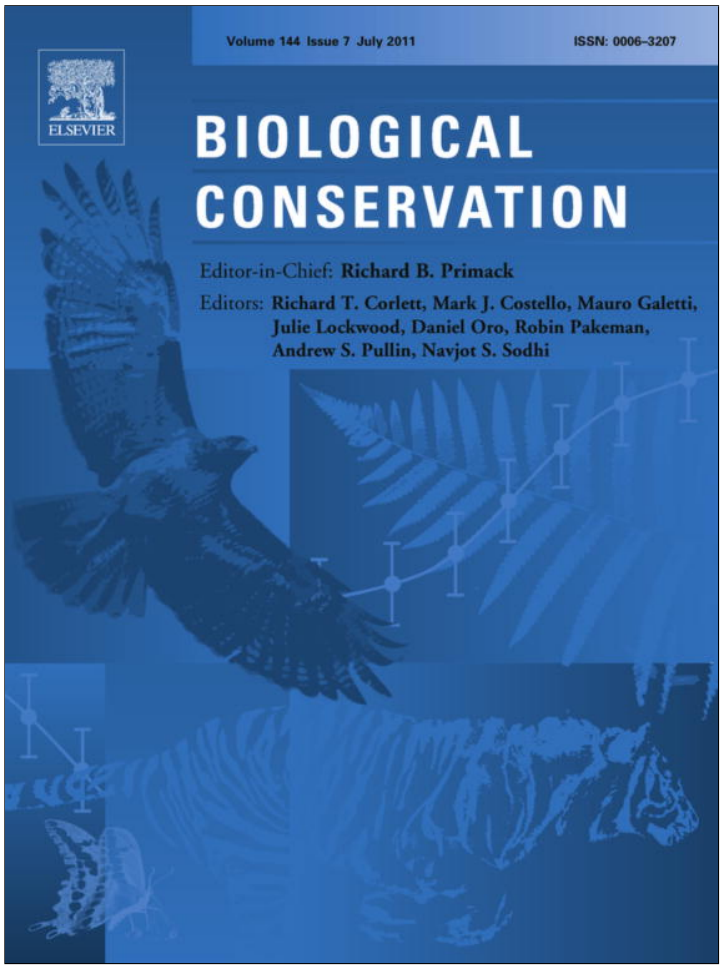
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Biological Conservation 144 (2011) 2012–2019

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Once-yearly sampling for the detection of trends in biodiversity: The case of Willow Slough, California

Joshua M. O'Brien [a,*], James H. Thorne [a], Michael L. Rosenzweig [b], Arthur M. Shapiro [c]

[a] Department of Environmental Science and Policy, University of California, Davis, 1 Shields Ave., Davis, CA 95616, USA
[b] Department of Ecology and Evolutionary Biology, University of Arizona, Tuscon, AZ 85721, USA
[c] Center for Population Biology, University of California, Davis, CA 95616, USA

ARTICLE INFO

Article history:
Received 19 April 2010
Received in revised form 11 April 2011
Accepted 16 April 2011
Available online 8 May 2011

Keywords:
Butterfly
Citizen-science
Diversity
Fisher's alpha
Life history
Monitoring

ABSTRACT

The butterfly fauna at Willow Slough, Yolo County, California has been censused for 32 years as part of a participatory citizen-science project, the Fourth of July Butterfly Count. While the utility of a once-a-year census as a monitoring tool is potentially compromised by lack of standardization in counting protocols and variation in observer skill, at Willow Slough these issues have been minimized.

We examined the Willow Slough count data for trends in both faunal diversity and the probability of presence of individual species. During the study, the number of species observed at a visit declined by 39%. Regressions of per-visit species counts against time did not detect a statistically significant decline until year 24. In contrast, Fisher's α, a statistic designed to reduce sample-size bias, detected the decline as early as year 13. Twelve of the 24 species analyzed showed significant declines in probability of occurrence; a further nine exhibited negative but non-significant trends. Butterflies that overwinter as eggs or larvae were more likely to decline than those that overwinter as pupae or adults. Many species in decline at Willow Slough have also been observed less frequently at nearby sites which are monitored year-round, supporting the value of once-a-year monitoring. Although correlations with climatic data have been identified, they are too weak to account for the observed faunal decline. We suspect broader patterns of land use and habitat continuity are implicated in butterfly declines across the region.

We conclude that once-a-year sampling, if properly and rigorously done, is in fact useful as a monitoring tool for butterfly faunas, and that Fisher's α is well suited to early detection of trends in repeated diversity sampling.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Concerns about biodiversity loss and global change have triggered an upsurge of interest in "citizen science". Members of the public, often already-committed amateur naturalists, are enlisted to monitor populations or biota in the hope of spotting trends in time for intelligent action to be taken (Lundmark, 2003; Silvertown, 2009). One of us (MLR) has mentored such an effort in hopes that anthropogenic habitats—including cities—would not be forgotten (www.tucsonbirds.org; Anonymous, 2009; McCaffrey, 2005; Turner, 2003). Such projects can generate long-term data sets that may contribute to our recognizing larger-scale trends.

In North America, the annual Audubon Christmas Bird Count is the best-known example, and it has spawned imitators, of which one of the oldest is the Fourth of July Butterfly Count (Kocher and Williams, 2000; Swengel, 1990). This continent-wide activity was begun by the Xerces Society in 1975 and is now administered by the North American Butterfly Association (NABA) (Wander, 2009; at www.naba.org). In recent years NABA has included from 400 to 500 counts, each with several participants. In its description of the program, NABA claims (Wander, 2009, p. iv) that "Count results provide abundant information about the distribution and relative population sizes of butterflies. Comparisons across years can be used to monitor changes in populations and study the effects of weather and habitat changes on butterflies." But of course, from a statistical perspective such claims are fraught with reservations. How comparable are the data either among routes or among years within routes? This is an issue of standardization and quality control. Although NABA provides a framework for the conduct of counts, there are numerous potential sources of error. The least-likely major source of error is variation in sampling route or coverage, since counters are admonished to standardize this. On the other hand, the number of counters may vary significantly from year-to-year, along with their degree of skill in field identification (a significant issue in many butterfly

* Corresponding author. Address: Center for Animal Disease Monitoring and Surveillance, 1 Shields Ave., Davis, CA 95616, USA. Tel.: +1 916 317 1594; fax: +1 530 752 1618.
E-mail address: jobrien@ucdavis.edu (J.M. O'Brien).

