Journal of Insect Conservation **5**: 197–206, 2001.

Analysis of transect counts to monitor population size in endangered insects

The case of the El Segundo blue butterfly, Euphilotes bernardino allyni

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Received 30 June 2000; accepted 30 May 2001

Key words: death rate estimation, endangered butterflies, Lycaenidae, population size estimation, restored habitat

Abstract

Before, during and after habitat restoration from 1984 to 1994, we monitored population size of the federally listed endangered El Segundo blue butterfly, *Euphilotes bernardino allyni* (Shields). In the subsequent formalization of a recovery plan for the species, the U.S. Fish and Wildlife Service established several recovery criteria, including a requirement of ‘a scientifically credible monitoring plan’ to track population size annually. To avoid detrimental effects of the extensively used mark-release-recapture method on the delicate El Segundo blue butterfly, which would conflict with protection afforded by the Endangered Species Act, we chose instead to perform transect counts to estimate relative population size. Herein, we analyze the results of our transect counts by three different methods, developed by or modified from Pollard, Watt *et al.* and Zonneveld. Qualitatively, the three methods, which have different assumptions, produced similar results when applied to the same data. Zonneveld’s model estimates death rate in addition to an index of population size, thus providing more information than the other two methods. The El Segundo blue butterfly’s sedentary nature and the close relationship of its adult and early stages to one foodplant permits extrapolation of the index of population size based on transect counts, to an estimate of actual population size. Our data document butterfly numbers increasing from 1984 to 1989, but then declining until the end of our observations in 1994. Based on analysis of our El Segundo blue butterfly data, we propose an implementation of a scientifically credible monitoring plan.

Introduction

The El Segundo blue butterfly, *Euphilotes bernardino allyni* (Shields)[1] inhabits remnants of the El Segundo sand dunes habitat in coastal Los Angeles County, California. Over 90% of these sand dunes having been destroyed for urban uses, the butterfly is now restricted to only three localities (Mattoni 1992), the largest of which is a 115 ha area at the Los Angeles International Airport (LAX). The 1974 listing of the El Segundo blue butterfly as endangered under the Endangered Species Act (41 Federal Register 22041) resulted in the protection of 80 ha of the dunes at LAX as a reserve (Mattoni 1992). Because long-term survival of this population was compromised by habitat disturbance and invasion of non-indigenous plants, Mattoni (1993a)

[1] Pratt and Emmel (1998) place *allyni* within *E. battoides* whereas Sheilds and Reveal (1988) and Mattoni (1989) and place *allyni* in *E. bernardino*.

designed and initiated a program to re-establish the historical complement of perennial plants at densities that mimic those of undisturbed fragments. In this paper we evaluate the results of that program, and relate these results to a key recovery criterion – assessment of population size and growth rate over time – in the recently approved Recovery Plan for the El Segundo blue butterfly (U.S. Fish and Wildlife Service 1998a).

The Recovery Plan prescribes that population size should be monitored by a 'scientifically credible monitoring plan,' but no protocol is specified (U.S. Fish and Wildlife Service 1998a). For a non-endangered species, population size monitoring probably would be conducted by mark-release-recapture (MRR) techniques (Gall 1985), and MRR was applied to the El Segundo blue butterfly before 1984 (Arnold 1983). Although MRR techniques are arguably appropriate for many species, they have been criticized because handling may damage small butterflies (Singer & Wedlake 1981; Morton 1982; Gall 1984). Certainly the El Segundo blue butterfly is at risk from detrimental effects of capture and handling (Mattoni & Murphy 1984; Murphy 1988): even the most careful netting of butterfly specimens damages wings and legs, modifies behavior (Singer & Wedlake 1981), and reduces efficiency in ovipositing (Mattoni, unpub. data). MRR techniques, therefore, are not suitable for the El Segundo blue butterfly. Behavioral characteristics of El Segundo blue butterfly adults, however, allow us to estimate with transect data total population size in circumscribed populations.

Transect walks have been developed as a quick and efficient method to monitor yearly population changes of butterflies (Pollard 1977; Watt *et al.* 1977; Thomas 1983). Pollard's original transect scheme involved the computation of an index equal to the sum of the mean weekly counts of a species throughout a flight season (Pollard *et al*. 1975; Pollard 1977). While Pollard's index made no attempt to reflect the total size of seasonal population, Watt *et al*. (1977) calculated seasonal brood size by dividing total number of butterflies observed during a season by residence time, calculated from MRR methods. With known longevity, this method is applied easily to transect walks. Later refinements of the transect walk method involved standardizing area and effort (Thomas 1983; Warren *et al*. 1984), but they did not incorporate estimating total population size by integrating the number of butterflies observed and dividing by longevity.

