.540 (0.027)	0.880 (0.017)	0.936 (0.012)	0.899 (0.014)	1.00 (0.00)
Mean	0.855	0.861	0.809	0.884	0.912	0.933	0.891

addition, the spurious results for time-dependent estimates of survival under all but one of the conventional methods we examined (Table 3) appear unsettling when survival rates need to be analysed as a function of explanatory variables. It is likely that a relationship between survival rate and covariates might also be distorted when using conventional methods. It has to be noted that the spurious unity survival estimates are a structural problem of these methods that does not have anything to do with the particular values of survival.

A more formal comparison of methods would ideally involve simulated data to gauge the bias in each method. We have not done this here, because both the CJS and the multistate models are very well studied theoretically and their estimates are known to be asymptotically unbiased if the assumptions are met (Carothers 1973, Sandland and Kirkwood 1981, Brownie et al. 1993, Kendall et al. 1997, Williams et al. 2002, Schaub et al. 2004). In contrast, all conventional methods yielded spurious unity estimates for survival for either the aboveground or the dormant state (Table 2a), and for either the first or the last periods of a study (Table 3). This fact alone should suffice to discourage their further use. In addition, the presence of spurious estimates does not foster optimism regarding the unbiasedness of estimates from conventional methods.

The strong assumption made about the duration of dormancy enables conventional methods to obtain estimates for all parameters in the model  $\{S_{\text{state} \times \text{time}}, \Psi_{\text{state} \times \text{time}}\}$ , i.e. including independent, time varying survival rates for the dormant state. However, the resulting estimates may be of questionable value, as we show here. In contrast, an apparent cost of using the multistate capture–recapture model is that independent, time-dependent survival rates may not be obtained for the dormant state under this model, nor can constant survival rates for the dormant state be obtained for some simpler models such as  $\{S_{\text{state}}, \Psi_{\text{state}}\}$ . Since the dormant state is unobservable, estimation turns out to be more complicated.

Some multistate models with time-dependency in either survival or state transitions allow the estimation of state specific survival rates. However, since parameters in the nested model without time-dependency are not identifiable, only biased or very imprecise estimates may be obtained if there is no such time variation in the data, even when an intrinsically identifiable model is used (Catchpole et al. 2001). In the *Cleistes* data we did not find numerical solutions to models with state specific survival rates. This may be due to a flat ridge of the likelihood surface or to sparse data. The numerical algorithm designed to find the highest point of this surface may then fail.

We see three ways how to obtain time varying survival rates. First, one can try to use models with different

Table 4. Comparison between estimation methods for the annual fraction of the population that is in the dormant state (SE) of *Cleistes bifaria* from 1991–1999. Estimates were obtained from Cormack–Jolly–Seber capture–recapture model ( $S_{\text{time}}$ ,  $\Psi_{\text{time}}$ ) as 1 minus the annual recapture rate  $p_t$ , and from the proportion of plants in the dormant state for five conventional methods (see text for details). No time varying estimates are obtainable with multistate capture–recapture models. SEs under the CJS model are adjusted for overdispersion, and for conventional methods, are based on the variance of a binomial random variable for conventional methods. Fraction dormant cannot be estimated for 1990. ... – not estimable, <sup>a</sup>mean for 1991–1998.

Method/year	MS capture– recapture model	CJS capture– recapture model	Method 1 1st terminal 0 = death	Method 2 1st terminal 0 - > -> dormant	Method 3 1st–2nd terminal 0 - > -> dormant	Method 4 1st–3rd terminal 0 - > -> dormant	Method 5 Intermediate approach
1991	...	0.180 (0.040)	0.109 (0.023)	0.268 (0.030)	0.268 (0.030)	0.268 (0.030)	0.109 (0.023)
1992	...	0.464 (0.050)	0.357 (0.039)	0.507 (0.035)	0.589 (0.032)	0.589 (0.032)	0.357 (0.039)
1993	...	0.465 (0.050)	0.364 (0.039)	0.442 (0.038)	0.562 (0.034)	0.629 (0.030)	0.364 (0.039)
1994	...	0.435 (0.048)	0.320 (0.036)	0.382 (0.036)	0.444 (0.035)	0.547 (0.031)	0.320 (0.036)
1995	...	0.163 (0.035)	0.077 (0.017)	0.125 (0.020)	0.176 (0.022)	0.232 (0.024)	0.077 (0.017)
1996	...	0.217 (0.032)	0.173 (0.024)	0.303 (0.027)	0.334 (0.030)	0.369 (0.027)	0.173 (0.024)
1997	...	0.289 (0.036)	0.196 (0.024)	0.267 (0.026)	0.365 (0.026)	0.390 (0.026)	0.267 (0.027)
1998	...	0.175 (0.037)	0.065 (0.014)	0.178 (0.020)	0.230 (0.021)	0.308 (0.022)	0.230 (0.021)
1999	...	...	0.459 <sup>a</sup> (0.027)	0.459 <sup>a</sup> (0.027)	0.523 (0.026)	0.554 (0.025)	0.554 (0.025)
Mean	...	0.299 <sup>a</sup> (0.037)	0.207 <sup>a</sup> (0.027)	0.309 <sup>a</sup> (0.027)	0.371 <sup>a</sup> (0.026)	0.417 <sup>a</sup> (0.025)	0.237 <sup>a</sup> (0.025)