0006-3207/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2011.04.023

Author's personal copy

groups). Moreover, NABA allows a leeway of several weeks in count scheduling (merely centered on the fourth of July). Not only can sampling date introduce error; it may also interact with weather-driven year-to-year phenological variation to create a false impression of change in population size (Tryjanowski and Sparks, 2001). These issues might be partially addressed post hoc by multivariate statistical analysis, assuming climatological data are available, but this has not been routinely done. Until it is, apparent trends in the 4th of July data are merely suggestive. These issues are recognized for most if not all "citizen science" projects, and are coming under increased scrutiny by biostatisticians and conservation biologists (Link and Sauer, 1996; Link et al., 2006).

There is one 4th of July survey route designed to obviate as many of these problems as possible. One of us (AMS), beginning in 1977 and continuing to the present, has carried out a count at Willow Slough, Yolo County, California alone, using absolutely standardized protocols. In just one year, 1989, the count was done by a surrogate who, like AMS, was already a seasoned lepidopterist who had extensive experience with the local fauna. The count has always been on July 4, a fact made possible by the Mediterranean climate of the California Central Valley which virtually assures good weather. Standardization of method also should minimize species detectability as an issue. Thus Willow Slough can serve as a test of what information of conservation value—if any—can be extracted from a once-a-year butterfly-monitoring regime under the best of circumstances.

Willow Slough is also unusual in another way. Since 1972, AMS has been monitoring entire butterfly faunas along a transect covering 10 sites including several in the region of Willow Slough. Sites along the Shapiro California transect (http://butterfly.ucdavis.edu) are sampled biweekly throughout the year, using the same protocol as at Willow Slough. One of these sites, West Sacramento, sampled since 1988, is <15 km from Willow Slough at similar elevation and shares most of the same butterfly fauna. The record of flight timing at West Sacramento provides a check on whether apparent population changes at Willow Slough might actually be byproducts of regional variations in seasonal phenology. It also allows comparisons of apparent population trends through time at Willow Slough, sampled only once-a-year, to the performance of populations of the same species at the much-more-closely-monitored West Sacramento site over extended periods. Long-term (>25 year) butterfly monitoring datasets, of sufficient length to detect declines in diversity at specific locations, are rare, being essentially limited to the British Butterfly Monitoring Scheme (Pollard and Yates, 1993). Similar schemes have begun in the Ukraine (1983), in Germany (1989), in the Netherlands and Finland (1990), in Belgium (1991), and in Spain (1994) (Marttila et al., 2001; van Swaay et al., 2008).

This study presents an analysis of a 32-year record of butterfly species diversity at Willow Slough. We asked, has butterfly species diversity at Willow Slough changed over the past 32 years? If so, by how much? The raw number of species observed in a sample (here referred to as "species count"), depends strongly on sample size, the number of individuals encountered. It is thus a relatively poor estimator of species diversity (Gotelli and Colwell, 2001), the actual number of species in a fauna, a quantity often referred to elsewhere as "species richness". Sample size in our data set varied considerably, so we estimated relative species diversity using Fisher's alpha, a bias-reducing index of species diversity that was designed to facilitate comparison between samples of different sizes (Fisher et al., 1943; Rosenzweig, 1995). A second goal of our study was to compare the sensitivity with which trends in the fauna were detected using alpha versus raw species counts.

Butterflies are sensitive to weather conditions, leading to their frequent appearance in studies of the biotic impacts of climate change (Hellmann et al., 2008; Parmesan and Yohe, 2003; Wilson et al., 2007). The third goal of the paper was to assess whether observed changes in species diversity (as estimated by species counts and by Fisher's alpha) and abundance were associated with variation of local weather variables.

The assemblage-level metrics mentioned so far give no indication of which species have been observed with decreasing or increasing frequency. The paper's final goal was to determine which butterfly species were increasing or decreasing in probability of occurrence and to test whether butterfly life history attributes predicted the species' trends.

2. Materials and methods

2.1. Study site

Willow Slough (38 37 40 N, 121 44 00 W, elevation 15 m) is a partly-channelized perennial stream located 3.5 km north of Davis, Yolo County, CA. The area was seasonal wetland prior to agriculturalization in the 19th Century (Shapiro, 2009; Thompson, 1960). Beyond the levees enclosing the floodplain row crops and alfalfa are grown today. The ungrazed floodplain contains both woody and herbaceous riparian and wetland vegetation. The woody vegetation is periodically removed manually because it impedes free flow in winter. The herbaceous vegetation is very dynamic due to periodic inundation and sedimentation, but is dominated by perennials, many of which are clonal and form large patches. It is documented narratively each year and photographically from time to time, but no quantitative vegetation sampling has been done. The makeup of the perennial vegetation has changed dramatically over time, as discussed elsewhere in this paper. The vegetation on the levees, which are kept free of woody plants, consists mainly of naturalized annual grasses and forbs, which are burned annually after drying commences in late spring or early summer.

2.2. Sampling

AMS walks a standardized 11-km course, originally laid out in 1977 to maximize habitat coverage, in one direction only, requiring 5.5–6 h. His sampling protocol is essentially identical to the "Pollard Walk" used in the U.K. Butterfly Monitoring Scheme (Pollard and Yates, 1993), except that in the "Pollard Walk" only butterflies within a 5 m "box" ahead of and to the sides of the observer are counted. In contrast, AMS counts to the limits of his visual acuity in those directions, generally beyond 5 m. The course has been held constant despite changes in the vegetation. In all 4th of July counts the observer records weather conditions at the start and end of the count, but for our analyses we use the University of California/National Oceanic and Atmospheric Administration climate station in Davis, California (38 32 07 N, 121 46 30 W); the observation site is 7 km SSW of Willow Slough. Because extreme afternoon heat may cause butterflies to seek shelter and be unobservable, the count is begun 15–30 min earlier on days expected to exceed 35 °C.

2.3. Analysis of faunal diversity

Because the number of butterflies seen at Willow Slough varies considerably, we were concerned that year-to-year variation in sample size might introduce enough noise to obscure any underlying trend in species diversity of the fauna. We thus calculated Fisher's alpha (α), the oldest bias-reducing statistic (Fisher et al., 1943), for each year's data using the R package "vegan" (Oksanen et al., 2010), and compared the results of analyses carried out using α with those that used raw species counts.

