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The utility of repeated presence data as a surrogate for counts: a case study using butterflies

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Abstract Abundance data are widely used to monitor long-term population trends for management and conservation of species of interest. Programs that collect count data are often prohibitively expensive and time intensive, limiting the number of species that can be simultaneously monitored. Presence data, on the other hand, can often be collected in less time and for multiple species simultaneously. We investigate the relationship of counts to presence using 49 butterfly species across 4 sites over 9 years, and then compare trends produced from each index. We also employed simulated datasets to test the effect of reduced sampling on the relationship of counts to presence data and to investigate changes in each index's power to reveal population trends. Presence and counts were highly correlated for most species tested, and population trends based on each index were concordant for most species. The effect of reduced sampling was species-specific, but on a whole, sensitivity of both indices to detect population

trends was reduced. Common and rare species, as well as those with a range of life-history and behavioral traits performed equally well. The relationship between presence and count data may break down in cases of very abundant and widespread species with extended flight seasons. Our results suggest that when used cautiously, presence data has the potential to be used as a surrogate for counts. Collection of presence data may be useful for multi-species monitoring or to reduce the duration of monitoring visits without fully sacrificing the ability to infer population trends.

Keywords Presence · Count data · Monitoring methods · Butterflies · Population trends · Sampling frequency

Introduction

Understanding and predicting species abundances is a fundamental goal of ecology (Andrewartha and Birch 1954), and doing this for rare or vulnerable species is central to conservation. Balancing the type and quality of data collection with financial and logistical constraints can entail compromise; therefore utilizing data to its fullest extent often becomes imperative. A range of indices and techniques are employed to track populations through time such as: presence-absence data (MacKenzie 2005), point counts (Ralph et al. 1995), transect counts (Pollard 1977), and mark-recapture (Skalski et al. 1983). Most monitoring programs are aimed at detecting changes in population density through time, and the majority are implemented within severe logistical constraints (Marsh and Trenham 2008), making effective collection and utilization of data a critical issue.

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Collection of presence data can be done with much shorter observation time because sampling can be discontinued after a single observation and therefore has the potential to be cost effective compared to more demanding methods of counts or mark-recapture. Presence data may be the only feasible option if monitoring entire faunas or floras simultaneously over large areas is necessary, especially if many species are involved. Often, though, abundance measurements are desired to monitor the longer-term dynamics of a population or focal suite of species. In particular, relative abundance data are important in identifying species in decline (Browne and Hecnar 2007; Doady et al. 2009), the rise of invasive species (Engeman and Whisson 2006; Harrington et al. 2008), the success of management strategies (Coelho and Manfrino 2007; Homyack and Haas 2009), as well as geographical differences in population dynamics (Okuda et al. 2009). Presence data are already used to predict abundance in gridded plot surveys (Conlisk et al. 2009). Here we address the question of whether presence data can be used profitably as a surrogate for count data in a butterfly fauna within the context of detecting long-term, demographic trends.

While abundance values are most accurately estimated by counting individuals and incorporating detection probabilities (MacKenzie and Kendall 2002), detection probability models suggest that changes in the detection of a species over time might also reflect changes in the relative abundance of a species. Animal abundance is among the most important sources of heterogeneity in detection probability (Royle and Nichols 2003). Under certain assumptions this source of heterogeneity may, in turn, be utilized in repeated presence surveys to infer changes in abundance.

Given that a species is present, if y is the count of individuals observed at site i , the probability of detecting at least 1 individual in a population can be expressed as:

$$p_i = \Pr(y_i > 0 | N_i) = 1 - \Pr(y_i = 0 | N_i) \\ = 1 - (1-r)^{N_i}$$

where p is the conditional probability of detecting occupancy of a species, given that it is present, with N individuals, each with a binomial sampling probability of r (Royle and Nichols 2003). The animal-specific detection probability, r , is the detectability of an individual based on traits such as crypsis and behavior in a certain habitat structure (Boulinier et al. 1998). For our purposes, we will consider r to be an average detectability for individuals of a unique population. Because r is population-specific, the precise nature of the relationship between N and p will vary with population (Royle & Nichols 2003), and will be biased if the detection probability changes over time (MacKenzie and Kendall 2002).

If the skill of the observer does not change, there are no systematic changes in the sites or monitoring conditions, and there are no behavioral changes in the animals that affect their detection, then the relationship of observed presence to observed counts should also remain constant through time.

Point-counts in which unique individuals are counted are commonly employed to estimate population abundance. The Royle and Nichols (2003) presence-absence model (above) and a point-count model developed by Royle (2004) provide equivalent estimators for site occupancy through identical definitions of N and r , and the shared assumption that detection is dependent on the average abundance of individuals available for detection (for a more complete explanation see Dorazio 2007). Equivalency of the presence-absence and point-count models establishes a connection between observed presence and observed abundance. Dorazio (2007) used simulation studies to test the performance of the point-count and Royle-Nichols presence-absence models, which assume abundance-dependent detection, against a presence-absence model that assumes independence between detection and abundance (MacKenzie et al. 2002) to detect trends in occupancy. The Royle-Nichols model was similar to the trend depicted by point-counts, and both of these models, which assume abundance-dependent detection, more accurately characterized the trend than the abundance-independent model.

In this paper we report an empirical study on the relationship between observed presence data and observed count data. Detection probabilities, and therefore true abundances, of each population were not estimated for this study because we were more interested in changes in relative abundance rather than true abundance. Sites were visited approximately every 2 weeks by a single individual over 9 years from a study designed to investigate inter-annual differences in butterfly presence and phenology. This study examines 151 populations of 49 species across 4 sites. Since exhaustive sampling, such as this effort, may not be feasible or practical for other taxonomic groups or monitoring schemes, we simulated data sets with lower frequency sampling and tested performance. Our goal was to (1) investigate the relationship between observed presence and observed count metrics for each population, (2) test the ability of each metric to detect population trends over time, and (3) examine the importance of sampling frequency to goals (1) and (2).

Methods

Monitoring methods

Beginning in 1999, both count and presence data were collected at 4 Central Valley sites. The Pollard count

method (Pollard 1977) was employed, in which a defined transect was walked and species observations were recorded. The sampling unit for each site was a single transect between 6.5–10 km in length meant to sample all local habitats at that location. Each site with a transect is bordered by a natural barrier such as the Sacramento River or Suisun Marsh or a non-habitat land cover such as a road or industrial area, making the sites relatively confined and therefore almost the entirety of each site can be observed from the transect. Although transects were of variable lengths, they remained fixed through time, and therefore differences in transect length had no effect for analyses within sites. Surveys were only conducted during weather conditions suitable for butterfly flight. Hereafter we refer to observed count data as “counts” and observed presence data as “day-positives”, in recognition that absences may only be a failure to detect (Gu and Swihart 2004). Between 1999 and 2007, each of the four valley sites—North Sacramento (NS), Rancho Cordova (RC), Suisun Marsh (SM), and West Sacramento (WS)—were visited at roughly two-week intervals with a range of 26 and 35 visits per year, and an overall total of 1,094 observation days.

Analyses

Correlation between day positives and counts within populations

To measure the relationship between annual counts and day-positives for individual populations, we performed separate Spearman correlations for each population (individual species at each site; $N = 151$). Day-positive data was derived from count data. As an exemplar site, day-positive and count data for the West Sacramento site are presented in Appendix Table 3. To account for differences in the number of visits between sites and years, count and day-positive values were divided by the number of visits to the site in that year to give counts per visit and day-positives per visit. Only years with at least one observation were included in the analysis. To explore variation among species in the correlation between day-positives and counts, we performed a Kruskal-Wallis test using the Spearman correlation coefficient, ρ , and species as a categorical variable ($N = 49$; total number of species). All analyses were carried out using the R statistical environment (R Development Core Team 2012).

