

**BUTTERFLY MONITORING METHODS:
THE IDEAL AND THE REAL WORLD**

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ABSTRACT

Butterflies may serve as indicators of biodiversity trends, but for this purpose reliable methods of monitoring their distribution and abundance are essential. We discuss advantages and disadvantages of the currently used methods and suggest potential refinements, based on methodological advances achieved in other organisms. While assessing butterfly distribution, it is vital to account for imperfect species detection at investigated sites. This can be achieved through conducting repeated presence–absence surveys within a single season, and analyzing data with statistical models that estimate detection probability and site occupancy by a species. Transect counts, predominantly used for assessing butterfly abundance in monitoring programs, are cost-effective and easy to implement, but less reliable than mark–release–recapture sampling frequently applied for the same purpose in research studies. Deficiencies of transect counts stem from the fact that they do not account for individual detection probability and temporal fragmentation of butterfly populations, i.e., the situation in which just a small fraction of individuals belonging to a single generation is present on any day of a season. Consequently, transect counts can only yield relative abundance indices, which presumably correlate well with daily butterfly numbers, but not necessarily with their seasonal population sizes. Possible refinements to transect counts that would allow the estimation of individual detection probability include double observer or double zone approaches. In contrast, finding an effective way to estimate longevity (a measure of temporal fragmentation) with transect counts seems impossible. Instead, efforts should be made to evaluate how variation in longevity affects transect-count results.

Keywords: abundance, detection probability, distribution, mark–release–recapture, population size, temporal fragmentation, transect counts

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INTRODUCTION

Halting the process of biodiversity decline, or at least significant reduction of its rate, is at present one of the global challenges facing humankind. It has been addressed by several fundamental international agreements, including the EU Sustainable Development Strategy adopted at the 2001 Gothenburg summit (European Commission, 2001) as well as the 2002 Johannesburg Convention on Biological Diversity (Balmford et al., 2005a). In order to assess if the ambitious targets of these agreements are being met, comprehensive biodiversity monitoring, especially at species, community, and habitat levels, is essential (Balmford et al., 2005b; Dobson, 2005).

Butterflies, together with birds and vascular plants, represent the most frequently monitored taxonomic groups (de Heer et al., 2005; Thomas, 2005), which is mostly due to their extreme popularity among amateur naturalists. Apart from this, several ecological characteristics make butterflies promising biodiversity indicators: (i) due to short (typically annual) life cycles they are more sensitive than other groups to changes in their habitats (Thomas, 1994; Thomas et al., 2004; van Swaay and Warren, 1999); (ii) breeding even in small habitat patches, they are likely to reflect changes occurring at a fine scale (van Swaay et al., 2006); (iii) they may be expected to be representative for a wide range of terrestrial habitats (van Swaay et al., 2006), and, more importantly, to be adequate indicators for many groups of terrestrial insects (Thomas and Clarke, 2004; Thomas, 2005), which themselves constitute the predominant fraction of biodiversity. Consequently, butterfly monitoring have been suggested as a potential tool for assessing large-scale biodiversity trends (Thomas, 2005; van Swaay and van Strien, 2005; van Swaay et al., 2006).

To effectively use butterflies as indicators, it must be possible to infer trends in their occurrence and abundance in an unbiased and relatively precise way, rather than to rely on so-called "expert judgment", as frequently happens nowadays (e.g., European Commission, 2005). In other words, butterfly monitoring programs have to apply proper survey designs as well as reliable methods of data collection and statistical analysis so that their results are scientifically sound and robust. The issues of survey design and statistical analysis of monitoring data are, in principle, independent of the species studied. Possibly the only peculiarity of butterflies in this respect is the fact that their populations, as compared with those of vertebrates, are subject to considerable annual fluctuations induced by both inherent population dynamics and environmental variation, e.g., weather patterns (Pollard, 1988; Roy et al., 2001). As a consequence, longer time-series are typically required to distinguish between such fluctuations and actual temporal trends (van Strien et al., 1997; Thomas, 2005). Furthermore, the issues of survey design and statistical analysis are well described in the existing literature (e.g., Bookhout, 1994; Thomas, 1996; Williams et al., 2002; Pollock et al., 2002) and thus beyond the scope of this paper. Instead, we shall focus on the problems of data collection methods (i.e., field techniques, sampling designs), which are equally important for the success of butterfly monitoring programs. This is because reliability of analytical methods relies on theoretical assumptions, the validity of which can be ensured only through adequate

field sampling methods. Even cutting-edge analyses can hardly compensate for biases resulting from poor field methods.