The first effort to obtain both population size and longevity estimates from transect counts was put forward by Zonneveld (1991). His method estimates four population parameters from transect counts, relying on a simple model for adult emergence and death. The model applies to species with discrete, non-overlapping generations, a condition that applies to the univoltine El Segundo blue butterfly (Mattoni 1992).

The close relationship between El Segundo blue butterfly adults and their foodplant provides an opportunity to further refine population size estimates based on transect counts. Both sexes of El Segundo blue butterflies predominately use flowerheads of a perennial shrub, Coastal Buckwheat (*Eriogonum parvifolium*), for nectaring and perching (90% of time), mate location (>90%), and oviposition sites (100%) (R. Mattoni unpub. data & Mattoni 1992). Most movement is within 10 m of foodplant patches; a few adults move greater distances within suitable habitat (Arnold 1986). These behavioral characteristics increase our confidence that the number of adults counted constitutes a substantial fraction of the total present in the transect. In addition, the close association of adults with flowerheads justifies extrapolating to obtain an estimate of total population size based on flowerhead distribution and density of adults on flowerheads.

Methods

Butterfly transects

In 1984, Mattoni (1990) established five transects to sample all areas occupied by the El Segundo blue butterfly at LAX as a way to monitor population size (Figure 1). Transect #1 (477 m, 1500 ft) traverses the toe of the backdune slope of the northernmost undisturbed natural habitat of the dunes. In 1984, *E. parvifolium* in this transect was restricted to five discrete patches, but 1986 plantings linked the original patches. Transect #2, (172 m, 560 ft) crosses an undisturbed native backdune slope that was more densely planted later. Transect #3 (630 m, 2050 ft) traverses undisturbed foredune characterized by few foodplants, which all appear stressed (i.e., producing fewer flowerheads than plants on the backdune). Transect #4 (37 m, 120 ft) crosses an isolated, dense, undisturbed patch of foodplants at the top of a 0.2 ha backdune fragment of habitat. Transect #5 (581 m, 1890 ft) extends across the largest undisturbed section of foredune.

From 1984 to 1994, we censused weekly from first adult emergence throughout the flight season. We walked at a slow pace along transects and recorded every butterfly observed within a 5-m-wide area

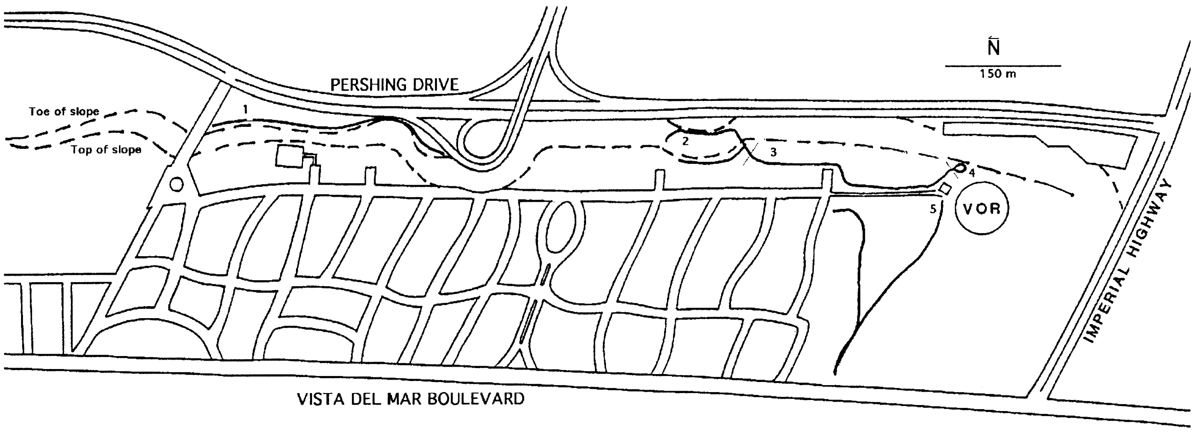

Figure 1. Butterfly monitoring transects ($n = 5$) on the El Segundo dunes at the Los Angeles International Airport that sample all areas occupied by El Segundo blue butterflies, 1984–1994. Streets between Pershing Drive and Vista del Mar Boulevard are remaining infrastructure from previous residential development that was removed.

projected ahead of the observer (Pollard 1977; Thomas 1983). Because El Segundo blue butterflies are sedentary and difficult to spot when they perch, we disturbed flowerhead visitors by sweeping a net above each plant. Reliable surveys would be impossible otherwise, because of the small size of the butterfly and the dense clusters of flowers in which the butterfly rests on many plants (3000 per m^2 on one plant). Mattoni made counts in 1984, 1986–1990; R. Rogers made counts during 1991–1994.

