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ORIGINAL PAPER

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

Kayce L. Casner · Matthew L. Forister · Karthik Ram · Arthur M. Shapiro

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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

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Section of Evolution and Ecology and Center for Population Biology, University of California, Davis, CA 95616, USA e-mail: theochila@gmail.com 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.

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; Doody 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 abundancedependent 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 twoweek 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, daypositive 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-Wallace test using the Spearman correlation coefficient, p, 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/daypositive 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 rho value. We tested a linear and quadratic regression term for flight window on correlation strength (rho). 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 rho 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 daypositive 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.

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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 interannual 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

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

 Sacramento site
 Page 100 (2000)

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

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

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	t value	p 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

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 Satyrium 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



Fig. 1 Relationships for quadratic regressions between Spearman's rho (ρ) and **a** the mean flight window, and **b** the mean count per daypositive. 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. lygdamus, 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 daypositive 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 daypositives 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 (slope_{count} = -0.83, slope_{day-posi-} $_{\text{tive}} = -0.42$), 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 daypositives 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 presenceabsence 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 daypositives).

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 (Glaucopshyche 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 bellcurve 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. Acknowledgments This project was funded by the NSF databases and informatics program (DBI-0317483 to A.M.S. and J. F. Quinn). We thank James Thorne, Joshua O'Brien, David Waetjen and Colin Rundel for statistical advice and constructive commentary.

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

Species	Year	Count	Day-positive
Coenonympha tullia	2002	0	0
Coenonympha tullia	2003	0	0
Coenonympha tullia	2004	1	1
Coenonympha tullia	2005	0	0
Coenonympha tullia	2006	0	0
Coenonympha tullia	2007	0	0
Colias eurytheme	1999	197	20
Colias eurytheme	2000	285	20
Colias eurytheme	2001	213	22
Colias eurytheme	2002	945	23
Colias eurytheme	2003	268	20
Colias eurytheme	2004	385	18
Colias eurytheme	2005	259	25
Colias eurytheme	2006	1,180	17
Colias eurytheme	2007	241	24
Danaus plexippus	1999	14	6
Danaus plexippus	2000	21	9
Danaus plexippus	2001	22	11
Danaus plexippus	2002	17	11
Danaus plexippus	2003	9	6
Danaus plexinpus	2004	29	15
Danaus plexippus Danaus plexippus	2005	33	11
Danaus plexippus Danaus plexippus	2005	12	7
Danaus plexippus Danaus plexippus	2000	10	, 7
Frynnis tristis	1999	8	4
Erynnis tristis	2000	19	6
Erynnis tristis	2000	2	2
Erynnis tristis	2001	5	2
Erynnis tristis	2002	10	2
Erynnis tristis	2003	37	5
Erynnis tristis	2004	17	5
Erynnis tristis	2005	17 8	3
Erynnis tristis	2000	0 17	8
Erynnis tristis Fuchloc ausonidas	1000	17	8
Euchioe ausonides	2000	26	3
Euchioe ausonides	2000	20	7
Euchioe ausonides	2001	59 10	7
Euchioe ausonides	2002	10	5
Euchioe ausonides	2005	1	1
Euchioe ausonides	2004	0	0
Euchioe ausonides	2005	0	0
Euchioe ausonides	2000	0	0
Eucnice ausonides	2007	1	14
Everes comynias	1999	0/ 57	14
Everes comynias	2000	27	0
Everes comyntas	2001	29	ð 11
Everes comyntas	2002	47	11
Everes comyntas	2003	57	11
Everes comyntas	2004	44	14

