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BIODIVERSITY RESEARCH

Estimation of the occupancy of butterflies in diverse biogeographic regions

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ABSTRACT

Aim We explored the extent to which occupancy of butterflies within three biogeographic regions could be explained by vegetation structure and composition, topography and other environmental attributes; whether results were consistent among regions; and whether assumptions of closure were met with assemblage-level sampling designs.

Location Chesapeake Bay Lowlands (Virginia), central Great Basin (Nevada) and western Great Basin (Nevada and California) (all USA).

Methods We applied single-season occupancy models that either assumed closure or relaxed the closure assumption to data from 2013 and 2014 for 13–15 species in each region.

Results Maximum single-year estimates of detection probabilities ranged from 0.14 to 0.99, and single-year occupancy from 0.28 to 0.98. The assumption of closure was met for a maximum of 54% of the species in a given region and year. Detection probabilities of > 90% of the species in each region increased as the categorical abundance of nectar or mud increased. Measures of the dominance or abundance of deciduous woody species and structural heterogeneity were included in the greatest number of occupancy models for the Chesapeake Bay Lowlands, which may in part reflect the intensity of browsing by white-tailed deer (*Odocoileus virginianus*). Elevation and precipitation were prominent covariates in occupancy models for Great Basin butterflies.

Main conclusions Because occupancy models do not rely on captures or observations of multiple individuals in a population, they potentially can be applied to a relatively high proportion of the species in an assemblage. However, estimation of occupancy is complicated by taxonomic, temporal and spatial variation in phenology. In multiple, widely divergent ecosystems, all or some associations between covariates and detection probability or occupancy for at least one-third of the species could not be estimated, often because a given species rarely was detected at locations with relatively low or high values of a covariate. Despite their advantages, occupancy models may leave unexplained the environmental associations with the distributions of many species.

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Keywords
Chesapeake Bay Lowlands, closure, detection, elevation, Great Basin. Lepidoptera, nectar, phenology, vegetation structure, white-tailed deer.

INTRODUCTION

The data required to precisely estimate abundance and other demographic parameters can be expensive and difficult to obtain (MacKenzie *et al.*, 2004). Single-species models of occupancy (MacKenzie *et al.*, 2002) have been used to explore the dynamics of populations, species and communities. Because occupancy models do not require data from

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captured individuals, or detections of multiple individuals in a population, they potentially can be applied to species that are problematic to handle, and to a relatively high proportion of the species in an assemblage.

Among the core assumptions of the original, single-season occupancy model (MacKenzie *et al.*, 2002) is that occupancy at a given location does not change among surveys (i.e. the closure assumption). Conducting all surveys within a relatively short period of time reduces the probability of violating this assumption (Rota *et al.*, 2009). However, doing so may not be feasible when conducting assemblage-level surveys for taxonomic groups in which species composition, phenology or activity patterns vary considerably within a season or geographically, such as anurans or invertebrates (e.g. Harms *et al.*, 2014).

The population dynamics of individual species of butterflies have been examined via both mark–recapture analyses (e.g. Brown & Ehrlich, 1980; Fleishman *et al.*, 2002; Leidner & Haddad, 2011) and occupancy models (e.g. Pellet, 2008; van Strien *et al.*, 2011; Bried *et al.*, 2012; Roth *et al.*, 2014). Collection of data on occupancy of many species within a butterfly assemblage, and therefore application of occupancy models to many species rather than to one or a small number of species, is complicated by many sources of variation in phenology (e.g. Baughman *et al.*, 1988; Weiss *et al.*, 1988). Moreover, the number of generations per year varies among and within species and can be plastic. Accordingly, it is quite difficult to gauge, *a priori*, the period in which a given species is available for sampling.

Assemblage-level surveys of butterflies traditionally addressed variation in phenology by conducting surveys every 1–3 weeks across the assemblage's flight season. This method maximizes the likelihood that at least one or two surveys will coincide with each species' flight. However, one survey is insufficient to estimate detection probability, and over several weeks, butterfly assemblages are not closed. If the flight season of a species can be estimated, then multiple surveys potentially can be used to develop a detection history. But the occupancy status of sample units is not constant across the season, and changes in occupancy are not random. Therefore, detection estimates that treat multiple surveys as replicate samples of the same species may be negatively biased, and the resulting estimates of occupancy positively biased. Another possibility, not mutually exclusive, is to sample each site repeatedly on each sampling date (the robust design; Kendall *et al.*, 1997). A third option is to relax the closure assumption by assuming that species are available for sampling at different times (Kendall *et al.*, 2013).

We explored the extent to which occupancy of butterflies in three assemblages – the Chesapeake Bay Lowlands, central Great Basin and western Great Basin – could be explained on the basis of vegetation, topography and other environmental attributes. Study locations in the central and western Great Basin fall within two different zoogeographic regions (Toiyabe and Inyo; Austin & Murphy, 1987). We included survey-specific covariates of detection probability, and we modelled occupancy and detection in multiple years as a function of the same covariates to examine the temporal transferability of results. We also examined whether results for species that occur in two of the assemblages were geographically consistent. Furthermore, we examined the degree to which assumptions of closure at the single-species level were met with an assemblage-level sampling design.

METHODS

Field methods

In the Chesapeake Bay Lowlands, our study area included the Virginia Peninsula between Toano and Hampton (Charles, City, Henrico, James City, Newport News, Williamsburg, and York Counties, Virginia) and the Middle Peninsula near West Point (King and Queen County and King William County, Virginia). Our central Great Basin study area included much of the adjacent Shoshone Mountains and Toiyabe and Toquima Ranges (Lander and Nye Counties, Nevada). In the western Great Basin, our study area included the east slope of the Sierra Nevada and the adjacent Wassuk Range and Sweetwater Mountains (Mono County, California and Mineral, Douglas, and Lyon Counties, Nevada).