Fisher's α is calculated by solving the following non-linear equation:

Author's personal copy

$$S = \alpha \ln(1 + N/\alpha) \quad (1)$$

where S is the number of species seen on a single July 4th, and N is the number of individual butterflies counted then. While many diversity indices incorporate both the number of species and a measure of evenness (the proportional representation of individuals among species), species abundances enter α's calculation only through their contribution to total sample size. Fisher's α assumes that species abundances follow a log-series distribution. The parameter of that distribution, α, has two simple interpretations. In large samples, it gives the expected number of "singletons" (species represented by a single individual) (Fisher et al., 1943). Alpha is also the number of additional species expected when the size of a sample is increased by a factor of e (where $e \approx 2.718$ is the base of the natural logarithm) (Fisher et al., 1943). Essentially, α estimates the rate at which the number of species observed is expected to increase as sample size increases.

To compare how long it took before a trend in species diversity became detectable using the raw species counts and Fisher's α, we performed a series of linear regressions of each diversity estimator against time, first using only the first three years of data, then adding the fourth year, then the fifth, and so on through the 32nd and latest year of the dataset.

We investigated possible impacts of weather on α, S and N by regressing all three variables against the following weather variables: total precipitation, average daily maximum, and average daily minimum temperature during summer and fall of the previous year and during winter, spring, and the start of summer (through July 4th) of the year in question; and maximum and minimum air temperature on the 4th of July. Cloud cover was not included in our analyses because it did not vary; July 4th was sunny in all 32 years.

2.4. Treatment of individual species

To test for long-term trends in occurrence of individual species, we performed binary logistic regressions of presence against time, using the standard logit link function and coding each year with 1 if the species was present and 0 if it was absent. We were specifically interested in detecting species that are being lost from the fauna, so we tested for significance using a one-sided null hypothesis of no decrease in probability of occurrence.

Because our goal was to identify species that are being lost from the fauna, we analyzed presence/absence rather than abundance data. There is a key qualitative distinction between seeing zero representatives of a species (in which case the species might actually be absent or extinct) and seeing one or more individuals (in which case it certainly isn't). Presence/absence data highlight that distinction, whereas in analyses of abundance data, between-year variability of population size can obscure the qualitatively important (but numerically small) difference between seeing one or a few individuals, and seeing none at all.

We therefore removed six species that have been present at every census (*Plebejus acmon*, *Atalopedes campestris*, *Pyrgus communis*, *Colias eurytheme*, *Strymon melinus*, and *Pieris rapae*) from the logistic regression analyses. We also excluded the three species that were absent just once (*Junonia coenia*, *Brephidium exile*, and *Pyrgus scriptura*) and three species that were only seen once (*Euchloe ausonides*, *Zerene eurydice*, and *Ochlodes sylvanoides*), leaving 24 species for this part of the analysis.

Whether individually significant or not, the slope coefficients associated with the effect of year in the logistic regressions provide estimates of the magnitude of each species' trend. We used the regression slopes in a series of comparisons aimed at determining whether butterfly life history attributes were associated with species' trends.

We tested four life-history variables for correlation with trends in species occurrence, *i.e.*, host-plant class (monocot or dicot); host-plant woodiness (woody or herbaceous); butterfly overwintering stage (egg, larva, pupa, or adult); and "weediness" of the butterfly's life history. As we define the term (Shapiro et al., 2003; Thorne et al., 2006), "weedy" species are those characterized by frequent apparent local population extinctions and recolonizations and are typically highly dispersive; "non-weedy" species have low vagility and relatively stable populations. We did not include voltinism, because nearly all of the species analyzed, including the three species that overwinter as adults, are multivoltine; only one (*Lycaena xanthoides*) is single-brooded. In testing for an effect of overwintering stage, with four different levels, we used a Kruskal–Wallis rank sum test (a non-parametric analogue of ANOVA) to compare regression coefficients between the groups. For all of the other predictor variables, we used two-sample Wilcoxon rank sum tests (a non-parametric alternative to the t-test) to compare the coefficients.

Butterflies at Willow Slough are recorded on the same date in each year, so trends in occurrence could potentially reflect either real changes in population abundance or changes in phenology. To assess the possibility that phenological shifts are driving the observed trend in diversity, we used results from an earlier study by Forister and Shapiro (2003). They analyzed trends in date of first flight (DFF) for 23 Central Valley California butterfly species (including many of those present at Willow Slough), regressing each species' DFF against time over a 31-year period. For those species contributing most to the observed decline in diversity at Willow Slough (defined as those whose probability of occurrence has declined significantly at the $P < 0.10$ level), we examined evidence of shifts in population phenology from Forister and Shapiro's earlier analysis.

All analyses were performed using the software package *R* (R Development Core Team, 2009).

3. Results

3.1. Faunal diversity

Thirty-six species and 42,961 individual butterflies were observed at Willow Slough over the course of the study. The number of individuals (N) recorded each year ranged from 618 to 2613 (mean: 1343; SD: 618), while the number of species (S) observed each year ranged from 13 to 30.

Butterfly diversity at Willow Slough on the 4th of July, whether estimated by S or by Fisher's α, declined significantly over the past 32 years (Fig. 1). The regressed value of S fell by 39% (adjusted $r^2 = 0.521$, $P < 10^{-5}$) between 1977 and 2008. (with 95% confidence intervals, and 1977 coded as year 0, its regression equation was $S = 26.1(\pm 2.0) - 0.33(\pm 0.11) * \text{year}$). Over the same period, the expected value of α has dropped from 4.79 to 2.49 (adjusted $r^2 = 0.657$, $P < 10^{-7}$; $\alpha = 4.79(\pm 0.34) - 0.074(\pm 0.019) * \text{year}$), a decline of 48% in α.

Regression of S against time yielded residuals that represent fluctuation of the species counts around their generally downward trend. These residuals were highly correlated with N ($r = 0.53$, $P < 0.005$), confirming our expectation that species count would depend on sample size, and motivating our use of the bias-reducing statistic for the estimation of species diversity.

