

## IMPROVING THE PRECISION OF ESTIMATES OF THE FREQUENCY OF RARE EVENTS

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PLATE 1. *Darlingtonia californica*, a rare carnivorous plant species endemic to the Siskiyou Mountains of Oregon and northern California, which grows in a threatened plant community type—serpentine fen. Photo credit: A. M. Ellison.

*nica* (Sarraceniaceae), to illustrate methods by which the precision of estimates of the probability of rare events can be increased (see Plate 1). Although prey capture by carnivorous plants provides nutrients required for successful sexual reproduction (reviewed in Ellison and Gotelli 2001), prey capture may be infrequent or rare (Zamora 1995, Zamora et al. 1998); most insects that enter pitcher-plant traps are not captured (Newell and Nastase 1998).

Like other pitcher plants in this family, *Darlingtonia* grows as a rosette of leaves that are modified to form pitcher-shaped traps (Arber 1941). These pitchers secrete copious nectar that attracts foraging insects, especially vespid wasps (*Vespula atropilosa*) and ants (*Tapinoma sessile*). As part of a long-term study of the demography of *Darlingtonia*, we recorded the frequency with which *Darlingtonia* captures wasps and estimated the conditional probability of a successful capture:  $\pi = P(\text{capture} \mid \text{visit})$ . During July 2002, Ellison, Gotelli and their colleagues observed 753 *Darlingtonia* plants for one-half hour each, for a total of 376.5 plant-hours of observation (A. M. Ellison, R. J. Emerson, E. J. Farnsworth, N. J. Gotelli, C. M. Hart, H. R. Steinhoff, and S. E. Wittman, *unpublished data*). During this time,  $N = 157$  wasps were seen to visit the pitchers, and  $n = 2$  of these wasps were captured. For each visit, we also recorded the time a wasp spent in each pitcher, and we measured the orientation of the pitcher's opening (as degrees east of north). Assuming that the observed visits are a simple random sample of visits, the frequentist

estimate of  $\pi$  is  $\hat{p} = n/N = 2 \text{ captures}/157 \text{ visits} = 0.0127$ . The estimated standard error for  $\hat{p}$  is  $SE_{\hat{p}} = \sqrt{\hat{p}(1 - \hat{p})/N} = 0.0089$ . These estimates do not assume that the per-visit probability of capture is the same for all visits. When the sample is a simple random sample, heterogeneity in the population is irrelevant (Thompson 2002). Because the probability of capturing a wasp is very low and the total sample size is small, the precision of this frequentist estimate ( $\hat{p}$ ) of capture probability by *Darlingtonia* is poor:  $CV_{\hat{p}} = 70.2\%$  and precision (defined below) = 1.26.

#### MEASURES OF PRECISION OF A PROBABILITY

Precision “refers to the dispersion of the observations” (Marriott 1990). It can be quantified by at least four different, but related, measures (Table 1). The most familiar are measures of absolute precision, the standard error (SE) and variance ( $s^2$ ). Because more precise estimates have smaller SEs, it is also common to define precision as  $1/s^2$ , especially in the Bayesian literature (Gelman et al. 1995:43).

When used to compare events that have different probabilities, absolute measures of precision have the counter-intuitive property that rarer events are more