In the Chesapeake Bay Lowlands, we sampled butterflies in 2013 and 2014 along 65 0.5-km transects within upland coniferous and deciduous forests and within riparian forests [for species composition, see Monette & Ware (1983) and Weakley *et al.* (2012)]. In the central and western Great Basin, we located transects along the full elevational gradients of montane canyons. We sampled 64 transects in the central Great Basin in 1995. We sampled 46 of those, and another 39 transects, in 2013 and 2014. In the western Great Basin, we sampled the same 100 transects in 2013 and 2014. Among the dominant land cover types in the Great Basin are coniferous woodlands, shrubsteppe dominated by sagebrush (*Artemisia* spp.) and riparian woodlands dominated by deciduous trees and shrubs. We sampled each transect approximately every 2 weeks throughout the majority of the flight season (late May through mid-August; generally six visits per season). During every visit, we walked the length of each transect at a near-constant pace and recorded all species detected (Pollard & Yates, 1993; Pullin, 1995).

During each visit in 2013 and 2014, we recorded the relative abundance (none, low, moderate, high) of individual plants (primarily forbs) from which one or more species of butterflies in those ecosystems are known to take nectar and, in the Great Basin, the relative abundance of sources of mud, such as stream crossings (none, low, moderate, high). Female fecundity in some species is related to nectar volume (Boggs & Ross, 1993), and many species feed on dissolved minerals in moist soil (Scudder, 1889; Arms *et al.*, 1974). We grouped some nectar and mud classes for analyses

because the number of transects in a given class was small. In the Chesapeake Bay Lowlands, we grouped the none and low nectar classes in 2013 and referenced the new class as low abundance; we grouped nectar classes none, low and moderate in 2014 and referenced the new class as low. In the Great Basin, we grouped the none and low nectar classes and referenced the new class as low. We grouped mud classes moderate and high and referenced the new class as moderate.

We included five covariates in occupancy models for butterflies in the Chesapeake Bay Lowlands: the length (km) of all edges between forest and agriculture, ruderal or herbaceous-developed land cover; structural heterogeneity of the understorey from 0 to 3 m above the ground [the approximate height of the white-tailed deer (*Odocoileus virginianus*) browse line (Allombert *et al.*, 2005; Bressette *et al.*, 2012)]; the proportion of the basal area of trees (≥ 10 cm dbh) that was deciduous; the number of deciduous stems (single- or multiple-stemmed trees or shrubs; 1 to < 10 cm dbh) below the canopy; and the categorical abundance of nectar. We included categorical abundance of nectar as a detection covariate. To derive edge length, we first obtained data on land cover at 30-m resolution (2013 Existing Vegetation Type data; www.landfire.gov). Next, we delineated edges between land cover types in Geospatial Modeling Environment (www.spatialecology.com/gme/index.htm). We then derived edge length in ARCGIS 10.1 (ESRI, Redlands, CA, USA) as the mean of the 30-m cells within a 90-m buffer on either side of the transect. We used light detection and ranging (LIDAR) data that were captured from 22 April through 10 May 2010 and 21 through 31 March 2013 to estimate structural heterogeneity of the understorey on the basis of density of returns at 10-m resolution, averaged among the 10-m cells within the 90-m buffer. We measured the proportion of basal area of trees that was deciduous within three circular plots (15 m radius) that were randomly placed within the 90-m buffer. We counted the number of deciduous stems within three circular plots (7.5 m radius), each of which was embedded within one of the 15-m plots.

We included elevation, the square of elevation, terrain roughness, precipitation in the water year (1 October–30 September) of sampling and categorical abundance of nectar and mud as covariates of occupancy in the Great Basin. All reasonably might be expected to affect habitat quality for many butterfly species (e.g. Fleishman *et al.*, 2001a,b). We included categorical abundance of nectar and mud as detection covariates. We derived mean elevation of the transect from a 10-m digital elevation model (www.ned.usgs.gov), assuming that the sampled area included 25 m on either side of the transect. We used a digital elevation model to derive terrain ruggedness (Riley *et al.*, 1999) within 30-m circular neighbourhoods and then averaged terrain ruggedness for the transect. We derived precipitation at 4-km resolution from the Parameter–elevation Relationships on Independent Slopes Model (PRISM).

Analysis methods

We used single-season occupancy models to analyse the data collected from all transects and on all visits during 2013 and 2014 for 13 species of butterflies in the Chesapeake Bay Lowlands and 15 species each in the central and western Great Basin (Table 1). We generally restricted our analyses to species that were detected in ≥ 30% and ≤ 70% of the transects in each year and that are not migrants, highly vagile (e.g. thousands of metres), or do not complete their entire life cycle in the ecosystem. We also modelled single-season occupancy of the 15 species in the central Great Basin in 1995.

We fit two parameterizations (MacKenzie *et al.*, 2002; Kendall *et al.*, 2013) of the single-season occupancy model. Both include the parameters ψ_i, the probability that a given species occupies transect i, and p_{ij}, the probability that the species is detected given that it is present on transect i during visit j. Kendall *et al.*'s (2013) model also allows a single entry and exit of the species from each transect during the sampling period; the probabilities of entry and exit between visits j and $j + 1$ are denoted as β_{ij} and d_{ij}, respectively. The model assumes that between the species' entry and exit, it is present and therefore available for sampling. However, p_{ij} may vary during the period in which the species is available. Because we focused on estimating ψ_i and p_{ij}, we do not report estimates of β_{ij} and d_{ij}. Prior to the analysis, we identified attributes of transects that we hypothesized could affect ψ_i and p_{ij}, and specified mathematical models [referenced as submodels (Taylor *et al.*, 2005; Pilliod & Scherer, 2015)] to represent those relations.

We fit models to the occupancy data in two stages. In the first stage, we evaluated submodels of p_{ij}, β_{ij} and d_{ij} and tested the assumption of closure. For both parameterizations, the sets of submodels of p_{ij} included effects of categorical abundance of nectar (calculated as the maximum abundance on any visit during the season), mud (in the Great Basin; the maximum abundance on any visit) or both. In all cases, we used the highest abundance class of nectar or mud as the intercept. For example, in the Great Basin and in the Chesapeake Bay Lowlands in 2013, we estimated whether p_{ij} was different on transects with no or little nectar, or on transects with a moderate abundance of nectar, than on transects with a high abundance of nectar. We report maximum single-year p_{ij} in the text and all p_{ij} in Appendix S3 in Supporting Information.

