

LIFE HISTORY TRADE-OFFS IN A RARE ORCHID: THE COSTS OF FLOWERING, DORMANCY, AND SPROUTING

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Abstract. We tested for life history trade-offs among dormancy, sprouting, and flowering in a seven-year study of a threatened, perennial plant, the small yellow lady's slipper orchid (*Cypripedium calceolus* ssp. *parviflorum* (Salisb.) Fernald). The aboveground states of 629 genets were monitored over seven years in a wet meadow in northeastern Illinois, USA. With mark–recapture statistics, survival, resighting, and stage transitions were calculated among three stage classes of individuals: dormant, vegetative, and flowering. The best-fit and most parsimonious models suggested that (1) survival was constant among years, but varied by stage; (2) dormant individuals suffered significantly higher mortality and were more likely to become dormant in future years than sprouting or flowering individuals; (3) flowering individuals had significantly higher survival and were more likely to flower in the future than sprouting and dormant individuals; and (4) sprouting individuals had a significantly higher stage transition to dormancy from the vegetative state than to any other state. Thus, our results identified costs of dormancy and sprouting to survival and future reproduction, but no costs of reproduction either to survival or future flowering effort. Dormancy seems unlikely to be adaptive except perhaps as a bet-hedging strategy under catastrophic conditions. Applying mark–recapture models to test predictions from life history theory provided a robust means to explore hypothetical trade-offs that may not have been observed in a conventional analysis and allowed dormancy to be estimated robustly without biasing survival estimation.

Key words: adult plant dormancy; bud dormancy; cost of reproduction; cost of sprouting; *Cypripedium calceolus*; demography; lady's slipper orchids; life history trade-offs; matrix modeling; multistrata mark–recapture; survivorship; trade-offs.

INTRODUCTION

Evolutionary theory predicts that life histories evolve subject to constraints imposed by trade-offs among fitness components. A key tenet of life history theory is that increased efforts or risks incurred in reproduction in one breeding season may have a cost to survival or reproduction in the same or a future breeding season (Fisher 1930, Calow 1979, Stearns 1992). In geophytes, plants whose perennating structures occur only belowground (Lesica and Steele 1994), flowering can be a costly aspect of reproduction (Snow and Whigham 1989, Ackerman and Montalvo 1990, Primack and Hall 1990; but see Primack and Hall 1988, Gill 1989). However, measuring reproductive costs can be complicated in many geophytes, in particular orchids, by the phenomenon of dormancy, in which no aboveground shoots develop during the growing season

though metabolic activity and root/rhizome growth continue (Lesica and Steele 1994).

Two hypotheses have been proposed to explain the function of dormancy in geophytes. Dormancy may occur at a cost to the plant as a result of stress. Whole genet dormancy might arise from an inability to compensate for harsh environmental conditions or for herbivory on the above ground shoot or on buds of the root mass during the previous or current growing season (Tamm 1972, Kull 1995). When dormant, the plant lacks resources to sprout new photosynthetic tissue, loses photosynthetic opportunity for the rest of the growing season and one or more future growing seasons, and may suffer an increased likelihood of mortality. For example, mortality rates were higher in dormant individuals of the European orchid, *Ophrys sphegodes*, than in sprouted individuals (Hutchings 1987a). Alternatively, dormancy could benefit plants by allowing them to conserve energy and survive harsh periods (Dahms 1995), and could be a bet hedging strategy to minimize temporal variance in fitness caused by environmental factors (Seeger and Brockman 1987, Philippi and Seeger 1989). Dormancy may be an effective way to avoid population-wide catastrophes, and may

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allow a plant to sample environments across time, similarly to dispersal as a means of sampling space (Levin and Cohen 1991, Wiener and Tuljapurkar 1994, McPeck and Kalisz 1998). In this case, dormant individuals should survive better than nondormant individuals. Thus, life history trade-offs in geophytes may be expected to occur between dormancy and survival, between sprouting and survival, and between flowering and dormancy in addition to the standard trade-offs between survival and flowering and between flowering and sprouting.