constraints. For example, it may be possible to produce identifiable parameters using models in which survival rate of only one state is different from that of the other two. For instance, model  $\{S_{(V=D,F)*\text{time}}, \Psi_{\text{state} \times \text{time}}\}$  is identifiable. Still, the same problem as described above may apply here also, i.e. if there is little variation of survival rates over time, no useful estimates may be obtained for a particular data set. Second, a Bayesian approach may be promising because Bayesian procedures often yield unbiased estimates even when the likelihood surface has a flat ridge (Brooks et al. 2000). Third, one could make the unobservable state at least partially visible by excavating some plants in years in which they do not appear aboveground. This would allow dormant plants to be distinguished from dead plants. We are currently investigating how this additional information can be incorporated into a multistate capture–recapture model that includes an additional state “dead”. In one orchid species, excavation did not negatively affect plants (Light and MacConaill 1991), therefore, this may be a viable option. If excavation was deemed too intrusive and a species is sufficiently common, repeated samples might be taken of plants that are not part of a long term survey.

### Population dynamics of *Cleistes bifaria*

A comparison of the demographic estimates from this study with those from previous studies of terrestrial orchids is complicated because most have applied conventional estimation methods (Hutchings 1987, 1989, Gregg 1991, Wells and Cox 1991, Waite and Farrell 1998, Willems and Melser 1998). In *Cleistes*, survival rate varied by year and averaged 0.86 (SEs  $\leq 0.01$ ), close to that for genets of another orchid, *Cypripedium calceolus* when it was analysed using the CJS model (0.88, SE = 0.02; Shefferson et al. 2001). Most surviving plants in *Cleistes* remained either in the same state or moved to the vegetative state. Few surviving dormant plants directly became flowering plants in the next year in *Cleistes*. The fraction dormant in *Cleistes* averaged 0.29 but with up to half the population staying dormant in some years. This is again similar to CJS results from *Cypripedium calceolus*, where the fraction dormant averaged 0.32 (SE = 0.024) but varied annually from 0.19–0.59 (Shefferson et al. 2001). In two populations of another lady’s slipper, *Cypripedium reginae*, the average ramet survival rate was estimated at 0.96 and 0.95 and the average fraction dormant at 0.12 and 0.02, respectively (Kéry and Gregg 2004).

There were large annual fluctuations in both survival and transition rates in *Cleistes*. As a result, the annual fraction dormant fluctuated even more strongly. This is highly typical for orchid populations that have long been

Table 5. Effects of climate on survival and state-transition rates in *Cleistes bifaria*. Survival was studied under model  $\{S_X, \Psi_{\text{state} \times \text{time}}\}$ , where transition rates are fully state- and time-dependent. Similarly, transition rates were studied under model  $\{S_{\text{time}}, \Psi_{\text{state} \times X}\}$ . In both cases, X denotes the structure shown under Source of variation. Table entries are the deviance corrected for overdispersion (QDevi), the proportion of QDeviance explained by a model (% QD), the number of estimable parameters (np), the overdispersion corrected AIC (QAIC<sub>c</sub>) and Akaike weights (w) for each model. All models are nested in the global model  $\{S_{\text{time}}, \Psi_{\text{state} \times \text{time}}\}$  on which we based estimation of overdispersion ( $\hat{c}=1.575$ ). Numerical convergence was not achieved for covariate Precipitation June<sub>i-1</sub>–May<sub>i</sub> in Table 5a.