We also included a fixed effect of visit (i.e. we estimated p_{ij} for each survey) in the submodels. Furthermore, the submodels included additive effects of nectar and visit and of mud and visit. For the models in which the closure assumption was relaxed, we estimated β_{ij} and d_{ij} as linear and quadratic functions of visit. We specified full models that included every combination of the submodels of p_{ij}, β_{ij} and d_{ij} with an intercept-only submodel of occupancy. We used Akaike's information criterion adjusted for small sample sizes (AIC_c) and Akaike weights (w_m), where m indexes models, to compare submodels of p_{ij}, β_{ij} and d_{ij} (Burnham &

Table 1 Maximum single-year probabilities of detection and occupancy of butterflies in three ecosystems.

	Detection			Occupancy		
	1995	2013	2014	1995	2013	2014
Chesapeake Bay Lowlands						
Ancyloxypha numitor		0.49* (0.27–0.71)	0.31 (0.17–0.50)		0.51 (0.33–0.69)	†
Poanes zabulon		0.74 (0.48–0.90)	0.57 (0.31–0.80)		0.40 (0.27–0.55)	0.43 (0.27–0.62)
Epargyreus clarus		0.46 (0.27–0.66)	0.43*(0.24–0.64)		0.84 (0.28–0.99)	0.47 (0.27–0.67)
Papilio troilus		0.64*(0.48–0.78)	0.48 (0.36–0.61)		0.75 (0.55–0.88)	0.72 (0.40–0.91)
Calycopis cecrops		0.64* (0.41–0.82)	0.48* (0.32–0.65)		0.55 (0.34–0.75)	0.67 (0.40–0.86)
Cupido comyntas		0.73 (0.60–0.83)	0.63* (0.43–0.80)		0.67 (0.51–0.80)	0.42 (0.30–0.55)
Celastrina ladon		0.34 (0.20–0.52)	0.28* (0.21–0.36)		0.89 (0.59–0.98)	0.65 (0.47–0.79)
Phyciodes tharos		0.31 (0.23–0.41)	0.34* (0.20–0.52)		0.85 (0.31–0.99)	0.66 (0.32–0.89)
Vanessa virginiensis		0.53* (0.26–0.79)	0.16* (0.08–0.30)		0.52 (0.26–0.78)	0.28 (0.14–0.48)
Limenitis arthemis		0.41* (0.23–0.63)	0.14* (0.09–0.22)		0.83 (0.45–0.97)	0.51 (0.25–0.76)
Lethe appalachia		0.51* (0.21–0.81)	0.42 (0.26–0.61)		0.38 (0.18–0.63)	0.41 (0.21–0.64)
Hermeuptychia sosybius		0.70* (0.53–0.83)	0.58* (0.42–0.72)		0.71 (0.57–0.83)	0.65 (0.51–0.76)
Cercyonis pegala		0.53 (0.28–0.77)	0.63 (0.42–0.80)		0.30 (0.19–0.44)	0.34 (0.23–0.47)
Central Great Basin						
Hesperia comma	0.67 (0.57–0.75)	0.60 (0.41–0.76)	0.42 (0.26–0.59)	0.85 (0.70–0.94)	0.83 (0.59–0.94)	0.66 (0.39–0.85)
Papilio rutulus	0.90 (0.80–0.96)	0.84 (0.65–0.94)	0.74 (0.57–0.86)	0.98 (0.16–1.00)	0.79 (0.59–0.91)	0.71 (0.53–0.84)
Lycaena heteronea	0.69 (0.47–0.85)	0.50 (0.32–0.68)	0.56 (0.35–0.75)	0.60 (0.41–0.76)	0.79 (0.44–0.94)	0.44 (0.29–0.60)
Satyrium behrii	0.69* (0.45–0.86)	0.77 (0.59–0.89)	0.67* (0.52–0.80)	0.75 (0.60–0.86)	0.82 (0.69–0.90)	0.88 (0.59–0.97)
Incisalia eryphon	0.81 (0.66–0.91)	0.74 (0.58–0.86)	0.81 (0.33–0.97)	0.76 (0.60–0.87)	0.60 (0.42–0.76)	0.71 (0.52–0.84)
Celastrina ladon	0.71* (0.52–0.84)	0.97 (0.78–1.00)	0.63 (0.52–0.73)	0.69 (0.54–0.81)	0.78 (0.36–0.96)	0.73 (0.55–0.85)
Glaucopsyche piasus	0.91 (0.80–0.96)	0.67 (0.44–0.83)	0.42 (0.25–0.62)	0.85 (0.73–0.92)	0.61 (0.40–0.78)	0.79 (0.60–0.91)
Speyeria callippe	0.87 (0.17–1.00)	0.62 (0.40–0.79)	0.77* (0.58–0.90)	0.83 (0.67–0.93)	0.78 (0.58–0.90)	0.69 (0.48–0.84)
Nymphalis antiopa	0.55 (0.42–0.68)	0.50* (0.42–0.58)	0.63 (0.44–0.78)	0.92 (0.33–1.00)	0.72 (0.54–0.85)	0.67 (0.46–0.82)
Limenitis weidemeyerii	0.86 (0.71–0.94)	0.95 (0.86–0.98)	0.88 (0.77–0.94)	0.92 (0.72–0.98)	0.57 (0.46–0.67)	0.77 (0.61–0.88)
Chlosyne acastus	0.86 (0.45–0.98)	†	0.96 (0.69–1.00)	0.62 (0.46–0.76)	0.47 (0.36–0.57)	0.46 (0.34–0.59)
Phyciodes pulchellus	0.71 (0.44–0.88)	0.28 (0.17–0.41)	0.75 (0.52–0.90)	0.61 (0.44–0.76)	0.78 (0.30–0.97)	0.54 (0.36–0.71)
Euphydryas anicia	0.50 (0.29–0.71)	0.85 (0.05–1.00)	0.65 (0.15–0.95)	0.89 (0.42–0.99)	0.48 (0.28–0.69)	0.77 (0.52–0.91)
Coenonympha tullia	0.92 (0.73–0.98)	0.83 (0.68–0.92)	0.74 (0.30–0.95)	†	0.80 (0.65–0.89)	0.77 (0.59–0.89)
Cercyonis sthenele	0.89 (0.79–0.95)	0.94 (0.82–0.98)	0.82 (0.69–0.91)	0.69 (0.53–0.81)	0.68 (0.56–0.78)	0.69 (0.54–0.80)
Western Great Basin						
Hesperia juba		0.84* (0.71–0.92)	0.54* (0.40–0.67)		0.57 (0.46–0.67)	0.78 (0.62–0.88)
Hesperia comma		0.93 (0.77–0.98)	0.84 (0.66–0.93)		0.62 (0.50–0.73)	0.62 (0.51–0.72)
Polites sonora		0.39 (0.21–0.59)	0.63* (0.31–0.86)		0.52 (0.28–0.75)	0.48 (0.32–0.64)
Papilio rutulus		0.81 (0.59–0.92)	0.58 (0.48–0.67)		0.73 (0.53–0.86)	0.75 (0.63–0.84)
Lycaena arota		0.73 (0.36–0.93)	0.63 (0.44–0.79)		0.51 (0.39–0.62)	0.55 (0.39–0.70)
Satyrium behrii		0.66 (0.45–0.82)	0.58* (0.38–0.76)		0.67 (0.31–0.90)	0.59 (0.42–0.74)