Here, we investigate life history trade-offs using multistrata mark-recapture statistics to evaluate demographic costs in a seven-year study of the small yellow lady's slipper orchid (*Cypripedium calceolus* ssp. *parviflorum* (Salisb.) Fernald), hereafter the lady's slipper orchid, a state-listed endangered species in Illinois. Survival in these orchids has been shown to be high and temporally constant, while dormancy fluctuated widely among patches within the population (range: 18–70% of the population; Shefferson et al. 2001). We were unable to experimentally test our hypotheses about the function of dormancy because it is not possible to force dormancy or to force dormant individuals to sprout, and because this species is endangered, which precludes experimentation. Instead, we focused on measuring the costs and benefits of the act of sprouting. We hypothesized that if dormancy is beneficial, then the probability of survival should be higher for dormant than for nondormant individuals. Alternatively, if dormancy occurs at a cost to the plant, then the probabilities of mortality and dormancy in the next growing season will be greater for dormant individuals than for sprouting individuals. If sprouting occurs at a cost to the plant, then sprouting individuals will be more likely to become dormant in the next season than to sprout again. Finally, we hypothesized that if lady's slipper orchids experience a cost of reproduction from flowering, then flowering individuals should experience decreased survival and an increased likelihood of becoming vegetative or dormant compared to individuals with no flowers.

METHODS

Study organism and study site

The lady's slipper orchid is a perennial geophyte occurring primarily in the Great Lakes region of the United States (Fuller 1933, Case 1987, Swink and Wilhelm 1994). 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, flowering occurs annually from mid-May through mid-June (Swink and Wilhelm 1994). Pollination is by deceit of insect vectors, and the tiny seeds lack nutritional reserves, requiring impregnation by the

appropriate mycorrhizal fungi for germination and growth (Fuller 1933, Curtis 1943, 1959). The first aerial leaf typically develops three years after germination, with the first mature flowering shoot appearing seven to thirteen years later (Curtis 1943, 1959, Kull 1995). The lateral rhizome of a single genet can initiate multiple stems (Harper and White 1974). Ramets grow from adjacent nodes as little as 0.5–1.1 cm apart (Curtis 1954, Kull 1987, Kull and Kull 1991). Kull and Kull (1991) estimated that a typical rhizome may have as many as 20 annual increments of growth, with the oldest increments decaying at the end of the rhizome.

This study was conducted from 1995 to 2001 in a 3-ha open wet meadow at Gavin Prairie Nature Preserve in Lake County, Illinois, USA (42°23' N, 88°8' W). See Shefferson et al. (2001) for a description of the site, which 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 ranged from 850 mm to 1000 mm during the study, with peaks in late spring and early summer.

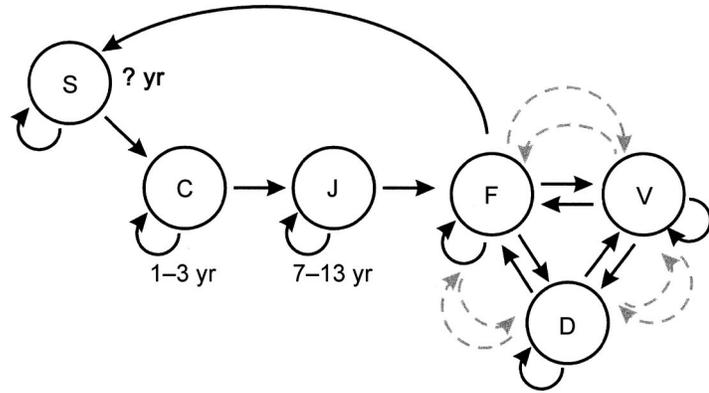
Field methods

We monitored a total of 629 mature genets occupying eight patches, separated by areas without orchids. In each patch, we established one permanent stake and attempted to locate and map 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. No fruiting censuses were conducted, due to the fragility and quality of this rare wetland habitat. 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 (Shefferson et al. 2001).

