

Seasonal variation in detectability of butterflies surveyed with Pollard walks

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Abstract Monitoring protocols should be designed to maximize the probability of detecting target species with limited resources. Most species are imperfectly detected, hence, they will often be overlooked at sites where they actually occur, resulting in false-negative errors (i.e. false absences). Uncertain detection of target species has profound implications for conservation, but can be dealt with by using adequate survey designs and statistical models. Butterflies often are monitored with repeated, fixed-route transect counts (Pollard walks). Even though this survey method is widely used in temperate regions, its efficiency in terms of detection probability has never been rigorously assessed in part owing to a lack of suitable analysis methods. Here, I use site-occupancy models to explore the seasonal patterns in detection probability of four California butterflies using Pollard walks. In an effort to inventory the butterfly fauna in two natural areas in the eastern foothills of the Santa Cruz mountains (California), I surveyed twelve 250 m long transects weekly for 22 weeks. I estimated the detection probability (the probability of recording a species during a single transect walk, given it is present) of four species. The probability of detecting each species depended mostly on the monitoring week. Average detection probability across the season was 64% for *Cercyonis pegala*, 56% for *Limenitis lorquini*, 76% for *Euphydryas chalcedona*, and 50% for *Lycaena arota*.

Based on the mean detection probability, I then inferred the number of visits necessary to be statistically confident that a given species was indeed absent from a transect where it was not observed (i.e. obtaining a false absence rate <5%). Knowledge of detection probabilities is fundamental to the optimal design of monitoring programs and the interpretation of their results. The methods applied in this study provide an efficient and evidence-based method to optimally allocate butterfly monitoring resources across space (number of transects) and time (number and timing of visits).

Keywords Detection probability · Monitoring · Fixed route transect · Jasper Ridge Biological Preserve · Site-occupancy models · Rhopalocera · Surveys

Introduction

Biodiversity monitoring programs are used for a variety of purposes, including species distribution atlases, habitat models, red list assessments, detection of spatial and temporal trends, evaluation of environmental impacts, and habitat management (Niemela 2000; Yoccoz et al. 2001; Nichols and Williams 2006). Because the reliable estimation of abundance is in many cases either impossible or financially/logistically prohibitive, so-called presence/absence data are often used as a substitute for population size (Williams et al. 2002; Koleff et al. 2003; MacKenzie 2005). This is especially true for large-scale programs or programs that target cryptic, rare, or endangered species (Stork and Samways 1995; MacKenzie et al. 2005).

A confounding factor in all monitoring programs is that species detection probability (the probability of detecting a species, given that it is present) is imperfect. False

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absences (assuming that a species is absent from a site where it is actually present but was overlooked) lead to underestimates of the geographic distribution of the species. This issue has been recognized as fundamental in many taxonomic groups, including reptiles, amphibians, birds and mammals (e.g. Bart and Schoultz 1984; Azuma et al. 1990; Kéry 2002; MacKenzie et al. 2002; Stauffer et al. 2002; Pellet and Schmidt 2005; MacKenzie et al. 2006; Thorne et al. 2006). In addition, false absences have been recognized as a source of bias in models of habitat quality (Tyre et al. 2003; Gu and Swihart 2004; Lütolf et al. 2006, MacKenzie 2006) and metapopulation dynamic (Moilanen 2002), as well as red list assessments (Gardenfors et al. 2001; Rodrigues et al. 2006) and conservation planning (Boulinier et al. 1998; Kéry and Schmid 2004).

For these reasons, presence/absence monitoring protocols should be designed to maximize the probability of detecting the target species with limited resources (Stork and Samways 1995; Zonneveld et al. 2003). This is especially true for taxa that are widely used as environmental state indicators such as butterflies, and for which biased inferences can cascade down to other taxonomic groups of interest (Thomas 2005).

In many countries with temperate climates, butterfly monitoring is often conducted by some variation of so-called Pollard walks (Pollard 1977; Pollard and Yates 1993), a standardized transect along which butterflies are counted. This method is popular because its standardized approach allows more rigorous statistical analysis than other methods (Jeffcoate 1995; Royer et al. 1998; Mattoni et al. 2001; Thomas 2005; Collier et al. 2006; Thorne et al. 2006). Pollard walks are based on fixed-route transects that are surveyed weekly. During each visit, observers count each butterfly observed along the route and within a fixed distance to the route.