Population size estimates

Three methods were used to estimate size of the population from transect counts.

Method I. Pollard Index. Pollard's (1977) population index consists of the sum of weekly mean of observed numbers throughout the flight period. The method is widely accepted and is easily calculated (Pollard 1984). Because counts were conducted approximately weekly, this index was quite close to the total number of butterflies observed.

Method II. Modified Watt et al. Method. Watt *et al.* (1977) estimated 'total animals [butterflies] present in the brood' by estimating daily butterfly numbers through MRR and extrapolation, summing them to calculate total animal-days, and multiplying this number by the death rate (determined by MRR). As our transect counts did not produce daily butterfly numbers, we linearly interpolated our data for days between counts. The sum of all butterfly counts, both actual and extrapolated, represent the number of 'butterfly-days'. We divided butterfly-days for each transect by the mean of longevity estimates provided by Arnold (6.1 d; 1983) to calculate a population estimate for each transect, which we then summed.

Method III. Zonneveld Model. Zonneveld's (1991) model for population size is more difficult to apply, but provides an estimate death rate (the inverse of longevity). His method also calculates the standard deviations of parameter estimates, which are lacking in the other methods. The model assumes absence of net migration, a constant death rate over the season, and logistically distributed emergence times. These assumptions yield the following description of changes in the number of butterflies:

$$\frac{d}{dt}x = N\frac{b}{\beta(1+b)^2} - \alpha x \quad \text{with } b = e^{(t-\mu)/\beta}.$$

In this equation, x describes the time-dependent density of the butterflies, N is the number of pupae that eclose during the flight period. The parameter μ is the mean date of emergence, whereas β characterizes the dispersion in the emergence times. The initial condition is that at the onset of the flight period no butterfly is present. We integrated the differential equation with Adams Predictor Corrector method (Burden & Faires 1985: 245) with a step size of 0.1 d.

To relate the model to the transect counts, we have to estimate parameter values from the counts. To do this, we assume that a constant fraction of the butterflies is observed. Because of the sedentary nature of the species, this assumption is robust and the fraction approaches unity. Furthermore, we assume that counts follow a Poisson distribution with the mean given by the model. Zonneveld (1991) presents the derivation of the maximum-likelihood estimators for parameters of this model, which we used.

Adjustment for flowerhead distribution

Numbers of mature *E. parvifolium* plants and flowerheads on each individual plant were mapped for the entire habitat in 1986, 1989 and 1993. The 1986 census represents the population before habitat was revegetated. By 1989 about 400 of the planted buckwheat seedlings matured, and by late 1993 over 5000 more seedlings were planted. However, only flowering plants were recorded, so those seedlings that did not produce flowerheads until after the study concluded were not mapped. Flowerheads were summed for each transect and for the patches that each traversed.

To provide an estimate of the total population size of the butterfly, the results of the three transect count analysis methods were extrapolated to the whole habitat area as measured by flowerheads. For each transect, we multiplied the number of butterflies per flowerhead on the transect by total number of flowerheads in the area sampled by the transect. The flowerhead adjustment was defined as the ratio of this adjusted butterfly number to the number of butterflies observed as follows:

$$FH_{\text{adj}} = \frac{\Sigma_{x=1}^{5}(n_x/FH(\text{transect})_x)FH(\text{area})_x}{\Sigma_{x=1}^{5}n_x},$$

where FH_{adj} is the flowerhead adjustment, n_x is the number of butterflies observed on transect x, $FH(\text{transect})_x$ is the number of flowerheads on transect x, and $FH(\text{area})_x$ is the number of flowerheads in the area sampled by transect x.

For years between foodplant surveys, we linearly interpolated flowerhead numbers, based on experience with the species and reflecting gradual maturation of flowerheads on buckwheat plants set out in 1989. The buckwheat plants set out in 1993 and 1994 did not produce flowerheads until after our surveys were complete. We used the 1986 buckwheat survey for 1984, and the 1993 survey for 1994.