Table 1 Continued.

	Detection			Occupancy		
	1995	2013	2014	1995	2013	2014
Incisalia eryphon		0.97* (0.88–0.99)	0.81 (0.62–0.92)		0.46 (0.33–0.59)	0.67 (0.42–0.85)
Plebejus saepiolus		0.88 (0.64–0.97)	0.94 (0.67–0.99)		0.47 (0.30–0.65)	0.55 (0.39–0.71)
Icaricia icariodes		0.89 (0.72–0.96)	0.99 (0.94–1.00)		0.67 (0.54–0.78)	0.70 (0.59–0.80)
Icaricia lupini		0.77* (0.59–0.89)	0.95* (0.86–0.98)		0.48 (0.36–0.61)	0.52 (0.39–0.65)
Speyeria zerene		0.34* (0.20–0.53)	0.57 (0.31–0.79)		0.34 (0.22–0.47)	0.31 (0.21–0.45)
Phyciodes pulchellus		0.57 (0.31–0.79)	0.95 (0.64–0.99)		0.47 (0.27–0.68)	0.46 (0.32–0.60)
Limenitis weidemeyerii		0.91 (0.71–0.98)	0.82 (0.59–0.94)		0.42 (0.29–0.55)	0.36 (0.27–0.46)
Cercyonis sthenele		0.70 (0.53–0.83)	†		0.45 (0.35–0.56)	0.49 (0.39–0.59)
Cercyonis oetus		0.84 (0.71–0.92)	0.89 (0.72–0.96)		0.58 (0.47–0.68)	0.49 (0.37–0.61)

Lower and upper 95% confidence intervals in parentheses. Occupancy probabilities were obtained from models that did not include environmental covariates. Nomenclature for butterflies in the Great Basin follows Fleishman *et al.* (1997) and Austin (1998). We included all models of detection probability within 2 AIC_c of the highest ranked model in our models of occupancy; we present the highest ranked models here.

*AIC_c of the highest ranked closure model > 2 AIC_c higher than that of the highest ranked relaxed closure model.

†Value could not be estimated.

Anderson, 2002). We retained all models from the first stage of modelling with AIC_c values within 2 units of the highest ranked model and included them in the second stage of modelling.

In the second stage of modelling, we evaluated submodels of ψ_i. The set of submodels included effects of each covariate (with classes of nectar and mud grouped as described above). For the Chesapeake Bay Lowlands, our submodels also included an interaction between edge length and structural heterogeneity. For the central and western Great Basin, our submodels also included five nonlinear effects or combinations of effects: elevation and the square of elevation, to account for a potential quadratic relationship between elevation and ψ_i; and additive effects of elevation and terrain ruggedness; elevation and mud; elevation and nectar; and nectar and mud. We combined all submodels of ψ_i with the submodels of other parameters from the model that was ranked highest in the first stage. Because many models that included covariates generated highly imprecise occupancy estimates, we report ψ_i from the intercept-only submodel. Complete model-selection results are in Appendix S2.

We standardized and centred all continuous covariates. We calculated Pearson's product–moment correlations between continuous covariates. We did not include two continuous covariates in a given model if their correlation coefficient was ≥ 0.60. We examined box-and-whisker plots, created in R (R Core Team, 2013), to assess correlations between continuous and categorical covariates. We used the plots to anticipate potential confounding effects of multicollinearity. When a strongly supported model included both a continuous and a categorical covariate, we examined whether the magnitude or direction of regression coefficients in the latter model and in models that included each of those covariates alone was considerably different. We included a maximum of two covariates in additive models.

We characterized the strength of association between response variables and covariates on the basis of the AIC_c values of the models in which they were included and the degree to which estimates of the 95% confidence intervals (CIs) of the regression coefficients overlapped zero. If a covariate was included in the model with the lowest AIC_c, or in a model with an AIC_c value within 2 units of the model with the lowest AIC_c, we considered it to be associated with p_{ij} or ψ_i and report it below. We considered the strength of association of a covariate with p_{ij} or ψ_i to be greater if its CIs did not overlap zero than if its CIs overlapped zero. We report associations with continuous covariates as regression coefficients and associations with categorical covariates as effect sizes.

When data are limited or probabilities approach 0 or 1, parameters may not be estimated correctly. Evidence of incorrect estimates includes noticeably high values of parameters or their standard errors and estimates of standard errors that are near zero. We examined estimates of model parameters and used the diagnostics in Program MARK to

identify potentially questionable estimates. We also considered regression coefficients or effect sizes with absolute values ≥ 10 to be questionable; because this criterion is arbitrary, we report values of the coefficients and their CIs in Appendix S3.

RESULTS

In the Chesapeake Bay Lowlands, we detected 59 species in 2013 and 55 species in 2014. In the central Great Basin, we detected 77 species in 1995, 70 in 2013 and 75 in 2014. In the western Great Basin, we detected 86 species in 2013 and 83 species in 2014. Species lists are in Appendix S1.