Several characteristics of this survey method has been previously evaluated (Pollard 1977; Thomas 1983), but single species detection probability in Pollard walks has rarely been assessed (Thorne et al. 2006; Kéry and Plattner 2007). Although Pollard walks were originally developed to detect trends in species abundance, the lack of correspondence between species non-detection (a monitoring reality) and species absence from site (a biological reality) clearly needs to be assessed in order to obtain unbiased data on species distribution. Here, I estimated the probability of detecting four different species of butterflies on any given visit. I further used estimates of detection probability to support quantitative arguments for refining future butterfly monitoring protocols making it possible to examine the ability to statistically infer species absence from a transect.

Methods

Study area

I inventoried the butterflies along twelve 250 m transects located on the eastern foothills of the Santa Cruz Mountains, California. Eight of these transects were located within Stanford's Jasper Ridge Biological Preserve (San Mateo county, 37°24'17" N, 122°13'28" W) and four were located in Palo Alto's Foothills Park (Santa Clara county, 37°21'34" N, 122°10'57" W). Transects were placed in order to represent the major vegetation associations present at both locations. Vegetation is typical of the Upper Sonoran Life Zone (Merriam 1898) and consists mainly of open oak-madrone woodland (characterized by *Quercus douglasii*, *Q. agrifolia*, *Arbutus menziesii*, *Heteromeles arbustifolia*), mixed chaparral (*Rhamnus californica*, *Artemisia californica*, *Mimulus aurantiacus*, *Baccharis pilularis*, *Rubus* spp.), and grasslands (*Lolium multiflorum*, *Bromus hordeaceus*, *Brachypodium distachyon*, *Briza maxima*, *Avena fatua/barbata*, *Centaurea solstitialis*).

Monitoring protocol

The monitoring protocol was based on Pollard walks (Pollard 1977; Pollard and Yates 1993). Each transect was visited weekly for 22 weeks between March and September 2006. Transects were visited between 10:00 and 17:00 on clear days. Wind speed was on average 1.4 m/s (minimum 0.4 m/s, maximum 4.8 m/s) and temperature was on average 23.7°C (minimum 12.4°C, maximum 36.5°C). Transects were walked in one direction at a slow and even pace (~1–2 km/h) for a duration of 15–20 min. Each butterfly (Rhopalocera: Papilionoidea and Hesperioidea) seen within a virtual 5 m observation cube projected ahead of the observer was counted (see state of the art in Thomas 2005; Pollard and Yates 1993). Individuals were either identified by sight (sometimes using close-focus 10× binoculars) or captured with a net for closer examination. Nomenclature follows the North American Butterfly Association (Cassie et al. 2001).

Statistical analysis

In order to estimate both single-visit detection probability (p) and site (transect) occupancy (ψ), I applied a method similar to mark-release-recapture (MacKenzie et al. 2002). This model is based on a species' detection history on multiple transects. A detection history documents whether a species was seen (1) or not (0) on each visit. This so-called site-occupancy modeling framework assumes that occupancy state of a site by a species does not change across the sampling occasions. In capture–recapture jargon, this is the

closure assumption (MacKenzie and Kendall 2002; MacKenzie et al. 2006). Transects are thus assumed to be either occupied or empty during the study period. I therefore restricted analyses for each species to the time span during which the species was flying in at least one transect.

I selected species that were univoltine or multivoltine with identifiable broods (in which case distinct analyses were performed for each brood), because they were the most likely to have a clearly identifiable flight periods. I only considered resident species with low vagility (tens to hundreds of meters) and species that were detected in at least three of the 12 transects. Ecological data on the species were collated from Scott (1986), Fleishman et al. (1997), and Glassberg (2001). Four species (Table 1) were included in the analysis: *Cercyonis pegala* (subfamily Satyrinae), *Euphydryas chalcedona* (Melitaeninae), the first brood of *Limenitis lorquini* (Limenitidinae), and *Lycaena arota* (Lycaeninae).