The typical parameters monitored include distribution and population size of a species. These are also the common criteria for evaluating species conservation status. Standards for assessing butterfly distribution and abundance have been developed 2–3 decades ago (reviews in Gall, 1985; New, 1991) and have been widely applied ever since. However, it appears that butterfly monitoring has not benefited much from recent methodological advances in this field achieved for vertebrates, especially birds. Our aim is thus to review and compare the advantages and disadvantages of the standard approaches with a special emphasis on how they meet the assumptions of the underlying statistical models. We shall also suggest some potential refinements to currently used methods as well as discuss which of the newly developed general methods could be applied for butterflies.

ASSESSING BUTTERFLY DISTRIBUTION

Estimating distribution of a species is based on recording its presence or absence at visited sites. Therefore, it is technically rather straightforward—any technique may be used that makes it possible to detect the species, regardless of whether this involves detecting its adults, eggs, larvae, or pupae. In fact, detecting non-adult life stages, especially larvae or pupae, may be more reasonable because their presence can typically be regarded as tantamount to the species breeding on the site and thus to its *de facto* occurrence, whereas recording the presence of adults may lead to overestimation of the distribution if dispersers are mistaken for resident individuals. Nevertheless, it is inevitable that the majority of schemes monitoring butterfly distribution has to rely on recording adults for practical reasons, namely lower cost and attractiveness to volunteer recorders, the involvement of which is essential in large-scale programs (Newman et al., 2003; Ellis and Waterton, 2004; Thomas, 2005).

Conceptual difficulty in recording presence or absence of a species, virtually untouched in butterfly studies until very recently (but see Kery and Plattner, 2007), lies in its imperfect detection (MacKenzie et al., 2002; Kery and Schmid, 2004). Recording a species indicates its presence, as long as species misidentifications are avoided, which requires adequate field skills. However, non-detection is not necessarily equivalent to the absence of a species, because it may go undetected when present. Thus, the estimates of distribution ranges of monitored species are negatively biased, unless imperfect detection is accounted for in the analysis (MacKenzie et al., 2002). Similarly, trends in distribution inferred from monitoring results uncorrected for detection probability are biased if this probability varies from year to year (Kery and Schmid, 2004). Apart from this, uncorrected occupancy results may have serious consequences also for metapopulation theory, the development of which has been largely based on butterfly studies (Thomas and Hanski, 1997, 2004). In particular, they may lead to negatively biased estimates of the incidence function estimates, which is a key parameter in popular stochastic patch occupancy models (SPOMs, Ovaskainen and Hanski, 2004), and also to

induce so-called pseudo-dynamics in these models, i.e., artifact extinction or colonization events (Moilanen, 2002).

Admittedly, in most butterflies the problem may be slightly less acute than in other groups, because of their typically high occupancy rate of suitable habitats (Baguette, 2004) and high population densities leading to relatively high species detection probabilities (Dorazio et al., 2006). Rare species are clear exceptions in this respect; Kery and Plattner (2007) report that in the Swiss Butterfly Monitoring program detection probabilities for certain species were below 0.3, though regrettably they do not mention the species names. More importantly, even in the case of relatively common species it is extremely naive to ignore the problem completely, assuming either perfect (i.e., equal to 1) or at least constant detection probability, because it clearly depends on sampling intensity (e.g., the time spent per visit to a site, number of observers, their experience, etc.) as well as butterfly abundance on a given day, related to the part of flight period (Zonneveld et al., 2003; Pellet, 2008).

The standard approach to the problem is to maximize species detection probability through increased sampling effort and/or optimized survey plan (Zonneveld et al., 2003). However, more promising are recent methodological developments in vertebrate studies that provide an effective framework for the estimation of species detection probability (MacKenzie et al., 2002). The basic idea is similar to that of mark–release–recapture (MRR) surveys, but individuals are replaced by sites monitored. Each site has its own species-detection history in which 1's and 0's indicate whether the species has or has not been detected there on consecutive sampling occasions. Species-detection histories for all the sites form a matrix with columns representing sampling occasions and rows representing sites. Hence the difference with conventional MRR is that detection histories with only 0's are possible. The crucial assumption is that of a “closed” system, i.e., no sites experience local extinctions or colonization by the species during the survey. The implication of this for adult butterfly studies is that a single survey has to be restricted to one season, and optimally to the mid part of the flight period. The parameters of the basic model include species detection probability (s ; it should be noted that p is used instead in the original reference, but we opt for s to distinguish it from individual detection probability introduced further in this paper) and site occupancy rate (i.e., fraction of sites occupied by the species, ψ). These parameters are estimated using maximum likelihood approach (for details see MacKenzie et al., 2002). MacKenzie et al. (2002) suggest that an effective sampling design should consist of at least 20 sites and at least 5 sampling occasions, but in the case of butterflies 2–3 sampling occasions may sometimes be enough concerning their typically high s and ψ . According to the simulation results, the model is fairly robust to missing data; occasional lack of sampling of a given site on a given occasion is not a problem until in total such cases do not exceed 20% of the entire data set.