Although a decline in species diversity was eventually apparent using either raw species counts or α as its metric, the trend was detectable much earlier using α (Fig. 2). After 23 years of sampling, raw counts of butterfly species number still did not reveal any consistently significant trend. Only since 2000, when the trend line of species count at the site indicated a decline of 18%, has the p-value of the regression stabilized. For α, a significant trend was apparent

Author's personal copy

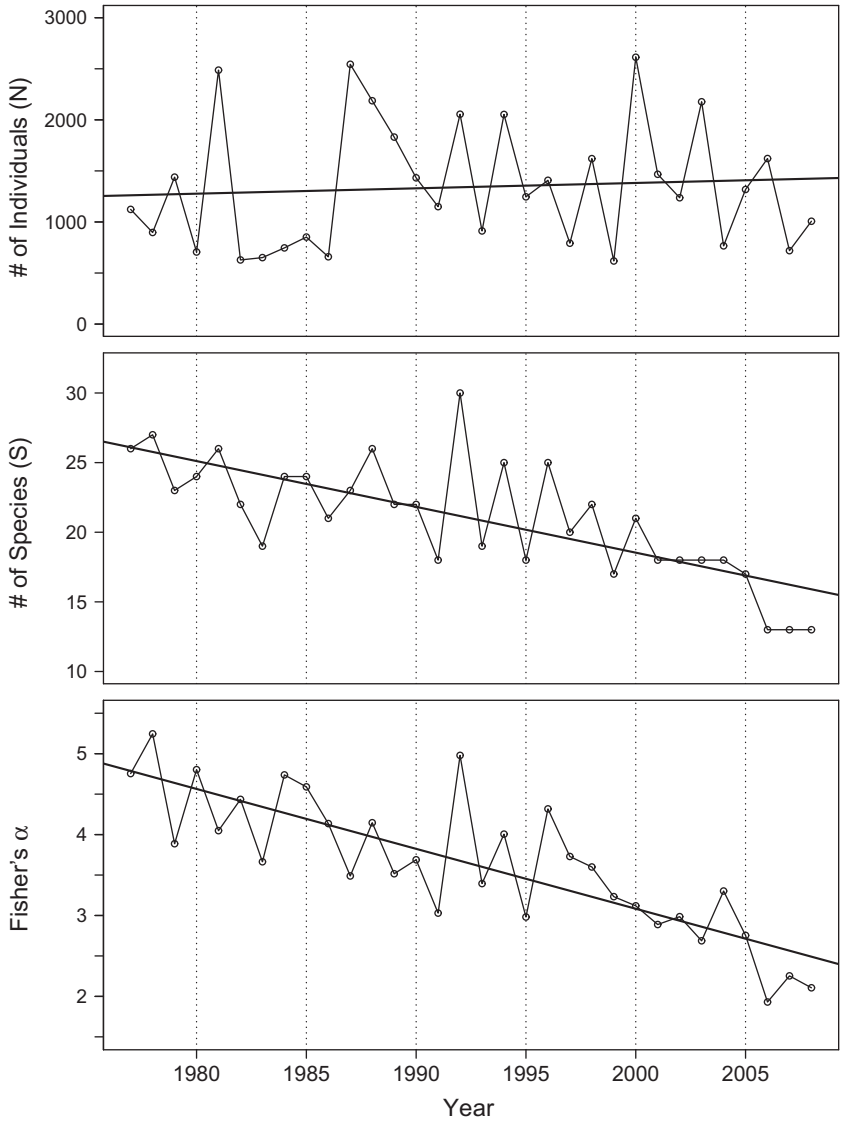


Fig. 1. Plots of number of individuals (N), number of species (S), and Fisher's α recorded on July 4th at Willow Slough in each of the past 32 years. Both S ($p < 0.001$) and α ($p < 0.0001$) have declined significantly. Regression lines (bold) fitted to S and α indicate, respectively, losses from the biota of 7.1 species (28%) and 8.7 species (33%). The number of individuals observed showed no significant trend over time.

much sooner. The negative trend of Fisher's α was significant as early as the 13th census ($p = 0.033$ in 1989) and has remained so ever since (except for the 16-year data set, for which $p = 0.066$).

During the past 32 years Willow Slough has become warmer. Trends of average minimum and maximum temperature vs. year were positive for all four seasons (Table 1). Previous summer maximum temperature increased significantly over the course of the study, and was negatively associated with S ($p = 0.0001$), N ($p = 0.033$), and α ($p = 0.019$). Fall, spring, and previous summer minimum temperatures also warmed significantly, but none of them exhibited a significant relationship to S, N, or α. There has been no clear trend in the amount of precipitation in any season nor was there a significant trend in maximum temperatures on the 4th of July itself (see Table 1 for the full results of tests of trend and of relationship to S, N, and α, for all weather variables examined).

3.2. Individual species

Both S and α reveal a decline in species diversity at Willow Slough, but neither gives any indication of which species have been observed less frequently, nor of whether there was any common factor associated with their decline. The results of the logistic regression tests, reported in Table 2, indicated that twelve species have been present at Willow Slough significantly less frequently over the past 32 years ($p < 0.05$ for a one-sided test). In all, 21 of the 24 species analyzed showed negative, if not significant, trends.

Overwintering stage was the only life history trait tested that was significantly associated ($p = 0.040$) with the strength of species' declines: host plant class, host plant woodiness, and "weediness" of butterfly life history showed no relation to species decline. Because there were so few species in some overwintering categories (just three species overwinter as adults, and three species as eggs) our data did not give us sufficient power to decompose the overall significant Kruskal–Wallis test into its component contrasts. Butterflies overwintering as larvae (six species) experienced, as a group, a significantly steeper decline than did those overwintering as pupae (seven species) ($p = 0.017$). Comparing the group of species that overwinter as eggs or larvae with the group that overwinter as pupae or adults, there was an even more significant difference ($p = 0.003$).

Of the 16 Willow Slough species that exhibited negative trends in occurrence with $p < 0.10$, 10 were among those analyzed by