I constructed a set of four models representing four major hypotheses regarding detection probability and applied the models to all four species. All models assumed that site occupancy was constant [denoted $\psi(\cdot)$]. Because the data set was relatively small, I kept candidate models simple (i.e. with few parameters). Model 1 represented the hypothesis of a constant detection probability [denoted $p(\cdot)$] across the flight season of a species. Model 2 assumed that detection probability was a function of the species' seasonal abundance, modeled with a quadratic relationship between survey week and detection probability [$p(\text{WEEK} + \text{WEEK}^2)$]. To test whether weather affected detection probabilities within the range of temperature and wind speed considered, I constructed two additional models. Model 3 [$p(\text{TEMP} + \text{TEMP}^2)$] assumed that there was an optimal survey temperature maximizing detection probability (detection probability as a quadratic function of temperature). Model 4 [$p(\text{WIND})$] assumed that wind speed affected detection probability in a linear fashion. Weather data (hourly temperature and wind speed) were collected from Stanford's Jasper Ridge Biological Preserve weather station.

I used an information theoretic approach to model selection (Burnham and Anderson 2002; Johnson and Omland 2004). As recommended when the ratio between sample size and number of model parameters is less than 40 (Burnham and Anderson 2002), I used the Akaike Information Criterion (AICc) for small samples. AICc model weights were derived and models ranked in a decreasing weight order. The sum of all Akaike weights across all candidate models is one. Models with lowest AICc were considered most parsimonious, and pairs of models with an absolute difference in AICc of less than 2 were considered equally good (Burnham and Anderson 2002).

Detection probability was calculated for each visit by averaging across all four models (Burnham and Anderson 2002). This procedure derives parameter estimates (detection probability p and occupancy ψ) for each week from all candidate models on the basis of each model's weight. I then used the model-averaged detection probabilities obtained for each visit and calculated both the maximum (p_{max}) and the average detection probability (p_{mean}) for each species across its flight period. Maximum likelihood optimization, model selection and model averaging were performed with program MARK 4.3 (Cooch and White 2001).

If detection probability is known, one can estimate the probability of recording a false absence (Tyre et al. 2003; Pellet and Schmidt 2005). After one visit, the probability of a false absence is $(1 - p)$. After n visits, the probability decreases to $(1 - p)^n$. To be 95% confident that a given species with p_{mean} average detection probability is absent from a site, a minimum of $N_{\text{min}} = \log(1 - 95\%) / \log(1 - p_{\text{mean}})$ visits must be made during the flight period.

Results

Monitoring results

All four species were imperfectly detected when present in a given transect, with a number of weeks detected always less than the length of the flight period (Table 1).

Table 1 Survey data of four butterfly species in twelve 250 m transects of the Santa Cruz Mountain foothills

Species	Apparent occupancy	Flight season (weeks)	Times detected (when present) (SD)	Average number of individuals recorded per visit (when present) (SD)	Total number of records
<i>Cercyonis pegala</i>	0.50	9	5.7 (1.6)	2.0 (1.9)	68
<i>Euphydryas chalcedona</i>	0.75	9	6.3 (1.7)	6.7 (1.1)	399
<i>Limenitis lorquini</i> (1st brood)	0.42	9	5.0 (1.6)	1.8 (1.2)	40
<i>Lycaena arota</i>	0.50	8	3.8 (1.3)	3.2 (2.7)	74

The apparent occupancy is the proportion of transects where the species was detected. The flight season is defined as the interval between the first and the last observation of the species. Transects were walked weekly

E. chalcidona was by far the most abundant species, while all three other species had relatively comparable abundance (total number of individuals recorded).

