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ESTIMATING DORMANCY AND SURVIVAL OF A RARE HERBACEOUS PERENNIAL USING MARK–RECAPTURE MODELS

RICHARD P. SHEFFERSON,[1] BRETT K. SANDERCOCK,[1] JOYCE PROPER,[2] AND STEVEN R. BEISSINGER[1,3]

[1]*University of California, Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management,*
151 Hilgard Hall, Berkeley, California 94720-3110 USA
[2]*Lake County Forest Preserve District, 36946 North Fairfield, Lake Villa, Illinois 60046 USA*

Abstract. Mark–recapture statistics have rarely been applied to plants, yet they can be useful for estimating plant demographic traits where individuals may be missed or unobservable. We applied mark–recapture statistics based on an information theory approach to estimate annual probabilities of dormancy in a five-year study of a threatened, perennial plant, the small yellow lady's slipper orchid (*Cypripedium calceolus* ssp. *parviflorum* (Salisb.) Fernald). The aboveground states of 548 genets in eight patches were monitored over five years. Apparent survival probabilities (ϕ), corrected for dormancy, were calculated. The best-fit model suggested that apparent survival was constant throughout the study for all patches, while dormancy varied additively with time among patches. The mean probability of dormancy was 0.320 ± 0.024, with a mean maximum overestimation of 0.067 as calculated using an estimate of the probability of detection. Dormancy typically lasted for no longer than two consecutive years, although dormancy as long as four years was observed. Dormancy displayed a strong covariate relationship with spring frost days, although effects of precipitation and mean spring temperature were almost equally strong. Mean apparent survival probabilities were high in each patch ($\phi = 0.878$), but dormancy probabilities varied considerably among patches ($d = 0.188$–0.672). Conventional resprouting probabilities underestimated apparent survival by a mean difference of 0.288 (range: 0.150–0.589). This novel application of mark–recapture statistics to plant demography allowed robust survival estimates that accounted for uncertainty due to an unobservable, dormant life stage.

Key words: adult plant dormancy; bud dormancy; Cypripedium calceolus; *demography; information theory; lady's slipper orchids; mark–recapture; maximum likelihood estimation; open population dynamics; survivorship.*

INTRODUCTION

> *Although plants do not present the problems of capture, mark and recapture that haunt animal demographers, observations on plant survival . . . are extremely laborious and time consuming. Another problem is that a considerable proportion of the plant is below ground where it is not visible.*
>
> —Solbrig (1980:4)

Demographic approaches to monitoring are central to assessing plant population trends and viability (Davy and Jefferies 1981, Schemske et al. 1994). One of the most integrative ways to evaluate the status of a threatened plant is to study its population persistence and critical life history stages through the use of Lefkovitch stage-based population matrices (Menges 1986, 1990, Silvertown et al. 1993, Fiedler et al. 1998). However, the paucity of demographic data for endangered plants hampers the development of population viability models (Menges 1986, Schemske et al. 1994, Beissinger and Westphal 1998). Unpredictable phenomena such as seed and adult dormancy pose particular difficulties for estimating population parameters, such as fecundity and survival (Gilbert and Lee 1980, Lesica and Steele 1994, Rasmussen and Whigham 1998, Sanger and Waite 1998).

Most demographic studies assume that all live plants can be detected (Gilbert and Lee 1980, Menges 1986, Lesica and Steele 1994). However, aboveground shoots may not give an accurate indication of total population size if much of a population remains dormant in the soil as seeds or root structures. This may be of particular concern for the monitoring of endangered plants that experience dormancy because population size could be greatly underestimated by overlooking individuals that have not sprouted. Alexander et al. (1997) approached the monitoring difficulties associated with dormancy by using mark–recapture statistics. These statistical methods are best known for applications that evaluate apparent survival and resighting probabilities of free-living animals (Lebreton et al. 1992), but have broader applications, including analysis of colony-site dynamics (Erwin et al. 1998), extinction events (Nichols and Pollock 1983, Rosenzweig and Clark 1994), and species richness (Dawson et al. 1995). Alexander et al. (1997) used mark–recapture models based on

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[3] Address correspondence to this author.

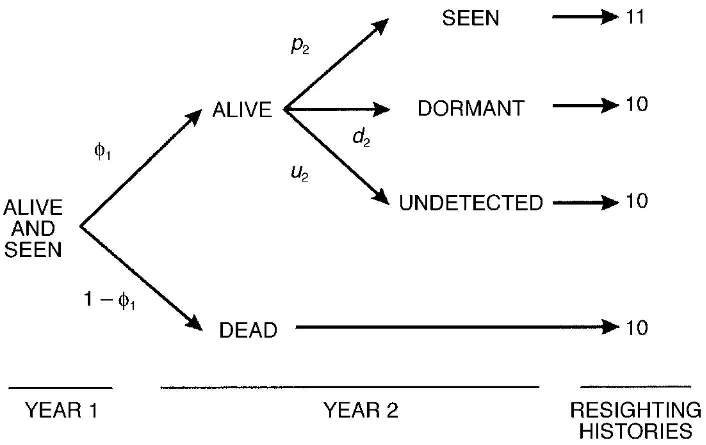

FIG. 1. Resighting histories over a two-year period for herbaceous perennials exhibiting dormancy. Resighting histories are developed as binary strings with successive digits corresponding to presence (1) and absence (0) in successive years. Terms include: ϕ (apparent survival), p (resighting probability), d (dormancy probability), and u (the probability of nondetection). Note that $p_i + d_i + u_i = 1$. If the probability of detection (p_i^*) equals $p_i/(p_i + u_i)$, then corrected dormancy (d_{corr}) is $1 - p/p^*$.

closed populations to estimate the population size of Mead's milkweed (*Asclepias meadii* Torr. ex A. Gray), a rare prairie perennial that grows in dense patches. Their results indicated that an annual census of aboveground shoots would most likely significantly underestimate the true size of the population.