The aforementioned basic model assumes that s is constant for all the sampling occasions and uniform across all the sites, but, in reality, species detection probability strongly depends on abundance—any species is easier to detect if more individuals are present. Since abundance of adult butterflies within their flight period varies greatly

both in time and in space, none of these assumptions is likely to hold. Moreover, if the same observer conducts sampling on consecutive occasions, one may expect a positive behavior response (*sensu* Otis et al., 1978) of species-detection probability, because observers would be likely to unintentionally look for the species more intensively on the sites where they had seen it previously. Time variation in s can be easily incorporated into the basic model (MacKenzie et al., 2002), while its extension developed by Royle and Nichols (2003) makes it also possible to account for its heterogeneity across sites. In contrast, to our knowledge, no model dealing with behavior response has been made available so far, and thus employing independent observers for consecutive sampling occasions may be worth consideration. For practical reasons (e.g., cheaper transport) it may be sometimes easier if these observers visit the sites together at one time. This is possible as long as the protocol ensures that they do not influence species detection by one another, e.g., they should not communicate.

It is worth mentioning that the extended model can even derive the estimates of local abundances from species detection/non-detection data; however, for at least two reasons we recommend caution in trying this application for butterflies. First, the model assumption of constant local abundance during the survey is unlikely to be met in butterfly populations. A possible exception would be the situation that all sampling occasions are carried out on the same day, which for a large enough number of sites seems difficult for logistic reasons. More importantly, the estimation of local abundances (N_i) is based on the relationship between the detection probability of the species on a given site (s_i) and that of an average individual (p) expressed by the equation: $s_i = 1 - (1 - p)^{N_i}$ (Royle and Nichols, 2003). This implies that \hat{N}_i estimates can be derived reliably only if they are relatively low, while p is relatively high. This may be true for passerine birds, on which Royle and Nichols (2003) tested their model, but in butterflies the usual situation involves local (daily) numbers of several tens to several hundred adults combined with extremely low individual detection probabilities.

ASSESSING BUTTERFLY ABUNDANCE

Two standard methods for quantifying butterfly abundance are Pollard transect counts and MRR sampling (Gall, 1985; New, 1991; Warren, 1992). The former method is cheap and time-efficient though less reliable (*cf.* hereafter), whereas MRR provides fairly precise estimates of population size, but at the expense of considerable fieldwork. Another problem with MRR is sometimes their negative effect on the populations investigated, either direct, due to catching and handling of a large fraction of individuals, or indirect, through habitat destruction by intensive trampling (C. Schultz, *pers. commun.*). Consequently, transect counts are widely applied in extensive large-scale and/or long-term monitoring programs, including the well-known British Butterfly Monitoring Scheme (Pollard and Yates, 1993) and the European Grassland Butterfly Indicator (van Swaay and van Strien, 2005), while the use of MRR has to be restricted to intensive small-scale and short-term research projects (Fig. 1). Few butterfly population studies with the help of MRR last for long enough to be able to monitor their trends. Comprehensive MRR