Model selection and estimates of detection probabilities

In three out of four species (*C. pegala*, *E. chalcidona*, and *L. lorquini*), detection probability was best modeled as a function of monitoring week (seasonal abundance). For these species, model 2 [$p(\text{WEEK} + \text{WEEK}^2) \psi(\cdot)$] fitted the presence/absence data best (Table 2). The effect was especially strong for *E. chalcidona*, where model 2 had a weight of almost 1. For the fourth species (*L. arota*), however, model 1 [$p(\cdot) \psi(\cdot)$], which assumed a constant detection probability, performed as well as model 2 (absolute ΔAICc of less than 2). The model selection thus provides equal support to the two hypotheses. Across species, there was little support for the weather models 3 (temperature) and 4 (wind speed).

Model-averaged estimates of detection probabilities varied considerably over time for all four species, reflecting the strong weight of models based on seasonal abundance (Fig. 1). For all species, detection probability varied over time with a maximum detection probability (p_{max}) in the middle of the flight season. The maximum detection probability (p_{max}), however, varied considerably between species, from a high value of 99% for *E. chalcidona* to a low of 60% for *L. arota* (Table 2, Fig. 1). Similarly, the

average detection probability (p_{mean}) varied from 50% for *L. arota* to 77% for *E. chalcidona* (Table 2).

Given the average detection probability estimates (p_{mean}), I estimated the false absence rate (the probability of not detecting a species when it was present) as a function of the number of visits to each transect (Fig. 2). A protocol aimed to detect *E. chalcidona* in at least 95% of the locations where it is present should include a minimum of three visits per site across the flight season. A protocol designed to detect *L. arota* in at least 95% of the locations where it is present should include at least 5 visits spread across the flight season (Fig. 2). A minimum of four visits per transect appears necessary to detect *C. pegala* and *L. lorquini* (Table 2). Given the fact that I made between 8 and 9 visits to each transect during the flight period of those four species (Table 1), model averaged estimates of occupancy (ψ) were always within one SE of the apparent occupancy (Table 2), suggesting that the protocol I used allowed the detection of all four species in every transect where they were present.

Discussion

Specificities in detection probability

Monitoring programs should acknowledge the fact that species are unlikely to be perfectly detected and that uncertainty will remain between non-detection and true

Table 2 Model selection and parameter estimation. AICc is the model Akaike Information Criterion for small samples, ΔAICc is the absolute difference in AICc with the best model, w is the model weight, and K is the number of parameters included in the model

Species	Model	AICc	ΔAICc	w	K	p_{max} (SE)	p_{mean} (SE)	N_{min}	ψ
<i>Cercyonis pegala</i>	2 $p(\text{WEEK} + \text{WEEK}^2) \psi(\cdot)$	90.80	0.00	0.73	4	0.774 (0.108)	0.641 (0.149)	4	0.500 (0.144)
	1 $p(\cdot) \psi(\cdot)$	93.16	2.35	0.22	2				
	4 $p(\text{WIND}) \psi(\cdot)$	96.82	6.02	0.04	3				
	3 $p(\text{TEMP} + \text{TEMP}^2) \psi(\cdot)$	98.69	7.89	0.01	4				
<i>Euphydryas chalcidona</i>	2 $p(\text{WEEK} + \text{WEEK}^2) \psi(\cdot)$	70.25	0.00	1.00	4	0.985 (0.011)	0.766 (0.286)	3	0.727 (0.134)
	1 $p(\cdot) \psi(\cdot)$	87.54	17.29	0.00	2				
	4 $p(\text{WIND}) \psi(\cdot)$	91.46	21.21	0.00	3				
	3 $p(\text{TEMP} + \text{TEMP}^2) \psi(\cdot)$	92.54	22.29	0.00	4				
<i>Limnitis lorquini</i> (1st brood)	2 $p(\text{WEEK} + \text{WEEK}^2) \psi(\cdot)$	78.02	0.00	0.71	4	0.788 (0.109)	0.555 (0.196)	4	0.416 (0.142)
	4 $p(\text{WIND}) \psi(\cdot)$	80.83	2.81	0.17	3				
	1 $p(\cdot) \psi(\cdot)$	81.80	3.78	0.11	2				
	3 $p(\text{TEMP} + \text{TEMP}^2) \psi(\cdot)$	87.06	9.05	0.01	4				
<i>Lycaena arota</i>	1 $p(\cdot) \psi(\cdot)$	85.56	0.00	0.45	2	0.595 (0.134)	0.502 (0.091)	5	0.507 (0.146)
	2 $p(\text{WEEK} + \text{WEEK}^2) \psi(\cdot)$	85.64	0.08	0.44	4				
	4 $p(\text{WIND}) \psi(\cdot)$	89.21	3.65	0.07	3				
	3 $p(\text{TEMP} + \text{TEMP}^2) \psi(\cdot)$	90.55	5.00	0.04	4				