A model of closure was more strongly supported than a model of relaxed closure (AIC_c of the highest ranked closure model > 2 AIC_c higher than that of the highest ranked relaxed closure model) for seven of the 13 species in the Chesapeake Bay Lowlands in 1 year and for another four species in both years (Table 1). In the central Great Basin, a model of closure was supported in 1 year for three species and in 2 years for one species. In the western Great Basin, a model of closure was strongly supported in both years for two species and in 1 year for four species.

Below, we include the results of detection and occupancy models in which some parameters could not be estimated or were imprecisely estimated. By doing so, we aimed to be transparent and to allow one to draw their own context-specific inferences about the potential information to be gained from applying occupancy models to data on butterfly detections. Nevertheless, we caution that any other parameter estimates in these models may be unreliable. Parameter estimates in models for species for which detection parameters could not be estimated also may be unreliable.

Chesapeake Bay Lowlands

Maximum single-year estimates of detection probabilities (p_{ij}) ranged from 0.14 to 0.74 (Table 1). Nectar was associated with p_{ij} of nine species in one of 2 years and three species in both years. In all but one case, as the abundance of nectar increased, p_{ij} increased (Table 2). Effect sizes for any nectar class ranged from 4.35 (*Cupido comyntas*, 2013; negative association) to 0.38 (*Hermeuptychia sosybius*, 2013; negative) (Appendix S3). Abundance of nectar was not associated with p_{ij} of *Cercyonis pegala.*

Occupancy (ψ_I) ranged from 0.28 (*Vanessa virginiensis*, 2014) to 0.89 (*Celastrina ladon*, 2013) (Table 1). We identified covariates associated with ψ_i of five species in 1 year and eight species in 2 years (Table 3). In the latter cases, one or more of the same covariates were associated with ψ_i of five of the species in both years.

The deciduous proportion of the basal area of trees was associated with ψ_i of nine species in 2013 and six species in 2014 (Table 3), with regression coefficients from −5.57 (*Phyciodes tharos*, 2013) to 1.15 (*Lethe appalachia*, 2013) (Appendix S3). Occupancy of one species in 2013 and five species in 2014 was associated with the number of deciduous stems. Regression coefficients ranged from −5.15 (*C. pegala*, 2014) to 1.16 (*L. appalachia*, 2014). Structural heterogeneity was associated with ψ_i of four species in 2013 and two

Table 2 Direction of estimates of effect sizes in models with the lowest AIC_c, or in models with AIC_c values within 2 units of the model with the lowest AIC_c, indicating that abundance of nectar was associated with detection probabilities of butterflies in the Chesapeake Bay Lowlands.

	2013		2014
	None or low abundance, compared with high abundance	Moderate abundance, compared with high abundance	None, low or moderate abundance, compared with high abundance
Ancyloxypha numitor	–	–	*
Poanes zabulon	–	–	*
Epargyreus clarus	–	–	*
Papilio troilus	–	–	–
Calycopis cecrops	–	–	
Cupido comyntas	–	–	–
Celastrina ladon			–
Phyciodes tharos	*	–	*
Vanessa virginiensis	–	–	
Limenitis arthemis	–	+	–
Lethe appalachia	*	–	†
Hermeuptychia sosybius	–	–	
Cercyonis pegala			

Negative direction indicates that the probability of detection increased as the abundance of nectar increased. Shaded cells indicate that 95% confidence intervals did not include zero. Estimates of the effect sizes are in Appendix S3.
*Effect size could not be estimated.
†Estimated effect size was ≥ |10|.

Table 3 Direction of estimates of regression coefficients and effect sizes of covariates associated with occupancy of butterflies in the Chesapeake Bay Lowlands.

	2013					2014				
	Edge length + sh	Edge length	sh	Deciduous proportion of basal area of trees	The number of deciduous stems	Edge length	sh	Deciduous proportion of basal area of trees	The number of deciduous stems	Nectar abundance (none, low or moderate, compared with high)
Ancyloxypha numitor			−	+		*	*		†	
Poanes zabulon				+				*		
Epargyreus clarus							+			
Papilio troilus	−		+						†	
Calycopis cecrops			+						−	
Cupido comyntas				−				−		
Celastrina ladon					*	−		+	−	−
Phyciodes tharos		+	+	−	†			−		
Vanessa virginiensis				−				−		
Limenitis arthemis				−	−			−	−	
Lethe appalachia				+					+	
Hermeuptychia sosybius				+			−	+		
Cercyonis pegala				−					−	

sh, structural heterogeneity.

Regression coefficients and effect sizes are from models with the lowest AIC_c, or models with AIC_c values within 2 units of the model with the lowest AIC_c. Directions for abundance of nectar are relative to high abundance. Shaded cells indicate that 95% confidence intervals for estimates of the regression coefficient or effect size did not include zero. Estimates of the regression coefficients and effect sizes are in Appendix S3.

*Regression coefficient or effect size could not be estimated.

†Estimate of the regression coefficient or effect size was ≥ |10|.

species in 2014, with regression coefficients from −0.94 (*Ancyloxypha numitor*, 2013) to 3.06 (*Epargyreus clarus*, 2014). Edge length was associated with ψ_i of *P. tharos* in 2013 (regression coefficient 0.84) and *C. ladon* in 2014 (−0.30). In 2013, the interaction between edge length and structural heterogeneity was associated with ψ_i of *Papilio troilus* (regression coefficient −1.39).

Central Great Basin

Maximum single-year p_{ij} ranged from 0.28 to 0.97 (Table 1). Abundance of nectar was associated with p_{ij} of three species in 2013 only, two species in 2014 only and two species in both years (Table 4). Abundance of mud was associated with p_{ij} of two species in 2013 only, one species in 2014 only and six species in both years. Detection probability increased as abundance of nectar or mud increased in all but one case. Effect sizes for either nectar class ranged from 0.41 to 2.70 (both *Lycaena heteronea*, 2013; both negative associations) (Appendix S3). Minimum and maximum effect sizes for either mud class were 0.10 (*Nymphalis antiopa*, 2014; negative association) and 4.97 (*Papilio rutulus*, 2014; negative), respectively.