Author's personal copy

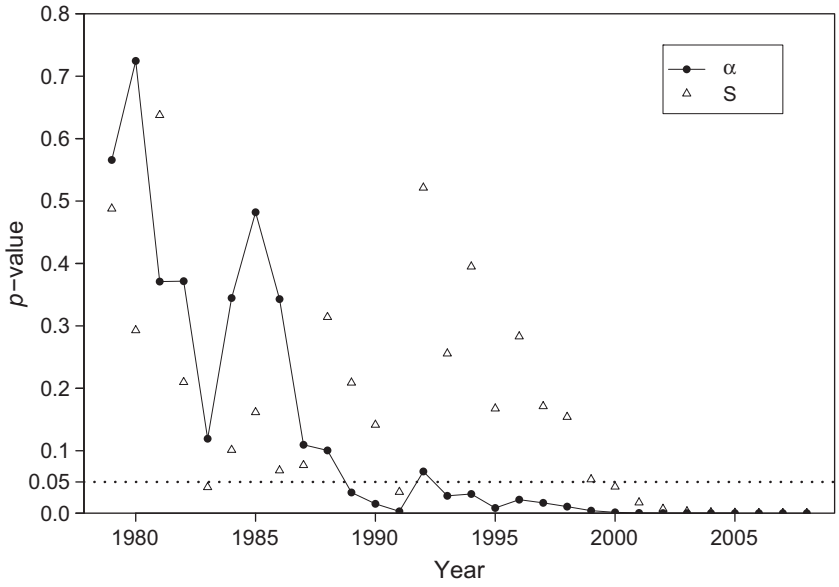


Fig. 2. *p*-values of regressions of species richness (*S*) and Fisher's α performed using successively greater numbers of years of data. The *p*-values from 1979 are based on three years of data, while, by 2008, they were based on 32 years of data. Because α corrects for sample size in its estimate of diversity, it consistently detected a significant decline seven to 11 years before a significant decline was detected using raw species counts (*S*).

Table 1
Trends of weather variables over time and the relationship of observed species number (*S*), abundance (*N*), and Fisher's α to weather variables. Slope and adjusted-r^2 and *p*-values for trends over time represent the results of regressions of each weather variable against time. Slope and adjusted-r^2 and *p*-values for the weather variables' relation to *S*, *N*, and α come from simple regressions of the assemblage-level metrics against each of weather variables. T_{max} and T_{min} are the average daily maximum and minimum temperature for each season, in °C. Seasonal precipitation is the total precipitation for each season, measured in millimeters. Seasons are defined as follows: fall = September, October, November of the preceding calendar year; winter = December, January, February; spring = March, April, May; summer (Prev.) = June, July, August; summer (current) = June and the first 4 days of July. Significance codes: $^{*}p < 0.05$, $^{**}p < 0.01$.

Weather variable	Trend over time			Relation to *S*			Relation to *N*			Relation to alpha		
	Slope	adj-r^2	*P*	Slope	adj-r^2	*P*	Slope	adj-r^2	*P*	Slope	adj-r^2	*P*
Summer (Prev.)												
Ppt	0.00	<0.01	0.649	7.93	0.00	0.307	1013.04	<0.01	0.375	0.78	<0.01	0.619
T_{max}	0.04	0.13	0.025*	−2.52	0.23	0.003*	−265.16	0.10	0.041*	−0.38	0.11	0.035*
T_{min}	0.04	0.25	0.002*	−2.54	0.17	0.011*	−249.15	0.06	0.101	−0.40	0.09	0.052
Fall												
Ppt	−0.02	0.02	0.187	−0.31	<0.01	0.784	−441.55	0.21	0.005*	0.23	0.00	0.315
T_{max}	0.03	0.02	0.196	0.77	0.03	0.180	229.45	0.22	0.004*	0.01	<0.01	0.948
T_{min}	0.04	0.16	0.012*	−0.90	0.00	0.339	−88.85	<0.01	0.521	−0.13	<0.01	0.499
Winter												
Ppt	0.02	<0.01	0.563	−0.19	<0.01	0.728	−94.43	0.01	0.242	0.02	<0.01	0.856
T_{max}	0.03	0.07	0.073	−0.61	<0.01	0.454	191.12	0.05	0.107	−0.22	0.03	0.181
T_{min}	0.04	0.04	0.126	−0.19	<0.01	0.717	−6.84	<0.01	0.929	−0.02	<0.01	0.877
Spring												
Ppt	−0.02	0.01	0.256	−0.32	<0.01	0.716	−58.11	<0.01	0.656	0.00	<0.01	0.982
T_{max}	0.06	0.08	0.061	0.01	<0.01	0.988	46.47	<0.01	0.503	−0.03	<0.01	0.719
T_{min}	0.04	0.17	0.011*	−0.70	<0.01	0.431	131.24	<0.01	0.314	−0.22	0.02	0.217
Summer (Current)												
Ppt	0.00	<0.01	0.855	−0.59	<0.01	0.851	7.55	<0.01	0.987	−0.23	<0.01	0.722
	0.02	<0.01	0.517	−0.23	<0.01	0.634	95.01	0.03	0.165	−0.10	<0.01	0.284
T_{min}	0.03	0.04	0.125	−0.74	<0.01	0.350	189.44	0.06	0.100	−0.26	0.06	0.094
July 4th												
T_{max}	0.08	<0.01	0.318	−0.32	0.07	0.069	−23.15	<0.01	0.388	−0.05	0.04	0.133

Forister and Shapiro (2003). Of those 10, not one showed evidence of significantly advancing date of first flight. Five species had regressions with (non-significant) positive slopes (indicative of a shift to later first appearance), and five had (non-significant) negative slopes. There was thus no clear trend of date of first flight among the species in steepest decline at Willow Slough, as would have been expected if the observed decline in diversity were the result of a simple shift in the phenology of the fauna.

4. Discussion

4.1. Regional context

The number of species observed per census of the Willow Slough butterfly fauna has eroded by about 40% over the last 32 years. This drastic decline has occurred in an unexceptional landscape in California's Central Valley, an area representative of

Author's personal copy

Table 2
Results of logistic regressions of presence vs. year for 23 species at Willow Slough (tested against a one-sided null hypothesis of no decrease in probability of occurrence). "Years present" is the number of years (out of 32) in which at least one representative of a species was observed; "number observed" is the total number of individuals seen over the course of the study.

Species	*p*-value	Slope	Overwintering stage	Years present	Number observed
Erynnis tristis	0.002	−0.19	Larva	19	55
Pholisora catullus	0.003	−0.18	Larva	21	187
Lerodea eufala	0.005	−0.16	Unknown	10	41
Polites sabuleti sabuleti	0.006	−0.16	Pupa	9	52
Papilio zelicaon	0.008	−0.15	Pupa	23	335
Lycaena helloides	0.01	−0.28	Egg	26	197
Vanessa cardui	0.018	−0.13	Migrant	25	936
Lycaena xanthoides	0.018	−0.12	Egg	24	328
Vanessa annabella	0.026	−0.3	All	28	261
Limenitis lorquini	0.032	−0.09	Larva	10	20
Danaus plexippus	0.034	−0.69	Migrant	28	559
Nymphalis antiopa	0.046	−0.09	Adult	7	8
Phyciodes campestris	0.059	−1.31	Larva	27	3310
Satyrium sylvinus	0.069	−0.14	Egg	3	3
Phyciodes mylitta	0.073	−0.07	Larva	24	111
Coenonympha tullia california	0.082	−0.52	Larva	2	2
Everes comyntas	0.107	−0.15	Larva	30	670
Vanessa virginiensis	0.225	−0.04	Adult	5	9
Vanessa atalanta	0.271	−0.02	Adult	16	26
Papilio rutulus	0.313	−0.02	Pupa	6	15
Atlides halesus	0.347	−0.03	Pupa	2	4
Battus philenor	0.707	0.05	Pupa	2	2
Pontia protodice	0.818	0.04	Pupa	9	73
Hylephila phyleus	0.888	0.08	Pupa	28	300

