

Evaluating Survival and Dormancy Rates of Rare Herbaceous Perennials with Mark-Recapture Statistics

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Why Use Mark-Recapture for Rare Herbaceous Perennials?

Demographic models may underestimate persistence of perennial plant populations if dormant plants are treated as dead. Mark-recapture statistics based on maximum likelihood estimation are often used to determine apparent survival and resighting rates of free-living animals, but have not been applied to plants. Here we use mark-recapture statistics to estimate dormancy in an endangered orchid. Analysis of resighting histories allows us to distinguish between death and dormancy (Fig. 1) and to obtain better estimates of survival.

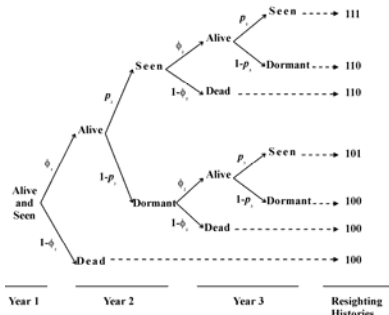


Fig. 1. Fates and associated probabilities of an herbaceous perennial exhibiting dormancy

Apparent survival (ϕ) refers to the product of the actual survival rate and the probability of shooting before death. Resighting rate (p) refers to the probability of shooting. Dormancy rate is given by $1-p$. Mortality is given by $1-\phi$. It is difficult to determine survival with conventional means when studying perennial species exhibiting adult dormancy. Mark-recapture statistics allow correction for dormancy rates, enabling better PVA models.

Case Study: The Small Yellow Lady's Slipper

The small yellow lady's slipper, *Cypripedium calceolus* var. *parviflorum* (Salisb.) Fernald, is a perennial orchid classified as endangered in Illinois. It typically occurs in tamarack swamps, wet woodland boundaries, wet meadows, and fens (Swink and Wilhelm 1994). In Lake Co., IL., flowering occurs annually from mid-May through mid-June. Seeds are tiny and lack nutritional reserves, requiring impregnation of soil mycorrhizae for germination and growth (Curtis 1959). The period of growth from seed germination until plant maturity is thought to range from 12 to 16 years (Curtis 1959). Vegetative reproduction also occurs through the growth of a lateral rhizome (Curtis 1954). Though its causes in orchids are unknown, dormancy is a phenomenon in which an aboveground shoot may fail to form in a given year without mortality to the plant (Curtis 1954).

This study was conducted from 1994 through 1998 in wet meadow habitat occupying approximately 7 acres of Grant Woods Forest Preserve, South Unit, in Lake County, IL. (42° 23' N, 88° 8' W). The meadow soil is saturated in its western and southern range and dominated by *Carex* spp. growing on tussocks. In its eastern range, it grades into a wet prairie dominated by grass spp. Due to the presence of 16 state-listed threatened and endangered plants, the site has been protected within the Illinois Nature Preserve System (Nuzzo 1990).

Field Methods

Eight populations of *C. calceolus* were considered in this study: three from 1994-1998, and five from 1995-1998. A permanent stake was established within each population. Every year during late anthesis, the location of each individual orchid observed within each population was recorded. A description of each plant was also recorded, including number of inflorescent stems, number of flowers per stem, and number of vegetative stems.

Due to the tendency of *Cypripedium* spp. to propagate vegetatively through the spread of rhizomes, we defined individual plants in terms of distance from previously recorded locations of individuals in each population. A plant located within 30cm of any previous year's record was considered the same plant. However, if several individuals were located within 30cm of a record, then only the closest individual was considered to be the same individual. This 30cm distance accounted for rhizome spread.

Statistical Analyses

In this study, 446 orchids were monitored on eight study plots. As a first step, we measured individuals alive for a minimum of three, four, and five years. We then modeled resighting histories for each population using Program MARK (White 1999) following methods described by Lebreton et al. (1992). All analyses began with the saturated CJS model ($\phi_{\text{time}} P_{\text{time}}$). Likelihood ratio testing was used to test time effects on apparent survival and resighting rates. Mean apparent survival and resighting rates were calculated using the model ($\phi_{\text{constant}} P_{\text{constant}}$). Resighting rates (the proportion of individuals shooting one year that also shoot the next) were calculated to examine the bias resulting from failure to consider dormancy within a demographic study. A final analysis was conducted on all eight populations in order to test for differences among the populations. This analysis began with the saturated CJS model ($\phi_{\text{population} \times \text{time}} P_{\text{population} \times \text{time}}$). Likelihood ratio testing was used to test time and population effects.



Results

Dormancy was common, but rarely lasted longer than 1 year (Fig. 2). Thirty-eight percent of the 230 individuals alive for a minimum of three years were dormant for part of the study. Ninety-two percent of those were dormant for only 1 year, and no orchids were dormant for three or more.

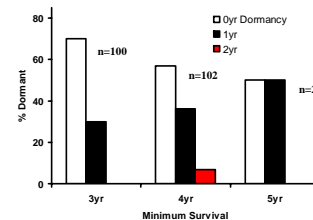


Fig. 2. Length of dormancy in orchids surviving at least 3 yrs. Orchids in different categories of minimum survival lengths are independent samples.

