

# Optimal design of butterfly occupancy surveys and testing if occupancy converts to abundance for sparse populations

Jason T. Bried · Jérôme Pellet

Received: 20 May 2011 / Accepted: 18 August 2011  
© Springer Science+Business Media B.V. 2011

**Abstract** Occupancy has several important advantages over abundance methods and may be the best choice for monitoring sparse populations. Here we use simulations to evaluate competing designs (number of sites vs. number of surveys) for occupancy monitoring, with emphasis on sparse populations of the endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov). Because conservation planning is usually abundance-based, we also ask whether detection/non-detection data may reliably convert to abundance, hypothesizing that occupancy provides a more dependable shortcut when populations are sparse. Count-index and distance sampling were conducted across 50 habitat patches containing variably sparse Karner blue populations. We used occupancy-detection model estimates as simulation inputs to evaluate primary replication tradeoffs, and used peak counts and population densities to evaluate the occupancy-abundance relationship. Detection probability and therefore optimal design of occupancy monitoring was strongly temperature dependent. Assuming a quality threshold of 0.075 root-mean square error for the occupancy estimator, the minimum allowable effort was 360 (40 sites × 9 surveys) for spring generation and 200 (20 sites × 10 surveys) for summer generation. A mixture model abundance estimator for repeated detection/non-detection data was biased low for high-density and low-density populations, suggesting that occupancy may not

provide a reliable shortcut in abundance-based conservation planning for sparse butterfly populations.

**Keywords** Butterflies · Study design · Survey effort · Detection probability · Distance sampling · Karner blue

## Introduction

The continuous index count is still among the most popular metrics for monitoring plant and animal populations (Thomas 2005; Marsh and Trenham 2008). However, count-index methods unrealistically assume the number of observed individuals is a constant fraction of the number actually present, such as detecting a constant proportion of butterfly abundance from year to year (Pollard et al. 1993; Roy et al. 2007; Harker and Shreeve 2008; Nowicki et al. 2008). Recently there has been strong discourse on whether population index methods accurately describe the parameter of interest, population size (Johnson 2008). Anderson (2001; 2003) asserts that index methods that do not account for detection probability ( $p$ ) are nearly worthless because the probability is almost never perfect ( $p = 1$ ) or constant among different habitats, observers, etc. Because  $p$  is almost always less than one and varies with myriad site-specific and time-varying factors (MacKenzie et al. 2006), a true population estimate requires, at a minimum, dividing the counts by  $p$ .

The Pollard-Yates index method and its derivatives have long been used for butterfly conservation planning (Pollard and Yates 1993; van Swaay et al. 2008). This approach involves counting the butterflies during repeated surveys and drawing inferences from the maximum or average number seen. There are several alternatives to relying on raw index counts for butterfly monitoring. Zonneveld

---

J. T. Bried (✉)  
Albany Pine Bush Preserve Commission, 195 New Karner Road,  
Albany, NY 12205-4605, USA  
e-mail: jbried@albanypinebush.org

J. Pellet  
A. Maibach Sàrl, CP 99, Ch. de la Poya 10,  
1610 Oron-la-Ville, Switzerland

(1991) developed a theoretical model to estimate butterfly mortality rate and provide an index of abundance from a sequence of Pollard-type counts. Although his model implicitly accounts for butterflies that eclose and die between survey events, the overall abundance (i.e., brood size, number of recruits in one generation) may be biased low because undetected butterflies present on surveys are not included. Distance sampling (Buckland et al. 2001) may overcome the false-absence problem on surveys, does not require handling of animals, and is being applied to butterflies (Brown and Boyce 1998; Powell et al. 2007; Pocewicz et al. 2010; Isaac et al. 2011), but it hinges on several restrictive assumptions, does not directly estimate brood size, and may not work well for extremely sparse populations (Bart et al. 2004). Mark and recapture methods account for detectability and adult turnover during the season and thus directly estimate brood size, but are labor-intensive, data-demanding (hard to attain sufficient recaptures with sparse populations), analytically complex, and potentially destructive for small and fragile animals (Singer and Wedlake 1981; Gall 1984; Murphy 1987; Mattoni et al. 2001; Haddad et al. 2008).

Another alternative to count-index methods is occupancy monitoring. In conservation, occupancy is typically regarded as inferior to abundance because it does not provide early warning of population declines (Pollock 2006; Joseph et al. 2006). However, by assuming that a species' detectability is largely a function of its abundance, and recognizing that change in population size typically accompanies change in proportion of area occupied (Gaston et al. 2000; Longcore et al. 2010), it is possible to reliably estimate abundance and population trend from occupancy data (He and Gaston 2000; Royle and Nichols 2003; Pollock 2006; Zhou and Griffiths 2007; Hui et al. 2009; Hwang and He 2011; but see Strayer 1999). Detection/non-detection data tend to approximate patch-level processes with far less effort than abundance surveys (MacKenzie et al. 2003; Zhou and Griffiths 2007), and may provide the best information under limited resources. For example, Joseph et al. (2006) determined that under financial constraints and for low density and/or hard-to-detect species, presence-absence methods rivaled or surpassed abundance methods at tracking changes in population size and assigning conservation status. Indeed, large year-to-year fluctuations may confound the detection of trends in butterfly abundance data (van Strien et al. 1997; Zonneveld et al. 2003).

Occupancy is often the best choice for monitoring endangered species and other taxa surviving at levels too low for abundance-based modeling (MacKenzie et al. 2006). Conservation of species persisting as small populations over large areas may require a shift in thinking from abundance to distribution (Zonneveld et al. 2003; Joseph

et al. 2006). Such may be the case for the endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) within portions of its range. Here we use simulations to evaluate competing designs (number of sites vs. number of surveys) for Karner blue occupancy monitoring, with emphasis on sparse populations (i.e., locally rare or low-density, <10 butterflies per hectare). However, because conservation planning is usually abundance-based, we also ask whether detection/non-detection data may reliably convert to abundance, hypothesizing that occupancy provides a more dependable shortcut when populations are sparse (the usual case for endangered species). Despite numerous studies on sampling and analysis issues for butterflies (e.g., Haddad et al. 2008; Isaac et al. 2011), ours may be the first to explore primary occupancy design tradeoffs and the macroecological occupancy-abundance relationship for sparse populations.