Single-year ψ_i ranged from 0.44 (*L. heteronea*, 2014) to 0.98 (*P. rutulus*, 1995) (Table 1). Regression coefficients could not be estimated or were ≥ |10| for *N. antiopa* in 1995, *L. heteronea* and *Satyrium behrii* in 2014 and *C. ladon* and *Phyciodes pulchellus* in 2013 (Table 5). In all other cases, one or more covariates were associated with ψ_i of all species in each year. Occupancy of *S. behrii* and *C. ladon* was associated with elevation only. At least some of the covariates that were associated with ψ_i of the other species varied among years.

Elevation (whether as a linear or a quadratic function) was associated with ψ_i of six species in 1995, 11 species in 2013 and 13 species in 2014 (Table 5). Regression coefficients ranged from −7.24 (*S. behrii*, 1995, linear relation) to 7.98 (*Coenonympha tullia*, 1995, linear) (Appendix S3). Occupancy of six species in 2013 and five species in 2014 was associated with mud abundance. Minimum and maximum effect sizes for either mud class were 0.04 (*Limenitis weidemeyerii*, 2013; positive association) and 4.35 (*P. rutulus*, 2014; positive), respectively. Precipitation was associated with ψ_i of seven species in 1995 and three species in each of 2013 and 2014, with regression coefficients from −5.15 (*Chlosyne acastus*, 1995) to 1.56 (*Speyeria callippe*, 1995). Nectar abundance was associated with ψ_i of four species in 2013 and five in 2014. Minimum and maximum effect sizes for either nectar class were 0.46 (*S. callippe*, 2013; negative association) and 8.00 (*Incisalia eryphon*, 2014; negative), respectively. Occupancy of three species in 1995, four in 2013 and three in 2014 was associated with terrain ruggedness. Regression coefficients ranged from −1.02 (*Hesperia comma*, 2014) to 3.51 (*C. tullia*, 1995).

Table 4 Direction of estimates of effect sizes of covariates associated with detection probabilities of butterflies in the central Great Basin.

	2013				2014			
	Nectar abundance (compared with high abundance)		Mud abundance (compared with high abundance)		Nectar abundance (compared with high abundance)		Mud abundance (compared with high abundance)	
	None or low	Moderate	None	Low	None or low	Moderate	None	Low
Hesperia comma			–	–	–	–		
Papilio rutulus			–	–			–	–
Lycaena heteronea	–	–			–	+		
Satyrium behrii	*	*			–	–		
Incisalia eryphon			–	–			*	*
Celastrina ladon			–	–			–	–
Glaucopsyche piasus	–	–			*	*		
Speyeria callippe	*	–			–	–		
Nymphalis antiopa			–	–			–	–
Limenitis weidemeyerii			–	–			–	–
Chlosyne acastus							*	–
Phyciodes pulchellus			–	–			*	–
Euphydryas anicia	*	–			*	*		
Coenonympha tullia	–	–					*	*
Cercyonis sthenele			–	–			–	–

Effect sizes are from models with the lowest AIC_c, or models with AIC_c values within 2 units of the model with the lowest AIC_c. Low, low abundance; moderate, moderate abundance. Negative direction indicates that the probability of detection increased as the abundance of nectar or mud increased. Shaded cells indicate that 95% confidence intervals did not include zero. Estimates of the effect sizes are in Appendix S3.
*Effect size could not be estimated.

Western Great Basin

Maximum single-year p_{ij} for a given species ranged from 0.34 to 0.99 (Table 1). Abundance of nectar was associated with p_{ij} of two species in 2014 only and four species in both 2013 and 2014 (Table 6). Abundance of mud was associated with p_{ij} of four species in 2013 only, two in 2014 only and three in both years. Effect sizes for either nectar class ranged from 0.23 (*Polites sonora*, 2014; positive association) to 3.15 (*Icaricia lupini*, 2014; negative) (Appendix S3). Effect sizes for either mud class fell between 1.04 (*H. comma*, 2014; negative association) and 5.15 (*Plebejus saepiolus*, 2014; negative), respectively.

Single-year ψ_i ranged from 0.31 (*Speyeria zerene*, 2014) to 0.78 (*Hesperia juba*, 2014) (Table 1). Regression coefficients and effect sizes could not be estimated or were $\geq |10|$ for *P. rutulus* and *Lycaena arota* in 2014 and *S. behrii* in 2013 (Table 7). In all other cases, one or more covariates were associated with ψ_i of all species in both years. A single covariate was associated with ψ_i of *Icaricia icarioides* (elevation, quadratic form), *S. zerene* (precipitation) and *L. weidemeyerii* (precipitation) in both 2013 and 2014. At least some of the covariates that were associated with ψ_i of the other species varied between years.

Elevation (whether as a linear or a quadratic function) was associated with ψ_i of nine species in 2013 and six species in 2014 (Table 7). Regression coefficients ranged from −2.22 (*Cercyonis sthenele*, 2013, linear relation) to 2.71 (*P. saepiolus*, 2014, linear) (Appendix S3). Precipitation was associated with ψ_i of eight species in 2013 and seven in 2014, with regression coefficients from −4.06 (*H. comma*, 2013) to 8.14 (*S. zerene*, 2014). Occupancy of five species in either year was associated with terrain ruggedness. Minimum and maximum regression coefficients were −1.26 (*P. saepiolus*, 2014) and 1.70 (*L. arota*, 2013), respectively. Mud abundance was associated with ψ_i of *P. saepiolus* in 2013 and *P. sonora* in both years. Minimum and maximum effect sizes for either mud class were 1.00 (*P. sonora*, 2013; negative association) and 3.46 (*P. sonora*, 2014; negative), respectively. Nectar abundance was associated with ψ_i of two species in 2014. The minimum and maximum effect sizes for either nectar class, 0.07 (positive association) and 2.00 (negative), both were associated with ψ_i of *P. saepiolus* in 2014.

DISCUSSION

We estimated p_{ij} and ψ_i, and environmental covariates associated with those probabilities, for a majority of modelled butterfly species in three ecosystems while accounting for violations of the closure assumption. The extent to which the closure assumption was met varied among ecosystems and years, and was greater in the Chesapeake Bay Lowlands than in the Great Basin. Within each ecosystem, the number and identity of species for which the closure assumption was

Table 5 Direction of estimates of regression coefficients and effect sizes of covariates associated with occupancy of butterflies in the central Great Basin.