Earlier work by Curtis (1943) and Svedarsky et al. (1996) allowed us to assume that individual shoots located within 20 cm of each other are ramets of the same genet (Shefferson et al. 2001). 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 (Shefferson et al. 2001). In this study, we included only mature genets defined as having at least one ramet with two or more leaves (Curtis 1943). Genet resighting histories were determined by matching the location of each genet to locations recorded in previous years (Shefferson et al. 2001). The state, or flower stage, of each adult genet was determined as vegetative or flowering, yielding two observable stages at each monitoring occasion (Fig. 1).

As described previously in Shefferson et al. (2001), we determined the probability of detection by surveying the patch with the largest lady's slipper orchid population (Aspen) twice over a five-day period in 1999.

FIG. 1. Life history diagram of the lady's slipper orchid, *C. calceolus* ssp. *parviflorum*. Arrows indicate demographic stage transitions between nodes. Dashed lines indicate vegetative reproduction. Stages are abbreviated as: seed (S), corm (C), seedling or juvenile (J), dormant (D), vegetative (V), and flowering (F). As adults, genets exist as dormant, vegetative, or flowering.



Mark-recapture modeling

Building on the work of Alexander et al. (1997) and Shefferson et al. (2001), we applied mark-recapture models to estimate survival and dormancy. Here, we employed multistrata models that estimate probabilities of resighting and survival within, and the probabilities of transition between, life stages (Brownie et al. 1993, Cam et al. 1998, White and Burnham 1999).

Detection.—Applying mark-recapture models to estimate dormancy assumes that the probability of detection (p^*) approaches unity and does not vary by flower stratum, hereafter referred to as stage. We tested this assumption with closed population modeling using the “closed captures” option in the program MARK (Otis et al. 1978, Alexander et al. 1997, White and Burnham 1999). Shefferson et al. (2001) showed that the probability of detection (p^*) can be considered a function of three exclusive probabilities: (1) the probability of first detection, p_f (this is equivalent to the probability of initial capture, symbolized as p by Otis et al. 1978); (2) the probability of redetection in the same monitoring session, c ; and (3) the probability of redetection in future monitoring sessions, r . Resighting, which we symbolize as p , can be simplified to r only if dormancy does not occur. The bias due to dormancy can be excluded by measuring redetection, c , during the same monitoring session. The parameter c reflects lack of detection due only to observer error. First detection (p_f) has no specific effects on resighting (p).

Here we describe the two-occasion monitoring session we performed to estimate our detection likelihoods for all aboveground orchids. We assumed a closed population during this special monitoring session conducted over a one-week period in patch Aspen in 1999. The probabilities of first detection (p_f) and redetection in the same monitoring session (c) were calculated separately using a step-down modeling strategy for all orchids beginning with model $p_{f(s)}, c_s, N_s$, in which all parameters varied by flower stage. Here, the subscript, s , refers to flowering stage, and N_s refers to the population size within each flowering stage (White and Burnham 1999). This model simultaneously and independently estimates

each parameter for each flowering stage, while ignoring all other sources of variation, such as year. Of the three components of detection, p_f and c are not affected by dormancy, but r is. Thus, to estimate lack of detection due to observer error, we must focus on p_f and c . Consequently, we did not develop model estimates of r . In the Aspen patch, 73 genets were detected and 29 were flowering, of which 76% had only one flower. Thus, only two flower stages were used to estimate the probabilities of detection: vegetative and flowering. While p_f was calculated using the full two-occasion data set, c was calculated using the same modeling strategy but applied only to those orchids capable of being redetected (i.e., the subset of orchids that had been previously sighted in 1998 or earlier).