## Methods

### Study system

The Albany Pine Bush Preserve (42°42'N, 73°52'W, elevation 79–110 m) is located near the Mohawk and Hudson rivers confluence in the densely populated capital region of east-central New York State. The area is characterized by a gently rolling sand plain and cold-temperate humid climate (Barnes 2003). Major vegetation types in the preserve include xerophytic early-successional barrens, thickets, and forests dominated by scrub oak (*Quercus ilicifolia* Wang., *Q. prinoides* Willd.) and pitch pine (*Pinus rigida* Mill.), along with semi-natural grasslands, red maple swamps, Appalachian oak-pine forests, and successional hardwood forests. Key threats include fire suppression and invasive plants along with continuing economic pressure to develop the area for housing, commerce, and industry.

The Pine Bush is one of four metapopulation recovery areas in the New York federal Karner blue recovery unit (USFWS 2003). It is the type locality for the Karner blue, which now survives in open-canopy scrub oak barrens, old fields, powerline corridors, and other herbaceous or shrubby dominated areas supporting its host plant, wild blue lupine (*Lupinus perennis* L.). Preserve managers use controlled burns, seed collection and plantings, mechanical treatments, and herbicides to create, restore, and maintain Karner blue habitat (Bried 2009; Bried and Braun 2009).

The Pine Bush is ideally suited for the study objectives because its Karner blue population has steadily declined in recent years (Albany Pine Bush Preserve Commission, unpublished data). Most if not all subpopulations in this study area are currently (2010 field season) below the 10 butterflies per hectare threshold mentioned earlier to define

“sparse”. Brood size evaluation in 2010 estimated fewer than 1,000 adult Karner blue recruited across 90 ha of sampled Pine Bush habitat, compared with over 25,000 adult Karner blue across 100 ha sampled in a recovery area (Saratoga Sandplains) located about 50 km north. With low encounter rates ( $<1$  butterfly per 100 m of transect), Karner blue abundance monitoring in the Pine Bush is becoming statistically inefficient and difficult to assess.

### Surveys

Surveys of Karner blue imagos were conducted in 50 habitat patches across preserve land, where a “patch” is defined mainly by the presence of lupine (Grundel and Pavlovic 2007). Most patches in the Pine Bush are delimited by roads, forest, and other well-defined edges. Many of the patches were originally mature, closed-canopy forest but are now fields planted with lupine, nectar species, and dense-foliage grasses. Few of the patches have ever been burned, but most have been mowed at least once in the past decade. Patches ranged in size from  $<0.1$  ha to 10.3 ha (mean  $\pm$  SD =  $1.7 \pm 2.6$  ha). Only one patch was isolated ( $>1$  km from all others), all but six were within 200 m of another study patch, and half were within 200 m of a patch known to be occupied during the study; dispersal of Karner blue is typically less than 1 km, and non-dispersal movement is confined within about 200 m (Knutson et al. 1999; USFWS 2003).

Data collection took place in 2010 during 18 May to 04 June (spring brood) and 29 June to 22 July (summer brood). Surveys were conducted at 2–5 day intervals between 0900 and 1800 h on non-rainy days and when air temperature exceeded 18°C. Surveys were repeated six times during spring brood and eight times during summer brood; the New York Karner blue recovery team currently sets an arbitrary minimum of five surveys per brood.

Different sets of patches were randomly assigned to seven trained observers, and there was no rotation of observers or patch order across surveys. Lack of rotation was due to logistical constraints, but we were able to incorporate observer and diel bias in the analysis. Modified Pollard-Yates transects (Pollard and Yates 1993) were used in 37 patches. Transect routes began from the site access point and zigzagged at approximate right angles across the site, with search time standardized by site area (see Kadlec et al. 2011). Observers walked at a steady pace gently swinging a butterfly net above the vegetation to stir any resting Karner blue into motion, and made frequent stops to scan the area for movement. All Karner blue seen at rest or in flight were counted. Observers tried to mentally track individuals and minimize double-counting, which was relatively easy given the generally low numbers across the study area.

Line-transect distance sampling (Buckland et al. 2001) was used in the remaining 13 patches. It was impractical to conduct distance sampling at 50 sites, so distance sampling was done at a subset of sites with historically high Karner blue numbers. This helped to increase observations for distance modeling and allowed estimating a large fraction of the preserve population. Transects were placed systematically from a random starting point 5–20 m from the patch edge. Transects were parallel and spaced 20 m apart except in the two largest sites where spacing was 30 m. Transects ran perpendicular to the patch’s longest axis and extended from one edge to the other. An observer walked slowly along each transect and recorded perpendicular distances to Karner blue in graduated intervals (0–0.5, 0.5–1.0, 1.0–1.5, 1.5–2.25, 2.25–3.0, 3.0–4.0 m) on both sides of the line. Distances were measured to the resting butterfly or its position prior to evasive movement. For butterflies in flight, distance was measured where the butterfly passed through an imaginary vertical plane oriented perpendicular to the transect line about an arm’s length in front of the observer. Butterflies showing communal behaviors of puddling, nectaring, chasing, or mating were recorded as cluster observations (Buckland et al. 2001), with distance measured at the geometric center.

### Optimal design for occupancy monitoring

We evaluated competing design options for occupancy using the Single-season Occupancy study Design Assistant (SODA). This new simulation-based software program helps to evaluate the tradeoff between spatial (site) and temporal (survey) replication (Guillera-Arroita et al. 2010). Design based on simulations rather than asymptotic properties of the estimators is superior under small sample size or when dealing with rare and elusive species (Guillera-Arroita et al. 2010). Depending on the project requirements, the SODA program allows the user to prioritize between maximizing estimator quality (minimize variance) or minimizing total effort. Users can run an automated search to explore different combinations of site and survey replication. Performance of the chosen design depends heavily on the simulation inputs, which are occupancy and detection probabilities. To estimate these parameters, we used the MacKenzie et al. (2003) multi-season extension to the closed population modeling framework of MacKenzie et al. (2002), as implemented in PRESENCE v3.1 (Patuxent Wildlife Research Center, United States Geological Survey, Laurel, MD). Rather than treat the broods as temporally separate entities, the multi-season approach implicitly incorporated potential density-dependent regulation from spring to summer generations (Pickens 2007; Fuller 2008). It also estimated the dynamic occupancy parameters of local extinction and colonization, helping

**Table 1** Covariates used to model metapopulation dynamics (patch use, colonization, extinction) and detection probability of Karner blue imagos in the Albany Pine Bush Recovery Area, New York State, USA