Results

Transect counts

The number of times the transects were sampled each year varied by the length of the flight season (Table 1). Butterflies were observed from mid-June through mid-August, except in 1991 when butterflies were seen well into September (Figure 2). The highest numbers were observed during the second half of July. The dates of onset and ending of the flight period differed among years, as did the length of the flight period, (i.e., the time between first and last observation). The length of the flight period depends on total number of butterflies observed, because with a higher number of butterflies, the probability increases to observe any butterfly in the tails of the flight period. This is shown by the significant linear regression of flight period on the total number of butterflies of either sex ($F_{1,16} = 11.3$, $p = 0.004$). We treated males and females separately to account for the phenomenon of protandry (i.e., males emerging before females; Zonneveld 1996).

The percentage of total butterflies observed on each transect varied substantially between years (Table 1), but because both the number of butterflies and available flowerheads showed annual changes, both contributed to the observed variability of butterfly densities. For the three years with flowerhead surveys, the number of butterflies per 1000 flowerheads ranged from 1.3 to 31.2. Densities were higher on average in 1989, on average almost three times greater than 1986 or 1993.

Model analysis

Calculations for the Pollard and Watt *et al.* population size indices are straightforward, in contrast with the more elaborate model of Zonneveld. This latter model estimated all four parameters for five of the years (1989, 1990, 1992–1994; see Table 2). As an example, Figure 3 shows the time course of abundance for the year 1993 with its model description. For 1984 and 1986 too few transect counts were available to fit the curve without constraint on the parameter values. For 1987, 1988 and 1991, counts were adequate, but data did not sufficiently meet model assumptions to achieve unambiguous results without intentionally constraining one parameter value. For those years in which the model did not provide estimates with a reasonable coefficient of variation for N, an unreliable estimate of death rate caused the problem. The estimate for this parameter is fixed by the decrease in numbers in the tail end of the flight season; without frequent surveys during this period, a reliable estimate of death rate is elusive. Therefore, we set the value for death rate for those years by applying the average value of the robust estimates, weighted by their coefficient of variation. This

Table 1. Number of butterfly surveys, adult E1 Segundo blue butterflies (ESB) counted by transect, and number of *E. parvifolium* flowerheads (FH) along transects and in the areas sampled by transects at LAX, 1984–1994.

Year (# surveys)	Transect number and length						
	#1 (477 m) toe of backdune	#2 (172 m) backdune slope	#3 (630 m) foredune	#4 (37 m) top of backdune	#5 (581 m) foredune	Total (*mean*)	Flowerhead adjustment
1984 (4)							2.13
Transect ESB	130	56	4	0	0	190	
1986 (5)							3.15
Transect ESB	64	109	2	67	9	251	
Transect FH	33 600	15 300	1500	4750	4940	60 090	
Area FH	55 275	49 700	3185	8280	89 605	206 045	
ESB per 1000 FH	1.9	7.1	1.3	14.1	1.8	4.2	
1987 (9)							2.04
Transect ESB	209	160	33	46	32	480	
1988 (10)							2.32
Transect ESB	522	319	31	144	37	1053	
1989 (11)							2.07
Transect ESB	782	431	43	143	46	1445	
Transect FH	76 250	31 100	1450	4580	13 530	126 910	
Area FH	108 200	92 800	2950	7900	76 400	288 250	
ESB per 1000 FH	10.3	13.8	29.7	31.2	3.39	11.3	
1990 (10)							2.25
Transect ESB	646	401	41	79	31	1198	
1991 (12)							2.77
Transect ESB	379	283	33	125	101	921	
1992 (15)							2.92
Transect ESB	467	302	6	144	127	1046	
1993 (10)							3.11
Transect ESB	318	406	10	117	74	925	
Transect FH	118 400	58 060	3410	9270	9840	198 980	
Area FH	243 500	191 500	7600	39 800	47 300	529 700	
ESB per 1000 FH	2.7	7.0	2.9	12.6	7.5	4.6	
1994 (8)							1.84
Transect ESB	782	172	5	37	65	1445	

resulted in setting the death rate at 0.21 d^{-1}, equivalent to a longevity of 4.8 d.

The standard deviation of the emergence times equals $(\pi/\sqrt{3})\beta = 1.81\beta$. The value of β shows little variation in those years for which an unconstrained estimate could be obtained; its mean value is 6.2 d. This gives an approximate emergence interval during which 95% of butterflies emerge within a period of ~45 days (4 times the S.D.) with little variation among these years (1989, 1990, 1992–1994). The observed flight period is also similar for these same years.