We expand the use of the mark–recapture approach to open populations of plants, which experience both real and observable fluctuations in population size, to develop robust estimates of adult dormancy and survival probabilities. Contemporary methods for open populations start from a global model such as the Cormack-Jolly-Seber (CJS) model, in which apparent survival and resighting probabilities vary by sampling intervals, or more complex models involving variation among multiple groups or stage classes (Brownie 1987, Clobert and Lebreton 1987, Lebreton et al. 1992). Plant resighting histories, which form the raw data for analysis, are coded for the yearly presence (1) or absence (0) of an aboveground shoot for each known individual (Fig. 1). Gaps in resighting histories may indicate that a plant was dormant, missed, or removed from an observable state (e.g., by herbivory). Observed resighting histories are converted into multinomial expansions, or likelihood functions, composed of apparent survival (ϕ) and resighting (p) terms that describe the temporal, spatial, and/or constrained nature of the model (Appendix). These expansions are then solved iteratively for the parameter values with the highest likelihood (Lebreton et al. 1992).

Plant demographers often estimate resprouting rates, or the percentage of marked plants observed in a subsequent year, and use it as a surrogate for survival. This term is equivalent to the ''return rates'' reported in wildlife literature (Lebreton et al. 1992). Using the open population mark–recapture approach, the resprouting rate may be decomposed into two probabilities: resighting (p) and apparent survival (ϕ; Nichols 1992). For models based on plant populations, the probability of resighting is the product of the probability that a live plant produces an aboveground shoot in a given year (i.e., sprouting or s) and the probability that the shoot is detected if present (i.e., detection or p^*). Apparent survival is an estimate of actual survival corrected for the resighting probability. The probability of dormancy (d) can be defined as the complement of resighting ($1 - p$) if the entire population is detected ($u = 0$; Fig. 1), an assumption that can be tested. An important consideration for estimating dormancy is the duration of the study, since a minimum of three years of mark–recapture data are required to estimate parameters for a single year (Lebreton et al. 1992). Furthermore, studies conducted for an interval shorter than the duration of dormancy may underestimate annual survival.

In this paper, we demonstrate the utility of mark–recapture models for estimating demographic parameters of long-lived plants. Here, we estimate adult dormancy and survival probabilities for the small yellow lady's slipper orchid, *Cypripedium calceolus* ssp. *parviflorum* (Salisb.) Fernald (hereafter the lady's slipper orchid). This rare, long-lived plant is threatened throughout its range, and estimates of the probability of dormancy for this orchid could have practical applications in future management and policy decisions. First, we evaluated the presence and extent of dormancy, and conducted sequential surveys to evaluate the validity of assuming unity in detection of surviving, nondormant individuals. Then, we used mark–recapture models to develop unbiased estimators of the probability of dormancy and apparent survival. We also show how this approach can be used to test life history hypotheses by conducting an initial exploration of the relationship between dormancy and several environmental covariates that influence the vital parameters of related orchid species. Lastly, we examined discrepancies between apparent survival estimates generated by our models and annual survival estimates generated as conventional resprouting rates that do not account for dormancy.

PLATE 1. A small yellow lady's slipper (*Cypripedium calceolus* ssp. *parviflorum*) genet with three flowers and a one-year-old seed pod in Gavin Prairie Nature Preserve, Lake Villa, Lake County, Illinois.

METHODS

Study organism and study site

The lady's slipper orchid is a perennial orchid occurring primarily in the Great Lakes region of the United States (Fuller 1933, Case 1987, Swink and Wilhelm 1994; see Plate 1). It is listed as endangered by the state of Illinois and by most other states in which it is found (Taft and Solecki 1990). It typically occurs in tamarack swamps, wet woodland boundaries, wet meadows, and fens (Case 1987, Swink and Wilhelm 1994). In Lake County, Illinois, anthesis (i.e., flowering) occurs annually from 18 May through 13 June (Swink and Wilhelm 1994). Pollination occurs through insect vectors, and the tiny seeds lack nutritional reserves, requiring impregnation of soil mycorrhizae for germination and growth (Fuller 1933, Curtis 1943). The first aerial leaf typically develops three years after germination, followed by another seven to thirteen years until the first mature flowering shoot is observed (Curtis 1943, Kull 1995). The seedling phase may be of particular importance to population persistence; in the related species, *Cypripedium acaule*, median longevity is 5.6 yr from germination, and 23.9 yr for plants that have survived to maturity (Gill 1989). A lateral rhizome can initiate the growth of multiple stems, or ramets, per individual plant, or genet (Harper and White 1974). Ramets can grow from adjacent nodes as little as 0.5–1.1 cm apart (Kull 1987, Kull and Kull 1991). Kull and Kull (1991) estimated that a typical rhizome may have as many as 20 live, annual increments of growth.

Although much debate exists regarding its cause, dormancy is a phenomenon in which an aboveground shoot may fail to form in a given year without mortality to the plant (Curtis 1954, Tamm 1972, Lesica and Steele 1994). This phenomenon may be an extreme form of ramet dormancy, in which shoots fail to form from a live annual growth increment of the rhizome (Kull 1995). However, plant demographers often acknowledge genet dormancy as a separate life history stage (Cochran and Ellner 1992, Kull 1995). Here, we use dormancy to refer to the absence of all shoots on a living, adult genet in a given year.

This study was conducted from 1995–1999 in eight patches of a 3-ha open wet meadow at Gavin Prairie Nature Preserve in Lake County, Illinois, USA (42°23′ N, 88°8′ W). The meadow had standing water in its western and southern range, and was dominated by *Carex* species growing on tussocks. In its eastern range, it graded into a wet prairie dominated by tallgrass species. Due to the presence of 16 state-listed threatened and endangered plants in the immediate vicinity, the site has been protected within the Illinois Nature Preserve System (Nuzzo 1990, Taft and Solecki 1990). Four soil series were identified in the wet meadow, with a pH range from 5.6 to 7.8 (Nuzzo 1990). Annual precipitation, measured from the start of one monitoring period to the next one, ranged from 850 mm to 1000 mm during the study, with peaks in late spring and early summer.

Field methods

We monitored a total of 548 mature genets occupying eight study patches (Table 1). We also monitored genets in three of the patches in 1994, but only used this data to analyze length of dormancy. In each patch, we established one permanent stake and attempted to locate all individual plants (genets), both flowering and vegetative. Every year during late anthesis, we recorded the location of each genet by marking its distance and direction from the permanent stake using a 50-m measuring tape and compass. Experienced field crews were used each year to maximize the probability of genet detection. Locating genets was relatively easy due to their low density and diffuse distribution (Table 1). Plants that lacked flowers were assumed to be *C. calceolus*, except in three patches where *C. candidum* and *C.* × *andrewsii* were also found. Members of these three species cannot be identified to species without flowers present (Swink and Wilhelm 1994), and 34 unidentifiable individuals were excluded from analysis (Table 1).

