Optimal Schemes to Detect the Presence of Insect Species

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Abstract: *Survey protocols to detect the presence of particular species should be organized to make optimal use of available resources. Current protocols mostly deal with this problem intuitively, but the problem can also be addressed with mathematical modeling. To this aim, we used a model that describes the abundance of a single, discrete generation of adult insects. Furthermore, we assumed that year-to-year variation in timing of the flight period was attributable to variation in peak emergence only. We determined the spacing of a given number of survey days on a transect that minimized the chance of missing a species when it was actually present. This spacing was fixed to a Julian date and applied to all years. We also calculated the probability of detecting the species, which depends on the number of survey days. For most parameter values, 5 survey days sufficed to detect with high probability (≥0.95) populations with an observable population size (total number of insects that can be observed in the transect over the entire flight period) exceeding 10. For observable population sizes under 10, achieving a detection probability of 0.95 may require many more than 5 survey days. As an example of the method, we constructed a survey-detection scheme for the Quino checkerspot butterfly (*Euphydryas editha quino*), based on the limited information available about its flight period. For an observable population size over 11, this scheme had a detection probability of >0.95. We also provide detection schemes for species whose death rate and variation in emergence time within and between years can at present be characterized only as small, moderate, or large. These survey schemes should maximize species detection and reduce uncertainty about absence.*

Planes Óptimos para Detectar la Presencia de Especies de Insectos

Resumen: *Los protocolos de prospección para detectar la presencia de determinadas especies debieran organizarse para hacer un uso óptimo de los recursos disponibles. La mayoría de los protocolos actuales tratan este problema de manera intuitiva, pero el problema también puede abordarse mediante el uso de modelaje matemático. Para ello utilizamos un modelo que describe la abundancia de una única generación discreta de insectos adultos. Más aún, suponemos que la variación anual en la sincronización del vuelo era atribuible solo a la variación en el pico de emergencia. Determinamos el espaciamiento de un determinado número de días de muestreo a lo largo de una transecta buscando minimizar la posibilidad de no registrar una especie cuando de hecho esté presente. Este espaciamiento se fijó en fechas según un calendario juliano aplicables a todos los años. También calculamos la probabilidad de detectar las especies, dependiente del número de días de muestreo. Para la mayoría de los parámetros, cinco días de muestreo fueron suficientes para detectar, con una probabilidad alta (≥0.95), poblaciones con tamaño poblacional observable (número total de especies que se pueden observar en la transecta a lo largo de todo el período de vuelo) mayor de 10. Para poblaciones observables <10, se pueden requerir mucho más de cinco días de muestreo para alcanzar una probabilidad de detección del 0.95. Como un ejemplo del método, construimos un plan de detección para la mariposa* Euphydryas editha quino *basado en la escasa información disponible sobre su período de vuelo. Este plan tenía una probabilidad de detección >0.95 para tamaños poblacionales observ-*

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ables mayores de 11. Además, proporcionamos planes de detección para aquellas especies cuya tasa de mortalidad y variación entre años o a lo largo de un mismo año en tiempo de emergencia solo pueden caracterizarse actualmente como pequeña, moderada o grande. Estos planes de prospección deberán maximizar la detección de especies y reducir la incertidumbre sobre la ausencia.

Introduction

Species-protection laws, notably the U.S. Endangered Species Act of 1973 (ESA) (16 U.S. Code section 1531), usually protect sites where a species is present, but they do not often protect unoccupied habitats. This is especially important when undeveloped land is slated for development. If during the environmental review process rare, threatened, or endangered species are detected, a site can be recognized and considered for protection. Detection of special-status species is thus central to conservation planning.

The ESA regulates any population of a listed species, however low its density. Detecting low-density populations poses special difficulties because not observing the species during surveys can be explained in contradictory ways. The species may indeed be absent. Alternatively, the species may be present but still not be detected because search efficiency is inadequate, too few surveys are conducted, or the surveys are improperly timed. To minimize the probability of not detecting a species, the surveyor should have the requisite skill and experience to maximize search efficiency. Moreover, survey number and timing should be optimally organized. With unlimited resources, this would amount to surveying daily during the period when the species is observable; for flying insects this implies surveying during the entire flight period. Funds to support daily surveys are typically not available, however, so the challenge to regulatory agencies is to design survey schemes that maximize the probability of detecting target species, given limited resources.

Designing such a scheme for insects is a challenge because no formal methods are available to carry it out. For example, the U.S. Fish and Wildlife Service (USFWS) designed a protocol to detect the presence of the endangered Quino checkerspot butterfly (*Euphydryas editha quino*) (USFWS 1999). The number of surveys required by the protocol was reduced from about 10 weekly surveys in 1999 to 5 in 2000 (USFWS 2000*b*). The original protocol and changes to it were formulated in consultation with experts and with reference to the scientific literature. However, the resulting protocols were not motivated by quantitative analysis of the detection probability.

The lack of quantitative analysis of detection probability is the rule rather than the exception, yet we contend that such analysis would be beneficial to the development of sound survey protocols. Moreover, we believe that this type of analysis is feasible if mathematical modeling techniques are used. Building on a previously published model for the abundance of adult insects during a single generation (Zonneveld 1991), we present an analysis of detection probability for a given survey protocol for such species. We also show how such a protocol can be optimized.

Two types of survey methods for adult insects can be distinguished. First, some methods aim to determine the absence or presence of all species within a particular taxon in a certain geographic area. Surveys for the detection of a single species can be considered a special case of this approach. The second type of survey method focuses on determining the abundance of particular species known in advance to be present. For insects, these include mark-release-recapture techniques (Gall 1985), Pollard walks (Pollard 1977), and line transects (Buckland et al. 1993; Brown & Boyce 1998). Both types of survey have been subject to mathematical analysis to optimize their design or to interpret their results. To the best of our knowledge, however, no mathematical analysis is available to optimize methods of detecting particular target species. Some researchers have calculated the probability of detecting a species based on the area surveyed, but without offering guidance about survey number or timing for detecting species with ephemeral presence and changing abundance (Green & Young 1993; Terrestrial Ecosystems Task Force 1998). When surveys to detect target species are undertaken, they are often modified based on the surveyor's experience. Such modification lacks a rigorous analysis of flight-period characteristics (e.g., Warren et al. 1984; Launer et al. 1992).