p_{max} and p_{mean} are the maximum and mean values of the model-averaged detection probability p . N_{min} is the minimum number of visits to be 95% confident that the species is absent and ψ is the proportion of transects in which the species was present

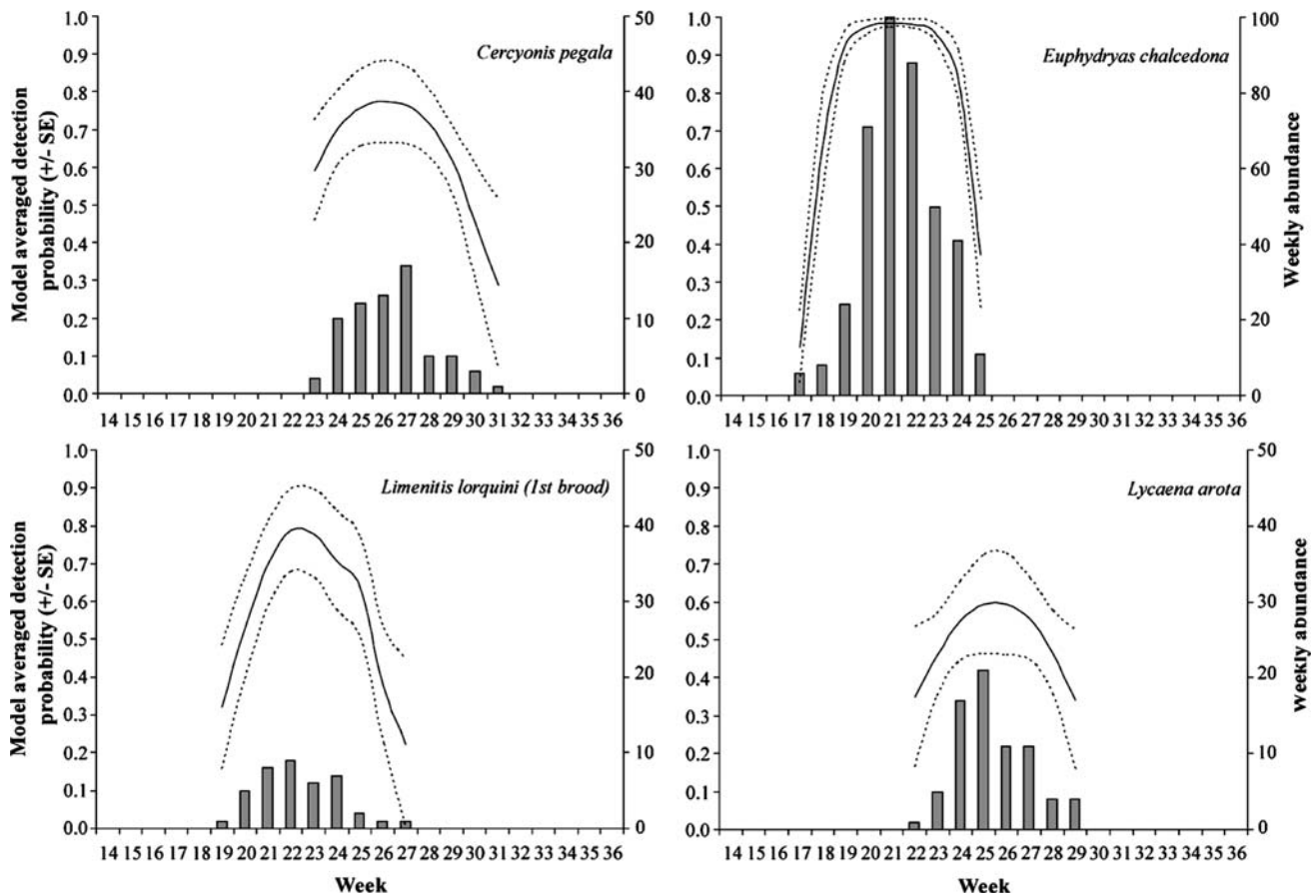


Fig. 1 Model-averaged detection probabilities (mean \pm SE: lines) and weekly abundance (bars) of four butterfly species of California