Table 3 continued

Table 3 continued

Species	Year	Count	Day-positive	Species	Year	Count	Day-positive
Everes comyntas	2005	46	14	Lycaena helloides	1999	49	11
Everes comyntas	2006	24	10	Lycaena helloides	2000	62	13
Everes comyntas	2007	80	18	Lycaena helloides	2001	51	13
Heliopetes ericetorum	1999	0	0	Lycaena helloides	2002	170	18
Heliopetes ericetorum	2000	0	0	Lycaena helloides	2003	52	11
Heliopetes ericetorum	2001	0	0	Lycaena helloides	2004	92	14
Heliopetes ericetorum	2002	0	0	Lycaena helloides	2005	169	14
Heliopetes ericetorum	2003	0	0	Lycaena helloides	2006	227	11
Heliopetes ericetorum	2004	0	0	Lycaena helloides	2007	330	14
Heliopetes ericetorum	2005	1	1	Lycaena xanthoides	1999	0	0
Heliopetes ericetorum	2006	1	1	Lycaena xanthoides	2000	3	2
Heliopetes ericetorum	2007	1	1	Lycaena xanthoides	2001	1	1
Hylephila phyleus	1999	40	12	Lycaena xanthoides	2002	6	2
Hylephila phyleus	2000	122	13	Lycaena xanthoides	2003	2	2
Hylephila phyleus	2001	68	13	Lycaena xanthoides	2004	2	1
Hylephila phyleus	2002	94	15	Lycaena xanthoides	2005	0	0
Hylephila phyleus	2003	254	15	Lycaena xanthoides	2006	0	0
Hylephila phyleus	2004	245	16	Lycaena xanthoides	2007	0	0
Hylephila phyleus	2005	194	16	Nymphalis antiopa	1999	22	5
Hylephila phyleus	2006	231	14	Nymphalis antiopa	2000	14	9
Hylephila phyleus	2007	183	14	Nymphalis antiopa	2001	12	5
Junonia coenia	1999	154	17	Nymphalis antiopa	2002	0	0
Junonia coenia	2000	334	21	Nymphalis antiopa	2003	1	1
Junonia coenia	2001	259	20	Nymphalis antiopa	2004	0	0
Junonia coenia	2002	201	20	Nymphalis antiopa	2005	3	3
Junonia coenia	2003	1,009	20	Nymphalis antiopa	2006	10	5
Junonia coenia	2004	290	20	Nymphalis antiopa	2007	3	3
Junonia coenia	2005	1,501	20	Nymphalis californica	1999	0	0
Junonia coenia	2006	254	16	Nymphalis californica	2000	1	1
Junonia coenia	2007	96	19	Nymphalis californica	2001	4	3
Lerodea eufala	1999	6	4	Nymphalis californica	2002	1	1
Lerodea eufala	2000	18	7	Nymphalis californica	2003	0	0
Lerodea eufala	2001	104	11	Nymphalis californica	2004	2	2
Lerodea eufala	2002	24	9	Nymphalis californica	2005	5	4
Lerodea eufala	2003	38	8	Nymphalis californica	2006	2	2
Lerodea eufala	2004	92	10	Nymphalis californica	2007	5	3
Lerodea eufala	2005	42	6	Papilio rutulus	1999	32	7
Lerodea eufala	2006	37	12	Papilio rutulus	2000	33	8
Lerodea eufala	2007	114	10	Papilio rutulus	2001	30	10
Limenitis lorquini	1999	26	8	Papilio rutulus	2002	12	7
Limenitis lorquini	2000	36	10	Papilio rutulus	2003	19	11
Limenitis lorquini	2001	7	4	Papilio rutulus	2004	10	7
Limenitis lorquini	2002	18	5	Papilio rutulus	2005	31	9
Limenitis lorquini	2003	4	4	Papilio rutulus	2006	13	4
Limenitis lorquini	2004	1	1	Papilio rutulus	2007	50	10
Limenitis lorquini	2005	5	3	Papilio zelicaon	1999	9	5
Limenitis lorquini	2006	4	3	Papilio zelicaon	2000	18	8
Limenitis lorquini	2007	16	6	Papilio zelicaon	2001	28	8