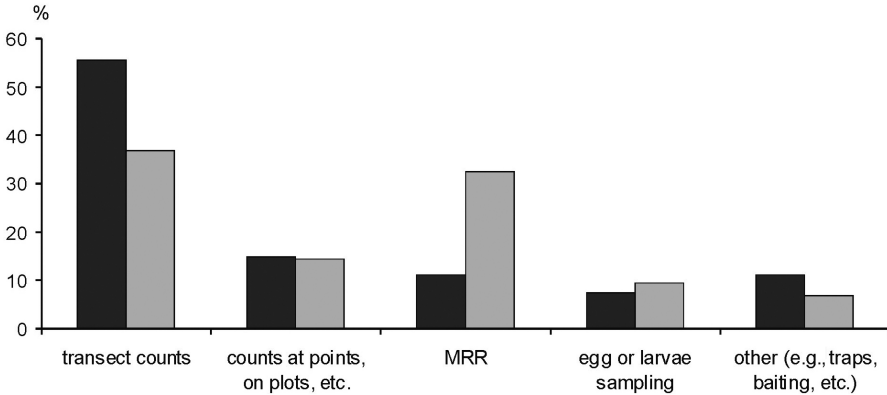


Fig. 1. The use of different methods for assessing butterfly abundance in monitoring programs currently conducted in Europe ($n = 27$; dark bars) and scientific studies published in 1996–2006 ($n = 160$; light bars). The sources of information were the database of species and habitat monitoring programs of the EuMon project (available at <http://eumon.ckff.si/monitoring>) and the ISI Web of Science. Only the monitoring programs assessing butterfly abundance and gathered in the EuMon database by 31 December 2006 were considered. The ISI Web of Science was searched through with the keywords “abundance” or “population size” combined with “butterfly”. Clearly irrelevant papers, e.g., those in which abundance or population size referred to subjects other than butterflies, or purely theoretical ones, were subsequently excluded. In addition, all 17 papers originating from the British Butterfly Monitoring Scheme were treated as a single entry to avoid bias made by this extremely successful program, while, in turn, the few studies using two independent methods were counted twice.

monitoring of the *Euphydryas editha bayensis* populations at the Jasper Ridge in California for over 35 years (Hellmann et al., 2003) is a unique example; in Europe similar projects reach at best a decade (e.g., Schtickzelle et al., 2002; Nowicki et al., 2005a).

Concerning reliability, the fundamental difference between transect counts and MRR is that only the latter method makes it possible to account for (i) imperfect detection of individuals and (ii) temporal fragmentation of butterfly populations, i.e., the situation that individuals belonging to a single generation are not all present at any single moment of time (Fig. 2). Because of neglecting the first issue transect counts can at most yield relative indices of abundance, and due to ignoring the second one these indices, though correlated with snapshot (usually daily) butterfly numbers, do not necessarily reflect seasonal population sizes, i.e., the sizes of generations, which should be the prime objective of monitoring.

In some cases sampling egg or larvae densities may be worth considering as an alternative method for monitoring butterfly abundance, which so far has been tremendously adult-biased. The useful property of non-adult life stages is that the problem of temporal fragmentation does not occur. The advantages and disadvantages of all three aforementioned methods are described in the following sections.

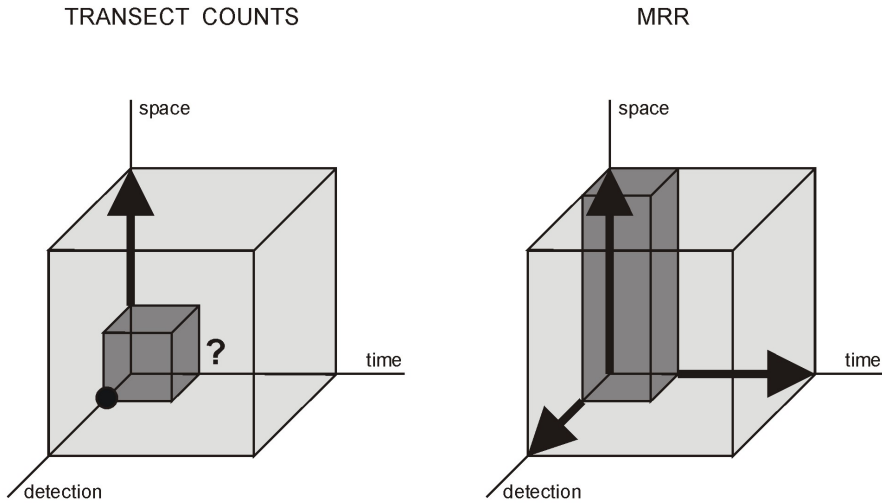


Fig. 2. Schematic relationship between total population (light block) and the fraction of individuals sampled (dark block) in standard transect counts and mark–release–recapture approach. To be sampled, individuals have to occur in the sampling period, be present in the sampled area, and get detected. A dot indicates that the fraction sampled is (presumably) constant along the particular “axis”, whereas an arrow means that it is estimated and thus the remaining fraction can be accounted for. A question mark represents the situation in which the fraction sampled is unknown and variable. In the case of MRR, estimating spatial coverage is possible, but typically the entire area occupied by a population is sampled (i.e., there is total coverage).

Other methods for assessing butterfly abundance available in literature (e.g., Owen, 1975; New, 1991; Hughes et al., 1998), include trapping adults with ground-covering net tents (Malaise traps) or bait traps. The former can yield the total count of adults eclosing throughout the season provided that tents are placed in the field for long enough, and the latter produces a relative abundance index. However, the focal area to which these outputs refer can only be very small in the case of Malaise traps, or undefined in the case of bait traps, because it is not known from how far butterflies are attracted. Moreover, both methods are labor-intensive, as traps have to be visited regularly to release captured individuals. Finally, the use of Malaise traps is technically difficult, whereas bait traps simply do not work for many species (authors’ unpubl. data). All considered, the deficiencies of the trapping methods seem to outweigh their merits and hence we shall not consider these methods any further in this paper.