many others in its combination of human impact and neglect. The decline in species diversity detected at Willow Slough, appears to be part of a broader local or even regional phenomenon. Three of the sites monitored by AMS as part of his 10-site transect across north-central California are, like Willow Slough, located on the floor of the Central Valley, and the faunas at all four sites overlap broadly in species composition. Furthermore, because they are visited year-round at roughly two-week intervals, local extinction can be positively identified at these sites with more confidence than they can be at Willow Slough. At West Sacramento, the nearest of the three sites, the probabilities of observation of 11 out of 39 species have declined since 1988 (unpublished data). Over the same period, no species have been observed significantly more frequently, and three have apparently gone extinct. The picture is similar at two more remote Central Valley sites, North Sacramento and the somewhat less ecologically-similar Rancho Cordova.

The emerging pattern of species decline in California's Central Valley is mirrored by reports of declining butterfly populations in intensively managed agricultural landscapes in other parts of the world. León-Cortés et al. (2000) estimated that the area occupied by *Lycaena phlaeas* in their study area in North Wales declined by 89% over the past century, largely due to conversion of semi-improved grasslands to improved grasslands by seeding, fertilizing, and the application of selective herbicides. During the second half of the 20th century, northern Belgium lost 30% of its butterfly fauna, and saw widespread declines in the ranges of its remaining specialist butterflies, a trend partly attributed to coincident intensification of agricultural practices (Maes and Van Dyck, 2001). Warren et al. (2001) found that habitat loss drove decreases in the distributions of 26 of 28 specialist butterflies in Britain between 1970 and 2000 despite broadly favorable change in climate during the same period. While lacking a time dimension, studies in northeastern Spain (Stefanescu et al., 2004) and southern Sweden (Bergman et al., 2004) have documented negative impacts on butterfly diversity of the amount of intensively managed agricultural land within 5 km of sampled transects.

Nearly all the species that have declined at Willow Slough are declining regionally. Several of these (*Nymphalis antiopa, Limenitis lorquini, Satyrium sylvinus, Coenonympha tullia california*) were never common at Willow Slough but were common to abundant at nearby transect sites and are apparently extinct there now. *Lycaena helloides* and *Pholisora catullus*, formerly frequent at Willow Slough, have declined catastrophically at most sites. In addition, one species that has declined catastrophically on a regional basis (*E. ausonides*) flies too early in the year to show up regularly on the Fourth of July count. One formerly abundant species at Willow Slough, *Phyciodes campestris*, is presumed locally extinct not only there but at all AMS' sites. Only one species in decline at Willow Slough, *Erynnis tristis*, appears to be doing well elsewhere in the region.

Because declines at other sites are documented by biweekly sampling, phenological artifacts in the once-a-year sampling regime are easily recognized and accounted for. Because the patterns of decline detected by such different sampling regimes are largely similar over the years documented, the utility of the once-a-year regime in spotting trends is supported. We will present a detailed analysis of the behavior of individual species, including comparisons of both abundance and phenology at Willow Slough and West Sacramento, in a separate paper.

Although the utility of once-a-year sampling was supported in the present study, it is worth emphasizing that the Willow Slough transect is something of a best case scenario, due to the consistency with which it has been observed, and the stable sunny climate that prevails at the season of observation. One shortcoming that holds for all once-a-year surveys is that they can by themselves provide no estimate of the number (or perhaps type) of species that they are likely to miss. Recent studies in California (Pellet, 2008) and Switzerland (Kéry and Plattner, 2007) which used repeated surveys to estimate species detectability indicate that the portion of the species missed in single surveys can be substantial. In both studies, the average detection probability of species known to be present was between 50% and 60%.

4.2. Role of climate

Climate at Willow Slough, like that of California as a whole, has warmed significantly over the past several decades (LaDochy et al., 2007). Studies elsewhere have shown that the number and diversity of butterflies seen in a survey can be affected by weather on the day of observation (Kocher and Williams, 2000) and in the season

Author's personal copy

preceding it (Pollard, 1988); therefore temperature is an obvious suspect in the search for the drivers of the observed decline in species diversity at Willow Slough.

We do in fact find some evidence consistent with an effect of increasing temperatures on the Willow Slough butterfly fauna. Mean temperature during the previous summer is a positive predictor of *N*, the number of individual butterflies seen the following 4th of July. Observed species counts, *S*, decline significantly by about 3.3 species for each 1 °C increase in the previous summer temperature. As mean summer temperatures have warmed by about 1.2 °C over the course of this study, that trend may account for the loss of about 3.9 species from the Willow Slough fauna. The actually observed decline of diversity at Willow Slough, however, is much greater: the fitted linear regression indicates a loss of 10.2 species over the same time period. Presumably α, which is not sensitive to *N*, declined because other factors, in addition to trends in climate, are involved in the observed decline of the Willow Slough fauna.

4.3. Life cycle correlations

While we have not positively identified any external driver of the decline in diversity, some species' life cycles apparently make them particularly vulnerable to decline. In particular, species that overwinter as larvae or eggs are significantly more likely to have declined than those that overwinter as pupae or adults. Our results parallel those of Bink (cited in Dennis (1993)) who studied correlates of vulnerability among 145 butterfly species of northwest Europe. Among those butterflies, overwintering stage was a predictor of vulnerability to habitat disturbance. Species hibernating as eggs were most vulnerable, followed by those overwintering as larvae and then by those overwintering as pupae or adults. Similarly, an analysis of trends over 35 years of 338 British moth species found the greatest declines among species overwintering as eggs, while the few species overwintering as adults increased on average (Conrad et al., 2004).