In all surveys, individual shoots located within 20 cm of each other were considered ramets of the same genet to account for the likely areal extent of each

TABLE 1. Characteristics of the eight patches of lady's slipper orchids, *Cypripedium calceolus* ssp. *parviflorum*, studied at Gavin Prairie, Lake County, Illinois, from 1995 to 1999.

Patch name	Total genets included in analysis	Percentage of genets with <5 ramets	Density (genets/m^2)
A	52	98%	1.389 ± 0.033
Aspen	143	99%	1.324 ± 0.064
C	35	94%	1.301 ± 0.053
T	53	89%	1.256 ± 0.033
Willow	42	95%	1.234 ± 0.046
X	128	94%	1.249 ± 0.023
Y	23	96%	1.033 ± 0.033
Z	72	97%	1.070 ± 0.049

Notes: ''Percentage of genets with <5 ramets'' is the percentage of total observed genets with a maximum of four ramets per year in all years of the study. Density of sprouting genets was determined for each patch on an annual basis. Genet locations were transformed into Cartesian (x, y) coordinates to account for the uneven distribution within each patch and to provide unbiased estimates of crowding. The study plots were treated as grids with 1-m^2 squares, and the total number of genets was divided by the total number of occupied squares.

orchid without including offspring and other orchids (Curtis 1943, Svedarsky et al. 1996). Thus, one genet could theoretically cover any area as long as each ramet was within 20 cm of at least one other ramet. Genets were assumed to be spatially segregated and nonoverlapping due to the low number of shoots (ramets) found per clump, and the low overall shoot density (Table 1; T. Kull, *personal communication*). Seedlings typically have one leaf, and the incidence of one-leafed ramets in mature plants of this genus is rare (Curtis 1943, Cochran 1986, Cochran and Ellner 1992). In this study, we only included mature genets with at least one ramet having two or more leaves.

Genet resighting histories were determined by matching the location of each genet to locations recorded in previous years. If two genets were located within 20 cm of each other in different years, they were considered to be of the same genet. Observations in consecutive years were then assembled into binary strings to develop the resighting histories (Fig. 1, Appendix).

An exploration of the prevalence of dormancy was conducted using resighting histories for 279 genets that were positively identified as being alive for a minimum of three to six years. Resighting data from 1994 were included in this analysis to see whether any genets were dormant for four years. To be included in this analysis, an orchid required a resighting history where it was known to be alive for a three- to six-year period.

To determine whether the probability of detection in this study approached unity, we surveyed the patch with the largest lady's slipper orchid population (Aspen) twice over a five-day period in 1999. During this short period, the population was assumed to be closed. Only two surveys were conducted to avoid damage from trampling, which would present extra risk to these threatened plants and could affect the probability of detection.

Mark–recapture modeling

Detection.—Mark–recapture analysis was used to examine the assumption that the detection probability was at unity. Specifically, closed population modeling through the ''Closed Captures'' option in program MARK was used (Otis et al. 1978, Alexander et al. 1997, White 1999). The overall probability of detection (p^*) was considered a function of two exclusive probabilities: the probability of first detection (f) and the probability of redetection (r). Assuming a closed population during the two-occasion extra monitoring session that we conducted in patch Aspen in 1999, the probability of first detection was calculated for all orchids using model f, c_c, N_c. In this model, f refers to the probability of first detection over the session, c refers to the probability of resighting, N refers to the population size, and the subscript ''c'' denotes constancy in the associated quantity or probability (White 1999). To determine the probability of redetection, or of resighting orchids located in previous years, we applied the same model to the subset of orchids that were sighted in 1998 or earlier, thus limiting the data to those orchids capable of being redetected. This approach corrected estimates of detection probability for small sample size, and enabled calculation of the associated standard errors. To be conservative, the lower of the two probabilities (f and r) was used as the overall probability of detection.

Dormancy and survival.—We conducted an open population mark–recapture analysis to estimate the probabilities of dormancy and apparent survival. To assess spatial and temporal variation in these rates, a global model was developed that incorporated site and annual variation (model $\phi_{\text{patch*time}}$, $p_{\text{patch*time}}$, abbreviated as $\phi_{p*t}\, p_{p*t}$), and then further models with reduced time and patch dependence were examined. Resighting histories were modeled for each patch using Program MARK (White 1999) following methods described by Lebreton et al. (1992) and Burnham and Anderson (1998). Maximum likelihood estimation of apparent survival and resighting probability was accomplished through the logit-link function (White 1999). Because correlations between population performance and environmental covariates have been found in other orchid species, models were developed that constrained dormancy as a linear function of annual variation in precipitation, mean spring temperature, and the number of freezing days in spring (hereafter, spring frost days). More complex models were not developed because we lacked a sufficiently long data set to adequately test alternative model structures. Precipitation (pre) was calculated as the total annual rainfall (mm) prior to anthesis (from June of the previous year until May of the study year: 1994, 833 mm; 1995, 849 mm; 1996, 883 mm; 1997, 892 mm; 1998, 999 mm; 1999, 864 mm). Spring frost days (sfd) were counted from March through May (1994–1999: 30 d, 25 d, 40 d, 35 d, 24 d, and 26 d, respectively). Mean spring temperature (mst) was calculated as the average of all daily high and low temperatures from March through May (1994–1999: 8.5°C, 7.7°C, 5.6°C, 6.7°C, 9.9°C, and 8.1°C, respectively). We expected rainfall and mean spring temperature to correlate negatively, and spring frost days to correlate positively with dormancy. Although spring frost days and mean spring temperature were negatively correlated (Spearman $r = -0.771$, $P = 0.072$), the use of both covariates in separate models does not hinder inferences from mark–recapture analysis and we had no a priori reason to include one covariate at the expense of the other.