Multistrata modeling.—We conducted an open population multistrata mark-recapture analysis using program MARK (White et al. 2002) for three stages, which we treated as strata: two observable, flowering (F) and vegetative (V), and one unobservable, dormant (D). Multistrata mark-recapture modeling allows the estimation of three conditional probabilities: (1) survival of an individual in stage k from time i to time $i + 1$ (S_i^k); (2) transition to stage l from k at time $i + 1$ (Ψ_i^{kl}); (3) and resighting in stage l at time $i + 1$ (p_{i+1}^l). These probabilities are considered to be independent of each other. Transitions from stage i to all stages must sum to 1.000, as transition estimates are independent of survival estimates. Furthermore, because this method separates the resighting, survival, and transition likelihoods into independent estimates, life history matrix transitions may be calculated by multiplying survival at stage i (S_i^i) by the transition from stage i to stage j (Ψ_i^{ij}). In all models developed, the resighting parameter was fixed to a known value—the estimate of redetection, c , from closed population modeling for each stage in 1999 (1.000, 0.977, and 0, for flowering, vegetative, and dormant stages, respectively; see *Results*). The accuracy and precision of this approach were tested using a replicated simulation (see Appendix), and both were found to be highly reliable.

Model development.—To assess temporal variation in demographic parameters and demographic hetero-

geneity within the population, we began by developing a global model in which survival, S , varied from year to year as well as independently by flower stage; stage transitions, Ψ , varied from year to year as well as independently by transition; and resighting, p , was fixed to the stage-specific values we determined through closed population modeling, with no annual variation (model $S_{\text{stage} \times \text{time}}, P_{\text{fixed}}, \Psi_{\text{stage transition} \times \text{time}}$, abbreviated as $S_{s \times t}, P_{\text{fixed}}, \Psi_{m \times t}$). This global model was the least constrained of the models developed. Additional models were parameterized by reducing interactions in a hierarchical method, as outlined in Shefferson et al. (2001). First, survival was reduced to additivity in which survival likelihoods varied from year to year in parallel across life stages (i.e., subscript “ $s + t$,” indicating an additive structure between stage and time). Then, survival was constrained to single variables, in which this parameter varied only by year or only by stage (i.e., subscript “ t ,” indicating time, or years, and subscript “ s ,” indicating stage). Finally, survival was reduced to a constant, with no variation allowed (i.e., subscript “ c ”). Survival was also parameterized as constant but differing by aboveground vs. belowground status (i.e., $S^F = S^V \neq S^D$), and by flowering vs. non-flowering status (i.e., $S^F \neq S^V = S^D$).

Once the model with the lowest AIC_c for survival was found, we continued model fitting by reducing independence and time variability in stage transitions, Ψ . First, stage-transitions were constrained to two modes of additivity (i.e., subscript “ $m + t$,” where “ m ” refers to stage transitions and “ t ” refers to time). In the first, stages were ranked ordinally with dormancy being the lowest rank and flowering being the highest. Stage transitions were then constrained as occurring in parallel across time among all stage transitions of equal rank change (e.g., a transition from dormancy to vegetative varied in parallel with a transition from vegetative to flowering, but was independent of all other transitions). In the second kind of additivity, all stage transitions of similar direction varied in parallel with one another (i.e., all transitions from a lower to a higher stage varied in parallel, but independently of transitions from a higher to a lower stage). Next, we created models with no annual variation in stage transitions (i.e., only the subscript “ m ,” indicating independence among transitions but no other variation modeled). Once the model with the lowest AIC_c was found, we remodeled survival in the same way as outlined in the preceding paragraph. Design matrices were used to develop the appropriate parameterizations. The link function used in estimation was the logit function.

Model inference.—Inference was made through a combination of AIC_c analysis, Akaike weighting, and likelihood-ratio testing. The model with the lowest AIC_c among all final models was considered the best-fit model. Models within two AIC_c units of the best-fit model were considered equally parsimonious, while models with AIC_c between two and ten units away had

weak support, and models over 10 AIC_c units away were strongly unsupported (Burnham and Anderson 1998). Further inference was made with Akaike weights, the relative likelihoods that a given model has the best fit given a set of models (these are normalized so that the weights of all models sum to 1.000; Burnham and Anderson 1998). Akaike weights were added across models containing a common parameter of interest to estimate cumulative Akaike weights, which examine the strength of a particular parameterization. To test whether dormancy changed significantly with flowering effort, we conducted a likelihood ratio test of model $S_s P_{\text{fixed}} \Psi_m$ with model $S_s P_{\text{fixed}} \Psi_{m(\text{FD=VD})}$, in which stage transitions were constrained so that the transition from flowering to dormancy was equal to the transition from a vegetative state to dormancy. Significance implied that transitions from the flowering and vegetative stages to dormancy varied more than expected by chance.