Dennis (1993) attributed Bink's results to a greater vulnerability of eggs and larvae to direct habitat disturbance. It is also possible is that overwintering stage is associated with the flexibility with which a species tracks fluctuations in climate. Forister and Shapiro (2003) found that over the past 30 years, the date of first flight of many Central Valley butterflies has come earlier in the year. For butterflies that overwinter as pupae, the change in date of first flight was significantly greater than for those overwintering as larvae. If pupal overwinterers are generally better able to track the phenology of nectar sources, host plants, or their natural enemies, they may be less vulnerable to directional change in regional climate. However, earlier emergence can be deleterious regardless of overwintering stage if it leads to either earlier onset of diapause or the production of an added late generation at high risk of weather-induced mortality.

4.4. Causation

We would of course like to know why the Willow Slough butterfly fauna is in decline, and likewise the broader regional fauna. Although we have identified some climatic correlations, they are, as noted previously, unlikely to be the sole or even the major drivers of decline.

Based on our familiarity with the natural history of the fauna, we suspect that successional vegetation change has contributed to the decline at Willow Slough. Since the mid-1980s two invasive, perennial, clonal weeds, *Lepidium latifolium* (Brassicaceae) and *Dipsacus sylvestris* (Dipsacaceae), have rapidly increased their combined areal coverage to approximately 50% of the floodplain. In the process they have displaced numerous butterfly resources, both nectar sources and larval host plants. This in itself may have been responsible for the unexpected apparent extinction/disappearance from the 4th of July count of *P. campestris*. Present for 26 years running and then absent in 5 out of the past 6 years, its host plant, *Aster chilensis* (Asteraceae) – which also served as a major seasonal nectar plant – has been reduced in coverage by an order of magnitude.

Other species adversely impacted and of butterfly importance include *Apocynum cannabinum* (Apocynaceae), *Asclepias fascicularis, Asclepias speciosa* (both Asclepiadaceae), *Phyla nodiflora* (Verbenaceae), *Malvella leprosa* (Malvaceae),and the important summer annual *Lotus purshianus* (Fabaceae). *L. latifolium*, a nectar source for various short-tongued Lycaenidae, is a larval host of the weedy butterfly *P. rapae,* whose numbers have actually increased at Willow Slough. *D. sylvestris* is not a larval host plant but is a nectar source for medium-to-large-size butterflies with long proboscides. However, local vegetation change alone cannot be driving the Willow Slough decline either, insofar as it is mirrored by declines in butterfly faunas at other sites on a regional basis. We suspect broader patterns of land use and habitat continuity are implicated in butterfly declines throughout the region.

5. Conclusions

The observed decline shows the utility of systematic, long-term monitoring efforts of the type carried out by many citizen scientists. Although the decline in species diversity at Willow Slough has been drastic, it would have been difficult to document (other than anecdotally) without the consistent record of monitoring that we have. Indeed, before analysis with Fisher's α, it was not evident to the observer (AMS) that a decline was taking place. Even the eventually dramatic decline in the raw number of species would have gone undocumented (and perhaps unnoticed) in a census less than 24 years long.

The results also illustrate how the use of a bias-reducing statistic can greatly improve estimates of relative species diversity and so improve our power to detect trends. There are many methods of estimating species diversity (Bunge and Fitzpatrick, 1993; Gotelli and Colwell, 2001; Magurran, 1988), not one of which, α included, is appropriate in every situation (Rosenzweig et al., 2011, 2003). However, if abundance data are available and one wants to detect trends or make comparisons between sets of similar taxa in space or time, Fisher's α may be the best. Compared to other diversity indices, including *S*, Fisher's α typically performs well in applications requiring a statistic with good "discriminant ability" (a term coined by Taylor (1978) to refer to the effectiveness of a statistic in detecting the effects of relevant independent variables (Magurran, 1988)). Discriminant ability is measured as the proportion of a statistic's among-sample variance that can be explained by the variables of interest. In our study, the discriminant ability of Fisher's α was clearly better than that of raw species count. 'Year' explained a much higher proportion of the variance in α (adjusted $r^2 = 0.657$) than in *S* (adjusted $r^2 = 0.521$).

Since its development by Fisher, the α statistic has proven effective in application to many collections, both biological and non-biological (e.g. (Buzas and Culver, 1999; Efron and Thisted, 1976; Taylor, 1978; Wolda et al., 1994)). Magurran (1988) attributes α's good performance to its near independence of sample size, its relative insensitivity to both the commonest and the rarest species, and its robustness with respect to deviations of the data from the theoretical log-series form. Indeed, α performs better than other indices even where the distribution of abundances is significantly different from a log-series (Boswell and Patil, 1971; Condit et al., 1998; Magurran, 1988). The ability to distinguish underlying trends from noise is especially important when what is being measured

Author's personal copy

may be a gradual erosion of diversity. So we recommend the application of α to other census or monitoring data that include the number of individuals seen.

Economic and logistical concerns often limit the thoroughness of ecological monitoring efforts. The Willow Slough case history demonstrates that even a once-a-year sampling program focused on short-lived, multivoltine insects can be of significant value in spotting and predicting trends in diversity if it is carried out in a consistent manner that assures statistical quality.

Acknowledgements

We thank Matt Forister and Mark Schwartz, colleagues at the University of Nevada and the University of California, for discussing early stages of the manuscript with us. This work was supported by an NSF Databases and Informatics Program grant (DBI-0317483 to A.M. Shapiro and J.F. Quinn).