We also tested the relationship between count/day-positive correlation strength (ρ) and two population-specific metrics to ascertain population traits that might contribute to high or low correlation values. To examine whether the length of the flight window affects correlation strength, we regressed the mean flight window (using circular dates, last day observed minus first day observed) for

a population against its ρ value. We tested a linear and quadratic regression term for flight window on correlation strength (ρ). We performed a similar test to explore the effect of abundance (during the population’s flight window) on correlation values by regressing the mean count per day-positive (in this case counts were divided by the number of day positives rather than the number of visits) against the Spearman ρ values. Again, a 1st and 2nd degree polynomial regression term for the mean count per day-positive was tested.

Detecting trends

We calculated slopes of temporal trends produced with counts and day-positives for each population using a general linear model (GLM) framework. Because GLMs are linear models, by definition they can only detect linear, rather than fluctuating trends. The number of sampling visits varied by year and site (between 26 and 35) so we included sampling effort in the models so that “year” and “visits” were independent variables and annually summed “counts” or “day-positives” was the dependent variable. The summed annual counts and day-positives for many of the butterfly populations were overdispersed, which is characteristic of count data (White and Bennetts 1996). We used the package *qcc* (Scrucca 2004) to identify populations with overdispersion, and if overdispersion was detected, we used a negative binomial error distribution with a log link from the *MASS* package (Venables and Ripley 2002), otherwise a poisson distribution with log link was used. Unlike the correlation analyses, we included years with zero observations in trend analyses. Populations with fewer than 3 years of positive observations in the 9-year period were excluded. To evaluate the overall concordance of day-positive and count trend lines, we performed a Pearson correlation on the slopes from the GLM analyses.

We also tested the relationship between correlation strength (from “Correlation between day positives and counts within populations” section) and concordance of day-positive and count trends to examine whether populations with strong correlative relationships show greater agreement in trends. We tested this by correlating each species’ correlation coefficient (from the relationship between presence and counts) with the absolute value of the difference between the slopes of day-positives and counts against years. We used a Spearman correlation for this analysis, and our choice of Spearman over Pearson correlation was motivated by our interest in detecting the relative strength of correlation rather than the actual magnitude. A significant correlation would indicate that species that have highly correlated day-positive and counts would also have a high level of correspondence between the day-positive and count slopes.

Additionally, we examined the relationship between the magnitude of trends through time and the level of concordance between day-positive and count trends. This analysis was driven by the question—does the severity of the trend based on counts influence the concordance of day-positive/count trend lines? We performed Spearman correlations between the absolute value of the count slope and the absolute value of the difference between day-positive and count slopes. We used absolute values because we were interested in understanding how the magnitude of a trend based on counts affects the ability of presence data to detect trends.

Simulations

We chose 12 exemplar species to investigate the effects of sampling interval on the relationship between day-positive and count data. We investigated the effect both on the correlation and the concordance of regression slopes. We chose species to represent a spectrum of the fauna in abundance (abundant and rare), duration of flight window (short and long), and population characteristics (high and low inter-annual variation). We also chose species with atypical results from the previous analyses so that we could investigate a range of possible responses to sampling frequency.

The goal of the simulation experiment was to understand how sampling frequency affects the strength of correlation and the concordance of regression slopes for day-positive and count data. The original dataset (January 1999–October 2007), which was based on a sampling scheme of approximately every 14 days, was resampled to simulate monitoring at 15, 30, 45, 60, 75 and 90-day intervals. We resampled the data for each species at each site by interval combination by choosing a starting point within the first 60-days of data collection, and continued sampling points closest to the chosen interval until we reached the end of the dataset. A simulated sampling result was created for each exemplar species at each location and for each sampling frequency and repeated 500 times to allow for accurate determination of 95 % confidence intervals for the subsequent calculations. Spearman correlation coefficients and GLM slope coefficients were calculated for species at the site level using methods described in “[Detecting trend](#)” section. In comparing correlation coefficients and trend slopes of simulated data, we assumed that the highest sampling frequency provided the closest approximation to the true value, and therefore the greatest accuracy.

Results

Of 151 total populations analyzed, 112 populations had highly correlated day-positives and counts ($\rho \geq 0.6$) (Table 1 and Appendix Table 3). A quadratic model was

Table 1 Results of correlations and GLM trend analyses for the West Sacramento site

Species	Correlations		Trends (slope)	
	rho	p value	day-positives	counts
Hesperiidae				
<i>Atalopedes campestris</i>	0.79	0.01	0.03 _p	0.17 _{nb}
<i>Erynnis tristis</i>	0.85	0.00	0.10 _p	0.08 _{nb}
<i>Heliopterus ericetorum</i>	1.00	0.00	1.74 _p	1.74 _p
<i>Hylephila phyleus</i>	0.71	0.03	0.01 _p	0.12 _{nb}
<i>Lerodea eufala</i>	0.55	0.12	0.06 _p	0.19 _{nb}
<i>Pholisora catullus</i>	0.80	0.01	−0.07 _p	−0.16 _{nb}
<i>Poanes melane</i>	1.00	0.00	−0.28 _p	−0.28 _p
<i>Polites sabuleti</i>	0.81	0.01	−0.06 _p	−0.25 _{nb}
<i>Pyrgus communis</i>	0.62	0.07	0.01 _p	0.07 _{nb}
<i>Pyrgus scriptura</i>	0.80	0.01	−0.07 _p	−0.13 _{nb}
Lycaenidae				
<i>Atlides halesus</i>	0.98	0.00	0.03 _p	0.00 _p
<i>Brephidium exile</i>	0.77	0.02	0.02 _p	−0.10 _{nb}
<i>Everes comyntas</i>	0.64	0.06	0.05 _p	0.02 _{nb}
<i>Lycaena helloides</i>	0.50	0.17	0.00 _p	0.23 _{nb}
<i>Lycaena xanthoides</i>	0.74	0.15	−0.72 _p	−0.76 _{nb}
<i>Plebejus acmon</i>	0.88	0.00	0.00 _p	−0.07 _{nb}
<i>Satyrrium sylvinus</i>	0.86	0.03	−0.08 _p	−0.09 _{nb}
<i>Strymon melinus</i>	0.03	0.93	0.02 _p	−0.04 _{nb}
Nymphalidae				
<i>Coenonympha tullia</i>	1.00	0.00	−0.28 _p	−0.28 _p
<i>Danaus plexippus</i>	0.84	0.01	−0.02 _p	−0.05 _{nb}
<i>Junonia coenia</i>	0.64	0.06	−0.01 _p	−0.14 _{nb}
<i>Limenitis lorquini</i>	0.93	0.00	−0.05 _p	−0.10 _{nb}
<i>Nymphalis antiopa</i>	0.89	0.01	0.00 _{nb}	0.02 _{nb}
<i>Nymphalis californica</i>	0.97	0.00	0.18 _p	0.21 _p
<i>Phyciodes campestris</i>	1.00	0.08	−0.62 _{nb}	−0.86 _{nb}
<i>Phyciodes mylitta</i>	0.70	0.04	−0.04 _p	0.00 _{nb}
<i>Vanessa annabella</i>	0.88	0.00	−0.09 _p	−0.10 _{nb}
<i>Vanessa atalanta</i>	0.86	0.00	0.05 _p	0.02 _{nb}
<i>Vanessa cardui</i>	0.92	0.00	0.10 _{nb}	−0.11 _{nb}
<i>Vanessa virginiensis</i>	1.00	0.00	0.00 _p	−0.01 _p
Papilionidae				
<i>Battus philenor</i>	0.90	0.01	0.09 _p	0.09 _p
<i>Papilio rutulus</i>	0.43	0.25	0.00 _p	0.06 _{nb}
<i>Papilio zelicaon</i>	0.93	0.00	−0.12 _p	−0.30 _{nb}
Pieridae				
<i>Colias eurytheme</i>	−0.44	0.24	0.01 _p	0.04 _{nb}
<i>Euchloe ausonides</i>	0.99	0.00	−0.31 _{nb}	−0.58 _{nb}
<i>Pieris rapae</i>	0.95	0.00	−0.02 _p	−0.05 _{nb}
<i>Pontia protodice</i>	1.00	0.00	−0.58 _{nb}	−0.67 _{nb}
<i>Zerene eurydice</i>	1.00	0.00	−0.80 _p	−0.8 _p

Subscripts p and nb represent the error distribution used - poisson or negative binomial, respectively. Results for other sites are in Appendix Table 4

the best fit for the regression between Spearman's rho (ρ , the relationship between day-positives and counts) and mean flight window. That relationship was generally flat for populations with flight windows of 0–100 days, and then declined (Table 2, Fig. 1). A quadratic model was also the best fit for the regression between correlation values (ρ) and the mean count per day-positive. Between a mean count per day-positive of 0 and 40 there was a significant decline in the correlation value, followed by an increase in ρ through a mean count per day-positive of 100 (Table 2, Fig. 1). The relationship between day-positives and counts differed among species (Kruskal–Wallis Chi squared = 101.1241, $df = 48$, $p = 1.171e-05$) suggesting that the strength of correlation between day-positives and counts was species dependent.