We adapted the Pollard transect method to maximize the detection probability of a target species. We investigated detection probability as dependent on the number of survey days and the parameters that describe the species' abundance curve during a season. We used a model for the species-abundance curve presented by Zonneveld (1991). This model, which is limited in its application to species with discrete generations, has been successfully used to describe data from a variety of butterfly species (Zonneveld 1991; Mattoni et al. 2001). Nevertheless, because none of the model's assumptions is specific to this taxon, it can also be applied to other insect taxa.

Our goal was to find an optimal detection scheme, with "scheme" defined as the number and spacing of survey days. We assumed that the species to be surveyed is present. We made a few assumptions about the flight period and about the year-to-year variation of the flight period. Taken together, these assumptions resulted in a model for the density of insects over time. The area covered by a transect times the density of insects yields the number of insects present in the transect. Because we would not see all the insects, we also needed a model for the statistical distribution of the observed number (i.e., given a certain number of insects, what is the probability of seeing k of them?). With the composite model we could calculate the probability of zero observed individuals at a particular time. Next, we needed to devise a scheme that minimized the chance of observing zero insects on all days. The scheme depended on the number of survey days and their timing. To investigate timing, we first had to choose a number of survey days. Once we had calculated optimal spacing of the survey days, we evaluated the effect of survey number on detection probability. When we designate a scheme as optimal, we always mean optimal with reference to the model we used.

Modeling Detection Probability

Zonneveld (1991) presented a model that describes adult insect abundance as it changes during the flight period. This model assumes a logistic emergence curve, random death, and the absence of net migration. The choice of the logistic emergence curve is not essential to our approach; instead, one could also choose the normal distribution (e.g., Manly 1974; Rothery & Roy 2001). The following differential equation describes changes in insect density during a single flight period:

$$\frac{dx(t)}{dt} = N\frac{b}{\beta(1+b)^2} - \alpha x(t) \text{ with } b = \exp\{(t-\theta)/\beta\} \tag{1}$$

and initial condition $\lim_{t\to-\infty} x(t) = 0$ (i.e., no insects are present at the onset of the flight season). In this equation, $x(t)$ is the instantaneous density of insects present at time t. Four parameters characterize presence: initial density of pupae that eclose, N; peak emergence time, θ; spread in emergence times, β; and death rate, α. None of these parameters can be dispensed with without seriously corrupting the model's ability to describe data. The solution to Eq. 1,

$$x(t) = Ne^{-\alpha(t-\theta)} \int_0^b \frac{r^{\alpha\beta}}{(1+r)^2} dr \tag{2}$$

describes the expected abundance curve. The peak in the expected abundance curve is reached some time after the peak emergence time.

To detect insects, establishment of a thorough, fixed transect through all suitable habitat (Pollard walk) allows for application of this model. Insects would not be observed exhaustively, so one must assume that a fraction of the total number is observed. The area covered by the transect, A, times the actual density of insects in the area, $x(t)$, yields the number of insects in the transect. An insect present at a particular survey day has a certain probability, say q, to be observed. The observable number, $\hat{x}(t)$, thus equals $qAx(t)$. If one applies this transformation in Eq. 2, it appears that the same argument must also apply to the initial density N. So we obtain a formal parameter, $\hat{N} = qAN$, which we call the observable population size. It is observable in the sense that one can estimate this quantity from transect counts. The density N is not observable because one does not know the sighting probability q. We thus treated $\hat{N}$ as the basic parameter in deriving detection schemes. Different values for q or A related to the choice of species or transects thus affect the outcome via $\hat{N}$.

The observable number presents the expected value, but chance processes will likely cause the actual observation, $X(t)$, to deviate from this. We assume the observations to be Poisson-distributed, with $\hat{x}(t)$ as the expected value. So the probability P of observing k insects obeys

$$P(X(t) = k) = \frac{e^{-\hat{x}(t)}[\hat{x}(t)]^k}{k!}. \tag{3}$$

The Poisson distribution is the simplest model for counts, often applied as a null model in the absence of more precise knowledge. It is important that this model for the actual observations introduces no new parameter, keeping the analysis as simple as possible.

Despite its conceptual simplicity, the model fits data on actual presence curves fairly often. For example, Fig. 1a shows data on the endangered Palos Verdes blue butterfly (*Glaucopsyche lygdamus palosverdesensis*), together with the model description. For some species, the abundance curve closely follows the emergence curve, which indicates that average life expectancy (i.e., the inverse of the death rate) is short relative to the duration of the flight period. The resulting abundance curve is near symmetrical, because it strongly resembles the emergence curve. Data from such an abundance curve may be difficult to analyze because they contain little information on the death rate. Analysis may still succeed, however, if one uses prior information on the death rate. Figure 1b shows an example of a nearly symmetrical abundance curve for the El Segundo blue butterfly (*Euphilotes bernardino allyni*), together with the model description. As prior information we used a sample of 20 death rates estimated for a variety of butterfly species. The freely available software tool INCA (The Urban Wildlands Group 2002) can perform analysis of transect-count data for the model used in this paper; it also allows the use of prior information on the death rate to an-