TRANSECT COUNTS

Counting butterflies on strip transects has a long tradition, but it was Pollard (1977) who laid grounds for their effective use in monitoring. His method is based on recording

individuals sighted within an imaginary $5 \times 5 \times 5$ m box in front of the observer walking at a uniform pace along a fixed route, divided into several sections reflecting major variations in habitat and management. Surveys are conducted only under strictly defined conditions concerning weather (> 17 °C, or 13 – 17 °C in sunny weather) and time of day (10:45–15:45), and repeated once a week for several months (April to September in UK)—see Pollard (1977) for more details. Weekly counts are summed for each species, and separately for each generation in multi-voltine species, to give their abundance index for a given site. The index (P) can be corrected for patch area (A) and transect length (L) to enable sites of different sizes to be compared, using the formula suggested by Thomas (1983): $P = 100 * N * A/L$, where N represents butterfly count per 100 m of transect.

From a theoretical point of view, transect counts belong to the class of relative abundance methods, in which the recorded value is the product of the true abundance and the corresponding detection probability of individuals: $C = N * p$. Hence any changes in the recorded value may not necessarily reflect the true changes in abundance, but instead they may be due to variation in detection probability. However, as long as p is constant, it is possible to infer temporal trends in abundance and their spatial patterns from the uncorrected count data. This underlines the importance of maintaining transect width constant (which seems obvious, but may occasionally prove difficult in field reality) as well as standardization of survey conditions that may affect p , such as weather, time of day, and experience of observers involved. Thorough testing of the transect-count routine (Pollard et al., 1975; Pollard, 1977) demonstrated that the effects of weather and time of day, within the pre-defined limits of both, on count results were insignificant. Similarly, the observer effect appeared negligible in comparison to typical year-to-year differences in butterfly abundance. All these findings are very encouraging; nevertheless, the authors of the method themselves cautioned against between-site comparisons and using different observers on a single site because of possible observer effect (Pollard et al., 1986). Therefore, apart from efforts given to keeping detection probability constant, it seems useful trying to develop method modifications that would allow estimating this probability. Simultaneous use of a second observer and subsequent application of a double observer approach (Caughley and Grice, 1982; Pollock and Kendall, 1987) for the data analysis is one promising solution. Another option could be transects with two recording bands (Greenwood, 1996), e.g., within and beyond 2.5 m on both sides of the transect line. Based on counts within and outside the central band (n_1, n_2) as well as central band width (W , in our case 5 m) and transect length (L), butterfly density can be estimated as $\hat{D} = \ln[(n_1 + n_2)/n_2] * (n_1 + n_2)/(W * L)$. However, the application of this approach may be problematic due to possible difficulties in species identification of butterflies sighted within the outer band. A generalization of the double zone approach would be the distance sampling method, in which the distance from the transect line is recorded for each individual observed. Results are then expressed in densities corrected for species-specific and transect-specific detection probabilities that are estimated from detectability vs. distance functions (Burnham et al., 1980; Pollock et al., 2002). Distance sampling has already been successfully attempted in butterflies (Brown and Boyce,