Bias in dormancy estimates.—Multiple checks during each year revealed no sprouting periods outside of the monitoring interval (J. Proper, R. Shefferson, K. Craft, and G. Vogt, *unpublished data*), and our records allowed us to detect over 90% of the lady's slipper orchids present (see *Results*). Thus, resighting (p) was assumed to be the probability of sprouting in a given year, and dormancy was calculated using $1 - p$ (Fig. 1). However, a corrected dormancy rate was also calculated to determine the maximum estimated bias in dormancy, where

$$d_{\mathrm{corr}} = 1 - [p/p^*] \qquad (1)$$

in which p is the probability of resighting from open population modeling and p^* is the probability of detection from the closed population modeling above. This corrected probability was calculated under the assumption that the probabilities of detection in other patches were similar to that of patch Aspen. This site was very likely to have a low, conservative p^* due to larger size and greater abundance of tallgrasses and dense vegetation compared to the other patches. Although the density of orchids at this site was slightly greater than in most other patches (Table 1), the difference was small and suggested little bias in the calculation of p^*.

Model selection

QAICc and overdispersion.—Following recent advances in mark–recapture theory, we adopted the information-theory approach to model selection and inference described by Burnham and Anderson (1998). This approach is starting to gain wider acceptance in the literature for its strong theoretical basis. The philosophy of the information-theory approach differs from likelihood ratio testing because it does not rely on arbitrary significance criteria and does not infer treatment effects where no experimentation was performed (Akaike 1973, Rice 1989, Lebreton et al. 1992, Burnham and Anderson 1998). Here, models were compared through the calculation of QAICc (corrected quasi-Akaike Information Criterion), a quantity derived from quasi-likelihood theory which evaluates each model's relative level of information loss from the original data set. QAICc calculates a single value that denotes the balance between the bias inherent in the parameters and the variance of the parameters (Akaike 1973, Burnham and Anderson 1998). Actual QAICc values have no intrinsic value because they are not on a ratio scale, but can be compared to values for other models in the same data set.

QAICc improves on conventional AIC (Akaike Information Criterion) because it incorporates corrections for small sample size and overdispersion (Cox and Snell 1989, Burnham and Anderson 1998). For a model M_j, it is given by Burnham and Anderson (1998) as:

$$\mathrm{QAICc} = -(2\log[\mathcal{L}\{\hat{\theta} \mid x, M_j\}]/\hat{c}) + 2K + (2K[K + 1])/(n - K - 1) \qquad (2)$$

where $\log[\mathcal{L}\{\hat{\theta} \mid x, M_j\}]$ is the log-likelihood of a set of parameter estimates $\hat{\theta}$ given data x and model j, K is the number of estimable parameters, and n is the effective sample size (White 1999). The variance inflation term, $\hat{c}$, corrects overdispersion, which occurs when a distribution has a larger-than-expected variance. When overdispersion is not corrected, relative differences in AIC in a suite of models are exaggerated, possibly resulting in false inference.

We tested the appropriateness of this approach with the program MARK bootstrap goodness-of-fit test for the global model. A distribution of expected deviance values was developed given the ideal conditions of independence of fate, equal detection, and lack of overdispersion (White 1999). The observed deviance of the global model was then compared to the ranked deviance values of 1000 simulations of the procedure, where deviance is given as follows:

$$\mathrm{deviance} = -2\cdot(\mathcal{L}[\hat{\theta} \mid x, M_{sat}]) - (-2\cdot[\mathcal{L}\{\hat{\theta} \mid x, M_j\}]) \qquad (3)$$

where M_{sat} refers to the saturated model (see White 1999 for definition) and M_j refers to the nested model under consideration (White 1999). If the bootstrapped deviance values are ranked in ascending order, the significance of an observed global deviance is given as the proportion of all bootstrapped values that are greater than the observed value (White 1999). When overdispersion was detected (see *Results*), we analyzed whether the magnitude of overdispersion was small enough to allow the use of QAICc. The variance inflation term, $\hat{c}$, was calculated by dividing the observed deviance in the global model by the mean expected deviance obtained from bootstrapping (G. White, K. Burnham, and D. Anderson, *unpublished manuscript*). Under this framework, $\hat{c} < 4$ allows the use of QAICc (Burnham and Anderson 1998).

Model development and ranking.—Model development was an iterative process consisting of reduction of time and patch dependence in apparent survival and resighting probability. To determine robust estimates of dormancy, we first reduced apparent survival. Once the model with the lowest QAICc for apparent survival was found, we continued model fitting by reducing time and patch dependence in the probability of resighting. The probability of resighting was also constrained to a linear fit of each environmental covariate. Apparent survival and resighting were modeled further using the model with the lowest QAICc from the previous iteration to examine if other reductions could be made. The model with the lowest QAICc overall was considered the best-fit model.

Models were ranked and parsimony was inferred according to differences in QAICc value relative to the best-fit model (i.e., ΔQAICc; Burnham and Anderson 1998). Models with $\Delta\text{QAICc} \leq 2$ from the best-fit model were considered equally parsimonious, those with $\Delta\text{QAICc} > 2$ and ≤ 10 had weak support, and those with $\Delta\text{QAICc} > 10$ had strong evidence against them (Burnham and Anderson 1998). Further inference was made with Akaike weights, which were determined to examine the likelihood that a particular model is the best model for the system. Akaike weights are given as

$$w_i = e^{(-\Delta\text{QAICc}_i/2)} \Big/ \sum e^{(-\Delta\text{QAICc}_j/2)} \qquad (4)$$

where ΔQAICc is again the difference in QAICc, i refers to the model under evaluation, and j refers to all models, whose $e^{(\Delta\text{QAICc}_i/2)}$ values are summed in the denominator (Buckland et al. 1997, Burnham and Anderson 1998).

Parameter estimation

The technique of model averaging was used to estimate patch-level vital rates and unconditional variances that reflected the uncertainty in model selection (Burnham and Anderson 1998; G. White, K. Burnham, and D. Anderson, *unpublished manuscript*). This technique uses Akaike weights to estimate vital parameters and variances that are weighted by the relative strength of each model, as in

$$\hat{\theta}_a = \sum w_i \hat{\theta}_i \qquad (5)$$

where the estimate $\hat{\theta}$ of parameter a is given by a weighted average of the parameter estimates for each model i according to the Akaike weight w of each model. Models with low QAICc values contribute the most to the final estimate of the parameter. Just as important as the calculation of the model-averaged estimate is the calculation of a standard error incorporating the level of model selection uncertainty. The appropriate quantity, per Buckland et al. (1997), is known as the estimated unconditional variance, given as

$$\text{var}(\hat{\theta}_a) = \left(\sum w_i \sqrt{[\text{var}\{\hat{\theta}_i \mid \text{M}_i\} + \{\hat{\theta}_i - \hat{\theta}_a\}^2]}\right)^2. \qquad (6)$$