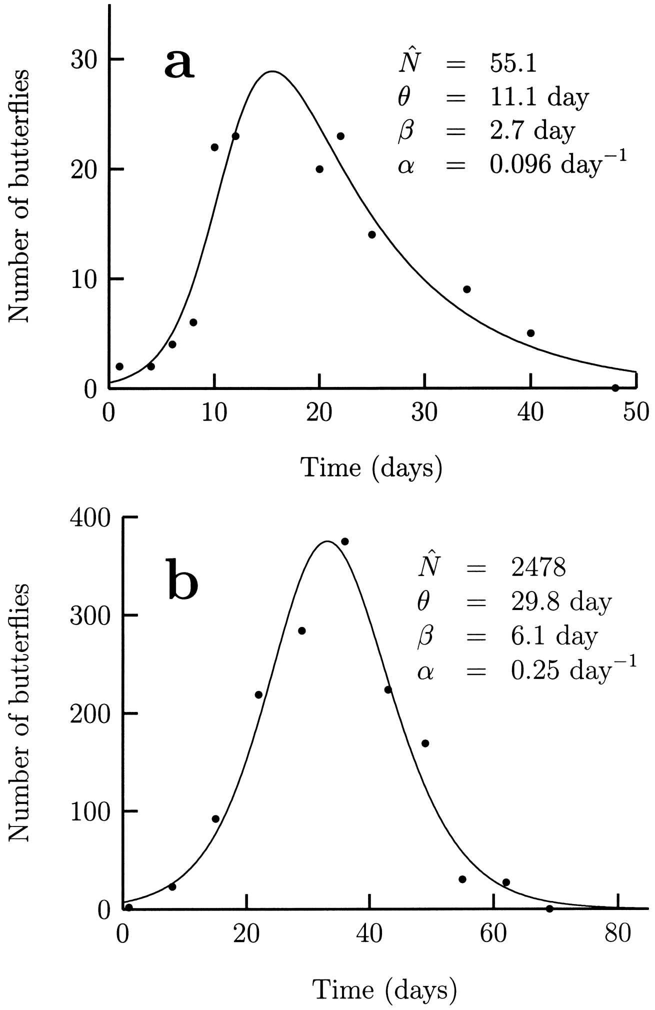

Figure 1. (a) Abundance of Glaucopsyche lygdamus palosverdesensis *during the flight period of 1998 at Defense Fuel Support Point, San Pedro, California (U.S.A.). Time* t = *0 corresponds to 27 February. Data are from Mattoni et al. (1998). (b) Abundance of* Euphilotes bernardino allyni *during the flight period of 1989 at Los Angeles International Airport, California (U.S.A.). Time* t = *0 corresponds to 16 June. Data reported by Mattoni et al. (2001).*

alyze nearly symmetrical abundance curves. Additionally, INCA contains many more data sets that are well described by the model.

The model defined by Eq. 2 describes the abundance curve in one particular year. However, the timing of the emergence peak depends to a substantial degree on weather conditions. In general, cold weather tends to delay emergence, whereas warm weather causes early emergence (Pollard 1988). Consequently, the flight period may differ substantially from year to year (Pollard & Yates 1993). Mattoni et al. (2001) found that over 11 years the emergence peak of the El Segundo blue butterfly (*Euphilotes bernardino allyni*) differed substantially among years, with a width of the 95% confidence interval of about 24 days. The other parameters determining the flight period and dispersion in emergence times and death rate also showed variation, but far less than peak emergence. We made the simplifying assumption that all year-to-year variation in flight period derives from variation in the emergence peak. We supposed that this parameter follows a normal distribution with zero mean and variance σ_θ^2 (i.e., $\theta \sim N[0, \sigma_\theta^2]$). The choice of zero mean means that, in our analysis, time centers around the expected emergence peak. Thus, the date of average peak emergence does not have to be fixed beforehand, making the approach more versatile.

To determine the likelihood of presence or absence of a particular species in an area, one would decide beforehand that counts have to be made on a limited number of days, say n. The question then arises of how these days should be spaced in time to minimize the chance of missing the species when it is present. The probability of failure to observe the butterfly on n days is

$$P(X(t_i) = 0, i = 1 \ldots n) = \int_{-\infty}^{\infty} \prod_{i=1}^{n} P(X(t_i) = 0|\theta)\phi(\theta)d\theta \tag{4}$$

$$= \int_{-\infty}^{\infty} \prod_{i=1}^{n} e^{\{-\hat{x}(t_i)|\theta\}}\phi(\theta)d\theta,$$

where $\exp\{-\hat{x}(t_i)|\theta\}$ is the probability of observing no insects on day t_i (from Eq. 3, with $k = 0$) given an emergence peak at θ; $\phi(\theta)$ is the probability density function for θ. The expected number depends on the emergence peak θ, as indicated by the vertical bar in the equation. We assumed that observations on different days are stochastically independent—that the outcome of one observation day should not affect the observation on the next day. If so, the probability of observing no insects on all survey days equals the product of the probabilities on each survey day of observing no insects (Π denotes this product). The value for this probability depends on the peak emergence time θ, which is variable. So we had to weigh the probability of observing no insects on all survey days for all possible values of θ. The integral in Eq. 4 accounts for this weighing.

The probability in Eq. 4 depends on the timing of the survey days through the values of t_i. Next we sought to find the values for t_i that minimize the probability in Eq. 4. To find these values, we differentiated Eq. 4 with respect to all t_i and set the resulting derivatives equal to zero. This yielded a system of n equations of the form

$$\frac{d}{dt_i}P(X(t_i = 0) = 0) \text{ for } i = 1, \ldots, \text{n}, \tag{5}$$

which has to be solved for t_i, $i = 1, \ldots, n$. Solutions can be minima or maxima, so it is necessary to check whether only minima have been found.

The solutions must be obtained numerically. First, we solved Eq. 1 by the Adams predictor-corrector method. Next, we calculated the probability of no observations on all days given by Eq. 4. We approximated the derivatives by the central-difference method. Finally, we applied the iterative Newton method to solve Eq. 5. We decided to study the optimal timing for $n = 5$ survey days. We also investigated the dependence of detection probability on the number of survey days.

Results and Discussion

Optimal Survey Timing

The optimal detection scheme varied with the parameter values (Fig. 2), and the pattern of the variation was similar for all four parameters. For $\hat{N} = 3$ (Fig. 2a), we saw five different solutions, indicating the times at which observations should be made. Of these five solutions, four followed the expected emergence peak. As we let $\hat{N}$ decrease, the spacing of survey times was compressed, until suddenly the two rightmost solutions collapsed to the same time. This means that survey days 4 and 5 (if we number survey days from early to late) fall on the same date. Lowering $\hat{N}$ even further eventually led to the collapse of days 1 and 2 to the same time. Further lowering of $\hat{N}$ then merged days 3 with 4+5, and finally 1+2 with 3+4+5. This implies that if $\hat{N} = 0.1$, for instance, then all five observations should be made at the same time.