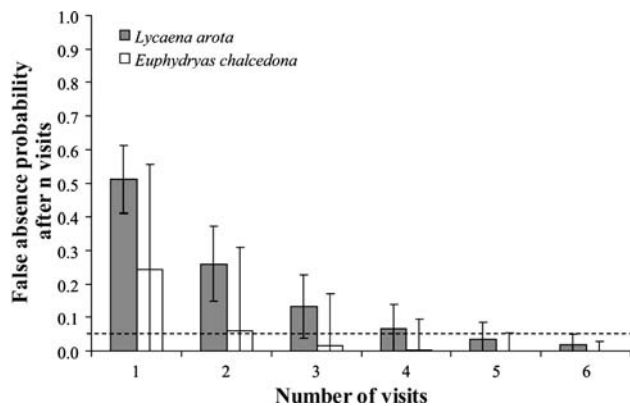


Fig. 2 False absence probability (mean \pm SE) after n visits for two species with different average detection probability (p_{mean}). The dashed line indicates the 5% false absence rate

absence. Here, I demonstrate that, in four California butterfly species, detection probability in Pollard walks is imperfect, that it is time-dependent, and strongly depends on species seasonal abundance.

The fact that all four species included in the analysis have detection probabilities strongly dependent on survey

week emphasizes the importance of emergence timing in the probability of detecting any given species, a pattern which is not surprising to any entomologist (Zonneveld et al. 2003). Species abundance is expected to be at a maximum in the middle of the flight season, thus maximizing individual detection probability (Fig. 1). In contrast, the maximum detection probability varied strongly among species, in part as a result of its behaviour. Males of *C. pegala* patrol all day in moist grassy area to seek females and courtship includes frequent vertical flights. Individuals of *E. chalcedona* also frequently patrol conspicuously on hilltops and clearings. Males of *L. lorquini* alternately perch and patrol about 3–4 m above the ground. *L. arota*, by contrast, inhabits open woodland and clearings where males perch and await passively for females (Scott 1986). *L. arota* also seldom flies more than tens of meters (Fleishman et al. 1997). These behaviours are evident in the results, where the three patrolling species were 18–40% more likely to be seen than the passive species. The average detection probabilities obtained here are comparable to those obtained by Pellet et al. (2007) for *Speyeria nokomis apacheana* (45%) and *Maculinea nausithous* (75%).

The fact that models including meteorological covariates did not perform well (total model weight for model 3 and model 4 on average 0.09 across all four species) reveals that the sampling conditions (temperature and wind speed) were generally adequate to monitor the presence/absence of the four target species. While weather did not seem to be a major factor affecting butterfly flight in our study area, it is very likely to be otherwise in regions with more variable daily weather (i.e. mountains, deserts, etc.) where butterflies have narrower flight windows.

Species relative abundance (as measured by the total number of individuals recorded) is arguably another factor that influences detection probability (Zonneveld et al. 2003). The apparent relative population size of *E. chalcidona* was high ($n = 399$), resulting in a high probability of detecting at least one individual per visit. Apparent relative abundance of the other three species was similar, but average detection probabilities were different (see Kéry and Plattner 2007 for another example). Detection probability of these species may depend largely on primary vegetation association (e.g. forest versus grassland species) and behaviour (Royer et al. 1998). It is also likely that a given species detection probability will vary between location (Link et al. 1994) as a result of the ability of the observer to efficiently detect the species in different transects. To test for heterogeneity of detection probability in various vegetation associations, I ran a mixture model [$p(2$ -group mixture) $\psi(\cdot)$] (Pledger 2000) for all four species using program PRESENCE (MacKenzie et al. 2006). For all four species, the mixture model ranked last or second before last (ΔAICc ranging from 4.5 for *L. arota* to 37.7 for *E. chalcidona*) suggesting that it was not necessary to model heterogeneity in detection probability explicitly.