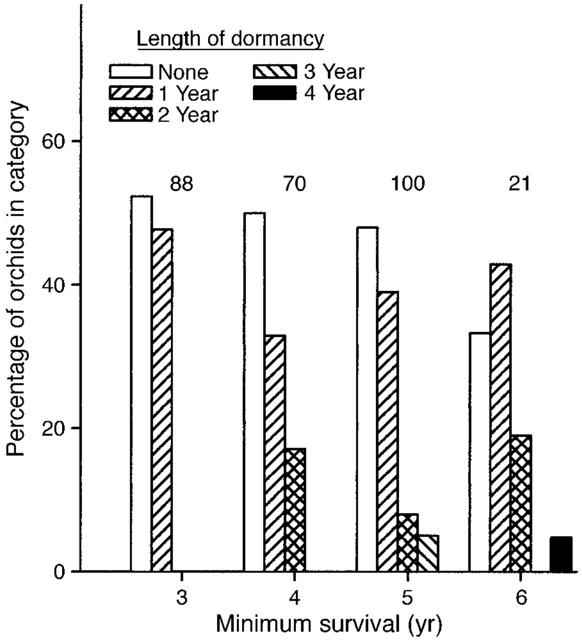

FIG. 2. Length of dormancy in orchids surviving at least three years, for lady's slipper orchids in eight patches at Gavin Prairie, Lake County, Illinois, monitored from 1995 to 1999. Data from three patches monitored in 1994 were included. Minimum survival lengths were treated as independent subsets, with each orchid assigned to only one category.

Patch-level and overall means of model-averaged parameter estimates were calculated, and standard errors were developed using the method of moments to propagate dependent random uncertainties (Taylor 1997: 212).

To examine the bias resulting from failure to consider dormancy, the resprouting probability was calculated as the proportion of individuals sprouting one year that also sprouted in the following year. The bias in using this probability as a proxy for survival was calculated as the difference between apparent survival and resprouting. Due to possible overestimation of dormancy, we also present dormancy estimates corrected for the probability of detection. All estimates are presented with ±1 SE.

RESULTS

Dormancy was commonly observed in the lady's slipper orchids, but rarely lasted longer than one year (Fig. 2). Of orchids that were known to be alive for three to six years, the number of individuals with dormant periods of one or more years was comparable to the number of individuals with no noticeable dormancy in all independent subsets of the resighting data: 143 orchids experienced dormancy, while 136 orchids did not. Seventy-nine percent of the former group were dormant for one year. Dormancy periods of two and three years were uncommon. Two-year dormants accounted for 12% of orchids alive for 4–6 yr, while

TABLE 2. Modeling resighting probability (p) and apparent survival (ϕ) for lady's slipper orchids in eight patches studied at Gavin Prairie, Lake County, Illinois, using data from 1995 to 1999.

Model	K	Deviance	ΔQAICc	w
Modeling ϕ				
$\phi_{p*t}\, p_{p*t}$	56	201.1	35.3	≤0.001
$\phi_{p+t}\, p_{p*t}$	42	226.1	22.7	≤0.001
$\phi_{p}\, p_{p*t}$	40	229.9	21.2	≤0.001
$\phi_{t}\, p_{p*t}$	35	234.4	13.7	≤0.001
$\phi_{c}\, p_{p*t}$	33	238.2	12.2	≤0.001
Modeling P				
$\phi_{c}\, p_{p+t}$	**12**	**281.3**	**0**	**≤0.294**
$\phi_{c}\, p_{p}$	**9**	**289.8**	**0.1**	**≤0.274**
$\phi_{c}\, p_{t}$	5	329.6	21.5	≤0.001
$\phi_{c}\, p_{c}$	2	339.5	22.8	≤0.001
$\phi_{c}\, p_{p+mst}$	**10**	**289.5**	**2.0**	**≤0.107**
$\phi_{c}\, p_{p+pre}$	10	289.8	2.2	≤0.099
$\phi_{c}\, p_{p+sfd}$	**10**	**289.2**	**1.8**	**≤0.121**
Further Models				
$\phi_{p+t}\, p_{p+t}$	21	272.1	11.9	≤0.001
$\phi_{p}\, p_{p+t}$	19	275.6	10.3	≤0.002
$\phi_{t}\, p_{p+t}$	14	278.6	2.1	≤0.101

Notes: Notation follows Burnham and Anderson (1998). K refers to the number of parameters. ΔQAICc is calculated as $\text{QAICc}_i - \min(\text{QAICc})$, where i refers to the model. The correction for overdispersion ($\hat{c}$) was 1.352. In the last column, w refers to the Akaike weight for each model using QAICc, where support for the model covaries with w. Subscripts include patch variation (p), annual variation (t), precipitation in mm (pre), number of freezing days in spring (sfd), mean spring temperature (mst), and constancy (c). The best-fit and equally parsimonious models are presented in boldface type.

three-year dormants accounted for only 4% of orchids alive for 5–6 yr (Fig. 2). Only one individual was dormant for four years. This analysis suggested that survival estimates that are not corrected for dormancy are likely to be biased.

Closed population modeling applied to patch Aspen indicated that the probability of detection was very high but that it deviated slightly from unity. The probability of first detection (f) was 0.920 ± 0.032. The associated probability of redetection (r) was 0.910 ± 0.035. An overall probability of detection (p^*) of 0.91 was assumed. Because these estimates were near unity, dormancy was assumed to be the complement of the probability of resighting ($d = 1 - p$) in subsequent analyses. However, corrected dormancy estimates were also calculated to explore the possible bias resulting from this assumption.

Significant overdispersion was observed in the global eight-patch, five-year model (program MARK bootstrap goodness-of-fit, $P = 0.001$). However, the mean expected deviance ($\text{deviance}_{\text{exp}} = 148.7 \pm 0.5$), calculated using the bootstrap GOF test, was close to the observed deviance of the global model ($\text{deviance}_{\text{obs}} = 201.1$), yielding an overdispersion factor that was relatively low ($\hat{c} = 1.352$). Thus, QAICc is an appropriate measure to analyze this suite of open population models.