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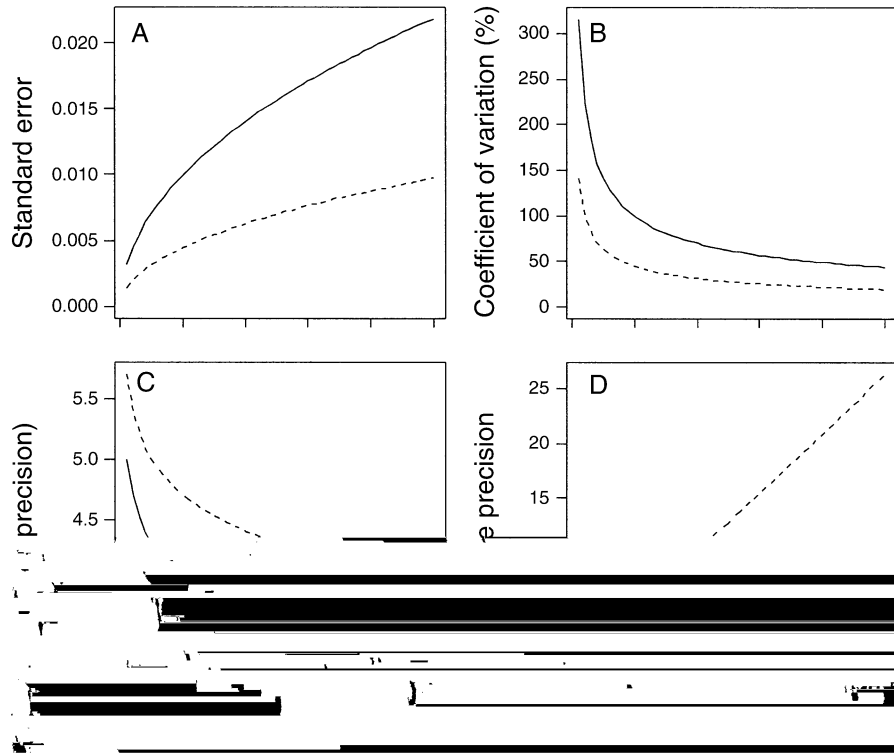


FIG. 1. The relationship between four measures of precision (Table 1) and the probability of an event when an event is rare (probability  $\pi < 5\%$ ). (A) standard error (SE), (B) coefficient of variation (CV), (C) absolute precision (presented as a log value), (D) relative precision,  $(1/CV)^2$ . Each measure of precision is calculated for sample sizes of  $N = 100$  (solid line) and  $N = 500$  (dashed line).

of the observations, and  $f(\pi \mid C, V)$  is the posterior. The vertical bars indicate which quantities are considered fixed. That is,  $f(C \mid V, \pi)$  is the probability distribution of  $C$  (the number of captures), conditional on the fixed values of  $V$  (the number of visits) and  $\pi$  (the capture probability). The integral in the denominator is a normalizing constant that ensures that the posterior distribution is a valid probability distribution (i.e.,  $0 \leq f(\pi \mid C, V) \leq 1$ ). Using Bayes' Theorem requires that the distributions of both the data and the prior be specified.

In the *Darlingtonia* data set, the data ( $f(C \mid V, \pi)$ ) are the number of captures observed in a certain number of visits. A binomial distribution is commonly used to model count data when the outcomes (capture or not) are independent, the probability of success (capture) is the same for all visits, and where the number of success (captures) cannot exceed the number of vis-