A similar pattern arose with variations in all parameters, the only deviation being in the parameter β, in which

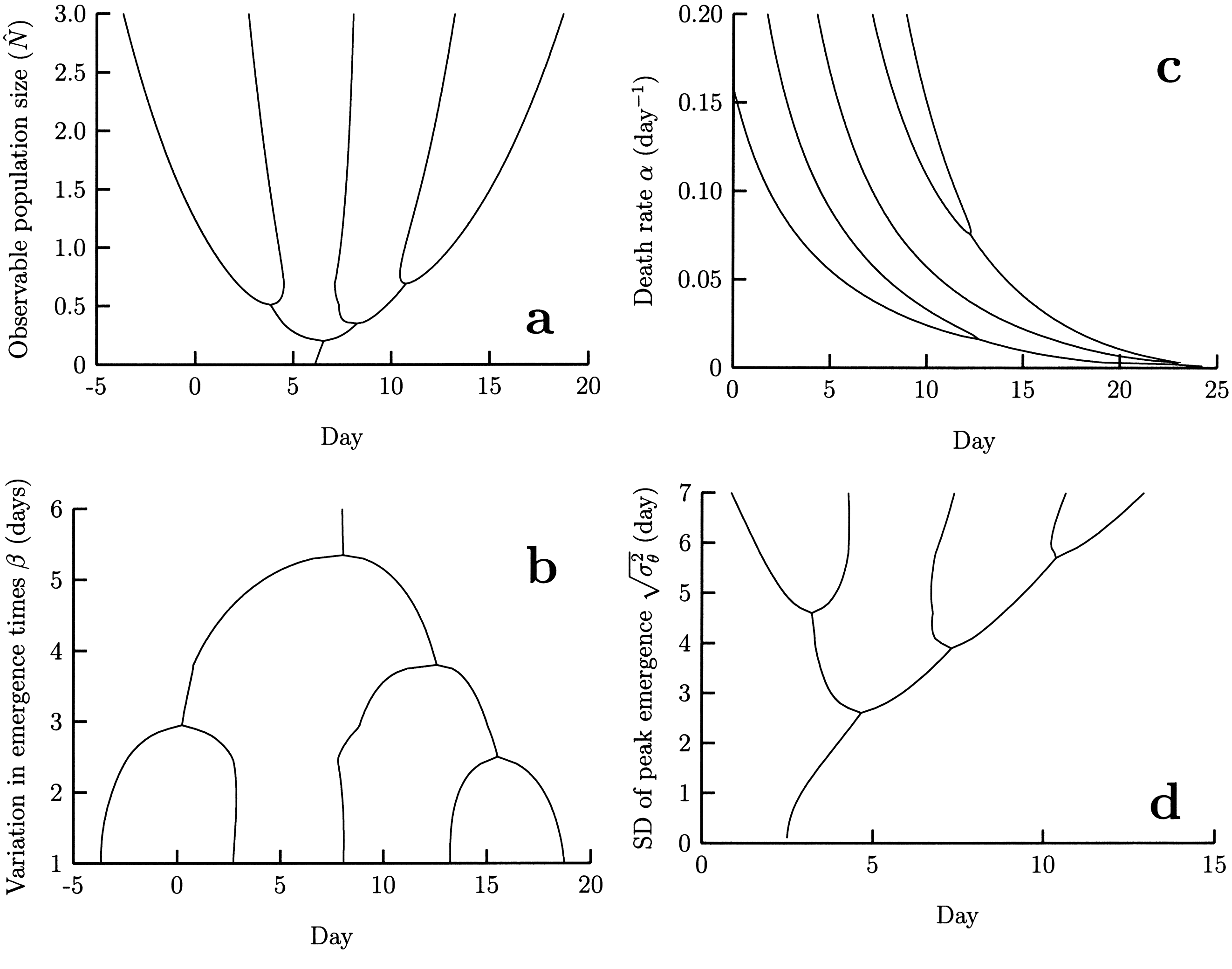

Figure 2. Optimal survey spacing for 5 survey days as a function of parameter values. The x *values give the times of the five surveys (the average peak emergence is set at zero). Survey days may coincide, so fewer than five solutions can be seen in the graphs for some parameter values. Parameter values are as follows: (a) $\beta = 1$, $\alpha = 0.1$, $\sigma_\theta^2 = 50$; (b) $\hat{N} = 3$, $\alpha = 0.1$, $\sigma_\theta^2 = 50$; (c) $\hat{N} = 0.75$, $\beta = 1$, $\hat{N} = 50$; (d) $\hat{N} = 1$, $\beta = 1$, $\alpha = 0.1$.*

low values yielded five different solutions and high values led to merging of the observation days. But in all, the order of merging was identical. This similarity is unlikely to be accidental: the probability of finding the same merging order for all four parameters by pure chance is $(1/24)^3 \approx 7.2 \times 10^{-5}$.

The similarity in the dependence of the detection scheme on the parameter values suggests that a single argument should suffice to explain the pattern. We believe that the pattern can be understood as the result of two opposing factors, both related to the possibility of not detecting a species during a survey (i.e., missing a species that has a local population). The first factor is the possibility of missing insects that are actually present during the survey. The second is the possibility of missing insects because survey days are incorrectly timed. These factors are opposing in the sense that they affect the detection scheme in opposite ways. The chance of missing insects because of low abundance favors concentrating all survey efforts near the peak of expected presence; the chance of missing insects because of incorrect timing favors spacing survey efforts throughout the potential flight period. The relative importance of the two factors depends on the parameter values, so the parameter values shape the detection scheme.

If the total number of insects, $\hat{N}$, is high, nondetection due to scarcity is unlikely. Nondetection due to poor timing of the survey is therefore the dominant factor shaping the detection scheme. This factor favors distribution of the effort over the flight period, so for sufficiently high values of $\hat{N}$ the optimal detection scheme consists of separated surveys. If the total observable number of insects is low, nondetection due to scarcity is more likely. As a result, optimal detection effort concentrates around the expected peak presence—which slightly follows peak emergence—in the optimal detection scheme.