To incorporate uncertainty in model selection, mark-recapture parameters and their unconditional variances and covariances were estimated robustly by model averaging (Buckland et al. 1997, White et al. 2002). To calculate errors for all derived parameter estimates, we used a first-order approximation to propagate dependent random uncertainties (Taylor 1997:212). All parameter estimates are presented with ± 1 SE. Hypotheses about differences among transitions and other demographic parameters were tested using program MARK's design matrix and model ranking, as well as likelihood ratio testing and program CONTRAST (Hines and Sauer 1989).

Goodness-of-fit.—Although no reliable method of testing goodness-of-fit exists for multistrata mark-recapture models, a rudimentary goodness-of-fit test in program MS-SURVIV was used to explore whether the global model failed to account for significant heterogeneity in the population (Hines 1994, Sandercock et al. 2000). Inference was made using the G statistic for MS-SURVIV's Model A, which is roughly equivalent to the global model in MARK, but with an unconstrained and unfixed parameterization for resighting (p). Lack of significance implied that overdispersion was not large enough to invalidate our inference using Akaike Information Criterion (AIC_c) values corrected for small sample sizes (Burnham and Anderson 1998).

RESULTS

Mark-recapture model assumptions.—Closed population modeling indicated that the probability of re-detection during a single monitoring occasion (c), and therefore resighting of nondormant orchids, did not vary by flower stage but the probability of first detection (p_f) did vary. All flowering individuals were highly likely to be detected; the probabilities of p_f and c for this stage were both estimated as 1.000 with a standard error $< 1 \times 10^{-5}$. For vegetative individuals, however, p_f and c were estimated as 0.810 ± 0.061

TABLE 1. Best seven models resulting from reducing survival (S) and stage-transitions (Ψ) and fixing resighting (p) assuming three flower stages (dormant, vegetative, and flowering) for lady's slipper orchids in Gavin Prairie, Lake County, Illinois.

Model	S	Ψ	K	Deviance	ΔAIC_c	w
1	$c(F = V \neq D)$	$m \times t$	41	1110.3	0	0.446
2	s	$m \times t$	42	1109.6	1.5	0.211
3	$c(F \neq V = D)$	$m \times t$	41	1111.8	1.6	0.203
4	c	$m \times t$	40	1115.3	2.9	0.105
5	$s + t$	$m \times t$	47	1103.9	6.3	0.019
6	t	$m \times t$	45	1108.9	7.1	0.013
7	c	$m + t, \pm$	17	1170.2	10.1	0.003

Notes: All models with Akaike weights (w) > 0.001 are presented. Resighting (p) fixed to 1.000, 0.977, and 0 for the flowering (F), vegetative (V), and dormant (D) stages, respectively. Notation after Burnham and Anderson (1998). K refers to the number of parameters. ΔAIC_c for the i th model is calculated as $AIC_{ci} - \min(AIC_c)$. The Akaike weight for each model using AIC_c is given by w , where support for the model is given by w on a scale of 0 (no support) to 1.0 (full support). Notation for survival and stage transitions: variation by flower stage (s), annual variation (t), and constancy (c) with equality among flower stages indicated in parentheses. Notations specifically for transition (Ψ) terms include: stage transitions varying independently by time ($m \times t$) and structured additivity between flower stage transition and time ($m + t$), where all transitions of equal sign are additively and linearly related (\pm i.e., additivity among transitions to lower flower stages, and among transitions to higher flower stages). The best-fit and most parsimonious models are presented in boldface type.

and 0.977 ± 0.022 , respectively. This suggests that as many as one-fifth of the previously undetected vegetative orchids present in any given year may have been aboveground, but undetected by observers, while

nearly all previously detected aboveground genets were redetected regardless of whether they were flowering or vegetative. Since resighting (p) is determined entirely by redetection of previously located individuals, this parameter was fixed at 1.000 and 0.977 for flowering and vegetative individuals, respectively, in all our models.