Mean population resighting rates were all less than 1.000, some as low as 0.636, suggesting mean population dormancy rates of between 0.097 and 0.364 (Table 1). Dormancy resulted in resighting rates that underestimated apparent survival by as much as 43.1% in one population, and 22.7% overall (Table 1).

Table 1. Resighting (R), apparent survival (ϕ), resighting (p), and dormancy (D) rates for eight populations of *Cypripedium calceolus* var. *parviflorum* (mean \pm 1 se).

No. Patch	Yrs	N	Resighting (R)	Apparent Survival (ϕ)	Resighting (p)	Dormancy (D)	Survival Bias ⁴
A	4	33	0.861 \pm 0.074	0.937 \pm 0.047	0.903 \pm 0.056	0.097	0.081
Aspen	4	120	0.613 \pm 0.086	0.879 \pm 0.029	0.694 \pm 0.043	0.306	0.303
C	4	33	0.653 \pm 0.105	0.902 \pm 0.062	0.731 \pm 0.087	0.269	0.276
T	4	45	0.739 \pm 0.075	0.915 \pm 0.084	0.741 \pm 0.099	0.259	0.192
Wil	4	32	0.766 \pm 0.025	0.927 \pm 0.043	0.818 \pm 0.063	0.182	0.174
X	5	121	0.698 \pm 0.064	0.837 \pm 0.028	0.807 \pm 0.037	0.193	0.166
Y	5	24	0.544 \pm 0.157	0.819 \pm 0.074	0.680 \pm 0.106	0.320	0.336
Z	5	50	0.496 \pm 0.082	0.871 \pm 0.052	0.636 \pm 0.068	0.364	0.431

Pool¹ 4. 446. 0.672 \pm 0.030. 0.869 \pm 0.016. 0.773 \pm 0.022. 0.227. 0.227.

¹ Resighting rate (R) calculated as the mean of all yearly resighting rates per population.

² Dormancy (D) = 1 - p

³ Survival bias = (ϕ - R) / ϕ

⁴ First year of data dropped from populations X, Y, and Z in order to pool the data set.

Annual estimates of apparent survival were typically high, but resighting rates varied considerably (Fig. 3). Though ϕ and p were not separable in 1998 due to time dependence in both rates, β_{1998} estimates ranged from 0.729 to 0.899 per population, suggesting high annual apparent survival and resighting rates in most populations. Annual resighting rate underestimated or, rarely, equaled annual apparent survival rate in all populations (Fig. 3).

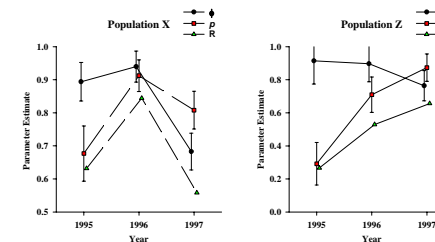


Figure 3. Annual resighting rate (R), apparent survival (ϕ), and resighting rate (p) in selected populations.

The eight populations had significantly different rates of apparent survival and resighting (Table 2). Apparent survival varied significantly with an interaction between time and population, while resighting rate varied significantly by population (Table 2).

Table 2. Summary of model testing for all eight populations.

Model	np ¹	DEV ²	AIC ³	Likelihood Ratio Test Results
Modeling p				
1) $\phi_{p_{yr}}$, $p_{p_{yr}}$	40	46.871	1164.843	
2) $\phi_{p_{yr}}$, $p_{p_{yr}}$	33	56.635	1159.037	Interaction between time (yr) and population on p , model 2 vs. 1: $\chi^2_{1df}=9.8$; $P=0.202$
3) $\phi_{p_{yr}}$, p_t	26	74.732	1161.882	Population effect on p , model 3 vs. 2: $\chi^2_{1df}=18.1$; $P=0.012$
4) $\phi_{p_{yr}}$, p_p	32	59.926	1160.130	Time effect on p , model 4 vs. 2: $\chi^2_{1df}=3.3$; $P=0.070$
Modeling ϕ				
6) $\phi_{p_{yr}}$, ϕ	18	92.051	1162.145	Interaction between time and population on ϕ , model 6 vs. 4: $\chi^2_{1df}=32.1$; $P=0.004$

¹ np = number of parameters

² Deviance (DEV) = -2lnL.

³ Aikake's Information Criterion (AIC) = DEV + 2np

⁴ The subscript 'p' refers to population; the subscript 't' refers to time.

Discussion

Dormancy was a common phenomenon in these populations of small yellow lady's slippers. This study is one of the first applications of mark-recapture to dormancy in plants. Demographic models that do not take dormancy into account would have underestimated the survival rates of these orchids by as much as 43.1%. Furthermore, population viability analyses equating survival with resighting rate would have underestimated overall population persistence. Any further monitoring efforts on these orchids or a similar species should incorporate a methodology to discern the prevalence of dormancy in the species, and its overall importance to the unbiased calculation of survival rates.

Significant differences among apparent survival and recaptures rates suggested that dormancy and survival of this species varies by micro-site related factors. In current studies, we are investigating the reasons for these differences.

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