Day-positive

Day-positive

Count

Table 3 continued

Year

Count

Table 3 continued	
Species	Year
Plebejus acmon	2005
Pleheius acmon	2006

Papilio zelicaon	2002	20	6	Plebejus acmon	2005	95	17	
Papilio zelicaon	2003	13	6	Plebejus acmon	2006	21	10	
Papilio zelicaon	2004	4	3	Plebejus acmon	2007	51	11	
Papilio zelicaon	2005	3	3	Poanes melane	1999	1	1	
Papilio zelicaon	2006	4	4	Poanes melane	2000	1	1	
Papilio zelicaon	2007	3	3	Poanes melane	2001	0	0	
Pholisora catullus	1999	64	12	Poanes melane	2002	0	0	
Pholisora catullus	2000	50	12	Poanes melane	2003	0	0	
Pholisora catullus	2001	19	9	Poanes melane	2004	1	1	
Pholisora catullus	2002	46	14	Poanes melane	2005	0	0	
Pholisora catullus	2003	37	13	Poanes melane	2006	0	0	
Pholisora catullus	2004	24	12	Poanes melane	2007	0	0	
Pholisora catullus	2005	16	7	Polites sabuleti	1999	185	15	
Pholisora catullus	2006	9	7	Polites sabuleti	2000	352	17	
Pholisora catullus	2007	23	9	Polites sabuleti	2001	158	16	
Phyciodes campestris	1999	13	6	Polites sabuleti	2002	203	18	
Phyciodes campestris	2000	24	7	Polites sabuleti	2003	153	17	
Phyciodes campestris	2001	11	5	Polites sabuleti	2004	220	18	
Phyciodes campestris	2002	2	2	Polites sabuleti	2005	79	12	
Phyciodes campestris	2003	0	0	Polites sabuleti	2006	51	10	
Phyciodes campestris	2004	0	0	Polites sabuleti	2007	44	12	
Phyciodes campestris	2005	0	0	Pontia protodice	1999	4	4	
Phyciodes campestris	2006	0	0	Pontia protodice	2000	0	0	
Phyciodes campestris	2007	0	0	Pontia protodice	2001	2	2	
Phyciodes mylitta	1999	125	17	Pontia protodice	2002	1	- 1	
Phyciodes mylitta	2000	109	20	Pontia protodice	2003	13	7	
Phyciodes mylitta	2001	115	16	Pontia protodice	2004	0	0	
Phyciodes mylitta	2002	63	17	Pontia protodice	2005	0	0	
Phyciodes mylitta	2003	24	11	Pontia protodice	2006	1	1	
Phyciodes mylitta	2004	85	17	Pontia protodice	2007	0	0	
Phyciodes mylitta	2005	50	13	Pvrgus communis	1999	159	16	
Phyciodes mylitta	2006	34	9	Pvrgus communis	2000	406	23	
Phyciodes mylitta	2007	106	14	Pvrgus communis	2001	348	23	
Pieris rapae	1999	895	25	Pvrgus communis	2002	548	25	
Pieris rapae	2000	2.196	29	Pvrgus communis	2003	389	24	
Pieris rapae	2001	2.199	27	Pvrgus communis	2004	547	23	
Pieris rapae	2002	2,537	30	Pyrgus communis	2005	585	24	
Pieris rapae	2003	3.109	31	Pyrgus communis	2006	463	19	
Pieris rapae	2004	2168	26	Pvrgus communis	2007	525	24	
Pieris rapae	2005	3.877	30	Pvrgus scriptura	1999	61	12	
Pieris rapae	2006	1.674	26	Pvrgus scriptura	2000	194	18	
Pieris rapae	2007	1,305	25	Pyrgus scriptura	2001	129	17	
Plebejus acmon	1999	7	6	Pyrgus scriptura	2002	198	17	
Plebejus acmon	2000	144	12	Pyrgus scriptura	2003	99	18	
Plebejus acmon	2001	87	14	Pyrgus scriptura	2004	101	15	
Plebejus acmon	2002	58	13	Pyrgus scriptura	2005	58	13	
Plebejus acmon	2003	48	11	Pyrgus scriptura	2006	2	2	
Plebejus acmon	2004	26	11	Pyrgus scriptura	2007	94	15	
•								