Trend lines using day-positives and counts are presented in Table 1 and Appendix Table 4. For most species, the slope of the trend line based on day-positive data was concordant with trends based on count data. Of 151

populations, 120 populations had an absolute day-positive/count slope difference of <0.1 . Trends, with sampling effort held constant at the mean value of 29.2 days/year, are presented for West Sacramento in Fig. 2.

Populations with correlated day-positives and counts tended to have more concordant day-positive/count trend lines, i.e. a smaller difference between trend lines ($\rho = -0.16$, p value = 0.053). Additionally, there was a significant positive correlation between the severity of the slope of the count line and the difference between count and day-positive trend lines ($\rho = 0.52$, p value = $6.99e-12$). In general, count trend lines with steep slopes were more divergent from associated day-positive slopes.

For most exemplar populations, the correlation between counts and day-positives diminished as the sampling effort declined (Fig. 3). For species with a single annual brood, such as *Glaucopsyche lygdamus*, *Lycaena xanthoides*, and *Satyrrium sylvinus*, correlations on simulated data with sampling intervals greater than 45 days failed because the occurrence of a population was often missed entirely in some years and there were not enough degrees of freedom to perform correlations. Correlations for double-brooded species such as *Coenonympha tullia* and *Ochlodes sylvanoides* also declined precipitously as sampling effort declined. The correlation between day-positives and counts only declined slightly for *Pholisora catullus*, which has multiple broods but occurs at low abundance. Correlation coefficients declined for populations of *Brephidium exile* and *Vanessa cardui*, which are multiple-brooded species with low to moderate abundances in most years but undergo occasional dramatic population explosions (mean

Table 2 Results of curvilinear regressions with population rho values from the count/day-positive correlations as the dependent variable and mean flight window (linear and quadratic) and mean count per day-positive (linear and quadratic) as the independent variables in separate regressions

	Estimate	Std. error	<i>t</i> value	<i>p</i> value
Mean flight window	9.37e−4	8.95e−4	1.05	0.30
Mean flight window ²	−6.77e−6	3.33e−6	−2.03	0.04
Mean count per dp	−3.26e−2	4.14e−3	−7.86	<0.01
Mean count per dp ²	3.52e−4	5.05e−5	6.97	<0.01

Fig. 1 Relationships for quadratic regressions between Spearman's rho (ρ) and **a** the mean flight window, and **b** the mean count per day-positive. Standard error is in grey and individual data points are open circles

Fig. 2 Population trends for West Sacramento from 1999 to 2007. Population trends over 9 years using day-positives (solid line) and counts (broken line) for 30 species. Slopes for regression lines are presented in Table 1

count_{standard deviation}. *B. exile*: NS = 72₄₉, RC = 2₂, SM = 9859₁₂₅₇₆, WS = 81₅₉; *V. cardui*: NS = 53₂₇₁₅, RC = 42₅₅₈₄, SM = 76₉₃₃₀, 54₃₈₅). Multi-brooded abundant populations such as *Colias eurytheme*, *Hylephila phyleus*, and *Pieris rapae* showed low day-positive/count correlations at all sampling intervals.

For most exemplar species, as sampling became less frequent, trends in population size (Fig. 4) became more erratic. Similar to the effect of sampling on correlations, the effects of sampling effort on trend results were species, and in some cases population, dependent. Results from single-brooded (*G. lydamus*, *L. xanthoides*, and *S. sylvinus*) and low-abundance (*P. catullus* and *C. tullia*) species remained consistent and accurate until a sampling interval of 75 to 90 days, at which point trend slopes for both indices became wildly inaccurate. Both count and day-positive slopes became less accurate for exemplar species with moderate to high abundance (*B. exile*, *C. eurytheme*, *H. phyleus*, *O. sylvanoides*, *P. rutulus*, *P. rapae*, and *V. cardui*) as sampling intensity decreased, although the effect was greater (increased variation) on count slopes ($t = -3.1$, $p = 0.003$).

Discussion

Day-positives and counts were correlated for the great majority of populations, and populations that did not display a strong correlation were clumped among certain species. Six species in particular—*A. campestris*, *C. eurytheme*, *H. phyleus*, *P. rapae*, *P. communis*, and *S. melinus*—had low day-positive/count correlation values, which accounted for over half of the low correlations. All of the aforementioned species were abundant, occurred at all sites, and had long flight windows which peak in abundance late in the flight season. Counts for *C. eurytheme*, *H. phyleus*, *P. rapae*, and *P. communis* varied by site and year, yet they were observed in almost all visits. In such cases the probability of detection, p , approached 1 even though N was variable, thus abundance and detection were effectively independent. Occupancy for large populations like *C. eurytheme*, *H. phyleus*, *P. rapae*, and *P. communis* may be better characterized by independent p and N , such as the model given by MacKenzie et al. (2002); (Dorazio 2007).

Populations with lower annual abundance and/or limited flight seasons exhibited higher correlations between counts

Fig. 3 Correlation coefficients with decline in sampling days. *Plots* show changes in the mean day-positive/count correlation coefficient with increasing time between simulated sampling intervals of 15, 30, 45, 60, 75, and 90 days

and day-positives. This suggests that day-positives are a particularly good proxy of counts for rare species. When counts were low, as with rare species, the data became more similar to binary presence data.

Correlation results based on simulations indicate that the effect of a reduced sampling regime on day-positive/count correlation coefficients was species-specific. Correlations for the exemplar species with short flight seasons were most affected by reduced sampling. *G. lygdamus*, *L. xanthoides*, and *S. sylvinus* produce only a single brood each year, and therefore, any reduction in sampling was likely to miss a portion or the entire flight season. *O. sylvanoides*, *C. tullia*, and *P. rutulus* produce only 2 broods per year, and the declines in their day-positive/count correlations with variation in sampling effort were between those of the single brooded and multi-brooded species. The other six exemplar species (*B. exile*, *C. eurytheme*, *H. phyleus*, *P. catullus*, *P. rapae*, and *V. cardui*) had multiple broods, and were minimally affected by a reduced sampling regime.

Temporal trends analyzed independently using day-positives and counts were concordant for most populations, although populations in severe decline, such as *Pholisora catullus* at SM, *Phyciodes campestris* at WS, *Pontia protodice* at RC, and *Euchloe ausonides* at NS, or rapidly growing populations, such as *V. cardui* at SM and *Incisalia augustinus* at RC and SM, showed high levels of discordance. In all of the above cases, count data represented a steeper slope than the corresponding day-positive data. When the slopes for these populations were considered relative to the slopes of other populations, both indices ranked populations similarly. For example, *E. ausonides* at NS has the greatest difference in absolute slopes of all populations at 0.41 ($\text{slope}_{\text{count}} = -0.83$, $\text{slope}_{\text{day-positive}} = -0.42$), but it ranked 6th and 2nd out of 151 populations in degree of population decline for day-positives and counts respectively. Therefore, by either index *E. ausonides* would be considered to be in severe decline relative to other populations. A previous study using

Fig. 4 Regression slopes for day-positives and counts using simulated data with a sampling frequency of 15, 30, 45, 60, 75, and 90 days. Plots are shown for twelve exemplar species at each site that it occurs

simulations found that presence-absence data has low to moderate power to detect all but the most severe declines in population densities (>50 %) (Strayer 1999). We found the converse—day-positive trends most accurately reflected count trends for populations that were not in extreme decline, although both indices performed equally well in determining relative declines of populations.