The best-fit and three equally parsimonious open population mark–recapture models indicated constancy in apparent survival among all patches and years (Table 2). Models that incorporated patch-level variation into apparent survival had weak support ($w \leq 0.002$; Table 2). Only one of the six best-supported models in our analysis incorporated annual variation in apparent survival (Table 2). This model, $\phi_t\, p_{p+t}$, had an Akaike weight 34% of that of the best-fit model, indicating that some annual fluctuations may occur (Table 2), although this assertion was only weakly supported.

Mark–recapture modeling indicated parallel annual trends in dormancy among patches (Table 2). Patch-level differences in dormancy were clearly observable in our best-fit ($\phi_c\, p_{p+t}$) and three equally parsimonious

TABLE 3. Probabilities of dormancy ($d = 1 - p$), corrected dormancy ($d_{\text{corr}} = 1 - p/p^*$), apparent survival ($\phi$), and resprouting ($R$), and bias in resprouting ($\phi - R$) for lady's slipper orchids in eight patches studied at Gavin Prairie, Lake County, Illinois, using data from 1995 to 1999 (estimate ± 1 SE).

Patch	Dormancy (d)	Corrected dormancy (d_{corr})	Apparent survival (ϕ)	Resprouting (R)	Bias in resprouting ($\phi - R$)
A	0.297 ± 0.071	0.228	0.878 ± 0.021	0.668 ± 0.077	0.210
Aspen	0.278 ± 0.042	0.206	0.878 ± 0.021	0.625 ± 0.100	0.253
C	0.188 ± 0.066	0.107	0.878 ± 0.021	0.677 ± 0.122	0.201
T	0.251 ± 0.063	0.177	0.878 ± 0.021	0.729 ± 0.078	0.150
Willow	0.239 ± 0.067	0.164	0.878 ± 0.021	0.698 ± 0.075	0.180
X	0.256 ± 0.045	0.182	0.878 ± 0.021	0.648 ± 0.062	0.230
Y	0.378 ± 0.109	0.316	0.878 ± 0.021	0.476 ± 0.121	0.402
Z	0.672 ± 0.060	0.639	0.878 ± 0.021	0.289 ± 0.049	0.589
Mean	0.320 ± 0.024	0.252	0.878 ± 0.021	0.590 ± 0.105	0.288

Notes: Apparent survival (ϕ) and resighting (p) probabilities were estimated using the technique of model averaging. Apparent survival (ϕ) was calculated as constant among patches due to the high cumulative Akaike weight of models incorporating no annual variation in that parameter. The probability of resprouting (R) was calculated as the mean proportion of sprouting plants at time $i - 1$ also aboveground at time i; it is equivalent to "return rates" in free-living animals (Lebreton et al. 1992). Dormancy (d) was calculated as the complement of resighting ($1 - p$).

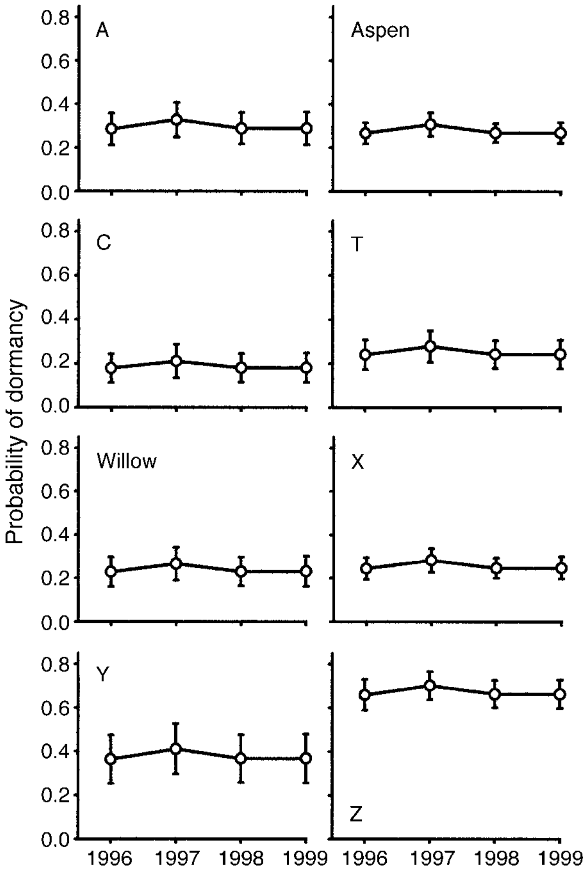

FIG. 3. Annual dormancy estimates for lady's slipper orchids in eight patches at Gavin Prairie, Lake County, Illinois, monitored from 1995 to 1999. Dormancy estimates were calculated by model averaging across all models considered. All parameter estimates are presented ±1 unconditional SE.

models (models $\phi_c\, p_{p+sfd}$, $\phi_c\, p_{p+mst}$, and $\phi_c\, p_p$ in Table 2). Three of these four models incorporated annual variation (models $\phi_c\, p_{p+t}$, $\phi_c\, p_{p+sfd}$, and $\phi_c\, p_{p+mst}$ in Table 2). The combined Akaike weight of these three models ($w_{combined} = 0.52$) relative to model $\phi_c\, p_p$ ($w = 0.27$) indicated that this annual variation was approximately twice as likely to occur as a constant probability of dormancy across all years. These results also indicated a high level of consistency among the annual probabilities of dormancy in the overall population, suggesting that any annual fluctuations in dormancy occurred synchronously among patches.

Dormancy probabilities varied substantially across all years and patches, and ranged from 0.179 to 0.702 (Table 3, Fig. 3). Dormancy occurred most frequently in all patches (Fig. 3) in 1997 ($d = 0.348 \pm 0.033$) and least often in 1996 ($d = 0.308 \pm 0.034$; Fig. 3). Annual estimates of dormancy were highest in patch Z (mean: 0.672 ± 0.060, range: 0.659–0.702) and lowest in patch C (mean: 0.188 ± 0.066, range: 0.179–0.211; Table 3, Fig. 3). The bias in dormancy, calculated by correcting for the probability of detection (p^*), suggested a possible overestimation of 0.067 on average (range across all patches: 0.032–0.080). This minor bias resulted from a high, though not ideal, probability of detection.