Species

Table 3 continued

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

Table 3 continued

Species	Year	Count	Day-positive
Vanessa virginiensis	2002	7	6
Vanessa virginiensis	2003	1	1
Vanessa virginiensis	2004	3	3
Vanessa virginiensis	2005	0	0
Vanessa virginiensis	2006	2	2
Vanessa virginiensis	2007	3	3
Zerene eurydice	1999	0	0
Zerene eurydice	2000	2	2
Zerene eurydice	2001	1	1
Zerene eurydice	2002	1	1
Zerene eurydice	2003	0	0
Zerene eurydice	2004	0	0
Zerene eurydice	2005	0	0
Zerene eurydice	2006	0	0
Zerene eurydice	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	
Atalopedes campestris	NS	-0.07	0.86	0.02 _p	-0.03 _{nb}	
Atlides halesus	NS	0.72	0.04	0.05 _p	0.13 _p	
Battus philenor	NS	0.80	0.03	0.11 _p	0.19 _{nb}	
Brephidium exile	NS	0.60	0.09	0.03 _p	0.02 _{nb}	
Colias eurytheme	NS	0.31	0.41	0.01 _p	0.15_{nb}	
Danaus plexippus	NS	0.91	0.00	0.02 _p	0.00_{nb}	
Erynnis persius	NS	1.00	0.00	0.23 _p	0.23 _p	
Erynnis tristis	NS	0.04	0.91	-0.03_{p}	0.04 _p	
Euchloe ausonides	NS	0.95	0.00	-0.42_{nb}	-0.83_{nb}	
Everes comyntas	NS	0.75	0.02	0.01 _p	0.07 _{nb}	
Glaucopsyche lygdamus	NS	0.81	0.02	-0.20 _p	-0.32 _{nb}	
Hylephila phyleus	NS	0.58	0.10	0.05 _p	$0.07_{\rm nb}$	
Junonia coenia	NS	0.66	0.06	0.02 _p	$0.17_{\rm nb}$	
Lerodea eufala	NS	0.73	0.03	0.15 _p	0.19 _{nb}	
Lycaena helloides	NS	0.85	0.00	-0.01_{p}	$-0.10_{\rm nb}$	
Lycaena xanthoides	NS	0.54	0.13	-0.03_{p}	-0.09_{nb}	
Nymphalis antiopa	NS	0.97	0.00	-0.06_{nb}	$-0.10_{\rm nb}$	
Nymphalis californica	NS	0.88	0.00	0.06 _p	0.10 _p	
Ochlodes sylvanoides	NS	0.25	0.55	0.10 _p	0.03 _{nb}	
Papilio rutulus	NS	0.66	0.05	0.04 _p	0.11 _{nb}	
Papilio zelicaon	NS	0.69	0.04	-0.04_{p}	-0.11_{nb}	
Pholisora catullus	NS	0.94	0.00	-0.10_{p}	$-0.10_{\rm nb}$	
Phyciodes mylitta	NS	0.87	0.00	0.06 _p	0.12 _{nb}	
Pieris rapae	NS	-0.03	0.95	-0.01_{p}	$0.05_{\rm nb}$	
Plebejus acmon	NS	0.39	0.30	0.05 _p	$0.10_{\rm nb}$	
Poanes melane	NS	0.95	0.00	0.09 _p	$0.17_{\rm nb}$	