The three methods for analyzing transect data yield similar results (Figure 4). Population size estimates derived by the different methods are highly correlated (Table 3). Although all estimates are based on the same data, different assumptions are involved in calculating each population size index. The two most related methods, those of Pollard and Watt *et al.*, yield the strongest correlation. We attribute the weaker correlation with Zonneveld's method to population estimates for 1989 and 1990. For these years, the model estimates death rates substantially greater than for other years (Table 2). By contrast, our application of the Watt *et al.* method uses a standard death rate for all years, irrespective of data, whereas Pollard's index does not include longevity in its calculation.

For all years, the population size index is lowest for the Pollard index, intermediate for Watt *et al.*'s method and highest for Zonneveld's model. Pollard's index is expected to underestimate population size, because it misses butterflies that emerge and die between consecutive transect counts. For Watt *et al.*'s method, we used Arnold's estimate of longevity, which exceeds the longevity estimated from the transect counts. Because the population size index is calculated by butterfly-days

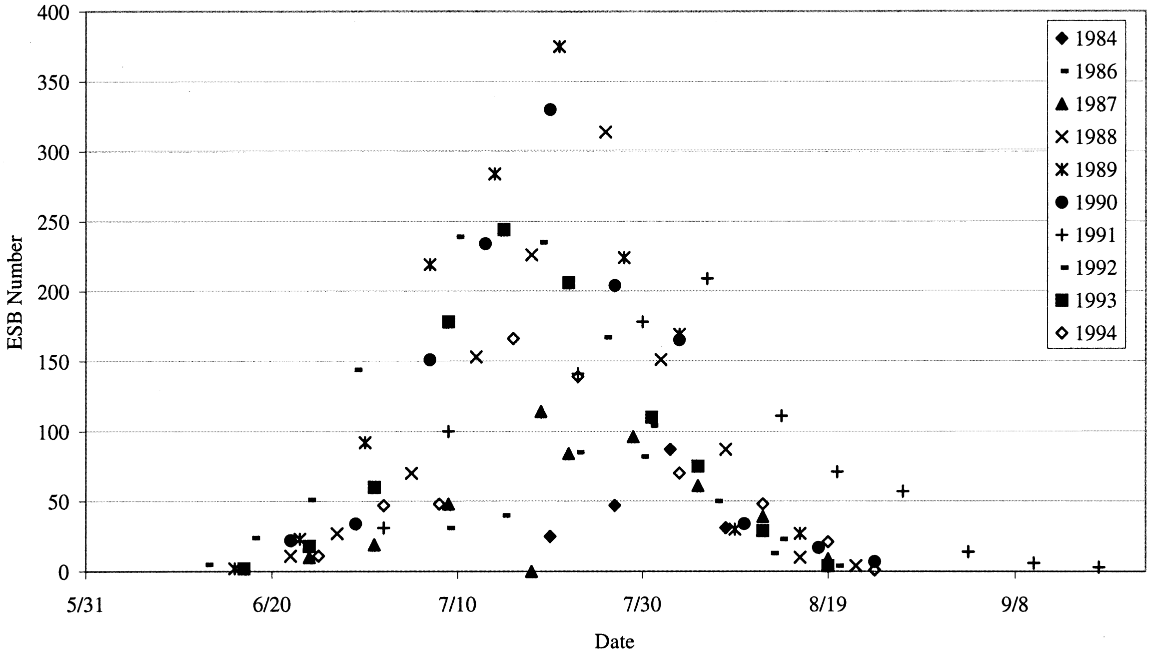

Figure 2. Number of El Segundo blue butterflies observed along transects at LAX, 1984–1994.

Table 2. Parameter estimates for Zonneveld's model fit to El Segundo blue butterfly transect data, 1984–1994. N is population size; μ is the mean day of emergence (measured in days after May 31); β is a measure for the dispersion in emergence times; α is the death rate; CV is the cofficient of variation of both N and α.

	N (#)	μ (d)	β (d)	α (d^{-1})	CV
1984	289	58	4.0	0.21[a]	
1986	445	51	5.2	0.21[a]	
1987	685	50	7.1	0.21[a]	
1988	1394	48	5.9	0.21[a]	
1989	2860	46	6.2	0.29	0.64
1990	2480	48	6.3	0.30	0.71
1991	1540	41	9.8	0.21[a]	
1992	1375	40	6.5	0.17	0.27
1993	1110	44	5.5	0.17	0.24
1994	765	47	6.5	0.17	0.43
1998[b]	3356	35	6.2	0.17	0.24

[a] α could not be estimated accurately (see text: Methods).
[b] Survey route different, N not comparable (see text: Coda).