The parameter β characterizes dispersion of the emergence times within a year. Small values for this parameter mean a short emergence window and hence a short flight period (given a reasonable death rate)—mayflies are a good example (Edmunds & Edmunds 1979). The possibility of missing a species because of incorrect timing is thus pertinent to the detection scheme. In the optimal scheme, the detection effort is therefore widely spread out. In contrast, a large β, with all other parameters held equal, causes a longer flight period. This makes it unlikely that one would miss a species because of incorrect timing. So the larger the dispersion in emergence times, the more important nondetection due to low numbers becomes. As a result, for large values of β the detection effort is best concentrated near the peak presence.

The effect of death rate can also be understood within this framework. A low death rate means presence over a long period. Missing the species because of incorrect timing is therefore unlikely. For that reason, all effort can be concentrated on a single time. A high death rate makes the flight period shorter, so nondetection due to wrong timing becomes more likely. As a result the effort is best spread out over different times.

Finally, the effect of the year-to-year variation of the emergence peak, characterized by σ_θ^2, is opposite to that of the within-year variation in emergence times. If peak emergence is highly concentrated around a fixed date each year, the chance of missing a species because of incorrect timing is very small indeed. Hence all detection effort should be concentrated near the peak presence. On the other hand, if peak emergence is unpredictable, incorrect timing of detection effort is more likely, so the best strategy is to hedge one's bets by widely spacing survey times.

The argument of two opposing factors explains that merging occurs for certain parameter values but not for others, but it does not explain the merging order or why the merging order is the same for variations in all parameters. We do not have an explanation for this particular result, but we expect that its cause is in some mathematical aspect of the model. Because we foresee no practical implications of this aspect, we did not further pursue the problem of merging order.

Given the optimal spacing of the surveys, we can now calculate the optimal detection probability. For reasonable observable population sizes, detection probability rapidly becomes saturated with increasing number of survey days (Fig. 3). For low observable population sizes, however, a disproportionate number of survey days is required to attain high detection probabilities.

Example Detection Scheme for Quino Checkerspot Butterfly

Although our analysis contributes to a better understanding of how to space a detection scheme, some additional issues have to be dealt with before the method can be applied. We want to illustrate these issues for a particular example, the Quino checkerspot butterfly (*Euphydryas editha quino*).

The Quino checkerspot butterfly is a lesser-known subspecies of the well-studied *Euphydryas editha*. Quino is listed as endangered under the ESA, and numbers of the six known metapopulations are low (USFWS 2000*a*). The habitat for the species was historically extensive, covering the coastal regions of southern California from Los Angeles southward into Baja California (Mattoni et al. 1997). This region has been under enormous development pressure, but the primary food plant for the butterfly, dwarf plantain (*Plantago erecta*), is still found, although patchily distributed, over a broad extent of the butterfly's historic range (Mattoni et al. 1997; USFWS 2000*a*). The USFWS therefore recommended surveys for the species in areas with appropriate habitat. Guidance for these surveys was provided in an official survey pro-

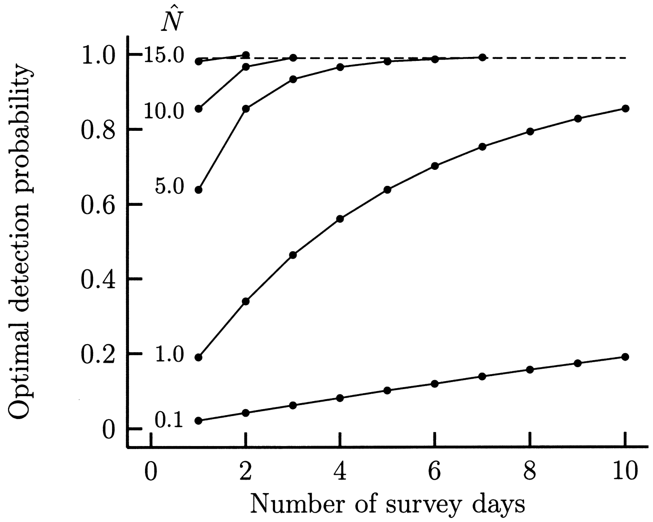

Figure 3. Optimal detection probability as a function of number of survey days. Parameter values are as follows: $\beta = 5$ day, $\alpha = 0.15$/day, $\sigma_\theta^2 = 50$ day^2; $\hat{N}$ indicated on figure. The dashed line indicates a detection probability of 0.99. For clarity of presentation, for each $\hat{N}$ only a single detection probability exceeding 0.99 is shown.

tocol, which has been revised (USFWS 1999, 2000*b*, 2001).

The method we have outlined offers the opportunity to optimize the scheme to detect Quino checkerspot adults. To this aim, we adopted values for the parameters that characterize the flight period of Quino checkerspot. Although these values are not currently known, we do have some data for the closely related *E. editha bayensis*, which we used to estimate death rate and dispersion of emergence within a year. We also have museum and survey records on the presence of Quino checkerspot from which we can estimate peak emergence and its variation. Iwasa et al. (1983) present data on male emergence during one flight season of the closely related *E. e. bayensis*. From these data we estimated that $\beta = 2.37$ day. Baughman et al. (1988) present death rates for 10 different years, and they varied from 0.092 to 0.344 per day. We neglected the year-to-year variation in the death rate and estimated an average death rate of $\alpha = 0.186$ per day.

To calculate the average date of peak emergence (θ) and the variation therein, we used Quino checkerspot incidence records from historical specimens and recent surveys, covering 1958–2000 (USFWS database; Fig. 4). We estimated the parameters by inspecting the Julian date (when available) of all relevant observations in the database. We assumed that the average date of peak emergence falls at the median of these observations, roughly 25 March. Of these records, 95% fell between 20 February and 10 May, an 80-day window. The 95% confidence interval approximately equals four times the standard deviation, so we calculated the variance of the observations as $(80/4)^2 = 400$. At least three important sources contributed to this variance: variation in emergence times, variation in longevity, and year-to-year variation in peak emergence. The variance of emergence times was $(\pi\beta/\sqrt{3})^2 \approx 18.4$, the variance of life expectancy was $1/\alpha^2 \approx 28.9$. The variance within years is the sum of these two (Rothery & Roy 2001). So the variance of year-to-year variation in peak emergence σ_θ^2 was roughly $400 - 18.4 - 28.9 \approx 350$. This yielded a window for peak emergence between 16 February and 1 May, which seems to be reasonable.