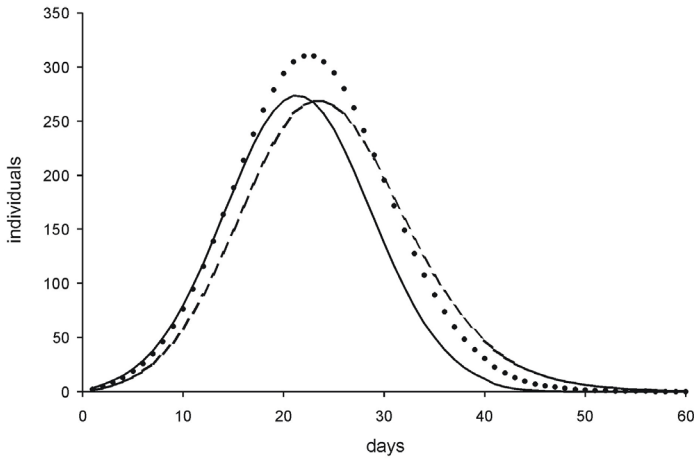


Fig. 3. The effect of seasonal population size and adult longevity on daily numbers of butterflies present throughout the flight period. It is assumed that individuals eclose for 40 days and their recruitment follows a Gaussian curve. The number of individuals flying each day (N_t) is the sum of newly eclosed ones (B_t) and those surviving from the previous day ($\phi * N_{t-1}$, where ϕ is daily survival rate). The total number of the individuals eclosed constitutes the seasonal population size ($N_{total} = \sum B_t$). The three following scenarios are presented: (i) $N_{total} = 2000$, $\phi = 0.6$ (solid line); (ii) $N_{total} = 1500$, $\phi = 0.75$ (dotted line); (iii) $N_{total} = 1000$, $\phi = 0.82$ (dashed line). The survival rates assumed correspond to adult life spans of 2, 3.5, and ca. 5 days, respectively. Noteworthy, the first and the third scenarios produce almost identical outcomes and are apparently indistinguishable for transect counts.

1998); however, its wider use is limited by technical difficulties in precise measuring of the distance at which butterflies are observed.

Following the successful testing of the constant detection probability assumption, it is not surprising that transect count results turned out to be highly correlated with population estimates obtained with MRR (Pollard, 1977; Thomas, 1983). However, it must be stressed that the latter represented merely the numbers of individuals present on the day of count, and not the seasonal population sizes. As already explained, in adult butterflies only a certain proportion of the seasonal population size is present on any given day because their life span is much shorter than the total time of occurrence (flight period). This proportion depends on the adult life span and flight period length (Nowicki et al., 2005b). In other words, the number of adults flying each day is a function not only of population size, but also of adult longevity, which should be viewed as a measure of the “accumulation” of daily cohorts in the course of the flight period (Fig. 3). Adult life span is highly affected by weather patterns, and can vary substantially from year to year within a single population (e.g., Brakefield, 1982; Courtney and Duggan, 1983; Warren, 1987). Consequently, higher population size may sometimes be followed by lower daily numbers (Fig. 3). The fact that transect-count results can be strongly influenced by variation in adult life span was noticed a long time ago (Owen, 1975), and also acknowledged

by Pollard (1977), but it has remained neglected ever since. In fact in the case of transect surveys little can be done to account for the extent of temporal fragmentation, because even if conducted weekly throughout the flight period transect counts alone do not provide any information on adult life span. Since transect count results cannot be easily corrected for differences in longevity, they should be at least interpreted with caution. One can imagine that relative abundance indices are somewhat overestimated in good weather seasons, and underestimated in bad ones.

Zonneveld (1991) proposed an interesting theoretical model allowing estimation of life span from transect count data, and more recently the free software Insect Count Analyzer (INCA) based on the model was made available (Longcore et al., 2003). Nevertheless, because of its rigorous requirements, e.g., logistically distributed recruitment and constant mortality throughout the season, the Zonneveld model remains difficult to apply and rarely used (examples of the model applications may be found in Mattoni et al., 2001; Longcore et al., 2003). In addition, transect counts should be repeated twice a week or even more frequently, especially at the end of flight period (Mattoni et al., 2001), but with this rather high sampling intensity life span estimates yielded by the model tend to be very imprecise (Gross et al., 2007). An alternative is the use of mixed methods, in which seasonal abundance is derived on the basis of transect counts corrected for adult life span estimated with a short-term MRR survey (Schultz and Dlugosch, 1999; Gross et al., 2007). This mixed approach is conceptually very similar to, but presumably slightly more labor-intensive than, the simplified MRR design (Nowicki et al., 2005b) that we describe at the end of the following section on mark–release–recapture. The lower labor requirements of the latter method are likely to stem from the fact that, apart from MRR sampling of relatively low intensity (required in both approaches), this method needs just recording the flight period length rather than a series of transect counts.

MARK–RELEASE–RECAPTURE

In MRR methods, both capture probability (p), which is conceptually equivalent to individual detection probability, and the turnover of adults within season expressed by daily survival rate (or residence rate in the case of spatially open populations) are directly estimated from the data. Therefore if the sampling has covered the entire flight period one can obtain the estimate of absolute population size for the investigated generation. The emphasis should be placed on ensuring that this estimate is unbiased, which can be achieved through proper fieldwork design and subsequent selection of an adequate MRR model for data analysis. From among the wide range of models available (reviews in Schwarz and Seber, 1999; Amstrup et al., 2005), the Jolly–Seber (JS) analytical model (Jolly, 1965; Seber, 1965) and its more advanced derivatives, i.e., the Cormack–Jolly–Seber (CJS)-type constrained models (Schwarz and Arnason, 1996), are the most popular in butterfly studies. Belonging to the class of open population models, they fit well butterfly populations in most situations and are easy to apply, thanks to the user-friendly MARK software (White and Burnham, 1999). However, a wider use of the Robust Design (RD) models (Pollock, 1982; Kendall and Pollock, 1992) should be advocated as they only re-