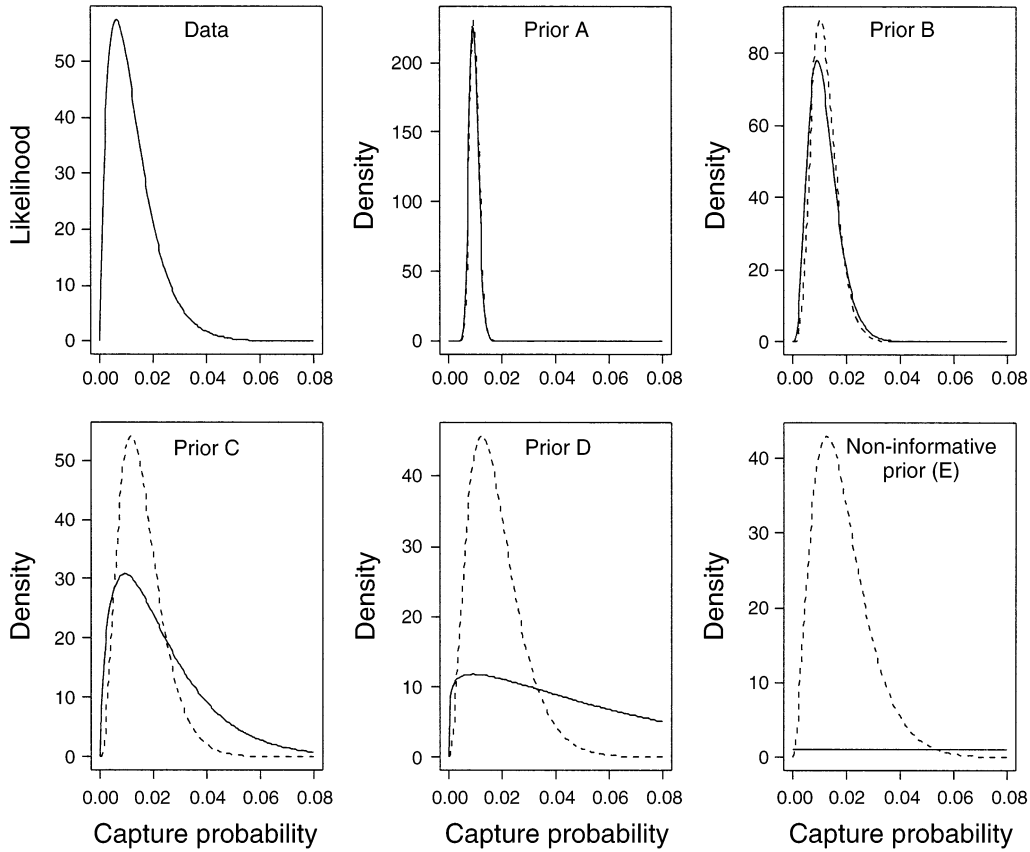


FIG. 2. Plots of the likelihood and prior (solid lines in density plots) and posterior (dashed lines in density plots) distributions for the five choices of prior distribution in Table 2. Note the different y-axis scales.

strata definition separates pitchers facing either 20° or 30° east of north from plants with all other orientations.

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TABLE 3. Precision of the estimate of the probability of capture using two different stratifications of the data.

Parameter	Stratum		Total
	A	B	
<b>Stratification 1†</b>			
Sample size (visits $V$ )	9	148	157
Number of captures ( $C$ )	2	0	2
Capture probability ( $\hat{p}$ )	0.222	0	0.0127
$SE_{\hat{p}}$	0.138	0	0.00792
$CV_{\hat{p}}$			62.1%
Precision			1.59
<b>Stratification 2‡</b>			
Sample size (visits $V$ )	19	138	157
Number of captures ( $C$ )	2	0	2
Capture probability ( $\hat{p}$ )	0.105	0	0.0127
$SE_{\hat{p}}$	0.0070	0	0.00852
$CV_{\hat{p}}$			66.9%
Precision			1.38

† Stratum A, plants with orientations of 20° or 30°; stratum B, all other plants.

‡ Stratum A, plants with orientations from 10° to 40°; stratum B, all other plants.

Estimating either  $\hat{p}$  (Eq. 6) or its variance  $s^2(\hat{p})$  (Eq. 7) requires knowledge of the relative sizes of the strata:  $N_A/(N_A + N_B)$ . The relative size of the strata may be estimated by independent criteria, such as stratum coverage or frequency in GIS databases. Because such information is lacking for the *Darlingtonia* population, we assume that the size of each stratum in the population is proportional to  $Lbh$ .