For observable population sizes exceeding 10, detection probability rapidly becomes saturated with increasing number of survey days (Fig. 5): five surveys give a detection probability of over 0.95. Smaller populations, however, require disproportionately more survey days to acquire this level of certainty. The survey protocol recommended by the USFWS (2000*b*) to detect Quino checkerspot prescribes five surveys. According to our model, five optimally spaced surveys would detect populations with observable population sizes of 10 or more butterflies with 95% confidence. The detection probability for the USFWS protocol is difficult to ascertain, however, because the season is opened at a different time each year. In the protocol, USFWS biologists decide to allow surveys to begin based on observations of larval phenology. Once the season is "opened," five weekly surveys are conducted. Opening the season based on observed phenology eliminates much of the uncertainty related to timing of peak emergence.

Rather than the current USFWS protocol, we propose use of a "bureaucratic" survey protocol, which amounts to setting the survey dates in advance, without knowledge of the actual flight period. We propose this for two reasons. First, with the USFWS protocol the detection probability cannot be determined. Although it might exceed that of the bureaucratic protocol, this is not guaranteed. If the phenology of the reference population is capriciously early, all survey days would be earlier than optimal, reducing detection probability. This situation is unlikely, but it can be avoided entirely with a bureaucratic approach. The second reason to suggest a bureaucratic protocol is one of cost. Not only must the observer monitoring the development of the butterfly be paid, but hiring observers for an uncertain survey period is much more expensive than hiring observers for a survey period of known timing.

For Quino checkerspot the bureaucratic protocol amounts to surveying on 28–29 February; 16 and 30 March; 14 April; and 1 May. The calculated detection probability for this scheme, with parameter values as described above, exceeds 0.95 for observable population sizes over 11. The realized survey dates may differ a few days from the scheduled dates without appreciably di-

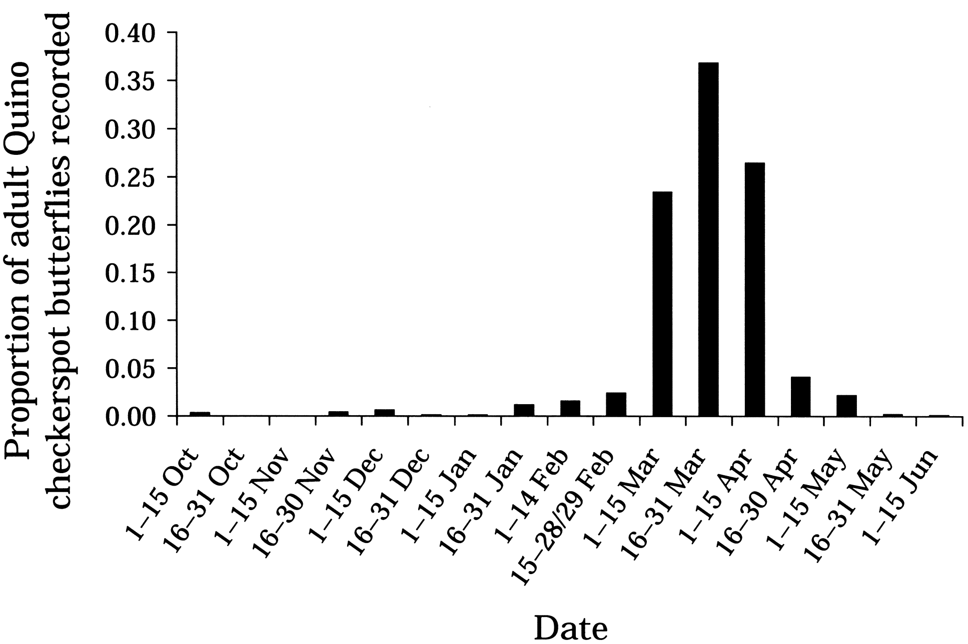

Figure 4. Incidence records of Euphydryas editha quino*, 1958-2000, from museum specimens and documented surveys (*n *= 953). The adults recorded in October through early December are associated with rare late-summer rains (Mattoni et al. 1997).*

minishing detection probability. A deviation of up to 3 days for all survey dates would reduce detection probability only a few percent. This leeway is necessary, for instance, to accommodate unfavorable weather conditions.

The applicability of the bureaucratic protocol is limited to sites and elevations within the range of the majority of those specimens from which estimates of peak emergence and its variation were derived. In the years following its listing as an endangered species, new Quino checkerspot populations have been located that extend upward to over 1300 m the range of elevations occupied by the species (Pratt 1999). Because the historic collections that constitute the majority of records in the database are from well-known lower elevations (<600 m), the resulting estimate of peak emergence and the subsequent detection scheme apply only to these lower elevations. Phenology at higher elevation is delayed, which reduces detection probability under the proposed protocol. For example, in 2001 Quino checkerspot was observed first on 27 March at a site at 610 m and on 24 April at 1310 m. At the higher elevation, only one of the optimal survey days would be within the actual 2001 flight period. This illustrates the need to choose parameters and applicable population ranges carefully.

Example Detection Schemes for Default Parameter Values

We obtained reasonable values for the parameters that characterize the flight period of Quino checkerspot because *Euphydryas editha* is one of the best-studied butterfly species (e.g., Singer & Ehrlich 1979; Iwasa et al. 1983; Ehrlich et al. 1984; Baughman et al. 1988; Mattoni et al. 1997). For many other species much less knowledge is available, and parameter values may be largely unknown. All one might be able to do is characterize the parameters as "small," "moderate," or "large" based on knowledge of the natural history of the species. To offer some guidance for such a situation, we present optimal spacing for five survey days for a range of parameter values (Table 1). This is the number of survey days already implemented in the protocol for the Quino checkerspot butterfly. Also, we believe that this number of survey days makes no unreasonable claims on resources.