References

Anonymous, 2009. The Tucson Bird Count. <http://en.wikipedia.org/wiki/Tucson_Bird_Count>.
Bergman, K.-O., Ekberg, O., Milberg, P., 2004. Landscape effects on butterfly assemblages in an agricultural region. Ecography 27, 619–628.
Boswell, M.T., Patil, G.P., 1971. Chance mechanisms generating the logarithmic series distribution used in the analysis of number of species and individuals. In: Patil, G.P., Pielou, E.C., Waters, W.E. (Eds.), Statistical Ecology, vol. 3. Pennsylvania State University Press, University Park, PA, pp. 99–130.
Bunge, J., Fitzpatrick, M., 1993. Estimating the number of species - a review. Journal of the American Statistical Association 88, 364–373.
Buzas, M.A., Culver, S.J., 1999. Understanding regional species diversity through the log series distribution of occurrences. Diversity & Distributions 5, 187–195.
Condit, R., Foster, R.B., Hubbell, S.P., Sukumar, R., Leigh, E.G., Manokaran, N., Loo de Lao, S., 1998. Assessing forest diversity on small plots: calibration using species-individual curves from 50-ha plots. In: Dallmeier, F., Comiskey, J.A. (Eds.), Forest Biodiversity Research, Monitoring, and Modeling: Conceptual Background and Old World Case Studies. United Nations Educational Scientific, and Cultural Organization, Paris, pp. 247–268.
Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R., Warren, M.S., 2004. Long-term population trends in widespread British moths. Journal of Insect Conservation 8, 119–136.
Dennis, R.L.H., 1993. Butterflies and Climate Change. Manchester University Press, Manchester.
Efron, B., Thisted, R., 1976. Estimating number of unseen species – how many words did Shakespeare know? Biometrika 63, 435–447.
Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12, 42–58.
Forister, M.L., Shapiro, A.M., 2003. Climatic trends and advancing spring flight of butterflies in lowland California. Global Change Biology 9, 1130–1135.
Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379–391.
Hellmann, J.J., Pelini, S.L., Prior, K.M., Dzurisin, J.D.K., 2008. The response of two butterfly species to climatic variation at the edge of their range and the implications for poleward range shifts. Oecologia 157, 583–592.
Kéry, M., Plattner, M., 2007. Species richness estimation and determinants of species detectability in butterfly monitoring programmes. Ecological Entomology 32, 53–61.
Kocher, S.D., Williams, E.H., 2000. The diversity and abundance of North American butterflies vary with habitat disturbance and geography. Journal of Biogeography 27, 785–794.
LaDochy, S., Medina, R., Patzert, W., 2007. Recent California climate variability: spatial and temporal patterns in temperature trends. Climate Research 33, 159–169.
León-Cortés, J.L., Cowley, M.J.R., Thomas, C.D., 2000. The distribution and decline of a widespread butterfly *Lycaena phlaeas* in a pastoral landscape. Ecological Entomology 25, 285–294.
Link, W.A., Sauer, J.R., 1996. Extremes in ecology: avoiding the misleading effects of sampling variation in summary analyses. Ecology 77, 1633–1640.
Link, W.A., Sauer, J.R., Niven, D.K., 2006. A hierarchical model for regional analysis of population change using Christmas bird count data, with application to the American black duck. Condor 108, 13–24.
Lundmark, C., 2003. BioBlitz: getting into backyard biodiversity. Bioscience 53, 329.
Maes, D., Van Dyck, H., 2001. Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? Biological Conservation 99, 263–276.
Magurran, A.E., 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, New Jersey.
Marttila, O., Saarinen, K., Lahti, T., 2001. The national butterfly recording scheme in Finland (NAFI) – Results of the first ten years (1991–2000). Baptria 26, 29–61.
McCaffrey, R.E., 2005. Using citizen science in urban bird studies. Urban Habitats 3, 70–86.
Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2010. Vegan: Community Ecology Package. R Package Version 1.17-4. <http://CRAN.R-project.org/package=vegan>.
Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
Pellet, J., 2008. Seasonal variation in detectability of butterflies surveyed with Pollard walks. Journal of Insect Conservation 12, 155–162.
Pollard, E., 1988. Temperature, rainfall and butterfly numbers. Journal of Applied Ecology 25, 819–828.
Pollard, E., Yates, T.J., 1993. Monitoring Butterflies for Ecology and Conservation: The British Butterfly Monitoring Scheme. Springer-Verlag, New York.
R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org>.
Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.
Rosenzweig, M.L., Donoghue, J.I., Li, Y.M., Yuan, C., 2011. Estimating species density. In: Magurran, A., McGill, B. (Eds.), Biological Diversity: Frontiers in Measurement and Assessment. Oxford Unversity Press, New York, pp. 276–287.
Rosenzweig, M.L., Turner, W.R., Cox, J.G., Ricketts, T.H., 2003. Estimating diversity in unsampled habitats of a biogeographical province. Conservation Biology 17, 864–874.
Shapiro, A.M., 2009. Revisiting the pre-European butterfly fauna of the Sacramento Valley, California. Journal of Research on the Lepidoptera 41, 31–39.
Shapiro, A.M., VanBuskirk, R., Kareofelas, G., Patterson, W.D., 2003. Phenofaunistics: seasonality as a property of butterfly faunas. In: Boggs, C.L., Watt, W.B., Ehrlich, P.R. (Eds.), Butterflies: Ecology and Evolution Taking Flight. University of Chicago Press, Chicago, pp. 111–147.
Silvertown, J., 2009. A new dawn for citizen science. Trends in Ecology & Evolution 24, 467–471.
Stefanescu, C., Herrando, S., Paramo, F., 2004. Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. Journal of Biogeography 31, 905–915.
Swengel, A.B., 1990. Monitoring butterfly populations using the 4th of July Butterfly Count. American Midland Naturalist 124, 395–406.
Taylor, L.R., 1978. Bates, Williams, and Hutchinson – a variety of diversities. In: Mound, L.A., Waloff, N. (Eds.), Diversity of Insect Faunas. 9th Symposium of the Royal Entomological Society. Blackwell Press, Oxford, pp. 1–18.
Thompson, K., 1960. Historic flooding in the Sacramento valley. Pacific Historical Review 29, 349–360.
Thorne, J.H., O'Brien, J., Forister, M.L., Shapiro, A.M., 2006. Building phenological models from presence/absence data for a butterfly fauna. Ecological Applications 16, 1842–1853.
Tryjanowski, P., Sparks, T.H., 2001. Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the red-backed shrike *Lanius collurio*. International Journal of Biometeorology 45, 217–219.
Turner, W.R., 2003. Citywide biological monitoring as a tool for ecology and conservation in urban landscapes: the case of the Tucson Bird Count. Landscape and Urban Planning 65, 149–166.
van Swaay, C.A.M., Nowicki, P., Settele, J., van Strien, A.J., 2008. Butterfly monitoring in Europe: methods, applications and perspectives. Biodiversity and Conservation 17, 3455–3469.
Wander, A., 2009. Introduction. In: Wander, A. (Ed.), 2008 Report, NABA Butterfly Counts. North American Butterfly Association, Morristown, NJ.
Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414, 65–69.
Wilson, R.J., Gutierrez, D., Gutierrez, J., Monserrat, V.J., 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. Global Change Biology 13, 1873–1887.
Wolda, H., Marek, J., Spitzer, K., Novak, I., 1994. Diversity and variability of Lepidoptera populations in urban Brno, Czech-Republic. European Journal of Entomology 91, 213–226.