Simulation results indicate that trends based on day-positives and counts become, in general, only slightly more discordant with reduced sampling, although accuracy of both indices declined. This was particularly apparent among single brooded and low-abundance species. *G. lygdamus* of RC, for example, maintained stable and concordant day-positive and count slope values around 0.0 up to a sampling regime of 90 days at which point the slopes jumped to 5.4 and 5.5 for day-positives and counts respectively (Fig. 3). Sampling affected *L. xanthoides*, *P. catullus*, and *S. sylvinus* similarly. The sampling threshold at which day-positive and counts became discordant or both indices lost accuracy in detecting trends was species dependent.

In a study simulating the outcome of monitoring programs based on count or presence-absence data, Joseph et al. (2006) found that count surveys are more reliable at detecting declines as the number of person days/year increased, while presence-absence is powerful when fewer days are dedicated. Likewise, counts out-perform presence-

absence as population size, N , and species-specific detectability, r , increase, but for species with lower detection, presence-absence surveys are more effective. For the Chestnut-rumped Hylacola (*Hylacola pyrrhopygia parkeri*), which has a probability of observation of 0.025, the “switching point” from presence-absence to counts is at 73 days of monitoring. For any number of days fewer than this, presence-absence performs better, and for more, counts more accurately capture the population trend.

Annual day-positives are an index for both the flight window (the length of a species’ flight season) and abundance. Few species are so conspicuous that a single individual is always detected, therefore the detection probability is usually less than 1, and the probability of seeing an individual of any species increases with the number of individuals present. The probability curve of observing a butterfly species is bell-shaped or has multiple peaks, depending on the number of broods, over the course of a species’ flight season (Thorne et al. 2006). The greatest variation in inter-annual observations of a species occurs early and late in the flight season. During years that a species is relatively more abundant, a higher number of individuals are flying during the “tails” of the season, which means that it is more likely that the species is detected, thereby increasing the day-positives for a species in that year (thus the correlation between counts and day-positives).

Correlations between presence-absence and count values rely on the dependence of detection probability, p , on true abundance, N , and the actual value of N has important implications for this relationship. If N is large and the species is almost always detected, there will be little variation in p , making it difficult to detect an association with N (Royle and Nichols 2003), and correlations may be weak, as was the case with *C. eurytheme*, *H. phyleus*, *P. rapae*, and *P. communis*. The exception is for species with explosive populations with short flight windows (*Glaucopteryx lygdamus* and *Brephidium exile*) or migratory populations (*V. cardui*). In these cases N was sometimes very large, but the short flight window or short period when it is present at a site, gives these species a seasonal bell-curve with longer or shorter seasonal tails depending on the magnitude of N , and thus relatively high correlations between presence and count values.

The strength of correlation between day-positives and counts was moderately associated with the concordance of trend lines ($p = 0.05$). Correlations between day-positives and counts measure the potential of day-positives to track inter-annual variation in abundance, while regressions measure long-term trends. Although most species have correlated day-positives and counts and concordant regression slopes, the association was not absolute. The few species that show little to no correlation in day-positive and count data, primarily *A. campestris*, *C. eurytheme*, *H. phyleus*, *P. rapae*, *P. communis*, and *S. melinus*, show a high level of similarity between regression slopes for most populations. For these species, day-positives poorly tracked the annual changes in abundance but adequately tracked long-term trends. This suggests that even trends for some species with independent detection, p , and abundance, N , may be tracked using presence data. The converse was also true. For example, *E. ausonides* at NS and *P. protodice* at RC have large differences in absolute slopes (0.41 and 0.31 respectively), but the correlation coefficient, ρ , for both populations was 0.99. In this case, day-positives successfully tracked inter-annual variation, but were less sensitive to long-term trends.

True abundance values underlie count values but they are not equal. The goal of most monitoring programs is to detect trends, and counts are the most commonly used metric (Marsh and Trenham 2008). Determining annual detection probabilities for individual populations, so that true abundances may be estimated, may not be feasible for many multispecies monitoring programs, especially when relative abundance rather than true abundance is of primary interest. We, as other monitoring programs, have made the implicit assumption in our analyses that the individual animal detection probabilities, r , for each population remained consistent over the course of the study. This is

reasonable as conditions and the same data collector were maintained throughout the project. We recognize that seasonality and weather may affect intra-annual detection probabilities (Harker and Shreeve 2007), though this variation is consistent through years, and therefore does not systematically affect detection probabilities. Additionally, aside from a few spot fires (less than 1 Ha in area) at NS, WS, and RC there was no directional succession at the sites to change habitat structure. Ensuring that monitoring conditions (weather, experience of observer, habitat structure, position of resources relative to transect) remain consistent for the duration of the project is important to maintaining consistent detection probabilities (Harker and Shreeve 2007; Wikström et al. 2008; Pellet et al. 2012).

This study was performed on a data set collected entirely by a single individual, thus avoiding errors that might result from multiple observers. This is the ideal situation for any monitoring regime and has allowed us to effectively explore the relationship between presence and count data. Differences in detection error imposed by multiple observers could diminish the congruence of trends based on presence and count data. Error imposed by multiple observers is problematic for many long-term monitoring schemes, although methods exist to account for error and determine observer-specific detection probabilities (Sauer et al. 1994; Nichols et al. 2000).

Additionally, the relationship of presence data to counts will likely vary across taxonomic groups, habitat types, life histories, and behaviors. We tested 49 species of butterflies across 5 families with a range of life-history traits and behaviors in 4 different habitats, and the relationship was consistent. Count data by date can easily be reduced to presence data and examined for concordance of population trends produced by both indices. This will allow managers to determine the reliability of the technique with their taxa before switching to monitoring based on presence. If count data are not available, it would be useful to collect training data as a way to test and calibrate future analyses. Use of day-positive data might be particularly useful for monitoring schemes with a similar fauna across multiple sites. The utility of this method can be extended to a range of other taxonomic groups once limitations are fully understood.

Presence-absence monitoring programs are becoming more common and currently make up more than 20 % of the programs initiated in the last 5 years in North America and Europe (Marsh and Trenham 2008), perhaps because monitoring is increasingly becoming more multi, rather than single, species based. Used cautiously, presence data has the potential to be used as a surrogate for counts, allowing scientists and managers to simultaneously monitor multiple species or reduce per-visit time without fully sacrificing the ability to infer population trends.

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Appendix

See Tables 3 and 4.