Variable	Definition and measurement
Brood	Spring versus summer generations
Canopy <sup>a</sup>	5–30% cover, or not (<5% or >30%), of woody vegetation structure at >2 m height
Captive-release <sup>b</sup>	Distance to the nearest study site receiving captive-reared Karner blue pupae during 2008–2010
Last treatment	Time (1–3, 4–5, >5 years) since last restoration or maintenance treatment (mowing, burning, tree removal)
Lupine <sup>c</sup>	Greater than or less than 970 stems per hectare
Observer	7 people total, each assigned to survey a fixed set of patches in both broods
Patch area	Estimated area of the site
Patch isolation <sup>d</sup>	Greater than or less than 200 m from an occupied patch
Peak count	Greatest number of Karner blue seen out of repeat surveys along modified Pollard-Yates transects or distance sampling transects
Sky cover	Clear (<5% cloud cover), mostly sunny (5–33%), partly sunny (33–66%), mostly cloudy (66–95%), or overcast (>95%)
Subpopulation	Single habitat patch, or any group of patches < 200 m apart
Temperature	Mean recorded for 3 min using a Kestrel <sup>®</sup> 2000 Pocket Weather Meter
Time of day	Start time (nearest minute) of a site survey
Wind speed	Mean recorded for 3 min using a Kestrel <sup>®</sup> 2000 Pocket Weather Meter

<sup>a</sup> Measured either by point-intercept sampling and densitometer along randomly placed transects (Bried and Braun 2009), or by a site-wide visual estimate; the desired cover range (5–30%) corresponds to reported benefits of partial canopy and shade for Karner blue oviposition and larval growth (Grundel et al. 1998a,b; Lane and Andow 2003; Pickens and Root 2008, 2009)

<sup>b</sup> See Gifford and O'Brien (2010) for Karner blue rearing and release protocols in the Pine Bush, and Webb (2010) for full details on Karner blue propagation efforts rangewide

<sup>c</sup> Measured by complete census or random sampling (Bried 2009; Bried and Braun 2009), stem threshold derived from Fuller (2008)

<sup>d</sup> “Occupied” = at least one Karner blue adult seen in 2010, and 200 m corresponds to the upper range of typical Karner blue flight distance (Knutson et al. 1999; USFWS 2003)

account for potential metapopulation structure (USFWS 2003; Guiney et al. 2010).

We tested a variety of auxiliary variables defined in Table 1. Detection probability was modeled in relation to air temperature, wind speed, sky cover, weather (temperature + wind speed + sky cover), time of day, and observer. Modeling diel heterogeneity in detectability is important (Bried et al. 2011) and in this case accounted for the inherent bias of not rotating the patch order. We also parameterized a model that allowed detection probability to vary between broods. We did not, however, estimate survey-specific probabilities (accounting for variation within broods; Pellet 2008) due to small sample to variable ratios and potential over-dispersion.

Occupancy (patch use) was modeled as a function of subpopulation, patch isolation, patch area, lupine, canopy, last treatment, and captive-release (see definitions in Table 1), all of which may influence Karner blue population dynamics (Grundel et al. 1998a, b; Lane and Andow 2003; Grundel and Pavlovic 2007; Pickens and Root 2008, 2009; Gifford and O'Brien 2010). Colonization was modeled as a function of patch isolation and captive-release, and extinction in relation to patch area and spring brood

peak count. Isolation and area of habitat patches are key drivers of metapopulation vital rates (Hanski et al. 1997; Pellet et al. 2007), and we view distance to the release site as a special case of isolation. Spring brood peak count served as a baseline for potential population growth between spring and summer broods.

Similar to Bailey et al. (2004), we first modeled the detection covariates one at a time while holding the other parameters constant, repeating for the covariates of occupancy, colonization, and extinction. The null model (no covariates) was included for reference in each comparison. We used Akaike's Information Criterion adjusted for small samples ( $AIC_c$ ) to select the best covariate(s) for each parameter, and then combined these terms into a final model. If multiple covariates were strongly supported ( $\Delta AIC_c < 2.0$ ; Burnham and Anderson 2002), we used model-averaging to attain the final occupancy and detection probabilities. To help with numerical convergence, all continuous covariates were standardized by their maximum value (peak count, captive-release, patch area) or to unit mean and variance (temperature, wind speed, time of day).

To find an optimal number of sites ( $S$ ) and surveys ( $K$ ) for future Karner blue occupancy monitoring, we

alternately used the mean and minimum of top-model occupancy ( $\hat{\psi}_{\text{mean}}$ ,  $\hat{\psi}_{\text{min}}$ ) and detection ( $\hat{p}_{\text{mean}}$ ,  $\hat{p}_{\text{min}}$ ) probabilities as inputs into SODA. Design was based on simulations rather than asymptotic approximations (MacKenzie and Royle 2005) because total study effort ( $S \times K$ ) was not especially large (in the statistical sense), and because we expected relatively low occupancy and detection probabilities due to small population sizes. The simulation goal was to minimize total effort based on estimator quality (precision) for various combinations of  $S$  and  $K$ . We assumed a maximum employable effort of 60 sites  $\times$  10 surveys per brood. Following Guillaera-Arroita et al. (2010), the optimal design was identified as the minimum  $S \times K$  yielding a root-mean square error (RMSE) below 0.075 for the occupancy estimator. We ran all combinations of  $S = \{10, 20, 30, 40, 50, 60\}$  and  $K = \{5, 6, 7, 8, 9, 10\}$  using 10,000 iterations. To help account for differences between broods, simulations were repeated for the spring and summer broods separately. Altogether, these 36 combinations of design parameters and four combinations of input parameters ( $\hat{\psi}_{\text{mean}}$  and  $\hat{\psi}_{\text{min}}$  coupled with spring and summer  $\hat{p}_{\text{mean}}$  and  $\hat{p}_{\text{min}}$ ) led to running 144 simulation scenarios.

#### Estimating abundance with occupancy data

Rather than restrictively assume abundance is equal across samples (as in MacKenzie et al. 2002, 2003), Royle and Nichols (2003) developed a model that reasonably assumes detection probability varies across sample locations primarily according to number of animals. Their model exploits how variation in abundance by sampled location ( $N_i$ ) creates distinct probabilities of detecting occupancy at each location. The net probability of detection at location  $i$  can be written as  $p(N_i, r) = 1 - (1 - r)^{N_i}$ , where  $r$  is a binomial sampling probability that a particular individual is detected (Royle and Nichols 2003). Average  $p$  is then estimated as a finite mixture of different detection probabilities conditional on  $N_i$ . The best (i.e., maximum likelihood) estimate of  $N_i$  is summed to estimate average abundance per sampled unit ( $\hat{\lambda}$ ). We assumed that patch-level abundances were Poisson distributed and estimated the parameters ( $r$ ,  $\lambda$ ) using PRESENCE.