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Table 4 continued

Table 4 continued				Table 4 continued							
Species	Site	Correla	tions	Trends		Species	Site	Correla	tions	Trends	
		rho	p value	D-p	Count			rho	p value	D-p	Count
Polites sabuleti	NS	0.73	0.03	-0.03 _p	-0.04 _{nb}	Vanessa annabella	RC	0.86	0.01	-0.02_{p}	-0.10 _{nb}
Polygonia satyrus	NS	0.87	0.33	-0.39_{p}	-0.57_{nb}	Vanessa atalanta	RC	0.90	0.00	0.01 _p	0.02 _p
Pyrgus communis	NS	0.36	0.35	0.01 _p	0.09 _{nb}	Vanessa cardui	RC	0.98	0.00	0.11 _{nb}	0.31 _{nb}
Pyrgus scriptura	NS	0.89	0.00	0.08 _p	0.04 _{nb}	Vanessa virginiensis	RC	0.99	0.00	0.01 _p	$-0.01_{\rm nb}$
Satyrium californica	NS	0.82	0.02	-0.19_{p}	-0.41_{nb}	Zerene eurydice	RC	1.00	0.00	-0.02_{p}	-0.02_{p}
Satyrium sylvinus	NS	0.12	0.77	-0.04_{p}	-0.31_{nb}	Adelpha bredowii	SM	0.89	0.00	0.05p	0.11 _p
Strymon melinus	NS	0.32	0.41	0.02_{p}	0.02 _{nb}	Agraulis vanillae	SM	1.00	0.00	-0.09_{p}	-0.09_{p}^{r}
Vanessa annabella	NS	0.72	0.03	-0.08p	-0.16 _{nb}	Atalopedes campestris	SM	0.23	0.55	0.02_{p}	0.00 _{nb}
Vanessa atalanta	NS	0.83	0.01	0.02 _p	0.03 _{nb}	Battus philenor	SM	0.99	0.00	0.31 _{nb}	0.36 _{nb}
Vanessa cardui	NS	1.00	0.00	0.1 _{nb}	0.28 _{nb}	Brephidium exile	SM	0.66	0.06	0.05 _p	0.03 _{nb}
Vanessa virginiensis	NS	0.66	0.08	-0.12_{p}	-0.08_{nb}	Coenonympha tullia	SM	1.00	0.00	$-0.10_{\rm p}$	$-0.10_{\rm p}$
Adelpha bredowii	RC	0.82	0.01	$-0.31_{\rm nb}$	-0.36_{nb}	Colias eurytheme	SM	0.13	0.73	0.01 _p	$0.02_{\rm nb}$
Atalopedes campestris	RC	0.24	0.54	-0.01_{p}	-0.10_{nb}	Danaus plexippus	SM	0.44	0.23	0.04 _p	-0.01nb
Atlides halesus	RC	1.00	0.00	0.08_{p}^{r}	0.08 _{nb}	Erynnis tristis	SM	0.96	0.00	-0.03_{p}^{r}	-0.05_{p}
Battus philenor	RC	0.09	0.82	0.00 _p	0.09 _{nb}	Euchloe ausonides	SM	0.63	0.07	$-0.11_{\rm p}$	$-0.23_{\rm nb}$
Brephidium exile	RC	0.77	0.04	$-0.16_{\rm p}$	$-0.07_{\rm nb}$	Everes comyntas	SM	0.85	0.00	0.00 _{nb}	$-0.01_{\rm nb}$
Coenonympha tullia	RC	0.88	0.00	-0.2_{nb}	-0.29_{nb}	Hylephila phyleus	SM	0.51	0.16	0.04 _n	0.14 _{nb}
Colias eurytheme	RC	0.27	0.48	0.02 _p	0.09 _{nb}	Incisalia augustinus	SM	1.00	0.33	0.30 _p	0.37 _{nb}
Danaus plexippus	RC	1.00	0.00	0.05 _p	0.03 _p	Junonia coenia	SM	0.59	0.09	0.00 _p	$-0.07_{\rm nb}$
Erynnis propertius	RC	1.00	0.00	0.02 _p	$-0.04_{\rm nb}$	Lerodea eufala	SM	0.92	0.00	0.03 _p	0.04 _n
Erynnis tristis	RC	0.37	0.32	0.06 _p	$-0.02_{\rm nb}$	Lycaena helloides	SM	0.26	0.50	0.01 _p	$-0.07_{\rm nb}$
Euchloe ausonides	RC	1.00	0.00	$-0.14_{\rm p}$	$-0.22_{\rm nb}$	Lycaena xanthoides	SM	0.73	0.04	$-0.04_{\rm p}$	-0.13_{nb}