Occupancy models allowing for imperfect detectability

Populations were assumed to be closed during the time frame analyzed. Although I restricted the analyses for each species to the time span during which that species was observed in at least one transect, microclimatic difference between transects might account for staggered emergences. However, given the fact that all transects experienced identical climate, and had relatively comparable slope and exposure, it is unlikely that staggered emergence could account for major changes in occupancy (although this fact does not exclude changes in abundance during the flight season). Violations of this the closed-population assumption would bias the values of detection probabilities at the beginning and end of the season (when populations are experiencing either delayed emergence or precocious population disappearance), thus affecting p_{mean} more than p_{max} .

I also restricted analysis to univoltine species and multivoltine species with clearly identifiable broods because the brood seasonal abundance curve was expected to be easier to model with quadratic terms. However, with a larger sample size, it would be relatively easy to model double-brooded species using higher polynomial (cubic) relationships.

Monitoring implications

Monitoring may be conducted for many reasons including: to provide an initial estimate of detection probability for a target species or to determine distribution patterns after detection probabilities have been estimated.

In the first case, it has been demonstrated that increasing the number of transects visited had little impact compared to increasing the number of visits to sites (Wintle et al. 2004) when trying to accurately estimate detection probability. Therefore, as illustrated by the present project, I would advise, as a rule of thumb, to apply a weekly count to a limited number of transects (>10) where species are likely to occur (MacKenzie and Royle 2005). Given that most species will be flying during at least 6–8 weeks, this should yield a long enough detection history to infer detection probability reasonably well, as was the case here with four relatively abundant species. However, for species with shorter flight period or a priori low detection probability, sampling should be intensified (to two or three visits per week) in order to obtain a detection history long enough (at least 8 sampling events) to make reliable and accurate inference on detection probabilities.

In the second case, I show here that, if prior knowledge of species flight period curve exists, then visits can be made at the time of peak abundance and the number of visits necessary (N_{min}) to reach a predefined level of false absence reduced accordingly, using the maximum detection probability estimate (p_{max}). Knowledge on when to visit transects to maximize detection probability usually relies on published materials and personal experience. In most cases, however, the emergence date of butterflies fluctuates each year as a result of climatic variability and uncertainty remains on the timing of peak activity (Weiss et al. 1993; Sparks and Yates 1997; Roy and Sparks 2000; Zonneveld et al. 2003, Nowicki et al. 2005). Therefore, the most adequate and conservative estimate of detection probability is the average across the species flight period (p_{mean}).

I demonstrated here that a given presence/absence survey can yield data of variable quality for different butterflies. It might be therefore difficult to design a generally efficient multi-species survey protocol (Barrows et al. 2005). When detection probabilities are taken into account, it is relatively easy to adapt the number of necessary

transect visits to be sufficiently confident that the false absence rate of a target species is kept below a predefined level (e.g. 5%). This might prove extremely important in the case of costly large scale monitoring program when both human and financial resources are limited (Field et al. 2005). In such situation, knowledge on the quality of data obtained through a given protocol can help allocate optimally survey efforts. The trade-off between number of sites (transects) visited and number of visits made to each site can then be made depending on the research questions that are being addressed (MacKenzie and Royle 2005).

Conclusions

Preliminary monitoring protocols should be designed to assess target species detection probability by surveying repeatedly a set of locations where the species is either known to occur or very likely to be present. Once quantitative data are available on a species detection probability, protocols can be implemented across larger areas and credible evidence-based occupancy data can be collected while optimizing financial resources allocation at the same time.

Because it is feasible to demonstrate with a predefined level of confidence that a target species is absent from a site, it is possible to reverse the burden of proof in environmental impact assessments and ask developers to demonstrate, not species presence, but species absence. This could generate a major paradigm shift in applied conservation science and practice.

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