We evaluated the Royle–Nichols approach against peak counts and distance sampling estimates. For peak counts, we compared the mixture model’s estimated number of Karner blue per patch ( $\hat{\lambda}$ ) to the mean raw peak count and, if necessary, the detection-adjusted peak count (raw peak divided by  $r$ ). We computed 95% confidence limits on the peak count by resampling the data 10,000 times with replacement. If the mean peak count exceeded the  $\hat{\lambda}$

interval, we concluded  $\hat{\lambda}$  was biased low and that no further testing was necessary. Otherwise, we repeated the interval estimation for means of detection-adjusted peak counts. Because the Royle–Nichols approach assumes that abundance is closed between surveys, we truncated surveys to the “peak period”, including only the peak survey and the surveys immediately before and after peak. For comparison, and because greater survey replication helps when detectability is low (Royle and Nichols 2003), the full survey data were also modeled. We ran the null model and a model parameterized with the best (lowest AIC<sub>c</sub>) occupancy and detection covariates from the previous analysis.

For comparison with distance sampling, we used distance transects as sampled units in two low-density Pine Bush subpopulations (37 and 14 transects) and two high-density Saratoga Sandplains subpopulations (35 and 16 transects). All four subpopulations received an equal number of surveys on similar dates and were analyzed using full surveys and peak period surveys. Distance sampling in Saratoga Sandplains was conducted in the same manner as described for the Pine Bush. Royle–Nichols density was estimated by truncating the line-transect distance counts to detection/non-detection data. The estimated number per transect was converted to estimated number per hectare by prorating the search area (transect length  $\times$  8 m width) out to patch area. This quantity was evaluated against the density modeling of program Distance v6.0 (Thomas et al. 2010). To help compensate for scarce observations, we fit a global model (combining both subpopulations within each recovery area) for the detection function and used this model to estimate a separate average probability density function in each subpopulation. We fit half-normal and hazard-rate key functions and added cosine adjustments to give a flexible model. The half-normal with cosine adjustment provided the best detection function for the Karner blue in Wisconsin (Brown and Boyce 1998), and the hazard-rate model with cosine adjustment was best for a group of butterfly species in forest and open-canopy habitats of Idaho (Pocewicz et al. 2010). Models were compared using AIC<sub>c</sub>, with sequential selection of cosine adjustment terms out to a maximum of five. Butterfly clusters were incorporated by regressing cluster size against the estimated detection function when significant ( $\alpha = 0.1$ ), or by using the mean cluster size if not.

## Results

### Occupancy model selection

Detection probability was most influenced by temperature (evidence ratio against the second best model = 12.6), occupancy probability by lupine and captive-release (6.9),

**Table 2** Model selection, where  $AIC_c$  is the model Akaike Information Criterion for small samples,  $\Delta AIC_c$  is the absolute difference in  $AIC_c$  with the best model,  $w$  is the model weight, and  $K$  is the number of parameters

Model	$AIC_c$	$\Delta AIC_c$	$w$	$K$
<b>Occupancy (<math>\psi</math>)</b>				
Lupine (L)	500.41	0.00	0.38	6
Captive-release (C)	500.81	0.40	0.31	6
Constant	503.16	2.75	0.10	5
Patch isolation	503.65	3.24	0.07	6
Canopy	504.31	3.90	0.05	6
Subpopulation	504.50	4.09	0.05	6
Patch area	505.54	5.13	0.03	6
Last treatment	507.74	7.32	0.01	7
<b>Detection (<math>p</math>)</b>				
Temperature (T)	503.16	0.00	0.88	5
Weather	508.32	5.15	0.07	7
Brood	510.63	7.47	0.02	5
Constant	511.57	8.52	0.01	5
Sky cover	511.68	8.41	0.01	4
Observer	513.96	10.80	0.00	5
Time of day	513.96	10.80	0.00	5
Wind speed	514.01	10.85	0.00	5
<b>Colonization (<math>\gamma</math>)</b>				
Captive-release	499.18	0.00	0.84	6
Constant	503.16	3.98	0.12	5
Patch isolation	505.18	6.00	0.04	6
<b>Extinction (<math>\varepsilon</math>)</b>				
Peak count (P)	498.44	0.00	0.78	6
Patch area	501.71	3.27	0.15	6
Constant	503.16	4.72	0.07	5
<b>Final models</b>				
$\psi(L)p(T)\gamma(C)\varepsilon(P)$	492.50	0.00	0.59	8
$\psi(C)p(T)\gamma(C)\varepsilon(P)$	493.22	0.72	0.41	8

colonization probability by captive-release (7.0), and extinction probability by peak count (5.2) (Table 2). In each case the covariate models outperformed the null model, undermining the constant probability assumption. As expected, occupancy probability increased with decreasing minimum distance to a captive-release site, and was greater at sites exceeding the lupine threshold (0.446) than at sites below it (0.146). Detection probability increased with temperature and was somewhat greater during summer brood surveys than spring brood surveys (Fig. 1). Because there were two competing factors for occupancy, two final models were run, one with occupancy constrained by lupine and the other by captive-release (Table 2). These models had similar support ( $\Delta AIC_c = 0.72$ ), thus we used model-averaged occupancy and detection probabilities for input into SODA.

## Optimal design for occupancy monitoring

We ran separate simulations for spring and summer broods to help account for the temperature-detectability relationship (Fig. 1). Assuming mean occupancy ( $\hat{\psi}_{\text{mean}} = 0.27$ ) and detection (see Fig. 1) inputs, even the smallest total effort (10 sites  $\times$  5 surveys) met the quality threshold of 0.075 RMSE for occupancy. We therefore based design recommendations on the conservative yet more informative lowest occupancy and detection probabilities (Table 3). At the 0.075 threshold, the minimum allowable effort was 360 (40 sites  $\times$  9 surveys) during spring brood and 200 (20 sites  $\times$  10 surveys) during summer brood. A sample of 20 sites instead of 40 during spring brood required 13 surveys to achieve  $RMSE < 0.075$ , and replication of 9 surveys instead of 10 during summer brood required 30 sites to achieve the threshold.