The strongest relationship among the analyzed covariates was the positive correlation between spring frost days and dormancy (logit slope coefficient $\beta = 0.009 \pm 0.015$). Relationships with precipitation and mean spring temperature were positive ($\beta = 0.001 \pm 0.037$) and negative ($\beta = -0.023 \pm 0.058$), respectively, and were supported due to parsimony and approximately equal Akaike weights among the covariate models (Table 2). However, only model $\phi_c\, p_{p+pre}$ was not parsimonious with the best-fit model, suggesting the weakest relationship between dormancy and precipitation.

Survival would have been underestimated greatly if dormant plants were assumed dead (Table 3). Apparent survival was calculated as 0.878 ± 0.021 across all years and all patches, due to the strong weight of models incorporating no variation in this parameter (Tables 2 and 3). Resprouting probabilities ranged from 0.289 to 0.729, with an average of 0.590 (Table 3). Thus, failure to consider dormancy resulted in resprouting probabilities that underestimated apparent survival by a difference of 0.288 on average (range: 0.150–0.589, Table 3).

DISCUSSION

Dormancy was a common phenomenon in this population of small yellow lady's slipper orchids (Table 3). Large proportions (19–67%) of this population became dormant each year, although dormant periods lasting longer than one year were rare (Fig. 2). It has been suggested that the buds of a dormant rhizome of this species may live as long as 10 yr, but with an increasingly small chance of resprouting with time (Kull 1995). Dormancy periods as long as four years were observed in this study (Fig. 2). This result is consistent with studies showing dormancy lengths of one to five years in other *Cypripedium* orchids (Gill 1989). However, the functional dormancy length in this population appears to be one to two years, after which the probability of regrowth becomes minute (Fig. 2). This supports Hutchings' (1987) observation of the high probability of death for *Ophrys sphegodes* individuals that were dormant for more than two years. The five year duration of our mark–recapture study was sufficiently long to account for dormancy length among individuals.

Dormancy of adults may be common among temperate Orchidaceae. Using conventional measures, Lesica and Steele (1994) determined that average dormancy probabilities for *Dactylorchis sambucina*, *Listera ovata*, *Ophrys sphegodes*, and *Orchis mascula* populations varied from 0.01 to 0.46, with probabilities as high as 0.85 for some years, and that dormancy usually lasted only one year. Willems and Melser (1998) noted that dormancy lasted a maximum of one year for *Coeloglossum viride,* although it was a rare phenomenon. Mehrhoff (1989) found an adult dormancy length of two years for *Isotria medeoloides,* one of the rarest endemic orchids in the continental United States. *Orchis militaris,* a lowland species occurring across Europe, had a maximum dormancy length of three years (Hutchings et al. 1998). Thus, the maximum length of dormancy in temperate orchids appears to be no more than five years.

Our use of mark–recapture methods to estimate dormancy was based on the premise that the probability of detection of genets was at unity. The estimated detection probability was 91%, and while not at unity, was high enough that it was reasonable to calculate the probability of dormancy as the complement of resighting ($d = 1 - p$, Fig. 1). We suspect three possible reasons for the lack of complete detection in our study. First, it is possible that seedlings were erroneously included in our data set. This was unlikely because exclusion of one-leafed individuals would have avoided this problem. Second, lady's slipper orchids of a repeatedly small stature or those growing in areas where visibility was hampered may have been less detectable, as noted by Alexander et al. (1997). Lastly, lady's slipper orchids may not have been detected as a result of observer error. Each of these scenarios could potentially result in overestimation of dormancy and, less likely, the underestimation of apparent survival. Given our high probability of detection, however, undetected individuals had only a small impact on our results. Correcting for the probability of detection would lower our dormancy estimates by 0.067 on average, which would comprise a slight degree of bias in dormancy in most patches (Table 3).

Our estimate of the probability of detection was calculated using a limited repeat-sampling strategy, where the number of sampling occasions was limited due to the conservation concerns and artifactual considerations posed by trampling damage. In systems where trampling is not an issue, more sampling occasions could be utilized. In this case, detection probabilities could be calculated annually and integrated into an open population study using models based on Pollock's robust design (Pollock 1982).

The bias due to overlooking dormancy in annual survival estimates for this species was quite high (Table 3), suggesting the need for caution in inference by demographers working with this and other species exhibiting adult dormancy. Not taking dormancy into account would have underestimated the survival probabilities of *C. calceolus* by as much as 0.588 in some patches, and on average by 0.287 (Table 3). Population viability analyses using resprouting rates as a surrogate for annual survival are likely to underestimate population growth rates and persistence, perhaps dramatically so (cf. Palmer 1987). Dormancy may be an important life history stage for many vascular plants, as evidenced by the wide variation in dormancy probabilities (Table 3; Fig. 3), the widespread occurrence of both seedling and adult dormancy within temperate species (Lesica and Steele 1994, Rasmussen and Whigham 1998), and the mycotrophic nature of seedling stages in some families like the Orchidaceae (Wells 1967). Given these conditions, the utility of stage-based demographic models for rare plants (Menges 1986) remains problematic unless future monitoring efforts incorporate methods to estimate dormancy and its overall importance to the unbiased calculation of survival probabilities.

Patch-level demographic trends, while similar, were not equal across the six years of our study, suggesting that differences in site-specific factors can have great impact on populations (Tables 2 and 3, Fig. 3). Constancy in survival and variability in resighting rate suggested that small yellow lady's slipper orchids may be regulated primarily through genet dormancy, with environmental influences driving this phenomenon. Our modeling revealed a relatively high level of variability in dormancy and suggested some influence from environmental conditions on the occurrence of dormancy (Fig. 3).

The most influential covariate on dormancy appeared to be the number of freezing days in spring, although precipitation and mean spring temperature appeared almost equally influential. Experimental studies have shown that prechilling has a positive effect on in vitro germination (Chu and Mudge 1994), although our modeling suggested a predominantly positive relationship between dormancy and spring frost days in model ϕ_c, p_{p+sfd} (Table 2). Other authors have noted treatment effects from environmental factors similar to those studied here on bud dormancy systems of other taxa (Takayama and Misawa 1980, Stimart et al. 1982, Aguettaz et al. 1990, de Klerk and Gerrits 1996). However, the covariates and linear models developed in this study were intended only as initial explorations of our data set. Another modeling analysis utilizing long-term data sets and higher order model structures could help discriminate the causes of among-patch variability.