	1995				2013								2014							
									Nectar abundance (compared with high abundance)		Mud abundance (compared with high abundance)						Nectar abundance (compared with high abundance)		Mud abundance (compared with high)	
	el	el^2	tr	pr	el	el^2	tr	pr	None/low	Mod	None	Low	el	el^2	tr	pr	None/low	Mod	None	Low
Hesperia comma	–	+	+		–			–					–	–	–					
Papilio rutulus				+					–	+	–	–	†						*	+
Lycaena heteronea				+	+		+	*						*		†				
Satyrium behrii	†				+	–							*				*	*		
Incisalia eryphon				–	–				–	+			–	–			†	†	–	–
Celastrina ladon	–								*	†			–	+					*	*
Glaucopsyche piasus	+			+	+						–	–	+	–			–	*		
Speyeria callippe				+	+			+	–	–			+	–		+	*	–	*	–
Nymphalis antiopa	†				+						–	–	–				–	–		
Limenitis weidemeyerii	–	+	+		–	–					–	+	–		–				–	–
Chlosyne acastus				–			+				–	+	–			–				
Phyciodes pulchellus		–			†				†	†			–				*	–		
Euphydryas anicia	+					–	+	–					+		+					
Coenonympha tullia	†		+		–		+							–						
Cercyonis sthenele				–	–				*	+	+	+	–			+			+	–

el, elevation; el^2, square of elevation; tr, terrain ruggedness; pr, precipitation; none/low, none or low abundance; mod, moderate abundance.
Regression coefficients and effect sizes are from models with the lowest AIC_c, or models with AIC_c values within 2 units of the model with the lowest AIC_c. Directions for abundance of nectar and mud are relative to high abundance. Shaded cells indicate that 95% confidence intervals for estimates of the regression coefficient or effect size did not include zero. Estimates of the regression coefficients and effect sizes are in Appendix S3.
*Regression coefficient or effect size could not be estimated.
†Estimated regression coefficient or effect size was ≥ |10|.

met also varied among years. It is possible that the canyon topography of the montane Great Basin leads to greater variation in emergence dates (e.g. because solar insolation, temperature and precipitation vary along gradients of elevation and aspect) and to more extensive movements of individuals (e.g. because air flow along the elevational gradient can be strong) than in the relatively flat Chesapeake Bay Lowlands. Additionally, 85% of the species we modelled in the Chesapeake Bay Lowlands always or sometimes have more than one brood per year (thus would be available for sampling more consistently), compared with 20% and 33% of the species in the central and western Great Basin, respectively.

Consistent with previous work in these systems, we observed considerable turnover in species composition (e.g. Fleishman & Mac Nally, 2003). We are among the first to estimate occupancy of a substantial proportion of butterfly species in an assemblage on the basis of surveys conducted throughout flight seasons over multiple years, and to evaluate the temporal consistency of associations between environmental covariates and occupancy. However, in each ecosystem, associations between one or more covariates and p_{ij} or ψ_i for at least one-third of the species – a total of 25 species-by-year models across the three ecosystems – either could not be estimated or seemed implausibly large (i.e. ≥ |10|). As noted above, other parameter estimates in these models may not be reliable. Examination of the raw data allowed us to identify potential causes of the estimation problems for about two-thirds of these models. In most cases, problems appeared to stem from clustering of detections at one end of the gradient of values of a covariate. For example, precipitation values for the transects in the western Great Basin on which *S. zerene* was detected in 2014 generally were relatively high. Similarly, in the same ecosystem, *P. sonora* was detected on four of the 37 transects on which nectar abundance was low. In a few cases, naïve occupancy may have been too low (e.g. 0.35) or too high (e.g. 0.66) to allow estimation of parameters.

Our estimates of abundance of nectar and mud were coarse; they were intended to be rapid and fairly repeatable among observers. Nevertheless, p_{ij} in one or more years was associated with abundance of nectar or mud for 92% of the species in the Chesapeake Bay Lowlands, all of the species in the central Great Basin and 93% of the species in the western Great Basin. In almost all cases, p_{ij} increased as the

Table 6 Direction of estimates of effect sizes of covariates associated with detection probabilities of butterflies in the western Great Basin.

	2013				2014			
	Nectar abundance (compared with high abundance)		Mud abundance (compared with high abundance)		Nectar abundance (compared with high abundance)		Mud abundance (compared with high abundance)	
	None or low	Moderate	None	Low	None or low	Moderate	None	Low
Hesperia juba			–	–	–	–		
Hesperia comma			–	–			–	–
Polites sonora	–	–			–	+		
Papilio rutulus			–	–				
Lycaena arota			*	*			–	–
Satyrium behrii							+	+
Incisalia eryphon			–	–				
Plebejus saepiolus			–	–			–	–
Icaricia icariodes	–	–			–	–		
Icaricia lupini	–	–			–	–		
Speyeria zerene					+	+		
Phyciodes pulchellus			–	–			–	–
Limenitis weidemeyerii			–	–				
Cercyonis sthenele								
Cercyonis oetus	–	–			–	*		

Effect sizes are from models with the lowest AIC_c, or models with AIC_c values within 2 units of the model with the lowest AIC_c. Low, low abundance; moderate, moderate abundance. Negative direction indicates that the probability of detection increased as the abundance of nectar or mud increased. Shaded cells indicate that 95% confidence intervals did not include zero. Estimates of the effect sizes are in Appendix S3.
*Effect size could not be estimated.

abundance of these resources increased. These relations are consistent with field experience. For example, species in the Papilionidae and Polyommatinae often are detected at mud. However, to the best of our knowledge, these relationships have not previously been quantified at the assemblage level. Detection probabilities tended to be relatively high for species that are abundant (e.g. *I. eryphon*, *C. comyntas*, *I. icariodes*), have limited vagility and circumscribed habitat (e.g. *P. saepiolus*) or are conspicuous (e.g. *P. troilus*, *L. weidemeyerii*). Detection probability tended to be associated more consistently than occupancy with abundance of nectar or mud. Continuous estimates of sugar mass may be more closely associated with occupancy than categorical abundance of nectar (Pavlik *et al.*, unpublished manuscript).