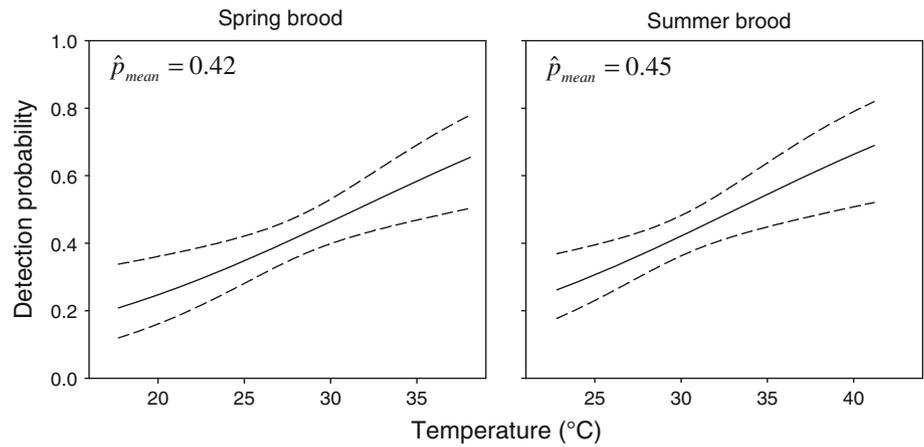
## Estimating abundance with occupancy data

Peak counts were as high as 12 butterflies in first brood and 73 butterflies in second brood. The mean observed peak number of butterflies per patch exceeded density estimates from the Royle–Nichols mixture model (Fig. 2), suggesting those estimates were biased low. Density was higher when modeled from full surveys compared to peak surveys. The Royle–Nichols estimate was also biased low compared to density estimates from program Distance, although not as severely for the low-density Pine Bush subpopulations (Table 4). Distance and Royle–Nichols point estimates were potentially similar in two cases, but the relationship was obscured by high standard error around the Royle–Nichols estimate. The Royle–Nichols estimate decreased with peak surveys whereas the Distance estimate increased (Table 4).

## Discussion

Although not central to the study objectives, results support the prevailing opinion that lupine is the most important factor controlling Karner blue population dynamics. Out of seven occupancy covariables, lupine abundance was rivaled only by distance to pupal release site in determining patch use. A caveat is that lupine stem counts for each site were simplified to binary form (using a threshold derived from Fuller 2008), potentially reducing sensitivity of the metric. Furthermore, not all factors expected to have influence (e.g., nectar diversity) were available for analysis. Grundel and Pavlovic (2007) found that host plant availability, microclimatic variables, matrix features, and spatial structure accounted for similar percentages of

**Fig. 1** Estimated temperature-specific detection probabilities ( $\hat{p}$ ) for the Karner blue butterfly. Dashed lines indicate 95% confidence intervals



**Table 3** Root-mean square errors for the occupancy estimator under competing design parameters ( $S$  = sites,  $K$  = surveys), using the minimum occupancy probability ( $\hat{\psi}_{min}$ ) and detection probability ( $\hat{p}_{min}$ ) from the final models in Table 2

Simulation input	$S$	$K$					
		5	6	7	8	9	10
$\hat{\psi}_{min} \approx 0.09, \hat{p}_{min} \approx 0.21$ (spring brood $\hat{p}$ )	10	0.4449	0.3611	0.3090	0.2628	0.2124	0.1894
	20	0.3734	0.2935	0.2365	0.1912	0.1512	0.1170
	30	0.3142	0.2368	0.1732	0.1320	0.0982	0.0838
	40	0.2609	0.1829	0.1247	0.0943	0.0627	0.0512
	50	0.2128	0.1369	0.0886	0.0612	0.0384	0.0281
	60	0.1631	0.0986	0.0630	0.0409	0.0282	0.0190
$\hat{\psi}_{min} \approx 0.09, \hat{p}_{min} \approx 0.26$ (summer brood $\hat{p}$ )	10	0.3536	0.2871	0.2312	0.1870	0.1443	0.1172
	20	0.2862	0.2086	0.1573	0.1211	0.0916	0.0680
	30	0.2246	0.1470	0.1000	0.0771	0.0596	0.0451
	40	0.1656	0.1129	0.0738	0.0538	0.0354	0.0241
	50	0.1285	0.0797	0.0461	0.0314	0.0206	0.0145
	60	0.0908	0.0516	0.0305	0.0187	0.0105	0.0079

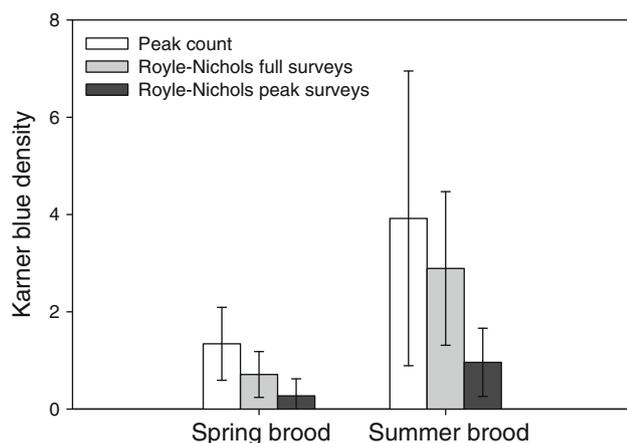
variation in Karner blue patch use, implying the need for multi-metric habitat monitoring in Karner blue recovery and not simply a focus on lupine. The New York Karner blue recovery team considers lupine as just one of many components of habitat quality (Bried 2009; Bried and Braun 2009).

Optimal design for occupancy monitoring

Butterfly activity is strongly regulated by the thermal environment (Wikstrom et al. 2009; Cormont et al. 2011), thus it was not surprising that temperature was the most important factor influencing Karner blue detection probability and therefore study design. Parietti (2009) found this to be true for a short-lived, endangered lycaenid in central Europe. Under cloudy or cool conditions butterflies are less active and harder to detect, requiring more surveys to confirm their absence with reasonable certainty. Based on our simulations, five surveys per brood, as previously

suggested for the Karner blue (Gifford and O’Brien 2010) and for other butterfly species (Zonneveld et al. 2003; Pellet 2008), may be sufficient to confirm absence in some sites but not all. For Karner blue occupancy monitoring in the Pine Bush, we recommend a design with at least 20 sites surveyed preferably 10 times each per brood. Under conservative input parameters, this design achieved a relatively precise (RMSE < 0.075) occupancy estimator during summer brood surveys. However, the strong temperature-detectability relationship suggests that more surveys ( $\geq 13$ ) may be needed during spring brood to compensate for lower temperatures and reduced butterfly activity.

Twenty sites could be prohibitive for long-term monitoring if 10 or more surveys are needed per site and brood. Removal sampling (MacKenzie and Royle 2005), where a site is no longer surveyed once presence is confirmed, would help make the monitoring program more affordable. If a removal design had been used in the



**Fig. 2** Estimated population density across 50 habitat patches based on peak counts and the Royle–Nichols mixture model for detection/non-detection data. Error bars depict 95% confidence intervals

current study, the total number of surveys (summed across sites) would have dropped from 287 to 235 during first brood and 385 to 251 during second brood, saving about 130 h of field time altogether. Removal sampling may not work for butterfly *abundance* monitoring because the survey period must span the flight period to accurately estimate peak emergence and brood size (Nowicki et al. 2005).