We varied three parameters: the death rate α, the variation of emergence times β, and the year-to-year variation of peak emergence σ_θ^2. We set a small, moderate, and large death rate equal to 0.1, 0.2, and 0.3/day, which corresponds to average life spans of 10, 5, and 3.3 days. Recorded values for the variation of emergence times β range from 0.9 (Zonneveld 1991) to 9.8 days (Mattoni et al. 2001). We therefore set small, moderate, and large values for β equal to 1, 5, and 9 days. For $\beta = 1$, 95% of the insects emerge in about 8 days; for $\beta = 5$ this window is about 36 days; and for $\beta = 9$ the emergence window is about 65 days. For the year-to-year variation of peak emergence $\sqrt{\sigma_\theta^2}$, we set small, moderate, and large equal to 5, 10, and 15 days, respectively. (Here we took the square root of the original parameter be-

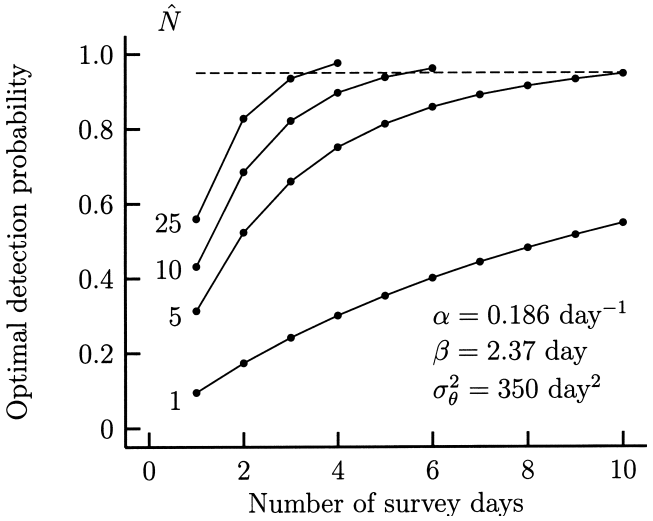

Figure 5. Optimal detection probability for Euphydryas editha quino *as a function of number of surveys. Average peak emergence θ is at 25 March. Dashed line indicates a detection probability of 0.95.*

cause the resulting standard deviation has more intuitive appeal.) This means that 95% of peak emergence dates fall within an interval of about 20, 40, or 60 days.

Table 1 presents optimal spacing for five survey days. The table also presents the population size that has a 0.95 detection probability. For larger populations, detection probability exceeds this threshold. Thus, the given population size is the minimal size that guarantees a detection probability of $\geq$0.95. We call this the detectable population size. The lower the detectable population size, the more sensitive the scheme.

With the number of survey days set, the scheme's sensitivity depends on the parameter values mostly in predictable ways. An increase in death rate causes fewer insects to be present at any time, so the scheme's sensitivity drops. An increase in the year-to-year variation of peak emergence leads to a decrease in sensitivity, again because expected numbers are lower. The effect of an increase in variation in emergence times within years, however, depends on the year-to-year variation of peak emergence. If between-year variation is large, sensitivity is highest for intermediate within-year variation in emergence times. For example, given a death rate of $\alpha = 0.1$/day and a year-to-year variation in peak emergence of $\sigma_\theta =$ 15 days, detectable population size is 4.8, 4.5, and 4.6 for within-year variation β equal to 1, 5, and 9 days, respectively. The following intuitive argument might explain this observation. Small within-year variation leads to a short flight period. If year-to-year variation in peak emergence is large, one might miss the flight period. With larger within-year variation in emergence, the flight period broadens, making it less likely to be missed as a result of unfortunate timing. If within-year variation in emergence becomes even larger, however, the expected number of insects decreases so much that the species might be missed because numbers are low.

The example schemes can be used as follows. First, an educated guess is made about the death rate, the variation in emergence times within years, and the year-to-year variation in peak emergence. The guess consists of classifying these parameters as small, moderate, or large. For the death rate this translates into the values 0.1, 0.2, or 0.3/day; for the variation in emergence times within years it translates into 1, 5, or 9 days; and for the year-to-year variation in peak emergence it translates into 5, 10, or 15 days. Second, one looks for the appropriate row in Table 1 under the heading "optimal detection scheme." The five columns under this heading show the timing of the survey as the number of days before (if negative) or after (if positive) the average date of peak emergence. So the third step is to choose a value for the average date of peak emergence to find the dates for the detection scheme. For practical purposes, the numbers in the optimal detection scheme must be rounded to the nearest integer. According to Table 1, two or more survey dates may coincide (e.g., in row four). This tells us that from the model's perspective the optimal strategy would be to perform the surveys at the same time, but this would be both impractical and unsatisfactory to the observer. We believe that good practical implementation would be to concentrate the surveys close to the optimal date. The interpretation of *close* depends on how reliable weather conditions are. Clearly, there is ample room for judgment based on expert opinion. The dominant feature of Table 1 is that for some parameter values it is a good strategy to concentrate detection efforts in a small time window, whereas for others it is better to spread the surveys over a longer time period.

Conclusion

Number of survey days, detection probability, and observable population size are interdependent. If two of them are decided, the third is automatically fixed (Fig. 5). Given a number of survey days and a detection probability, the observable population size that can be detected with this probability is fixed. For one thing, this implies that the optimal survey number, unqualified, does not exist. One has to make choices, motivated by issues such as resource availability and vulnerability of the species involved, about two of the three quantities that define the detection scheme: number of survey days, detection probability, and observable population size.