In general, our multistrata models fit the data relatively well. Overdispersion was not significant in the global three-stage, seven-year model (program MS-SURVIV goodness-of-fit: $G_{120} = 45.8, P = 1.000$), so the overdispersion factor was not used to modify AIC_c model ranks.

Life history trade-offs.—Survival did not vary appreciably among years, as models lacking temporal structure in survival had a high cumulative Akaike weight (models 1, 2, 3, 4, and 7, $w = 0.968$; Table 1). Additive effects and interactions between flower stage and time were also not supported (model 5, $w = 0.019$; Table 1). However, stage transitions varied highly with year and transition, suggesting potential environmental influences on flowering stage (Fig. 2). In the best six models, stage transitions varied with a transition \times time interaction for this population of lady's slippers (Table 1). There was strong support for this model structure (models 1, 2, 3, 4, 5, and 6, $w = 0.997$; Table 1), which indicates a temporally dynamic life cycle for adult genets.

A cost of flowering effort to future sprouting or reproductive effort was not observed. Current flowering was positively, rather than negatively, related to future flowering effort ($\Psi^{DF} = 0.164 \pm 0.020 < \Psi^{VF} = 0.264 \pm 0.019 < \Psi^{FF} = 0.474 \pm 0.025$; program CONTRAST test of homogeneity: $\chi^2_2 = 94.5, P < 0.001$). Variation in dormancy by flower stage was strongly supported (Table 1), but the probability of becoming dormant sig-

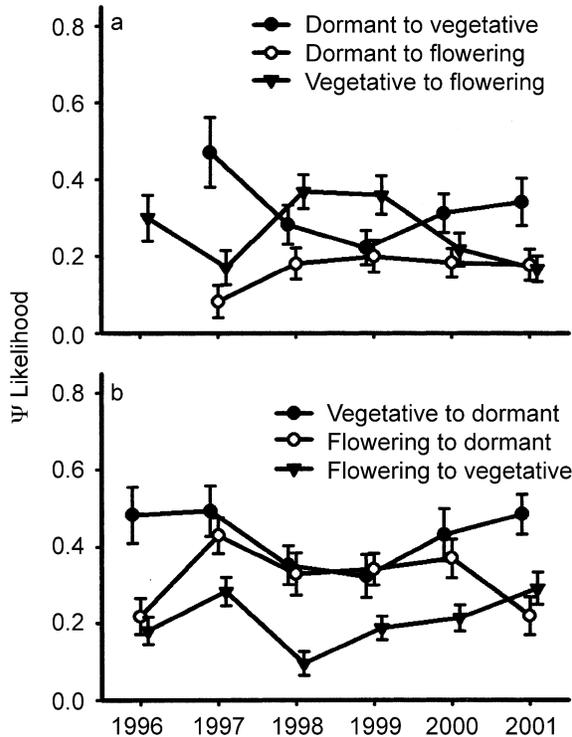


FIG. 2. Annual stage transitions (Ψ) estimated with model-averaged mark-recapture estimates for three flower stages (dormant, vegetative, and flowering) for lady's slipper orchids studied from 1995 to 2001 at Gavin Prairie, Lake County, Illinois: (a) positive transitions, (b) negative transitions. Error bars represent ± 1 SE.

TABLE 2. Model-averaged mark–recapture survival, stage transition, and resighting estimates for three stages (D, dormant; V, vegetative; and F, flowering) for lady’s slipper orchids studied from 1995 to 2001 at Gavin Prairie, Lake County, Illinois.