The parameter estimates and optimum designs found in this study may transfer to comparable systems, namely sparse populations of small-bodied, specialist butterflies in cold-temperate locations. In the absence of better information, the Pine Bush is already using the simulation inputs and results to help design occupancy surveys for the Frosted elfin (*Callophrys irus* Godart), another rare, lupine-feeding butterfly of barrens, prairies, and semi-natural grasslands.

Another option for occupancy monitoring is to use arbitrary effort and rely on occupancy-detection modeling to correct false absences. This approach has several obvious disadvantages. First and foremost, it often leads to “convenience sampling”, which will always be inferior to probability-based sampling and sampling according to objective criteria (Yoccoz et al. 2001). Second, emphasis should be placed on proper study design and quality-controlled data collection rather than relying on unnecessarily complex analyses to salvage information gathered on the basis of poorly designed protocols (MacKenzie and Royle 2005; Bailey et al. 2007; Nowicki et al. 2008). Third, occupancy-detection modeling requires repeat surveys (MacKenzie et al. 2006), which precludes removal sampling if detection occurs on the first survey at a large fraction of sites. Instead, we recommend a pilot study and simulations to estimate the minimum total effort (site  $\times$  survey replication) that allows precise interpretation of the occupancy rate, combining the recommendation with removal sampling if necessary. In the long-term, this evidence-based approach would benefit conservation programs operating under tight budgets and limited modeling capacity.

#### Estimating abundance with occupancy data

Patterns of occurrence are often a function of local population size and may carry almost as much information as counts for locally rare or low-density species (Lopez and Pfister 2001; Royle and Nichols 2003; Pellet et al. 2007). Indeed the Royle–Nichols approach has proven valuable for low-density birds (e.g., Dreitz et al. 2006; Bried et al. 2011). Bried et al. (2011) found that it increased raw point count densities of shrubland birds more than five-fold on average, and reported similar or slightly lower model abundance estimates from binary as compared to count data.

**Table 4** Karner blue estimated population density (no. ha<sup>-1</sup>) using detection/non-detection data modeling (Royle–Nichols approach) and count data modeling (Distance) in low-density (Pine Bush) versus high-density (Saratoga Sandplains) metapopulation recovery areas

Recovery area	Subpopulation	Effort <sup>a</sup>	Spring brood		Summer brood	
			Royle–Nichols (SE)	Distance (SE)	Royle–Nichols (SE)	Distance (SE)
Pine Bush	Apollo	Full	3.7 (4.1)	3.9 (1.2)	1.1 (0.4)	5.1 (1.4)
		Peak	Inestimable	7.1 (2.6)	0.8 (0.6)	5.7 (2.5)
	Kings road	Full	2.8 (1.4)	9.5 (2.8)	5.1 (6.6)	5.6 (2.4)
		Peak	2.0 (0.9)	16.3 (5.3)	0.9 (0.6)	9.7 (4.4)
Saratoga Sandplains	Edie road	Full	18.7 (8.9)	523.6 (48.9)	8.4 (2.6)	216.1 (33.0)
		Peak	10.5 (3.7)	748.7 (62.6)	8.7 (4.1)	358.7 (64.9)
	Old Gick	Full	6.0 (2.0)	111.6 (8.1)	23.6 (22.0)	232.2 (21.0)
		Peak	4.2 (1.4)	119.2 (11.0)	Inestimable	417.5 (39.3)

<sup>a</sup> Full = six first brood surveys and eight second brood surveys; Peak = three surveys per brood, including the peak count survey and the surveys immediately before and after

It makes intuitive sense for detection/non-detection data to underestimate abundance of large populations and to approximate or overestimate abundance of small populations. However, the Royle–Nichols model appeared to underestimate Karner blue abundance regardless of population size. The model may not work well for relatively high local abundances and low individual detection probabilities (Nowicki et al. 2008). Patch-scale peak counts ranged over several orders of magnitude with coefficients of variation exceeding 200%, indicating that not all patches contained low Karner blue densities. Additionally, individual detection probabilities were generally low ( $r < 0.3$ ), and our samples included fewer than the 10 surveys recommended when  $r < 0.3$  (Royle and Nichols 2003). Fewer surveys mean fewer possible detection histories and parameter space that is sparsely covered by the maximum-likelihood estimates, reducing estimator precision especially under low detectability (Guillera-Arroita et al. 2010).

Another explanation could be violation of the closure assumption (Nowicki et al. 2008), as butterflies undoubtedly emerged and died or immigrated and emigrated between surveys. Collapsing surveys around suspected peak emergence did not appear to mitigate the violation, perhaps because of lost power with only three surveys. To safely assume constant local abundance for short-lived animals, the model may need data gathered from spatial subsampling (Guillera-Arroita 2011) or repeat sampling on the same days (Nowicki et al. 2008; Parietti 2009). Another contributing factor may be that the Poisson (random) prior spatial distribution was not a reasonable assumption in the highly variegated, heavily managed Pine Bush landscape. Other error distributions are theoretically more reasonable for small or aggregated populations, such as the negative binomial or zero-inflated Poisson (Zhou and Griffiths 2007; Wenger and Freeman 2008; Joseph et al. 2009).

## Conclusions

Occupancy monitoring seems reasonable for situations like the Pine Bush where currently the wild Karner blue population is small and 60% of lupine patches are occupied. If populations are large and occupy most of the habitat area, then detection/non-detection data may not be able to discriminate patterns. None of the Pine Bush habitat patches during the 2010 survey exceeded the minimum threshold of 60 observations suggested for accurate distance data modeling (Buckland et al. 2001). As a result, reliable abundance estimates may not be attainable without prohibitively large survey effort. Nevertheless, we suspect that in many conservation programs detection/non-detection data will not gain acceptance unless those data convert to abundance.