This study is one of the first applications of mark–recapture to estimate dormancy in plants. Mark–recapture analyses incorporate the uncertainty in detection and result in robust estimation of plant vital rates (Alexander et al. 1997). This facilitates an understanding of temporal and spatial changes in vital rates, as well as life history responses to changing conditions. Mark–recapture methodology is especially useful for monitoring and observational studies of plant species where adult dormancy may result in biased estimates of survival. The mark–recapture methods presented here will be useful for herbaceous perennials and for investigating the dynamics of juvenile stages of shrubs and trees, especially in species that die back in fires and resprout from dormant root structures in the following growing seasons. Seedbank dynamics of annuals may also be modeled more effectively with a maximum likelihood approach, particularly in cases where seeds are too numerous to count accurately. Mark–recapture methods may also prove useful for intra-annual modular demography of highly plastic growth forms. Application of maximum likelihood estimation approaches that utilize information-theoretical model selection methods have the potential to enhance greatly the field of plant demography.

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APPENDIX

Maximum likelihood estimation in mark–recapture modeling

To familiarize plant demographers with mark–recapture techniques, we present a short summary of the theory behind this approach to modeling. Maximum likelihood estimation in mark–recapture modeling makes use of the multinomial likelihood function (Pitman 1993), given as

$$\mathcal{L}(\hat{\theta}_i \mid n, y_i) = C \prod (P_i^{y_i}) \tag{A.1}$$

where $\mathcal{L}(\hat{\theta}_i \mid n, y_i)$ refers to the likelihood of the parameter estimates given the data and the model structure, n refers to the total number of parameters, y_i refers to each individual parameter, and P_i refers to the probability value of each individual parameter. The multinomial coefficient, C, is given by Pitman (1993) as

$$C = \binom{n}{y_i} = \frac{n!}{\prod y_i!}. \tag{A.2}$$

Equation A.1 is often log-transformed to convert the right-hand product into a sum. Using a large number of iterations, probabilities can be evaluated for all parameters to find the parameter estimates with the maximum likelihood.

Table A1 shows the unique resighting histories for patch Y of our study site. In the multinomial expansion for each resighting history, ϕ_i refers to apparent survival from time i to time $i + 1$, p_i refers to the resighting rate at time i, β refers to the product of the final two time-dependent parameters, ϕ_4 and p_5, which cannot be estimated separately, and χ_i refers to the probability of not resighting an individual further if already seen at time i, as given by

$$\chi_i = 1 - \phi_i(1 - [1 - p_{i+1}]\,\chi_{i+1}) \tag{A.3}$$

where $\chi_5 = 1$. If an orchid is seen multiple times, then the multinomial expansion begins with the product of apparent survival (ϕ) and resighting (p) for the first occasion it was seen. The appropriate apparent survival/resighting products are multiplied together until all sightings are included, with a term denoting the sighting with no further resighting (χ_i) ending the multinomial expansion. If an orchid is seen only once, its multinomial expansion is composed of only one term: χ_i for the occasion it was observed.

The likelihood function for a population's estimated parameters ($\hat{\theta}_i$) given the number of parameters and associated parameter structure in model M_j and data x would be the product of the multinomial expansions, each to the power of their observed occurrences, and the multinomial coefficient, *C*. Each multinomial expansion is the probabilistic translation of an unique resighting history. Thus, the real resighting histories from lady's slipper orchids in this patch would yield the following function (Table A1):

TABLE A1. Resighting histories and multinomial descriptions for lady's slipper orchids monitored at patch Y in Gavin Prairie, Lake County, Illinois, from 1995 to 1999.

Resighting history	Number of orchids observed	Multinominal expansions
00001	2	No term
00010	4	χ_4
00011	2	β_5
00100	1	χ_3
01000	2	χ_2
01010	2	$\phi_2(1 - p_3)\phi_3 p_4 \chi_4$
01100	1	$\phi_2 p_3 \chi_3$
01111	2	$\phi_2 p_3 \phi_3 p_4 \beta_5$
10100	1	$\phi_1(1 - p_2)\phi_2 p_3 \chi_3$
11000	2	$\phi_1 p_2 \chi_2$
11011	3	$\phi_1 p_2 \phi_2(1 - p_3)\phi_3 p_4 \beta_5$
11111	1	$\phi_1 p_2 \phi_2 p_3 \phi_3 p_4 \beta_5$

Notes: Notation follows Lebreton et al. (1992): ϕ_i refers to apparent survival at time *i*, p_i refers to the resighting rate at time *i*, and β refers to the product of the final two time-dependent parameters, ϕ_4 and p_5, which cannot be estimated separately. The symbol χ_i refers to the probability of no further resighting given sighting at time *i*.

$$\begin{aligned}\mathcal{L}(\hat{\theta}\,|\,x, \mathrm{M}_j) = {} & C\chi_4^4\beta_5^2\chi_3^1\chi_2^2(\phi_2[1 - p_3]\phi_3 p_4 \chi_4)^2 \\ & \times \phi_2 p_3 \chi_3^1(\phi_2 p_3 \phi_3 p_4 \beta_5)^2 \\ & \times \phi_1[1 - p_2]\phi_2 p_3 \chi_3^1(\phi_1 p_2 \chi_2)^2 \\ & \times (\phi_1 p_2 \phi_2[1 - p_3]\phi_3 p_4 \beta_5)^3 \\ & \times \phi_1 p_2 \phi_2 p_3 \phi_3 p_4 \beta_5^1. \qquad \text{(A.4)}\end{aligned}$$

Equation A.4 was log-transformed to facilitate maximum likelihood estimation by turning the likelihood function into a sum rather than a product. If Eq. A.4 had been a binomial likelihood function, then the log-transformed equation could be solved directly with calculus. Multinomial functions need to be solved iteratively, however, due to their complex multivariate structure.

A linear model is ''linked'' to the maximum likelihood function through the use of a special function known as a ''link function''. These link functions constrain the parameter estimates in the maximum likelihood function to a dummy variable structure as entered into a design matrix, resulting in a constrained linear model (White 1999). Through link functions, external constraints can be placed on the data in the form of a model, including the additive linear structure used here and environmental covariates. Many studies in the literature, including this study of lady's slippers, have used the logit link, given as

$$\hat{\theta}_i = e^{d_i}/(1 + e^{d_i}),$$

where d_i refers to the appropriate element in the dummy matrix (White 1999).