Table 3 Day-positive and count data for all species at the West Sacramento site

Species	Year	Count	Day-positive
<i>Atalopedes campestris</i>	1999	58	11
<i>Atalopedes campestris</i>	2000	63	11
<i>Atalopedes campestris</i>	2001	123	16
<i>Atalopedes campestris</i>	2002	103	15
<i>Atalopedes campestris</i>	2003	227	17
<i>Atalopedes campestris</i>	2004	208	18
<i>Atalopedes campestris</i>	2005	152	17
<i>Atalopedes campestris</i>	2006	181	12
<i>Atalopedes campestris</i>	2007	298	17
<i>Atlides halesus</i>	1999	0	0
<i>Atlides halesus</i>	2000	0	0
<i>Atlides halesus</i>	2001	4	4
<i>Atlides halesus</i>	2002	3	2
<i>Atlides halesus</i>	2003	0	0
<i>Atlides halesus</i>	2004	1	1
<i>Atlides halesus</i>	2005	2	2
<i>Atlides halesus</i>	2006	1	1
<i>Atlides halesus</i>	2007	1	1
<i>Battus philenor</i>	1999	1	1
<i>Battus philenor</i>	2000	3	3
<i>Battus philenor</i>	2001	0	0
<i>Battus philenor</i>	2002	2	2
<i>Battus philenor</i>	2003	0	0
<i>Battus philenor</i>	2004	3	2
<i>Battus philenor</i>	2005	0	0
<i>Battus philenor</i>	2006	1	1
<i>Battus philenor</i>	2007	3	3
<i>Brephidium exile</i>	1999	12	4
<i>Brephidium exile</i>	2000	136	10
<i>Brephidium exile</i>	2001	130	10
<i>Brephidium exile</i>	2002	181	12
<i>Brephidium exile</i>	2003	93	7
<i>Brephidium exile</i>	2004	14	8
<i>Brephidium exile</i>	2005	31	9
<i>Brephidium exile</i>	2006	59	8
<i>Brephidium exile</i>	2007	69	10
<i>Coenonympha tullia</i>	1999	1	1
<i>Coenonympha tullia</i>	2000	1	1
<i>Coenonympha tullia</i>	2001	0	0

Table 3 continued

Species	Year	Count	Day-positive
<i>Coenonympha tullia</i>	2002	0	0
<i>Coenonympha tullia</i>	2003	0	0
<i>Coenonympha tullia</i>	2004	1	1
<i>Coenonympha tullia</i>	2005	0	0
<i>Coenonympha tullia</i>	2006	0	0
<i>Coenonympha tullia</i>	2007	0	0
<i>Colias eurytheme</i>	1999	197	20
<i>Colias eurytheme</i>	2000	285	20
<i>Colias eurytheme</i>	2001	213	22
<i>Colias eurytheme</i>	2002	945	23
<i>Colias eurytheme</i>	2003	268	20
<i>Colias eurytheme</i>	2004	385	18
<i>Colias eurytheme</i>	2005	259	25
<i>Colias eurytheme</i>	2006	1,180	17
<i>Colias eurytheme</i>	2007	241	24
<i>Danaus plexippus</i>	1999	14	6
<i>Danaus plexippus</i>	2000	21	9
<i>Danaus plexippus</i>	2001	22	11
<i>Danaus plexippus</i>	2002	17	11
<i>Danaus plexippus</i>	2003	9	6
<i>Danaus plexippus</i>	2004	29	15
<i>Danaus plexippus</i>	2005	33	11
<i>Danaus plexippus</i>	2006	12	7
<i>Danaus plexippus</i>	2007	10	7
<i>Erynnis tristis</i>	1999	8	4
<i>Erynnis tristis</i>	2000	19	6
<i>Erynnis tristis</i>	2001	2	2
<i>Erynnis tristis</i>	2002	5	2
<i>Erynnis tristis</i>	2003	10	3
<i>Erynnis tristis</i>	2004	37	5
<i>Erynnis tristis</i>	2005	17	5
<i>Erynnis tristis</i>	2006	8	3
<i>Erynnis tristis</i>	2007	17	8
<i>Euchloe ausonides</i>	1999	11	5
<i>Euchloe ausonides</i>	2000	26	7
<i>Euchloe ausonides</i>	2001	39	7
<i>Euchloe ausonides</i>	2002	10	3
<i>Euchloe ausonides</i>	2003	1	1
<i>Euchloe ausonides</i>	2004	0	0
<i>Euchloe ausonides</i>	2005	0	0
<i>Euchloe ausonides</i>	2006	0	0
<i>Euchloe ausonides</i>	2007	1	1
<i>Everes comyntas</i>	1999	67	14
<i>Everes comyntas</i>	2000	57	11
<i>Everes comyntas</i>	2001	29	8
<i>Everes comyntas</i>	2002	47	11
<i>Everes comyntas</i>	2003	57	11
<i>Everes comyntas</i>	2004	44	14

Table 3 continued

Species	Year	Count	Day-positive
<i>Everes comyntas</i>	2005	46	14
<i>Everes comyntas</i>	2006	24	10
<i>Everes comyntas</i>	2007	80	18
<i>Heliopetes ericetorum</i>	1999	0	0
<i>Heliopetes ericetorum</i>	2000	0	0
<i>Heliopetes ericetorum</i>	2001	0	0
<i>Heliopetes ericetorum</i>	2002	0	0
<i>Heliopetes ericetorum</i>	2003	0	0
<i>Heliopetes ericetorum</i>	2004	0	0
<i>Heliopetes ericetorum</i>	2005	1	1
<i>Heliopetes ericetorum</i>	2006	1	1
<i>Heliopetes ericetorum</i>	2007	1	1
<i>Hylephila phyleus</i>	1999	40	12
<i>Hylephila phyleus</i>	2000	122	13
<i>Hylephila phyleus</i>	2001	68	13
<i>Hylephila phyleus</i>	2002	94	15
<i>Hylephila phyleus</i>	2003	254	15
<i>Hylephila phyleus</i>	2004	245	16
<i>Hylephila phyleus</i>	2005	194	16
<i>Hylephila phyleus</i>	2006	231	14
<i>Hylephila phyleus</i>	2007	183	14
<i>Junonia coenia</i>	1999	154	17
<i>Junonia coenia</i>	2000	334	21
<i>Junonia coenia</i>	2001	259	20
<i>Junonia coenia</i>	2002	201	20
<i>Junonia coenia</i>	2003	1,009	20
<i>Junonia coenia</i>	2004	290	20
<i>Junonia coenia</i>	2005	1,501	20
<i>Junonia coenia</i>	2006	254	16
<i>Junonia coenia</i>	2007	96	19
<i>Lerodea eufala</i>	1999	6	4
<i>Lerodea eufala</i>	2000	18	7
<i>Lerodea eufala</i>	2001	104	11
<i>Lerodea eufala</i>	2002	24	9
<i>Lerodea eufala</i>	2003	38	8
<i>Lerodea eufala</i>	2004	92	10
<i>Lerodea eufala</i>	2005	42	6
<i>Lerodea eufala</i>	2006	37	12
<i>Lerodea eufala</i>	2007	114	10
<i>Limenitis lorquini</i>	1999	26	8
<i>Limenitis lorquini</i>	2000	36	10
<i>Limenitis lorquini</i>	2001	7	4
<i>Limenitis lorquini</i>	2002	18	5
<i>Limenitis lorquini</i>	2003	4	4
<i>Limenitis lorquini</i>	2004	1	1
<i>Limenitis lorquini</i>	2005	5	3
<i>Limenitis lorquini</i>	2006	4	3
<i>Limenitis lorquini</i>	2007	16	6