Stage at time i	Survival	Stage at time $i + 1$			Resighting
		D	V	F	
D	0.815 ± 0.057	0.510 ± 0.037	0.326 ± 0.031	0.164 ± 0.020	0
V	0.956 ± 0.051	0.427 ± 0.027	0.309 ± 0.033	0.264 ± 0.019	0.977
F	0.972 ± 0.037	0.318 ± 0.021	0.208 ± 0.015	0.474 ± 0.025	1.000

Notes: Transitions are estimated as independent of survival and sum to 1.000 within each life stage at time i . Stasis transitions for stage at time i are estimated as the complement to the sum of all estimated nonstasis transitions from stage at time i . All estimates are presented with ± 1 SE.

nificantly decreased (Table 2), rather than increased, with increased flowering effort in the previous growing season (Likelihood ratio test of model $S_s p_{\text{fixed}} \Psi_m$ vs. model $S_s p_{\text{fixed}} \Psi_m$ (FD=VD); $\chi^2_6 = 26.2$, $P < 0.001$).

The three most parsimonious models suggested a cost of dormancy (Table 1). Although one of the three best models suggested equal survival in the dormant and vegetative stages (model 3, $w = 0.203$; Table 1), models with lower survival for the dormant stage had three times more support (models 1, 2, and 5, $w = 0.676$; Table 1). Model-averaged survival of the dormant stage was significantly lower than survival of the vegetative and flowering stages ($S^D = 0.815 \pm 0.057$ vs. $S^V = 0.956 \pm 0.051$ and $S^F = 0.972 \pm 0.037$, program CONTRAST: $\chi^2_1 = 5.2$, $P = 0.022$).

Nonflowering individuals were more likely to stay nonflowering and to exhibit dormancy than flowering individuals (Table 2; Ψ^{VD} and Ψ^{VV} vs. Ψ^{VF} , program CONTRAST: $\chi^2_1 = 13.3$, $P < 0.001$; Ψ^{DD} and Ψ^{DV} vs. Ψ^{DF} , program CONTRAST: $\chi^2_1 = 65.7$, $P < 0.001$). The strongest tendency within the dormant and flowering stages was to remain within the same stage over time, but the vegetative stage was more likely to transition to dormancy than to any other stage (Table 2).

Flowering individuals survived better and became dormant less frequently than did vegetative individuals. Vegetative individuals had a greater tendency to transition to dormancy than to any other state ($\Psi^{VD} = 0.427 \pm 0.027$ vs. $\Psi^{VV} = 0.309 \pm 0.033$ vs. $\Psi^{VF} = 0.264 \pm 0.019$, program CONTRAST: $\chi^2_2 = 24.4$, $P < 0.001$; Table 2), and were significantly more likely to become dormant than were flowering individuals (likelihood ratio test of model $S_s p_{\text{fixed}} \Psi_m$ vs. model $S_s p_{\text{fixed}} \Psi_m$ (FD=VD); $\chi^2_6 = 26.2$, $P < 0.001$). Thus, sprouting may be associated with a survival cost in the vegetative stage, since vegetative individuals were more likely to go dormant in the next year than to sprout as either vegetative or flowering.

DISCUSSION

Building on work by Alexander et al. (1997) and Shefferson et al. (2001), we applied mark–recapture models to test for life history trade-offs in a rare and long-lived orchid. Mark–recapture modeling has been useful in answering life-history questions in animals

(Nichols et al. 1994, Nichols and Nichols 1995, Cam et al. 1998), and allowed us to develop robust estimates of annual probabilities of survival, sprouting, and current and future flowering. Using these methods, we rigorously tested for potential trade-offs that would be difficult to detect with conventional statistical methods because of complications created by dormancy and the long lifespan of the small yellow lady’s slipper orchid.