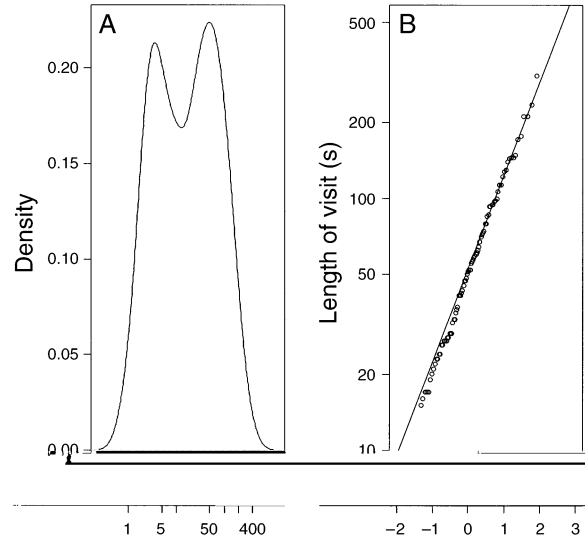


FIG. 3. (A) Probability density of visit length, estimated using a kernel smoother. The two modes are at 4 s and 50 s. The trough between the two peaks is centered at 13.5 s. (B) A log-normal quantile-quantile plot of the 86 visit lengths in the upper peak (visit lengths  $> 13.5$  s). The theoretical quantiles were calculated after accounting for truncation (no value less than 13.5 s) and censoring (two captures with lengths  $> 307$  s).

knowledge of wasp behavior and energetics. Lacking that information, we used a critical visit length of 307 s, the longest observed visit that did not result in a capture. The estimated capture probability  $\hat{p}$  is the probability that a visit exceeds 307 s:  $\hat{p} = 0.59[1 - \Phi(1.99)] = 0.0137$ . The estimate  $\hat{p}$  of  $\pi$  is very sensitive to the choice of critical visit length. For example, if the critical length is 360 s, the estimate  $\hat{p}$  decreases to 0.0090.

Bootstrap resampling can be used to estimate the precision of  $\hat{p}$  (Efron 1981, Dixon 2001). The bootstrapped standard error of the capture probability is estimated to be 0.0095, corresponding to a cv of 66% and precision of 1.10. The estimate from the threshold model is less precise than the frequentist estimate if precision is measured using an absolute measure ( $0.0001/s^2$ ) and more precise if precision is measured by a relative measure (cv).

#### *Using aggregated data from larger scales*

The primary data used to estimate the probability of a rare event come from observations of individuals, such as detailed observations of 753 individual *Darlingtonia* plants. Such data provide information about both the number of events (e.g., captures) and the number of trials (e.g., visits). At larger spatial or temporal scales, we can obtain samples of entire populations and observe the total number of rare events over a given interval of time or space (e.g., Lawson and Williams 1994, Plummer and Clayton 1996). This sample yields the product of the rate of occurrence of the event  $\times$  the number of trials (e.g., capture rate  $\times$  visitation rate). We can glean indirect information about the rate at which the rare event occurs from this product. Combining the direct and indirect information using a statistical model provides a more precise estimate of the capture probability.

We collected aggregate data on the total number of wasps captured by *Darlingtonia* individuals at several nearby sites over one-hour and two-day periods (A. M. Ellison, R. J. Emerson, E. J. Farnsworth, N. J. Gotelli, C. M. Hart, H. R. Steinhoff, and S. E. Wittman, *unpublished data*). These aggregate data were much easier to collect; we simply counted the number of wasps trapped in each pitcher after one hour or two days, rather than collecting direct behavioral observations. However in the aggregate data, we only recorded the number of wasps successfully captured per pitcher; the number of visits to each pitcher by wasps was not recorded.

Direct observations of wasp behavior suggests that wasps are actively foraging at *Darlingtonia* pitchers only for a 4-h period (10:00–14:00 hours) each day, so the 2-d aggregate data were assumed to reflect all captures made during 8 h of wasp activity. In the aggregate data, a total of six wasps were captured in a total of 1416 plant-hours (162 plants in the 2-d sample = 1296 plant-hours + 120 plants in the 1-h sample).

This aggregate information can be combined with the detailed data using a binomial distribution (Efron 1981, Dixon 2001).



TABLE

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