Table 3 continued

Species	Year	Count	Day-positive
<i>Lycaena helloides</i>	1999	49	11
<i>Lycaena helloides</i>	2000	62	13
<i>Lycaena helloides</i>	2001	51	13
<i>Lycaena helloides</i>	2002	170	18
<i>Lycaena helloides</i>	2003	52	11
<i>Lycaena helloides</i>	2004	92	14
<i>Lycaena helloides</i>	2005	169	14
<i>Lycaena helloides</i>	2006	227	11
<i>Lycaena helloides</i>	2007	330	14
<i>Lycaena xanthoides</i>	1999	0	0
<i>Lycaena xanthoides</i>	2000	3	2
<i>Lycaena xanthoides</i>	2001	1	1
<i>Lycaena xanthoides</i>	2002	6	2
<i>Lycaena xanthoides</i>	2003	2	2
<i>Lycaena xanthoides</i>	2004	2	1
<i>Lycaena xanthoides</i>	2005	0	0
<i>Lycaena xanthoides</i>	2006	0	0
<i>Lycaena xanthoides</i>	2007	0	0
<i>Nymphalis antiopa</i>	1999	22	5
<i>Nymphalis antiopa</i>	2000	14	9
<i>Nymphalis antiopa</i>	2001	12	5
<i>Nymphalis antiopa</i>	2002	0	0
<i>Nymphalis antiopa</i>	2003	1	1
<i>Nymphalis antiopa</i>	2004	0	0
<i>Nymphalis antiopa</i>	2005	3	3
<i>Nymphalis antiopa</i>	2006	10	5
<i>Nymphalis antiopa</i>	2007	3	3
<i>Nymphalis californica</i>	1999	0	0
<i>Nymphalis californica</i>	2000	1	1
<i>Nymphalis californica</i>	2001	4	3
<i>Nymphalis californica</i>	2002	1	1
<i>Nymphalis californica</i>	2003	0	0
<i>Nymphalis californica</i>	2004	2	2
<i>Nymphalis californica</i>	2005	5	4
<i>Nymphalis californica</i>	2006	2	2
<i>Nymphalis californica</i>	2007	5	3
<i>Papilio rutulus</i>	1999	32	7
<i>Papilio rutulus</i>	2000	33	8
<i>Papilio rutulus</i>	2001	30	10
<i>Papilio rutulus</i>	2002	12	7
<i>Papilio rutulus</i>	2003	19	11
<i>Papilio rutulus</i>	2004	10	7
<i>Papilio rutulus</i>	2005	31	9
<i>Papilio rutulus</i>	2006	13	4
<i>Papilio rutulus</i>	2007	50	10
<i>Papilio zelicaon</i>	1999	9	5
<i>Papilio zelicaon</i>	2000	18	8
<i>Papilio zelicaon</i>	2001	28	8

Table 3 continued

Species	Year	Count	Day-positive
<i>Papilio zelicaon</i>	2002	20	6
<i>Papilio zelicaon</i>	2003	13	6
<i>Papilio zelicaon</i>	2004	4	3
<i>Papilio zelicaon</i>	2005	3	3
<i>Papilio zelicaon</i>	2006	4	4
<i>Papilio zelicaon</i>	2007	3	3
<i>Pholisora catullus</i>	1999	64	12
<i>Pholisora catullus</i>	2000	50	12
<i>Pholisora catullus</i>	2001	19	9
<i>Pholisora catullus</i>	2002	46	14
<i>Pholisora catullus</i>	2003	37	13
<i>Pholisora catullus</i>	2004	24	12
<i>Pholisora catullus</i>	2005	16	7
<i>Pholisora catullus</i>	2006	9	7
<i>Pholisora catullus</i>	2007	23	9
<i>Phyciodes campestris</i>	1999	13	6
<i>Phyciodes campestris</i>	2000	24	7
<i>Phyciodes campestris</i>	2001	11	5
<i>Phyciodes campestris</i>	2002	2	2
<i>Phyciodes campestris</i>	2003	0	0
<i>Phyciodes campestris</i>	2004	0	0
<i>Phyciodes campestris</i>	2005	0	0
<i>Phyciodes campestris</i>	2006	0	0
<i>Phyciodes campestris</i>	2007	0	0
<i>Phyciodes mylitta</i>	1999	125	17
<i>Phyciodes mylitta</i>	2000	109	20
<i>Phyciodes mylitta</i>	2001	115	16
<i>Phyciodes mylitta</i>	2002	63	17
<i>Phyciodes mylitta</i>	2003	24	11
<i>Phyciodes mylitta</i>	2004	85	17
<i>Phyciodes mylitta</i>	2005	50	13
<i>Phyciodes mylitta</i>	2006	34	9
<i>Phyciodes mylitta</i>	2007	106	14
<i>Pieris rapae</i>	1999	895	25
<i>Pieris rapae</i>	2000	2,196	29
<i>Pieris rapae</i>	2001	2,199	27
<i>Pieris rapae</i>	2002	2,537	30
<i>Pieris rapae</i>	2003	3,109	31
<i>Pieris rapae</i>	2004	2,168	26
<i>Pieris rapae</i>	2005	3,877	30
<i>Pieris rapae</i>	2006	1,674	26
<i>Pieris rapae</i>	2007	1,305	25
<i>Plebejus acmon</i>	1999	7	6
<i>Plebejus acmon</i>	2000	144	12
<i>Plebejus acmon</i>	2001	87	14
<i>Plebejus acmon</i>	2002	58	13
<i>Plebejus acmon</i>	2003	48	11
<i>Plebejus acmon</i>	2004	26	11

Table 3 continued

Species	Year	Count	Day-positive
<i>Plebejus acmon</i>	2005	95	17
<i>Plebejus acmon</i>	2006	21	10
<i>Plebejus acmon</i>	2007	51	11
<i>Poanes melane</i>	1999	1	1
<i>Poanes melane</i>	2000	1	1
<i>Poanes melane</i>	2001	0	0
<i>Poanes melane</i>	2002	0	0
<i>Poanes melane</i>	2003	0	0
<i>Poanes melane</i>	2004	1	1
<i>Poanes melane</i>	2005	0	0
<i>Poanes melane</i>	2006	0	0
<i>Poanes melane</i>	2007	0	0
<i>Polites sabuleti</i>	1999	185	15
<i>Polites sabuleti</i>	2000	352	17
<i>Polites sabuleti</i>	2001	158	16
<i>Polites sabuleti</i>	2002	203	18
<i>Polites sabuleti</i>	2003	153	17
<i>Polites sabuleti</i>	2004	220	18
<i>Polites sabuleti</i>	2005	79	12
<i>Polites sabuleti</i>	2006	51	10
<i>Polites sabuleti</i>	2007	44	12
<i>Pontia protodice</i>	1999	4	4
<i>Pontia protodice</i>	2000	0	0
<i>Pontia protodice</i>	2001	2	2
<i>Pontia protodice</i>	2002	1	1
<i>Pontia protodice</i>	2003	13	7
<i>Pontia protodice</i>	2004	0	0
<i>Pontia protodice</i>	2005	0	0
<i>Pontia protodice</i>	2006	1	1
<i>Pontia protodice</i>	2007	0	0
<i>Pyrgus communis</i>	1999	159	16
<i>Pyrgus communis</i>	2000	406	23
<i>Pyrgus communis</i>	2001	348	23
<i>Pyrgus communis</i>	2002	548	25
<i>Pyrgus communis</i>	2003	389	24
<i>Pyrgus communis</i>	2004	547	23
<i>Pyrgus communis</i>	2005	585	24
<i>Pyrgus communis</i>	2006	463	19
<i>Pyrgus communis</i>	2007	525	24
<i>Pyrgus scriptura</i>	1999	61	12
<i>Pyrgus scriptura</i>	2000	194	18
<i>Pyrgus scriptura</i>	2001	129	17
<i>Pyrgus scriptura</i>	2002	198	17
<i>Pyrgus scriptura</i>	2003	99	18
<i>Pyrgus scriptura</i>	2004	101	15
<i>Pyrgus scriptura</i>	2005	58	13
<i>Pyrgus scriptura</i>	2006	2	2
<i>Pyrgus scriptura</i>	2007	94	15