Flowering did not appear to entail a cost to survival. Annual survival did not decrease with increasing flowering effort. Rather, it either increased (models 1, 2, 3, and 5, Table 1) or remained constant (models 4, 6, and 7, Table 1) for all flower stages across all years of study. Models supporting an increase in survival with increasing flower stage garnered approximately seven times more support than models with no flower stage differentiation in survival (models 1, 2, 3, and 5: cumulative $w = 0.879$; models 4, 6, and 7: cumulative $w = 0.121$; Table 1). Survival is often size dependent in clonal plants (de Kroon et al. 1992). As mortality risk is spread across ramets (Pitelka and Ashmun 1985), there is also increased opportunity for resource acquisition and competitive ability (Sutherland and Stillman 1988). This inference is supported by the fact that vegetative genets were more likely to go dormant in the following year than to become vegetative or to flower (Table 2). Furthermore, a lack of evidence for costs of flowering to sprouting, dormancy, and survival may be attributable to high resource levels in flowering plants (Tuomi et al. 1983, Biere 1995). Perhaps individuals may not risk flowering until they have a relatively large resource base.

We found little evidence of a cost of current flowering effort to future flowering effort. Flowering individuals exhibited a strong tendency to remain flowering the following year (Table 2). Although flowering may impose direct physiological costs in spent resources, and flowering individuals may be more visible and vulnerable to herbivores (Biere 1995), no demographic evidence of these costs was observed for the lady’s slipper orchid. Similarly, Hutchings (1987b) found no evidence that current flowering reduced future flowering in the early spider orchid, *Ophrys sphegodes*. In contrast, among Dutch populations of *Spiranthes spiranthes*, individuals tended to enter a vegetative

state following a flowering season (Willems and Dorland 2000). We also did not detect a cost of flowering to future sprouting. We predicted an increased likelihood of dormancy with increased flowering effort, but instead found the reverse relationship (Table 2). Any cost that might have increased the likelihood of dormancy with increasing flowering effort was apparently not large enough to offset the greater vigor of a genet that grows more flowering ramets.

Our results suggest that dormancy in *C. calceolus* occurs at a cost to survival and may not be adaptive. Dormant individuals had significantly lower survival and, if they survived, were more likely to remain dormant in the following year than vegetative and flowering individuals (Tables 1, 2). A cost of dormancy may be due to insufficient photosynthesis as a result of failing to keep a green shoot aboveground for one or more growing seasons. We postulated that mycorrhizae might provide a means of recouping the cost of not sprouting during dormant periods, although the exact mechanism by which energy might be obtained through nonphotosynthetic means is not understood (Wells 1967, Dixon et al. 1990, Leake 1994). Our results, however, suggest that any nutritional benefits derived from mycorrhizae appear unable to offset the loss of resources that can be obtained via photosynthesis.

Resource limitation may also be an important factor in the disparate levels of survival among dormant, vegetative, and flowering stages. Flowering individuals may occur in areas with greater resources, which enhance flower production and reduce the occurrence of dormancy. Such environmental heterogeneity could cause dormancy to be negatively correlated, and survival positively correlated, with genet size. Furthermore, the growth and maintenance of multiple ramets is costly and may influence future sprouting of smaller genets in low resource environments (Callaghan et al. 1992). Although our evidence does not suggest an adaptive benefit from dormancy, survivorship of dormant individuals ($S^D = 0.815$, Table 2) was still relatively high, so it is possible that dormancy may potentially function as a bet-hedging trait under catastrophic conditions.

In conclusion, our study suggests costs of dormancy to survival, which may result from foregoing photosynthesis for one or more growing seasons, but found no evidence for costs of reproduction, either to survival or future flowering effort. These life history patterns suggest that fitness may not be as sensitive to sexual reproduction as it is to mortality. Population growth rates of long-lived herbaceous plants and long-lived vertebrates are often highly sensitive to small changes in survival (Silvertown et al. 1993, Sæther and Bakke 2000). Consequently, selection for a high, relatively unvarying survival probability may be paramount to growth and persistence in this orchid population.

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APPENDIX

An appendix describing simulation tests of multistrata mark–recapture modeling for undetectable strata is available in ESA's Electronic Data Archive: *Ecological Archives* E084-027-A1.