Unfortunately, our study suggests that occupancy data may not provide a reliable shortcut in abundance-based conservation planning for sparse butterfly populations. Haddad et al. (2008) mentioned the Royle–Nichols model overcomes some of the limiting assumptions of distance sampling but needs further development for butterflies. Therefore, conservation planners dealing with sparse butterfly populations may have to find ways of incorporating occupancy as a metric in its own right, or find ways to work with raw counts. Despite obvious flaws, butterfly count-index methods may actually provide reliable population estimates (Collier et al. 2008; Haddad et al. 2008; Isaac et al. 2011; but see Harker and Shreeve 2008). Counting at peak emergence can facilitate simple estimation of brood size (Nowicki et al. 2005), and if peak counts are sufficiently large (e.g., >30 butterflies; Gross et al. 2007), then Zonneveld's (1991) model could help in tracking coarse population trends. Conservation programs for sparse butterfly populations should consider a combination of count-index and occupancy monitoring in lieu of mark-recapture, distance sampling, and other more costly methods.

**Acknowledgments** This project was enabled by the Environmental Protection Fund, New York State Department of Environmental Conservation. Stephen Bence, Beth Cooper, Amanda Dillon, Brandon Ferns, Garrett Grilli, Ashley Rathman, and Joanna Thompson conducted the butterfly surveys, and Amielle DeWan, Rebecca Shirer, and several anonymous reviewers offered valuable comments on earlier versions of the manuscript.

## References

- Anderson DR (2001) The need to get the basics right in wildlife field studies. *Wildlife Soc B* 29:1294–1297
- Anderson DR (2003) Response to Engeman: index values rarely constitute reliable information. *Wildlife Soc B* 31:288–291
- Bailey LL, Simons TR, Pollock KH (2004) Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecol Appl* 14:692–702
- Bailey LL, Hines JE, Nichols JD, MacKenzie DI (2007) Sampling design tradeoffs in occupancy studies with imperfect detection: examples and software. *Ecol Appl* 17:281–290
- Barnes JK (2003) Natural history of the Albany Pine Bush: Albany and Schenectady counties, New York. New York State Museum Bulletin #502, Albany, New York
- Bart J, Droege S, Geissler P, Peterjohn B, Ralph CJ (2004) Density estimation in wildlife surveys. *Wildlife Soc B* 32:1242–1247
- Bried JT (2009) Information costs of reduced-effort habitat monitoring in a butterfly recovery program. *J Insect Conserv* 13:615–626
- Bried JT, Braun DP (2009) Restoration monitoring for Karner blue butterfly recovery in New York State. State Wildlife Grant Service Contract #C006028, Albany, New York
- Bried JT, Langwig KE, DeWan AA, Gifford NA (2011) Habitat associations and survey effort for shrubland birds in an urban pine barrens preserve. *Landscape Urban Plan* 99:218–225
- Brown JA, Boyce MS (1998) Line transect sampling of Karner blue butterflies (*Lycaeides melissa samuelis*). *Environ Ecol Stat* 5:81–91

- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach (revised edn). Springer, New York
- Collier N, MacKay DA, Benkendorff K (2008) Is relative abundance a good indicator of population size? Evidence from fragmented populations of a specialist butterfly (Lepidoptera: Lycaenidae). *Popul Ecol* 50:17–23
- Cormont A, Malinowska AH, Kostenko O, Radchuk V, Hemerik L, Wallis-DeVries MF, Verboom J (2011) Effect of local weather on butterfly flight behavior, movement, and colonization: significance for dispersal under climate change. *Biodivers Conserv* 20:483–503
- Dreitz VJ, Lukacs PM, Knopf FL (2006) Monitoring low density avian populations: an example using mountain plovers. *Condor* 108:700–706
- Fuller SG (2008) Population dynamics of the endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov). Dissertation, State University of New York, College of Environmental Science and Forestry, Syracuse, New York
- Gall LF (1984) The effects of capturing and marking on subsequent activity in *Boloria acrocnema* (Lepidoptera: Nymphalidae), with a comparison of different numerical models that estimate population size. *Biol Conserv* 28:139–154
- Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH (2000) Abundance-occupancy relationships. *J Appl Ecol* 37:39–59
- Gifford NA, O'Brien K (2010) Karner blue butterfly recovery plan for the Albany Pine Bush Meta-population Recovery Unit. Management Plan and Final Environmental Impact Statement for the Albany Pine Bush Preserve: Appendix D. Available at [www.albanypinebush.org](http://www.albanypinebush.org)
- Gross K, Kalendra EJ, Hudgens BR, Haddad NM (2007) Robustness and uncertainty in estimates of butterfly abundance from transect counts. *Popul Ecol* 49:191–200
- Grundel R, Pavlovic NB (2007) Resource availability, matrix quality, microclimate, and spatial pattern as predictors of patch use by the Karner blue butterfly. *Biol Conserv* 135:135–144
- Grundel R, Pavlovic NB, Sulzman CL (1998a) Habitat use by the endangered Karner blue butterfly in oak woodlands: the influence of canopy cover. *Biol Conserv* 85:47–53
- Grundel R, Pavlovic NB, Sulzman CL (1998b) The effect of canopy cover and seasonal change on host plant quality for the endangered Karner blue butterfly (*Lycaeides melissa samuelis*). *Oecologia* 114:243–250
- Guillera-Arroita G (2011) Impact of sampling with replacement in occupancy studies with spatial replication. *Method Ecol Evol*. doi:10.1111/j.2041-210X.2011.00089.x
- Guillera-Arroita G, Ridout MS, Morgan BJT (2010) Design of occupancy studies with imperfect detection. *Method Ecol Evol* 1:131–139
- Guiney MS, Andow DA, Wilder TT (2010) Metapopulation structure and dynamics of an endangered butterfly. *Basic Appl Ecol* 11:354–362
- Haddad NM, Hudgens B, Damiani C, Gross K, Kuefler D, Pollock K (2008) Determining optimal population monitoring for rare butterflies. *Conserv Biol* 22:929–940
- Hanski IA, Gilpin ME (eds) (1997) Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego
- Harker RJ, Shreeve TG (2008) How accurate are single site transect data for monitoring butterfly trends? Spatial and temporal issues identified in monitoring *Lasiommata megera*. *J Insect Conserv* 12:125–133
- He F, Gaston KJ (2000) Estimating species abundance from occurrence. *Am Nat* 156:553–559
- Hui C, McGeoch MA, Reyers B, Cle Roux P, Greve M, Chown SL (2009) Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. *Ecol Appl* 19:2038–2048
- Hwang W-H, He F (2011) Estimating abundance from presence/absence maps. *Method Ecol Evol*. doi:10.1111/j.2041-210X.2011.00105.x
- Isaac NJB, Cruickshanks KL, Weddle AM, Rowcliffe JM, Brereton TM, Dennis RLH, Shuker DM, Thomas CD (2011) Distance sampling and the challenge of monitoring butterfly populations. *Method Ecol Evol*. doi:10.1111/j.2041-210X.2011.00109.x
- Johnson DH (2008) In defense of indices: the case of bird surveys. *J Wildlife Manage* 72:857–868
- Joseph LN, Field SA, Wilcox C, Possingham HP (2006) Presence-absence versus abundance data for monitoring threatened species. *Conserv Biol* 20:1679–1687
- Joseph LN, Elkin C, Martin TG, Possingham HP (2009) Modeling abundance using *N*-mixture models: the importance of considering ecological mechanisms. *Ecol Appl* 19:631–642
- Kadlec T, Tropek R, Konvicka M (2011) Timed surveys and transect walks as comparable methods for monitoring butterflies in small plots. *J Insect Conserv*. doi:10.1007/s10841-011-9414-7
- Knutson RL, Kwiilosz JR, Grundel R (1999) Movement patterns and population characteristics of the Karner blue butterfly (*Lycaeides melissa samuelis*) at Indiana Dunes National Lakeshore. *Nat Areas J* 19:109–120
- Lane CP, Andow DA (2003) Oak savanna subhabitat variation and the population biology of *Lycaeides melissa samuelis* (Lepidoptera: Lycaenidae). *Ann Entomol Soc Am* 96:799–809
- Longcore T, Lam CS, Kobernus P, Polk E, Wilson JP (2010) Extracting useful data from imperfect monitoring schemes: endangered butterflies at San Bruno Mountain, San Mateo County, California (1982–2000) and implications for habitat management. *J Insect Conserv* 14:335–346
- Lopez JE, Pfister CA (2001) Local population dynamics in metapopulation models: implications for conservation. *Conserv Biol* 15:1700–1709
- MacKenzie DI, Royle JA (2005) Designing occupancy studies: general advice and allocating survey effort. *J Appl Ecol* 42:1105–1114
- MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255
- MacKenzie DI, Nichols JD, Hines JE, Knutson MG, Franklin AB (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207
- MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, Burlington
- Marsh DM, Trenham PC (2008) Current trends in plant and animal population monitoring. *Conserv Biol* 22:647–655
- Mattoni R, Longcore T, Zonneveld C, Novotny V (2001) Analysis of transect counts to monitor population size in endangered insects. *J Insect Conserv* 5:197–206
- Murphy DD (1987) Are we studying our endangered butterflies to death? *J Res Lepidoptera* 26:236–239
- Nowicki P, Richter A, Glinka U, Holzschuh A, Toelke U, Henle K, Woyciechowski M, Settele J (2005) Less input same output: simplified approach for population size assessment in Lepidoptera. *Popul Ecol* 47:203–212
- Nowicki P, Settele J, Henry P-Y, Woyciechowski M (2008) Butterfly monitoring methods: the ideal and the real world. *Israel J Ecol Evol* 54:69–88