Source of variation	QDevi	% QD	np	QAIC <sub>c</sub>	w
a) Modeling survival rate <i>S</i>					
Year <i>i</i>	2466.2	100	55	2580.1	0.93
Precipitation June <sub>i</sub> –May <sub>i+1</sub>	2482.7	29	50	2585.9	0.05
No. Frost days March <sub>i</sub> –May <sub>i</sub>	2485.1	18	50	2588.4	0.02
Constant	2489.3	0	49	2590.4	0.00
Mean temperature March <sub>i</sub> –May <sub>i</sub>	2488.6	3	50	2591.8	0.00
b) Modeling state transition rates $\Psi$					
State $\times$ Year I	2466.2	100	55	2580.1	1.00
State $\times$ Prec. June <sub>i-1</sub> –May <sub>i</sub>	2623.6	25	20	2664.1	0.00
State $\times$ Mean temp. March <sub>i</sub> –May <sub>i</sub>	2633.9	20	20	2674.4	0.00
State $\times$ Frost days March <sub>i</sub> –May <sub>i</sub>	2661.5	7	20	2702.0	0.00
State	2675.8	0	14	2704.1	0.00
State $\times$ Precipitation June <sub>i-1</sub> –May <sub>i+1</sub>	2666.4	4	20	2706.9	0.00

a classic example of annual fluctuations especially in the number of flowering plants (e.g. *Ophrys apifera*, Wells and Cox 1991). Our results suggest that a greater part of

this variation may be due to redistribution of plants between life-states, and particularly, to transitions into the dormant state, and less to variation in survival. Such fluctuations may distort inference from projection matrix models when based on a few years of data only. Dormancy thus seems key to an understanding of the population dynamics of perennial plants with dormant states. Multistate capture–recapture models are suitable to directly model such effects on the transition rates.

In contrast to seed and bud dormancy, little is known about dormancy of adult life-states in plants, and its determinants are controversial. Earlier observations of a lack of synchronized dormancy in a terrestrial orchid seemed to contradict an effect of climate (Wells 1967). In contrast, in *Cleistes* we found evidence for climatic effects on both survival and state transition rates, although there was strong temporal variation in both rates. Although the correlative nature of our study warrants caution in interpreting these results, precipitation in particular seems to have a crucial effect on the population dynamics of *Cleistes* both for survival and for the redistribution of the ramet population among life-states. Years with more precipitation were associated with higher survival in the same year and with fewer transitions into the dormant state in the following year. Another recent capture–recapture study also found effects of climate on dormancy. In the lady’s slipper *Cypripedium calceolus*, dormancy was more frequent following low precipitation during the previous year, as well as after low mean spring temperatures and a larger number of spring frost days (Shefferson et al. 2001). The direction of the effect of mean spring temperature was the same in both studies, but in contrast to the *Cypripedium* study, we did not detect an effect of the number of spring frost days.

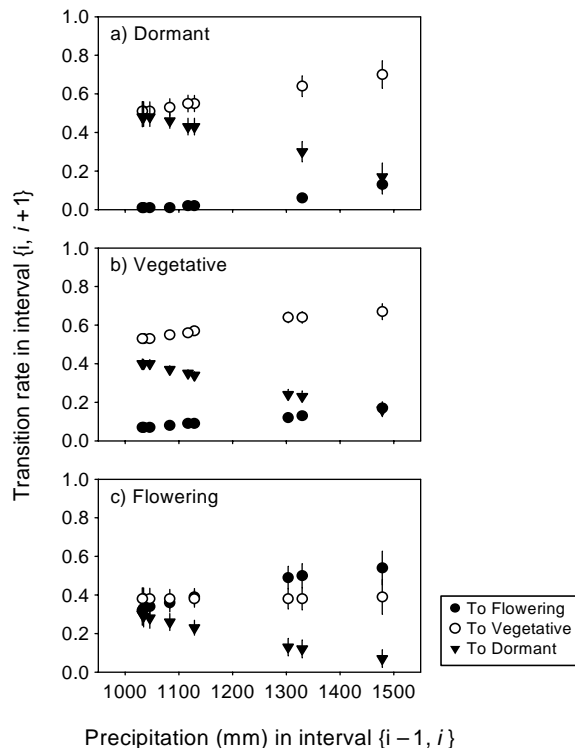


Fig. 1. Effect of total precipitation (in mm) in year *i*–1 on state-transition rates in year *i* in *Cleistes bifaria*. Estimates and SE are from model  $\{S_{\text{time}}, \Psi_{\text{state} \times \text{Prec}(i-1)}\}$  with transitions between year *i* and *i*+1 constrained to be logit-linear functions of total precipitation during the interval June<sub>i-1</sub>–May<sub>i</sub>. Panels a–c are for transitions from the dormant, vegetative, and flowering state, respectively, and symbols denote the state to which plants move.

### The assumption of a unity detection rate

A critical assumption made by all methods discussed in this paper is that the detection probability of all individuals in the aboveground state is equal to 1. This assumption needs to be tested, e.g. through a double-observer study (Kéry and Gregg 2003). In our study, detectability of the aboveground states of *Cleistes* was indeed  $\sim 1$ . However, this will not generally be the case in a plant demographic study, especially when only one survey is made per year. Estimates of demographic rates must then be adjusted for detection probability. There are three ways with which to accomplish this. First, if an estimate of detection probability is available (e.g. from a double-observer study), it can be used directly in capture–recapture models by fixing the corresponding detection probability. This also works well if detection probability is time- or state-dependent. Second, detectability could be estimated as an integral part of a study by conducting at least two full surveys every year. This would enable demographic estimates under the robust design (Kendall et al. 1997, Williams et al. 2002).