Table 3 continued

Species	Year	Count	Day-positive
<i>Satyrrium sylvinus</i>	1999	3	2
<i>Satyrrium sylvinus</i>	2000	11	5
<i>Satyrrium sylvinus</i>	2001	2	2
<i>Satyrrium sylvinus</i>	2002	3	2
<i>Satyrrium sylvinus</i>	2003	0	0
<i>Satyrrium sylvinus</i>	2004	1	1
<i>Satyrrium sylvinus</i>	2005	0	0
<i>Satyrrium sylvinus</i>	2006	0	0
<i>Satyrrium sylvinus</i>	2007	4	2
<i>Strymon melinus</i>	1999	49	11
<i>Strymon melinus</i>	2000	205	13
<i>Strymon melinus</i>	2001	94	18
<i>Strymon melinus</i>	2002	119	15
<i>Strymon melinus</i>	2003	108	13
<i>Strymon melinus</i>	2004	93	15
<i>Strymon melinus</i>	2005	198	15
<i>Strymon melinus</i>	2006	94	12
<i>Strymon melinus</i>	2007	89	16
<i>Vanessa annabella</i>	1999	20	14
<i>Vanessa annabella</i>	2000	26	16
<i>Vanessa annabella</i>	2001	19	9
<i>Vanessa annabella</i>	2002	16	11
<i>Vanessa annabella</i>	2003	26	16
<i>Vanessa annabella</i>	2004	18	10
<i>Vanessa annabella</i>	2005	55	16
<i>Vanessa annabella</i>	2006	26	14
<i>Vanessa annabella</i>	2007	6	5
<i>Vanessa atalanta</i>	1999	3	3
<i>Vanessa atalanta</i>	2000	9	9
<i>Vanessa atalanta</i>	2001	18	10
<i>Vanessa atalanta</i>	2002	1	1
<i>Vanessa atalanta</i>	2003	16	10
<i>Vanessa atalanta</i>	2004	14	11
<i>Vanessa atalanta</i>	2005	8	7
<i>Vanessa atalanta</i>	2006	14	11
<i>Vanessa atalanta</i>	2007	7	7
<i>Vanessa cardui</i>	1999	0	0
<i>Vanessa cardui</i>	2000	2	2
<i>Vanessa cardui</i>	2001	194	15
<i>Vanessa cardui</i>	2002	5	5
<i>Vanessa cardui</i>	2003	67	16
<i>Vanessa cardui</i>	2004	145	15
<i>Vanessa cardui</i>	2005	1188	24
<i>Vanessa cardui</i>	2006	7	5
<i>Vanessa cardui</i>	2007	12	9
<i>Vanessa virginiensis</i>	1999	1	1
<i>Vanessa virginiensis</i>	2000	2	2
<i>Vanessa virginiensis</i>	2001	3	3

Table 3 continued

Species	Year	Count	Day-positive
<i>Vanessa virginiensis</i>	2002	7	6
<i>Vanessa virginiensis</i>	2003	1	1
<i>Vanessa virginiensis</i>	2004	3	3
<i>Vanessa virginiensis</i>	2005	0	0
<i>Vanessa virginiensis</i>	2006	2	2
<i>Vanessa virginiensis</i>	2007	3	3
<i>Zerene eurydice</i>	1999	0	0
<i>Zerene eurydice</i>	2000	2	2
<i>Zerene eurydice</i>	2001	1	1
<i>Zerene eurydice</i>	2002	1	1
<i>Zerene eurydice</i>	2003	0	0
<i>Zerene eurydice</i>	2004	0	0
<i>Zerene eurydice</i>	2005	0	0
<i>Zerene eurydice</i>	2006	0	0
<i>Zerene eurydice</i>	2007	0	0

Table 4 Results of correlation and GLM trend analysis for North Sacramento (NS), Rancho Cordova (RC) and Suisun Marsh (SM)

Species	Site	Correlations		Trends	
		rho	p value	D-p	Count
<i>Atalopedes campestris</i>	NS	−0.07	0.86	0.02 _p	−0.03 _{nb}
<i>Atlides halesus</i>	NS	0.72	0.04	0.05 _p	0.13 _p
<i>Battus philenor</i>	NS	0.80	0.03	0.11 _p	0.19 _{nb}
<i>Brephidium exile</i>	NS	0.60	0.09	0.03 _p	0.02 _{nb}
<i>Colias eurytheme</i>	NS	0.31	0.41	0.01 _p	0.15 _{nb}
<i>Danaus plexippus</i>	NS	0.91	0.00	0.02 _p	0.00 _{nb}
<i>Erynnis persius</i>	NS	1.00	0.00	0.23 _p	0.23 _p
<i>Erynnis tristis</i>	NS	0.04	0.91	−0.03 _p	0.04 _p
<i>Euchloe ausonides</i>	NS	0.95	0.00	−0.42 _{nb}	−0.83 _{nb}
<i>Everes comyntas</i>	NS	0.75	0.02	0.01 _p	0.07 _{nb}
<i>Glaucopsyche lygdamus</i>	NS	0.81	0.02	−0.20 _p	−0.32 _{nb}
<i>Hylephila phyleus</i>	NS	0.58	0.10	0.05 _p	0.07 _{nb}
<i>Junonia coenia</i>	NS	0.66	0.06	0.02 _p	0.17 _{nb}
<i>Lerodea eufala</i>	NS	0.73	0.03	0.15 _p	0.19 _{nb}
<i>Lycaena helloides</i>	NS	0.85	0.00	−0.01 _p	−0.10 _{nb}
<i>Lycaena xanthoides</i>	NS	0.54	0.13	−0.03 _p	−0.09 _{nb}
<i>Nymphalis antiopa</i>	NS	0.97	0.00	−0.06 _{nb}	−0.10 _{nb}
<i>Nymphalis californica</i>	NS	0.88	0.00	0.06 _p	0.10 _p
<i>Ochlodes sylvanoides</i>	NS	0.25	0.55	0.10 _p	0.03 _{nb}
<i>Papilio rutulus</i>	NS	0.66	0.05	0.04 _p	0.11 _{nb}
<i>Papilio zelicaon</i>	NS	0.69	0.04	−0.04 _p	−0.11 _{nb}
<i>Pholisora catullus</i>	NS	0.94	0.00	−0.10 _p	−0.10 _{nb}
<i>Phyciodes mylitta</i>	NS	0.87	0.00	0.06 _p	0.12 _{nb}
<i>Pieris rapae</i>	NS	−0.03	0.95	−0.01 _p	0.05 _{nb}
<i>Plebejus acmon</i>	NS	0.39	0.30	0.05 _p	0.10 _{nb}
<i>Poanes melane</i>	NS	0.95	0.00	0.09 _p	0.17 _{nb}