Everes comyntas	RC	0.57	0.11	0.02 _p	-0.12_{nb}	Nymphalis antiopa	SM	1.00	0.00	$-0.10_{\rm p}$	$-0.10_{\rm p}$
Glaucopsyche	RC	0.75	0.02	0.05 _p	0.01 _{nb}	Nymphalis californica	SM	0.81	0.03	0.11 _p	0.14 _{nb}
lygdamus				r		Ochlodes sylvanoides	SM	0.71	0.03	0.02 _n	0.02 _{nb}
Hylephila phyleus	RC	-0.01	0.98	0.03 _p	0.00 _{nb}	Ochlodes yuma	SM	0.79	0.01	$0.02_{\rm p}^{\rm F}$	0.01 _p
Incisalia augustinus	RC	0.93	0.01	0.35 _p	0.60 _{nb}	Papilio rutulus	SM	0.88	0.00	0.04 _p	0.10 _{nb}
Junonia coenia	RC	0.82	0.01	0.00_{p}	0.00 _{nb}	Papilio zelicaon	SM	0.68	0.04	-0.03_{p}^{r}	-0.09_{nb}
Lerodea eufala	RC	0.79	0.02	0.01 _p	0.04 _p	Pholisora catullus	SM	0.97	0.01	-0.55_{nb}	$-0.72_{\rm nb}$
Limenitis lorquini	RC	0.97	0.01	0.01 _{nb}	0.02 _{nb}	Phyciodes campestris	SM	0.40	0.75	$-0.02_{\rm nb}$	$-0.09n_{\rm b}$
Lycaena helloides	RC	0.71	0.07	0.03 _p	0.00 _p	Phyciodes mylitta	SM	0.94	0.00	$-0.07_{\rm p}$	-0.14_{nb}
Nymphalis antiopa	RC	0.85	0.00	0.06 _p	0.03 _{nb}	Pieris rapae	SM	0.26	0.51	$-0.00_{\rm p}$	0.05 _{nb}
Nymphalis californica	RC	0.93	0.00	0.07 _p	0.10 _{nb}	Plebejus acmon	SM	0.72	0.03	$-0.04_{\rm p}$	-0.19_{nb}
Ochlodes sylvanoides	RC	0.26	0.51	0.03 _p	0.09 _{nb}	Poanes melane	SM	0.50	0.67	$0.32_{\rm p}^{\rm F}$	0.26 _p
Papilio multicaudatus	RC	0.82	0.02	-0.16_{p}	-0.18_{p}	Polites sabuleti	SM	0.60	0.09	0.01 _p	-0.02_{nb}
Papilio rutulus	RC	0.96	0.00	-0.01_{p}	0.04 _{nb}	Pontia protodice	SM	1.00	0.33	-0.31_{nb}	-0.33_{nb}
Papilio zelicaon	RC	0.35	0.36	-0.03_{p}	0.01 _p	Pyrgus communis	SM	-0.08	0.85	0.00 _p	0.00 _{nb}
Phyciodes mylitta	RC	0.42	0.30	-0.02_{p}	0.07 _p	Pyrgus scriptura	SM	0.65	0.08	-0.20_{nb}	-0.26_{nb}
Pieris rapae	RC	0.59	0.10	0.00_{p}	-0.06_{nb}	Strymon melinus	SM	0.50	0.17	0.00 _p	-0.06_{nb}
Plebejus acmon	RC	0.70	0.04	0.04 _p	0.06 _{nb}	Vanessa annabella	SM	0.90	0.00	-0.09^{r}_{p}	-0.24_{nb}
Poanes melane	RC	0.99	0.00	-0.18_{p}	-0.28_{nb}	Vanessa atalanta	SM	0.89	0.00	-0.07_{p}^{r}	-0.08_{p}
Pontia protodice	RC	0.97	0.00	-0.29_{nb}	-0.60_{nb}	Vanessa cardui	SM	0.97	0.00	0.11 _{nb}	0.41 _{nb}
Pyrgus communis	RC	0.60	0.09	0.02 _p	0.03 _{nb}	Vanessa virginiensis	SM	1.00	0.00	-0.13_{nb}	-0.13_{nb}
Satyrium californica	RC	0.33	0.39	-0.06_{p}	0.12 _{nb}	The owner distribution of		aub cari-	tad to the	trand real-	10 (n mair
Strymon melinus	RC	0.32	0.40	0.00 _p	0.02 _{nb}	son, <i>nb</i> negative binom	ial)	subscrip	icu to tile	uenu valu	ie (p pois-

son, nb negative binomial)

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