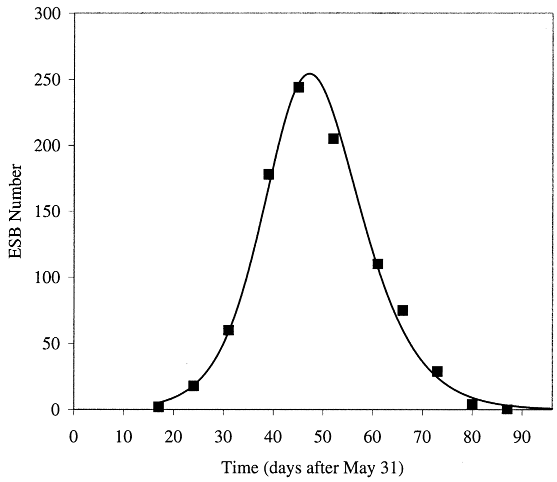

Figure 3. Zonneveld's model fit (line) for El Segundo blue butterfly transect count data (squares) collected at LAX in 1993.

divided by longevity, a higher estimate for longevity results in a lower estimate for population size.

Flowerhead survey

Most of the 1300 buckwheat plants that we censused at LAX in 1985 grew in patches, largely created by previous disturbance. By late 1993, numbers of mature buckwheat plants had more than doubled (Table 1). Revegetation had connected patches, except for differential survival of plants across unsuitable microhabitats. Relative to flowerhead numbers, the revegetation program was successful. During the 1994 revegetation more than 5000 *E. parvifolium* were set out and they matured in 1996–1997. Unfortunately, the lack of a consistent monitoring program since 1994 has obviated the opportunity to analyze the dynamics of this change.

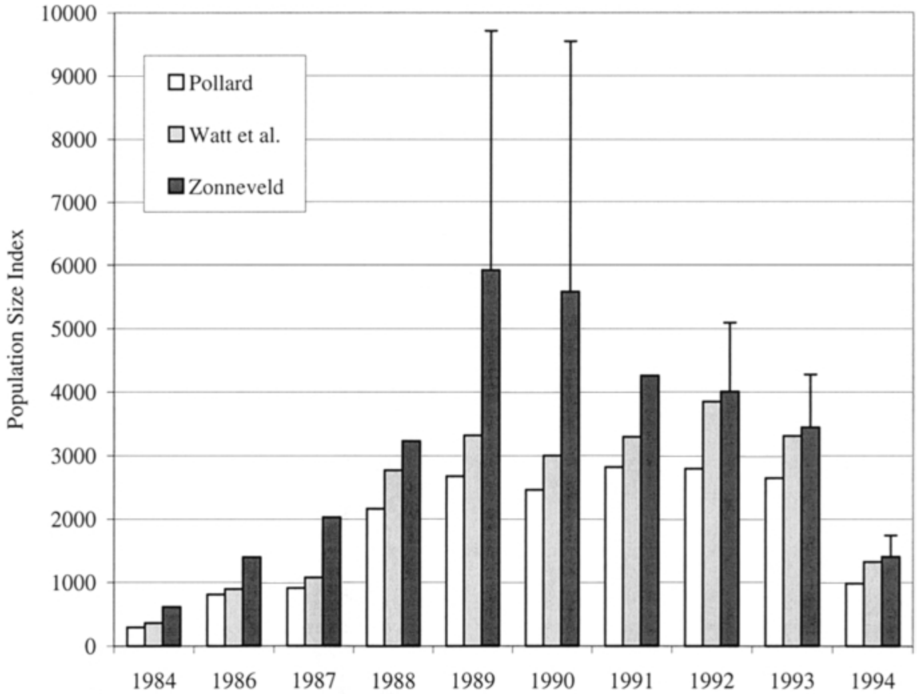

Figure 4. Calculated population size indices of El Segundo blue butterfly at LAX, 1984–1994 as determined by three different methods of analysis. Error bars indicate one standard deviation where transect counts were sufficiently frequent to allow its calculation by the Zonneveld model.

Table 3. Correlation coefficient(upper triangle) and significance (lower triangle) among population size estimates according to different methods.