cently gained some ground in butterfly research (Settele et al., 2000; Casula and Nichols, 2003; Nowicki et al., 2005c). Despite the fact that they require several capture sessions within a rather short time (ideally a single day), which is obviously a drawback, their clear advantage is that they allow individual and behavioral variations in p that (C)JS models do not. Additionally, since in monitoring studies the seasonal population size is of prime interest, rather than the dynamics of daily numbers throughout the season, models focusing on recruitment estimates (the sum of which constitutes seasonal population size) deserve more attention. The superpopulation approach incorporated in the POPAN software (Arnason and Schwarz, 1999) seems particularly useful in this respect.

Unfortunately, very few butterfly population studies using MRR make efforts to validate assumptions of the statistical model applied, though there are exceptions that can be recommended as examples to follow. For instance, Schtickzelle et al. (2002) provides a comprehensive guideline for dealing with the assumptions and the model selection routine of the CJS models, while Nowicki et al. (2005c) does the same for the RD approach. The most standard assumptions are those of (i) unique and permanent marking, (ii) equal capture probability, and (iii) spatial and demographic closure of population. The first assumption, implying that animals are individually marked and their marks are not lost or overlooked in subsequent samplings, is relatively easy to meet if proper marking procedure is used and sampling is done carefully enough. Writing numbers on the underside of hind wings with fine-tipped waterproof pens is by far the simplest and the most reliable technique (Gall, 1985), while the historical coding systems (Ehrlich and Davidson, 1960; Brussard, 1970) are obsolete nowadays.

The other two assumptions are more difficult to fulfill since they depend not only on survey properties, but also on characteristics of investigated populations. Capture probability may vary between capture occasions (time variation), vary between individuals (heterogeneity), or change once an individual has been captured (behavior response) (Otis et al., 1978). Robust Design models, as implied by the name, are robust to all three kinds of violations of the equal p assumptions as well as their combinations, while (C)JS models allow time variation and (to a limited extent) behavior response, but not heterogeneity. Time variation in p is a relatively common phenomenon in butterflies as their activity is weather dependent. Behavior response, also termed marking effect, has sometimes been reported in butterfly studies using ad hoc testing (Singer and Wedlake, 1981; Gall, 1984; Mallet et al., 1987; Kemp and Zalucki, 1999), but systematic analyses (e.g., Schtickzelle et al., 2002; Nowicki, 2005c) did not reveal its presence. According to our experience, behavior response does not occur if handling is done properly, which involves a firm grip of wings while the mark is being written and placing butterflies on plants, preferably nectar source ones, at release. Differences in capture probability, especially intersexual ones with females typically having lower p , occur frequently in butterflies. Therefore we strongly suggest that if (C)JS models are used, intersexual differences in p should always be tested for and, if detected, population size estimates should be derived separately for both sexes and summed up at the end. It must be stressed that even such a procedure does not always remove all heterogeneity in p , because individuals of the same sex may also differ in catchability. Nevertheless, the

impact of this intrasexual heterogeneity on the (C)JS population size estimates is usually an underestimation of up to 20% (authors' unpubl. data).

Population closure combines spatial closure, i.e., no emigration or immigration, and a demographic one, i.e., no recruitment or deaths. Obviously no real population is ideally closed except for short moments, but let us suggest a rule of thumb that a population can be regarded as effectively closed if its gain or loss of individuals does not exceed 10% within the investigated period. This can be achieved by conducting capture sessions within a period that is relatively short in comparison with residence time of an average individual. A practical difficulty in this respect is caused by patch size-dependant residence time in butterflies (Schultz and Crone, 2001; Crone and Schultz, 2003)—in small habitat patches the residence times may prove too short to allow spatial closure even in very intensive studies. Formally, population closure is only required within primary periods of the Robust Design (precisely speaking, only its simpler versions since recent advances to the RD theory relax this assumption; see Schwarz and Stobo, 1997). However, spatial closure is always desirable since it makes interpretation of population size estimates much easier. For this reason it is recommended that if possible, MRR sampling should cover the entire area used by a population. Kendall (1999) proved that even if sampling is restricted to a part of this area, the population size can still be correctly estimated, yet this is true only as long as animals move randomly into and out of the sampled area. In reality, butterflies do not move randomly, especially at patch edges (Schultz and Crone, 2001), whereas within larger habitat patches their movements may be constrained to smaller “home ranges” (Hovestadt and Nowicki, 2008, this issue). Demographic closure can normally be achieved by limiting each primary period to daytime hours of a single day, because butterflies tend to eclose in early morning hours (Thomas and Lewington, 1991) and die mostly at night (Warren, 1992).