The choice of which quantity to set probably differs for the parties involved. We assume that it is reasonable to ask for reliable conclusions, which means that the detection probability should be set first. We propose that a 0.95 de-

Table 1. Optimal spacing of species detection schemes and their sensitivity for a range of parameter values.[a]

Parameter			*Detectable population size*[b] $\hat{N}$	*Optimal detection scheme*[c]				
α	β	σ_θ		t_1	t_2	t_3	t_4	t_5
0.1	1	5	1.7	0.5	4.0	6.9	10.1	12.0
0.1	1	10	3.1	−6.7	1.6	8.7	15.6	23.4
0.1	1	15	4.8	−14.0	−1.4	9.6	20.7	33.5
0.1	5	5	2.0	7.0	7.0	7.0	7.0	7.0
0.1	5	10	3.1	−1.0	−1.0	10.5	17.0	17.1
0.1	5	15	4.5	−13.3	−1.5	9.2	20.5	30.9
0.1	9	5	2.7	7.8	7.8	7.8	7.8	7.8
0.1	9	10	3.3	8.6	8.6	8.6	8.6	8.6
0.1	9	15	4.6	−4.7	−4.7	11.3	22.0	22.0
0.2	1	5	3.0	−3.3	0.9	4.3	7.8	11.5
0.2	1	10	6.3	−11.3	−2.7	4.9	12.5	21.3
0.2	1	15	11.7	−18.4	−5.7	5.7	17.3	30.6
0.2	5	5	3.5	4.3	4.3	4.3	4.3	4.3
0.2	5	10	6.0	−5.8	−5.8	5.0	15.1	15.1
0.2	5	15	8.8	−19.1	−5.9	4.9	15.7	28.7
0.2	9	5	4.9	4.5	4.5	4.5	4.5	4.5
0.2	9	10	6.4	4.8	4.8	4.8	4.8	4.8
0.2	9	15	9.1	−10.0	−10.0	5.1	19.7	19.7
0.3	1	5	4.5	−4.9	−0.5	3.1	6.7	10.9
0.3	1	10	10.1	−12.9	−4.2	3.5	11.2	20.2
0.3	1	15	23.0	−19.9	−7.3	4.3	16.0	29.1
0.3	5	5	5.0	3.1	3.1	3.1	3.1	3.1
0.3	5	10	9.0	−9.1	−5.8	3.1	13.2	14.7
0.3	5	15	13.2	−21.0	−7.6	3.2	14.2	27.5
0.3	9	5	7.2	3.2	3.2	3.2	3.2	3.2
0.3	9	10	9.6	3.3	3.3	3.3	3.3	3.3
0.3	9	15	13.6	−11.9	−11.9	3.4	18.4	18.4

[a] *See text for complete explanation and guidelines for use.*

[b] *Detectable population size is the observable population size that can be detected with 0.95 probability.*

[c] *Optimal detection scheme is given in days relative to average peak emergence θ. Negative entries indicate number of days before average peak emergence θ; positive entries indicate number of days after average peak emergence.*

tection probability is fair, although efforts to detect species on the brink of extinction may warrant a higher detection probability of 0.99. Next, conservation biologists might opt to set observable population size. This might lead to unreasonable costs, however, so regulatory organizations might want to weigh cost considerations to set the survey number. The observable population size then follows. If this size is high, the survey protocol is not sensitive enough, and one may decide to increase the number of survey days. This, however, will not always result in the desired detection probability (Fig. 5).

So far we have treated the observable population size $\hat{N}$ as unipartite. Because it obeys $\hat{N} = qAN$, however, various factors contribute to it. Assuming that the area covered by the transect, A, is maximized, low observable numbers can be attributed to a low actual population density when detection probability q is high. When q is low, however, observable number will be low even if populations are substantial. Hence, we need some knowledge of q to safely interpret results from our analysis of the number of survey days required. For the Palos Verdes blue butterfly, search efficiency q was estimated to be 0.4 (Mattoni & Longcore 2000). For the El Segundo blue butterfly, based on behavioral characteristics, we presumed that search efficiency is very high and may be close to or exceed 0.9 (Mattoni et al. 2001). For other species, however, such as many hairstreak butterflies (Theclinae), q may be inherently low. Transect methods may then need to be supplemented with searches for different life stages. For example, the brown hairstreak butterfly (*Thecla betulae* L.) is more easily spotted as an egg during the winter than as an adult in late summer (Thomas & Lewington 1991). For regulatory agencies dealing with laws that have absolute prohibitions on take (e.g., the USFWS's enforcement of Section 9 of the ESA), the choice of an acceptable detection probability will be especially difficult for species with inherently low q values that result in low observable population sizes.

We argue that knowledge of detection probability is important in a regulatory context, but knowledge of this probability can also be important in the design of any study to determine the geographic range or shifts in range of a species. For instance, Parmesan (1996) inferred range shifts in *E. editha* from apparent changes in the occupation of known historical population sites throughout the species' range. In such a study, an estimate of detection probability could lend more confidence to rating a site as unoccupied after a given number of visits.

In recent decades, the population sizes of many insect species have declined precipitously, but their habitats have not been eliminated. When such species are not located for some years, conservation decisions depend on the level of certainty that the species has been extirpated, rather than that it may be persisting in low numbers. If the probability of having detected the species if present were 0.99, one might assume that the species had been extirpated and proceed with reintroduction efforts. If the probability of detection were only 0.75, however, the management decision might be to enhance the habitat until greater certainty is achieved.

The conclusion that a site is unoccupied, given no observations of a species during surveys that were part of a scheme with high detection probability, depends on additional assumptions. For instance, multiyear diapause would frustrate this conclusion. Multiyear diapause may not be the rule, but it is common in unpredictable climates, such as those of arid and Mediterranean regions (Scott 1986). For example, *E. editha* may enter multiyear diapause (Singer & Ehrlich 1979), and some observers have reported it in *E. e. quino* (USFWS 2000*a*). Furthermore, metapopulation dynamics complicate temporal patterns of occupation (Hanksi 1999). Surveys may conclude that a site is unoccupied with a high degree of certainty during 1 year, and the site may then be occupied through dispersal the next. The dynamic nature of occupation is not incorporated into the ESA, but briefly unoccupied habitat is critically important from an ecological perspective (Rohlf 1991). A conservative scheme to determine ecologically significant extirpation (i.e., with little probability of quick recolonization) would include more than one survey year. Only for sedentary species with low dispersal ability can a single negative survey result be interpreted as extirpation with high probability.

Finally, we stress that detection schemes are only as good as the field biologists who implement them. Even the best-designed scheme with high detection probability will fail if survey personnel are inexperienced or exercise poor judgment. As with all Pollard walks, survey routes must be thorough and carefully planned (Thomas 1983) and weather conditions must be appropriate. Math is no cure for bad biology. But with experienced observers, a well-designed detection scheme will allow greater confidence that if a species is present it will be detected.

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