	Pollard	Watt *et al.*	Zonneveld
Pollard	—	0.991	0.866
Watt *et al.*	0.0000	—	0.836
Zonneveld	0.0012	0.0026	—

Discussion

Increasing urbanization that destroys and fragments habitats is a major cause of the increase in the number of insect species and subspecies that are endangered. The El Segundo blue butterfly is a typical example, but many other insect species suffer similar fates, e.g., the quino checkerspot butterfly, *Euphydryas editha quino* (Mattoni *et al.* 1997), the Palos Verdes blue butterfly, *Glaucopsyche lygdamus palosverdesensis* (Mattoni 1993b; Mattoni 1994), and the Delhi sands giant flower-loving fly, *Raphiomidas terminatus abdominalis* (Rogers & Mattoni 1993). In all, 44 insects and arachnids are listed as threatened or endangered by the United States Endangered Species Act (50 CFR 17), while many equally imperiled species remain without formal protection.

For delicate endangered insects, tracking population size will require long-term monitoring protocols that do not harm individuals. Transect counts are, in principle, well suited for the purpose, but the death rate of the species must be known to obtain an estimate of population size. Pollard's method provides an index without knowledge of a death rate. However, this index is difficult to relate to the population size because it involves implicit assumptions regarding the fraction of butterflies not observed because of emergence and death of individuals between weeks. In our modification of Watt *et al.*'s method, investigators must use a constant death rate from other species or other years, or simultaneous MRR studies must be undertaken to establish an estimate of death rate. Such studies are often not allowed when monitoring endangered species with unknown death rates. The advantage of Zonneveld's method is that both death rate and an index of population size can be obtained if sufficiently frequent transect counts are made.

The difficulty in analyzing our transect data with Zonneveld's method largely resulted from a suboptimal frequency of transect counts. To obtain reliable estimates of death rate, an investigator especially needs frequent transect counts at the end of flight periods. If death rate is well fixed, the other parameters are usually fixed as well. (The statistical correlation between parameter estimates of population size and death rate is indicated by their nearly identical coefficients of variation.) For optimal analysis, counts should be conducted as frequently as manageable, throughout the entire flight period. The frequency of transect counts is relative to the length of the flight period. For the El Segundo blue butterfly counts should be conducted biweekly or at least weekly, each interval representing 5–10% of the maximum flight period for the species. The surveys analyzed herein were initiated by Mattoni before publication of the Zonneveld model, and did not incorporate this consideration. Nevertheless, the longevity estimates produced by our application of Zonneveld's model (3.3–5.9 d) are consistent with those from MRR studies for this species (2.3–7.3 d, Arnold 1983).

Another potential shortcoming of Zonneveld's model is the need for a minimum peak number of individuals observed on one day during transect counts (i.e., 25) to reliably use the method. If this condition cannot be approximately met, successful application of the model is doubtful. This number, however, can be used to determine the length of the transect for those species with sufficient abundance.

The estimated size of the El Segundo blue butterfly population, adjusted for flowerhead distribution, increased from 1984 to 1989, then decreased through 1994 (Figure 4). During 1984–1986, introduced California Buckwheat (*Eriogonum fasciculatum*) was removed from the LAX site (Mattoni 1990). This non-indigenous species was planted in 1975 instead of the native Coastal Buckwheat in a well-intentioned but flawed effort to revegetate after disturbance of the backdune during road construction. Pratt (1987) documented that the California Buckwheat provided habitat for other lepidopterous larvae (i.e., Gelechiidae and Cochylidae), thus placing the El Segundo blue butterfly at a competitive disadvantage. Competitors of the El Segundo blue butterfly increase their populations during the earlier flowering period of *E. fasciculatum* and thereby are more numerous competitors for the finite resources of the later-blooming *E. parvifolium*. The simultaneous removal of *E. fasciculatum* and planting of *E. parvifolium* probably contributed greatly to the rapid increase of the El Segundo blue butterfly from 1984–1989 (Longcore *et al*. 2000).

We are uncertain of the cause of the decrease from 1989 until observations ended in 1994. Density-dependent population regulation following increased population size may be implicated, but density-independent variables, such as rainfall, may also be involved. The precipitation significantly above average in 1992 and 1993 (Student's T, $p < 0.007$; mean 47.2 ± 7.4 cm vs. 21.6 ± 8.6 cm all other study years) may have contributed to the population decline. Climate is known to influence insect numbers, but its effect is dependent on the species involved and the effect on its predators and parasites as well (Uvarov 1931; Pollard 1988).