Table 4 continued

Species	Site	Correlations		Trends	
		rho	p value	D-p	Count
<i>Polites sabuleti</i>	NS	0.73	0.03	−0.03 _p	−0.04 _{nb}
<i>Polygonia satyrus</i>	NS	0.87	0.33	−0.39 _p	−0.57 _{nb}
<i>Pyrgus communis</i>	NS	0.36	0.35	0.01 _p	0.09 _{nb}
<i>Pyrgus scriptura</i>	NS	0.89	0.00	0.08 _p	0.04 _{nb}
<i>Satyrium californica</i>	NS	0.82	0.02	−0.19 _p	−0.41 _{nb}
<i>Satyrium sylvinus</i>	NS	0.12	0.77	−0.04 _p	−0.31 _{nb}
<i>Strymon melinus</i>	NS	0.32	0.41	0.02 _p	0.02 _{nb}
<i>Vanessa annabella</i>	NS	0.72	0.03	−0.08 _p	−0.16 _{nb}
<i>Vanessa atalanta</i>	NS	0.83	0.01	0.02 _p	0.03 _{nb}
<i>Vanessa cardui</i>	NS	1.00	0.00	0.1 _{nb}	0.28 _{nb}
<i>Vanessa virginiensis</i>	NS	0.66	0.08	−0.12 _p	−0.08 _{nb}
<i>Adelpha bredowii</i>	RC	0.82	0.01	−0.31 _{nb}	−0.36 _{nb}
<i>Atalopedes campestris</i>	RC	0.24	0.54	−0.01 _p	−0.10 _{nb}
<i>Atlides halesus</i>	RC	1.00	0.00	0.08 _p	0.08 _{nb}
<i>Battus philenor</i>	RC	0.09	0.82	0.00 _p	0.09 _{nb}
<i>Brephidium exile</i>	RC	0.77	0.04	−0.16 _p	−0.07 _{nb}
<i>Coenonympha tullia</i>	RC	0.88	0.00	−0.2 _{nb}	−0.29 _{nb}
<i>Colias eurytheme</i>	RC	0.27	0.48	0.02 _p	0.09 _{nb}
<i>Danaus plexippus</i>	RC	1.00	0.00	0.05 _p	0.03 _p
<i>Erynnis propertius</i>	RC	1.00	0.00	0.02 _p	−0.04 _{nb}
<i>Erynnis tristis</i>	RC	0.37	0.32	0.06 _p	−0.02 _{nb}
<i>Euchloe ausonides</i>	RC	1.00	0.00	−0.14 _p	−0.22 _{nb}
<i>Everes comyntas</i>	RC	0.57	0.11	0.02 _p	−0.12 _{nb}
<i>Glaucopsyche lygdamus</i>	RC	0.75	0.02	0.05 _p	0.01 _{nb}
<i>Hylephila phyleus</i>	RC	−0.01	0.98	0.03 _p	0.00 _{nb}
<i>Incisalia augustinus</i>	RC	0.93	0.01	0.35 _p	0.60 _{nb}
<i>Junonia coenia</i>	RC	0.82	0.01	0.00 _p	0.00 _{nb}
<i>Lerodea eufala</i>	RC	0.79	0.02	0.01 _p	0.04 _p
<i>Limenitis lorquini</i>	RC	0.97	0.01	0.01 _{nb}	0.02 _{nb}
<i>Lycaena helloides</i>	RC	0.71	0.07	0.03 _p	0.00 _p
<i>Nymphalis antiopa</i>	RC	0.85	0.00	0.06 _p	0.03 _{nb}
<i>Nymphalis californica</i>	RC	0.93	0.00	0.07 _p	0.10 _{nb}
<i>Ochlodes sylvanoides</i>	RC	0.26	0.51	0.03 _p	0.09 _{nb}
<i>Papilio multicaudatus</i>	RC	0.82	0.02	−0.16 _p	−0.18 _p
<i>Papilio rutulus</i>	RC	0.96	0.00	−0.01 _p	0.04 _{nb}
<i>Papilio zelicaon</i>	RC	0.35	0.36	−0.03 _p	0.01 _p
<i>Phyciodes mylitta</i>	RC	0.42	0.30	−0.02 _p	0.07 _p
<i>Pieris rapae</i>	RC	0.59	0.10	0.00 _p	−0.06 _{nb}
<i>Plebejus acmon</i>	RC	0.70	0.04	0.04 _p	0.06 _{nb}
<i>Poanes melane</i>	RC	0.99	0.00	−0.18 _p	−0.28 _{nb}
<i>Pontia protodice</i>	RC	0.97	0.00	−0.29 _{nb}	−0.60 _{nb}
<i>Pyrgus communis</i>	RC	0.60	0.09	0.02 _p	0.03 _{nb}
<i>Satyrium californica</i>	RC	0.33	0.39	−0.06 _p	0.12 _{nb}
<i>Strymon melinus</i>	RC	0.32	0.40	0.00 _p	0.02 _{nb}

Table 4 continued

Species	Site	Correlations		Trends	
		rho	p value	D-p	Count
<i>Vanessa annabella</i>	RC	0.86	0.01	−0.02 _p	−0.10 _{nb}
<i>Vanessa atalanta</i>	RC	0.90	0.00	0.01 _p	0.02 _p
<i>Vanessa cardui</i>	RC	0.98	0.00	0.11 _{nb}	0.31 _{nb}
<i>Vanessa virginiensis</i>	RC	0.99	0.00	0.01 _p	−0.01 _{nb}
<i>Zerene eurydice</i>	RC	1.00	0.00	−0.02 _p	−0.02 _p
<i>Adelpha bredowii</i>	SM	0.89	0.00	0.05 _p	0.11 _p
<i>Agraulis vanillae</i>	SM	1.00	0.00	−0.09 _p	−0.09 _p
<i>Atalopedes campestris</i>	SM	0.23	0.55	0.02 _p	0.00 _{nb}
<i>Battus philenor</i>	SM	0.99	0.00	0.31 _{nb}	0.36 _{nb}
<i>Brephidium exile</i>	SM	0.66	0.06	0.05 _p	0.03 _{nb}
<i>Coenonympha tullia</i>	SM	1.00	0.00	−0.10 _p	−0.10 _p
<i>Colias eurytheme</i>	SM	0.13	0.73	0.01 _p	0.02 _{nb}
<i>Danaus plexippus</i>	SM	0.44	0.23	0.04 _p	−0.01 _{nb}
<i>Erynnis tristis</i>	SM	0.96	0.00	−0.03 _p	−0.05 _p
<i>Euchloe ausonides</i>	SM	0.63	0.07	−0.11 _p	−0.23 _{nb}
<i>Everes comyntas</i>	SM	0.85	0.00	0.00 _{nb}	−0.01 _{nb}
<i>Hylephila phyleus</i>	SM	0.51	0.16	0.04 _p	0.14 _{nb}
<i>Incisalia augustinus</i>	SM	1.00	0.33	0.30 _p	0.37 _{nb}
<i>Junonia coenia</i>	SM	0.59	0.09	0.00 _p	−0.07 _{nb}
<i>Lerodea eufala</i>	SM	0.92	0.00	0.03 _p	0.04 _p
<i>Lycaena helloides</i>	SM	0.26	0.50	0.01 _p	−0.07 _{nb}
<i>Lycaena xanthoides</i>	SM	0.73	0.04	−0.04 _p	−0.13 _{nb}
<i>Nymphalis antiopa</i>	SM	1.00	0.00	−0.10 _p	−0.10 _p
<i>Nymphalis californica</i>	SM	0.81	0.03	0.11 _p	0.14 _{nb}
<i>Ochlodes sylvanoides</i>	SM	0.71	0.03	0.02 _p	0.02 _{nb}
<i>Ochlodes yuma</i>	SM	0.79	0.01	0.02 _p	0.01 _p
<i>Papilio rutulus</i>	SM	0.88	0.00	0.04 _p	0.10 _{nb}
<i>Papilio zelicaon</i>	SM	0.68	0.04	−0.03 _p	−0.09 _{nb}
<i>Pholisora catullus</i>	SM	0.97	0.01	−0.55 _{nb}	−0.72 _{nb}
<i>Phyciodes campestris</i>	SM	0.40	0.75	−0.02 _{nb}	−0.09 _{nb}
<i>Phyciodes mylitta</i>	SM	0.94	0.00	−0.07 _p	−0.14 _{nb}
<i>Pieris rapae</i>	SM	0.26	0.51	−0.00 _p	0.05 _{nb}
<i>Plebejus acmon</i>	SM	0.72	0.03	−0.04 _p	−0.19 _{nb}
<i>Poanes melane</i>	SM	0.50	0.67	0.32 _p	0.26 _p
<i>Polites sabuleti</i>	SM	0.60	0.09	0.01 _p	−0.02 _{nb}
<i>Pontia protodice</i>	SM	1.00	0.33	−0.31 _{nb}	−0.33 _{nb}
<i>Pyrgus communis</i>	SM	−0.08	0.85	0.00 _p	0.00 _{nb}
<i>Pyrgus scriptura</i>	SM	0.65	0.08	−0.20 _{nb}	−0.26 _{nb}
<i>Strymon melinus</i>	SM	0.50	0.17	0.00 _p	−0.06 _{nb}
<i>Vanessa annabella</i>	SM	0.90	0.00	−0.09 _p	−0.24 _{nb}
<i>Vanessa atalanta</i>	SM	0.89	0.00	−0.07 _p	−0.08 _p
<i>Vanessa cardui</i>	SM	0.97	0.00	0.11 _{nb}	0.41 _{nb}
<i>Vanessa virginiensis</i>	SM	1.00	0.00	−0.13 _{nb}	−0.13 _{nb}

The error distribution used is subscripted to the trend value (*p* poisson, *nb* negative binomial)

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