- Parietti D (2009) Optimal monitoring strategy for endangered short-lived butterflies. Thesis, University of Lausanne, Switzerland
- Pellet J (2008) Seasonal variation in detectability of butterflies surveyed with Pollard walks. *J Insect Conserv* 12:155–162
- Pellet J, Fleishman E, Dobkin DS, Gander A, Murphy DD (2007) An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biol Conserv* 136:483–495
- Pickens BA (2007) Understanding the population dynamics of a rare, polyvoltine butterfly. *J Zool* 273:229–236
- Pickens BA, Root KV (2008) Factors affecting host-plant quality and nectar use for the Karner blue butterfly: implications for oak savanna restoration. *Nat Areas J* 28:210–217
- Pickens BA, Root KV (2009) Behavior as a tool for assessing a managed landscape: a case study of the Karner blue butterfly. *Landscape Ecol* 24:243–251
- Pocewicz A, Morgan P, Eigenbrode SD (2010) Local and landscape effects on butterfly density in northern Idaho grasslands and forests. *J Insect Conserv* 13:593–601
- Pollard E, Yates TJ (1993) Monitoring butterflies for ecology and conservation. Chapman and Hall, London
- Pollard E, van Swaay CAM, Yates TJ (1993) Changes in butterfly numbers in Britain and the Netherlands, 1990–91. *Ecol Entomol* 18:93–94
- Pollock JF (2006) Detecting population declines over large areas with presence-absence, time-to-encounter, and count survey methods. *Conserv Biol* 20:882–892
- Powell AFLA, Busby WH, Kindscher K (2007) Status of the regal fritillary (*Speyeria idalia*) and effects of fire management on its abundance in northeastern Kansas, USA. *J Insect Conserv* 11:299–308
- Roy DB, Rothery P, Brereton T (2007) Reduced-effort schemes for monitoring butterfly populations. *J Appl Ecol* 44:993–1000
- Royle JA, Nichols JD (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790
- Singer MC, Wedlake P (1981) Capture does affect probability of recapture in a butterfly species. *Ecol Entomol* 6:215–216
- Strayer DL (1999) Statistical power of presence-absence data to detect population declines. *Conserv Biol* 13:1034–1038
- Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philos Trans R Soc B* 360:339–357
- Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *J Appl Ecol* 47:5–14
- [USFWS] U.S. Fish, Wildlife Service (2003) Final recovery plan for the Karner blue butterfly (*Lycaeides melissa samuelis*). U.S. Fish & Wildlife Service, Fort Snelling
- van Strien AJ, de Pavert RV, Moss D, Yates TJ, van Swaay CAM, Vos P (1997) The statistical power of two butterfly monitoring schemes to detect trends. *J Appl Ecol* 34:817–828
- van Swaay CAM, Nowicki P, Settele J, van Strien AJ (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodivers Conserv* 17:3455–3469
- Webb L (2010) Propagation handbook for the Karner blue butterfly, *Lycaeides melissa samuelis*, 1st edn. New Hampshire Fish and Game Department. Nongame Endangered Wildlife Program, Concord
- Wenger SJ, Freeman MC (2008) Estimating species occurrence, abundance, and detection probability using zero-inflated distributions. *Ecology* 89:2953–2959
- Wikstrom L, Milberg P, Bergman KO (2009) Monitoring butterflies in semi-natural grasslands: diurnal variation and weather effects. *J Insect Conserv* 13:203–211
- Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. *Trends Ecol Evol* 16:446–453
- Zhou S, Griffiths SP (2007) Estimating abundance from detection-nondetection data for randomly distributed or aggregated elusive populations. *Ecography* 30:537–549
- Zonneveld C (1991) Estimating death rates from transect counts. *Ecol Entomol* 16:115–121
- Zonneveld C, Longcore T, Mulder C (2003) Optimal schemes to detect the presence of insect species. *Conserv Biol* 17:476–487