Third, under some conditions detectability may be estimated as part of a multistate model from the same encounter history data discussed in this paper even if only one survey is conducted each year. Considering only one aboveground stage, Kendall and Nichols (2002) and Schaub et al. (2004) show that survival, transition, and detection rates can be estimated for a range of models provided that the transition probabilities are Markovian. Using computer algebra to assess parameter identifiability, we are currently exploring the same type of models for two aboveground states. Preliminary results indicate that if there is significant temporal variation in survival and transition rates, these models have a behaviour similar to those with only one aboveground state, and that many of the models in Table 1 may have identifiable parameters even when detection probability is estimated along with survival and transition rates. This is an important result, since it would make possible unbiased estimation of demographic rates even when no ancillary data are available on detection rate. Statistically rigorous demographic estimates based on multistate models may then also be obtained for ‘historic’ data sets for which it may be not possible anymore to conduct a sampling survey specifically to estimate detection probability. Still, there may be costs involved in terms of the precision of estimates. In addition, models are not identifiable when either survival or transition rates are time constant or nearly so. Therefore, the best solution is probably to collect data in such a way that they can be analysed with the robust design approach (Schaub et al. 2004).

### Additional issues in demographic studies of plants with dormant states

Many plant demographic studies involve estimation of the size of a population (Alexander et al. 1997, Slade et al. 2003). Such estimations are difficult for species with dormancy, especially if the annual fraction dormant fluctuates, as is so typical for many terrestrial orchids. As a solution, we suggest individually marking and surveying a sample of the population so that the fraction dormant can be estimated for each year  $i$  as  $(1 - p_i)$  via a time-specific CJS model. Annual counts ( $C_i$ ) of the visible, aboveground fraction of the population can then be adjusted for plants underground as  $\hat{N}_i = C_i / \hat{p}_i$ , where  $\hat{N}_i$  is the estimated population size in year  $i$  and  $\hat{p}_i$  the estimated fraction of the population aboveground.

With capture–recapture analysis, it is also possible to construct a projection matrix for a plant with dormancy. Models in our study condition on first observation of plants, i.e. they only describe the probability of events after first marking an individual. They therefore do not model the recruitment process, but instead model losses (the complement of survival) and redistribution between states (transition rates). The loss and state redistribution part of a projection matrix can easily be obtained by multiplying the matrix of state transitions by a vector of state-specific survival rates. Recruitment would then have to be added, information about which could either come from outside the main capture–recapture study or estimated directly using a Jolly–Seber type capture–recapture model, such as Pradel’s temporal symmetry model (Pradel 1996).

### Temporal emigration as a unifying concept

Unobservable life-states frequently occur in animal ecology, e.g. when some animals skip a breeding event and sampling is conducted only at the breeding sites. This is known as temporary emigration (Kendall et al. 1997, Schaub et al. 2004). A difference between the CJS model and the multistate model is that the former assumes that the state transitions are random, whereas in the latter models they are Markovian. This means that under the CJS model it is assumed that the probability of a plant to become dormant in the next year does not depend on whether or not the plant is dormant in the current year. Under the multistate model, the probability of a plant becoming dormant in the next year may depend on whether the plant was dormant, vegetative or flowering in the current year. These assumptions are testable. The CJS model could be adapted to allow Markovian transitions (Schaub et al. 2004), and the multistate model could be constrained in such a way that the transitions are random. Using formal model selection it is possible to test which form of transitions is appropriate for the data at hand.

## Conclusion

Our study shows that different available methods of studying demography of plants with dormancy may produce very dissimilar estimates of rates of survival, state transitions, and of the fraction of dormant individuals in the population. The differences within the class of conventional methods were considerable and show a high sensitivity of the parameter estimates to the additional assumptions that are required with the conventional methods. Further, conventional methods yield spurious estimates of survival rates. We formally show that many multistate capture–recapture models, which require the fewest assumptions of all methods considered, have parameters that are identifiable. These latter models yielded insights into the effects of climate on the demography of the orchid *Cleistes bifaria*, that might otherwise have been impossible to obtain in a statistically rigorous way. Our results suggest that orchid populations will be sensitive to climate change. We suggest that conventional methods should not be used for plant demographic studies involving dormant states. Better methods with less restrictive assumptions are now available. Life states are such a prominent feature of plants that multistate models offer a natural framework for analysing plant population dynamics.

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