Measures of the dominance or abundance of deciduous woody species and structural heterogeneity were included in the greatest number of occupancy models for butterflies in the Chesapeake Bay Lowlands. In part, this association may reflect that the larval host plants of five of the species we modelled are deciduous. Additionally, structural heterogeneity may be a surrogate measure of intensity of browsing by white-tailed deer. Areas in which white-tailed deer are abundant tend to have relatively little understorey, thus relatively few grasses or forbs that serve as larval host plants or nectar sources. Removal of the understorey also changes microclimate and may expose immature life stages to higher probabilities of predation.

Elevation and precipitation were among the most prominent covariates in occupancy models for butterflies in the central and western Great Basin. One or both covariates were associated with occupancy of all species in both ecosystems. Strong relationships between elevation and occupancy were consistent with previous work in these ecosystems (e.g. Fleishman *et al.*, 1998, 1999, 2001a,b). In the central Great Basin, about twice as many associations between occupancy and precipitation were observed in 1995, a water year with unusually high precipitation, than in 2013 or 2014. Moreover, in 1995, none of the 95% CIs for estimates of the regression coefficient included zero. The direction of the associations between occupancy and precipitation was inconsistent among species. Although extreme winters can increase mortality of overwintering life stages, especially larvae (Douglas, 1986; Dennis, 1993), precipitation may forestall senescence of host plants and nectar sources.

We found considerable temporal variation in whether covariates were associated with p_{ij} or ψ_i of a given species and, if so, the identity of those covariates. With respect to probabilities associated with abundance of nectar and mud, it is possible that outputs were affected by our use of transect-specific maxima rather than survey-specific values. The peak of the flight season for many species did not coincide with the maximum abundance of nectar or mud. Additionally, our models did not differentiate among broods. Terrain ruggedness was associated with occupancy of four species in

Table 7 Direction of estimates of regression coefficients and effect sizes of covariates associated with occupancy of butterflies in the western Great Basin.

	2013						2014							
					Mud abundance (compared with high abundance)						Nectar abundance (compared with high abundance)		Mud abundance (compared with high abundance)	
	el	el^2	tr	pr	None/low	Mod	el	el^2	tr	pr	None/low	Mod	None/low	Mod
Hesperia juba				–					+	–				
Hesperia comma				–			–		+	–				
Polites sonora		–		–	–	–		–			*	–	–	–
Papilio rutulus		–		+			†						*	*
Lycaena arota	–		+				*		*					
Satyrium behrii	*		*							–				
Incisalia eryphon	–		+	–						–				
Plebejus saepiolus	+		–		–	–	+	–	–		–	+		
Icaricia icariodes		–						–						
Icaricia lupini		–					+		+					
Speyeria zerene				+						†				
Phyciodes pulchellus	+		+					–						
Limenitis weidemeyerii				–						–				
Cercyonis sthenele	–		+							–				
Cercyonis oetus				–					+					

el, elevation; el^2, square of elevation; tr, terrain ruggedness; pr, precipitation; none/low, none or low abundance; mod, moderate abundance. Regression coefficients and effect sizes are from models with the lowest AIC_c, or models with AIC_c values within 2 units of the model with the lowest AIC_c. Directions for abundance of nectar and mud are relative to high abundance. Shaded cells indicate that 95% confidence intervals for estimates of the regression coefficient or effect size did not include zero. Estimates of the regression coefficients and effect sizes are in Appendix S3.

*Regression coefficient or effect size could not be estimated.

†Estimated regression coefficient or effect size was $\geq |10|$.

the western Great Basin but, in contrast to previous work in the region (Fleishman *et al.*, 2001b), no species in the central Great Basin. Again, the set of locations that were included in this analysis versus previous analyses may explain some of the discrepancy.

We modelled seven species that occurred in both the central and western Great Basin, but covariates associated with p_{ij} and ψ_i of those species, or the direction of association with the same covariate, often differed between ecosystems. This variation may reflect that our study locations in the central and western Great Basin are within different zoogeographic regions (Austin & Murphy, 1987). In many cases, different subspecies occupy the two regions, and their local ecology may be sufficiently distinct to affect covariate associations.

Occupancy rarely has been estimated for a high proportion of the species within an assemblage of butterflies, and our work highlighted some of the applications in which occupancy estimation has limitations. Single-species occupancy models often are applied to many species that were sampled simultaneously. These situations may require or lead to the assumption that sampling of each modelled species was sufficiently and equally robust. But given typical financial and logistical constraints, it rarely is tractable to sample an assemblage, especially one that is highly dynamic, with a design that is ideal for estimating occupancy of the majority of individual species. For example, assemblage-level surveys generally encompass areas that are unlikely to be occupied by a given species, which may complicate parameter estimation. Moreover, if organisms are sufficiently mobile that the occupancy status of fairly small sites is likely to change between surveys, as is the case with adult butterflies, inferences about the environmental variables that are associated with p_{ij} and ψ_i may become biased (e.g. Hayes & Monfils, 2015). Our work both elucidates trade-offs among application of occupancy models to multiple co-occurring species of butterflies and highlights a number of novel ecological relations, especially the extent to which detection probabilities may relate to ephemeral resources.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 All species detected in the Chesapeake Bay Lowlands (2013 and 2014), central Great Basin (1995, 2013, and 2014), and western Great Basin (2013 and 2014).

Appendix S2 Complete results of both stages of the model-fitting process for the Chesapeake Bay Lowlands and Great Basin in all years.

Appendix S3 For each species in each ecosystem and year, whether the assumption of closure or relaxed closure (*not closed*) was supported more strongly; values of the regression coefficients (for continuous covariates), effect sizes (for categorical covariates), and their lower (LCI) and upper (UCI) confidence intervals (CIs) in models of detection probability and occupancy that either were the most strongly supported (lowest AIC_c; in black) or within 2 AIC_c of the most strongly supported (in blue); estimates of occupancy and their CIs; and estimates of detection probability on each visit.

BIOSKETCH

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