Four criteria have been established to consider downlisting the El Segundo blue butterfly from endangered to threatened status under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1998a). These criteria are: (1) protection of four geographically specified populations, (2) management to maintain coastal dune habitat in these four areas, (3) a statistically upward trend in population size for at least ten years 'as determined by a scientifically credible monitoring protocol,' with population growth rates maintained though management at or above one, and (4) initiation of a public education program. In the following we consider only the third criterion and its interpretation.

A population growth rate for a species can be defined as the ratio of population sizes from one year to the next. Even with uncertainty of estimates of population size, statistical uncertainty of this ratio is not easily determined, which implies that it is impossible to verify annually whether the criterion of a positive population growth rate is being met. An alternative is to complete a trend analysis for a prolonged period, which is also difficult, even with extensive survey data (Thomas 1996; Van Strien *et al*. 1997). For the El Segundo blue butterfly, it seems inappropriate to use linear regression, because our data suggest that the initial increase in size of the population is not sustained in later years. The statistical uncertainties in interpreting population trends and population growth rates make it difficult to set success thresholds for implementing the criterion. Qualitatively, the population growth rates of three to five of the five last years of the study are below one, depending on the analysis method used. The recovery criterion is, indeed, prudent to require trends over a 10-year period. If the survey were restricted to 1984–1989, one would have inappropriately concluded that the El Segundo blue butterfly population was on its way to recovery. The choice of method for analysis of the transect data is also important to the trend analysis. The Zonneveld method shows a five-year increase, followed by a five-year decrease of the population size. Consideration of the Pollard index shows a population increase followed by stability for six seasons followed by a bad year in 1994.

Other U.S. Fish and Wildlife Service recovery plans for insects listed as threatened or endangered also contain criteria requiring scientifically credible monitoring (e.g., Delhi Sands flower-loving fly, *Raphiomidas terminatus abdominalis*, Oregon silverspot butterfly, *Speyeria zerene hippolyta*, Myrtle's silverspot butterfly, *Speyeria zerene myrtleae*, U.S. Fish and Wildlife Service 1997, U.S. Fish and Wildlife Service 1998b, U.S. Fish and Wildlife Service 1999). These plans, however, provide little guidance on technical aspects to implement such criteria. For butterflies and other conspicuous insects, we recommend that standardized transect counts be completed at intervals equal to 5–10% of the flight period (biweekly as a rule of thumb) and throughout the entire flight period. Transect lengths should be such that the peak number of individuals observed equals or exceeds 25. Other considerations may be needed to sample habitats with different population densities, or to extrapolate transect counts to entire population size based on habitat characteristics. Also, further issues may arise in dealing with metapopulation structures. These guidelines enhance the probability that data can be analyzed properly, so that counts actually provide necessary information to evaluate recovery criteria.

For many applications, a Pollard index, or our modified Watt *et al.* method is appropriate and easy to calculate from transect counts conducted as we recommend. However, for instances where total rather than relative population size is important and mark-release-recapture is prohibited, or where standard error measures are desired for trend analysis, data collected following these recommendations can be analyzed using the Zonneveld model. This method is most robust, and its ability to incorporate changes in longevity from year-to-year shows different patterns than the other methods.

Coda

Since 1994, consultants working for LAX performed various surveys of the El Segundo blue butterfly population there. The route followed by these surveys, however, was different (albeit similar) from the route used in this paper and many different observers conducted these counts. Two years (1995, 1998) involved surveys throughout the entire flight season, while in other years (1996, 1997) surveys were limited – with no scientific justification – to four dates 'near the peak of the butterfly's activity period' (Arnold 1998). No further quantification of buckwheat flowerhead abundance and distribution was undertaken. The differences in survey routes, failure to survey throughout the flight season, and lack of buckwheat flowerhead data prevent us from comparing the results from this period to those obtained for 1984–1994 in evaluating the ongoing response of the butterfly to revegetation. When sufficient surveys were conducted, however, we can use the results to further confirm the parameter estimates from the Zonneveld model. The 1998 survey does this well; the death rate exactly matches that determined in 1992–1994, and other parameters are similar. If the transect were assumed to be the same, the population estimate for the transect would be increasing (Table 2), and would constitute an expected response to the maturation of buckwheat planted in late 1993 and 1994.

Acknowledgements

The authors thank Rick Rogers, Julie Rolle, and Paul Principe for valuable field assistance. Ger Ernsting, Lawrence Gall, Jerry Longcore, Catherine Rich, and two anonymous reviewers provided constructive comments on the manuscript.

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