Whenever the cost of survey has to be optimized against the expected precision of its results, which is usually the case in monitoring programs, the simplified MRR design proposed by Nowicki et al. (2005b) may prove helpful. It is based on recording the start and the end of the flight period, and MRR sampling covering its mid part with at least 5 capture days, placed at intervals roughly equal to average adult life span, i.e., 2–3 days in small butterfly species and slightly more in larger ones. Seasonal population size can be then estimated from the number of butterflies flying at peak, their life span, and flight period length (for details see Nowicki et al., 2005b). This simplified design enables the cost of survey to be cut by about two-thirds.

SAMPLING OF NON-ADULT LIFE STAGES

Even though non-adult life stages may not be ideally synchronized, they last for long enough so that all individuals belonging to the same generation can be present together for some time. Consequently while sampling butterfly eggs or larvae instead of adults, one does not have to deal with the issue of temporal fragmentation. Similarly, detectability is not a problem provided that adequate searching techniques are available. As immobile or almost immobile objects, eggs and larvae can most often be detected almost perfectly, i.e., p is approaching 1. For instance, the detection rate of *Maculinea alcon* or

M. rebeli eggs exceeds 95% even if the survey is conducted rather quickly (authors' unpubl. data). When detection rate is so high, its variation has little effect on the population size estimates. Furthermore, the detection rate can be easily estimated through double sampling (Cochran, 1977).

Disadvantages of egg or larvae censuses are mostly practical ones, including little attractiveness for volunteers (though there are clear exceptions) and species-specific field techniques. Another argument against relying on eggs or larvae is that their abundance, although perfectly useful for monitoring population trends, is slightly less informative for assessing population status as compared with that of adults, because it is breeding individuals that define the effective population size. Moreover, the number of eggs or larvae cannot be easily converted into the number of adults in either the preceding or the following generation due to annual variation in fecundity as well as mortality in non-adult life stages (Warren, 1992).

All considered, sampling eggs or larvae does not have the potential to become widely applicable, but it remains an effective method for assessing abundance of selected species in which eggs or larvae are relatively conspicuous. Egg count has become the standard for assessing abundance of some lycaenids such as the two aforementioned *Maculinea* species (Elmes et al., 1996; Maes et al., 2004; van Swaay, pers. commun.) as well as *Lycaena dispar* (Duffey, 1968; Webb and Pullin, 2000). Larvae surveys, in turn, can be applied with relative ease to fritillary butterflies, e.g., *Melitaea cinxia* (Thomas and Simcox, 1982), *Euphydryas aurinia* (Schtickzelle et al., 2005), and *Euphydryas maturna* (Konvicka et al., 2005), the caterpillars of which aggregate in communal nests. In all the above cases, censuses of eggs or larvae can be conducted on plots, transects, or even the entire sites (total count) depending on their area. Labor requirements can be significantly reduced by a two-step procedure that comprises estimating average numbers of eggs per foodplant or larvae per nest on the basis of a limited sample, and sampling foodplant or nest density on the site.

CONCLUSIONS

Throughout this paper we have underlined the importance of imperfect detection in monitoring, regardless of whether it is manifested in the form of species detection probability in the case of distribution assessment or individual detection probability in the case of abundance estimation. Modifying studies of butterfly distribution in a way that would allow accounting for species detection probability appears relatively easy and should be widely popularized, despite specific constraints that we have presented. This basically implies conducting repeated surveys within a single season, preferably using independent observers, and applying novel statistical models for estimating detection probability and site occupancy by a species (MacKenzie et al., 2002; Royle and Nichols, 2003). Apart from this, relying on eggs or larvae in species where these life stages are fairly conspicuous deserves a wider use because their presence is biologically more meaningful for species occurrence than that of adults.

Concerning abundance estimation, a method combining the simplicity and low cost of transect counts with the reliability and precision of MRR would be an ideal solution.

The need for such a “reconciliation” between the transect counts and MRR was strongly voiced already more than two decades ago (Gall, 1985), but at present it still remains unachieved. Moreover, it is doubtful whether this ambitious goal is at all achievable. In the case of MRR there is apparently little space for reducing the labor requirements any further than has been accomplished by the simplified sampling procedure proposed by Nowicki et al. (2005b). Therefore it is, rather, refinements of transect surveys that should be sought. A vital advance would be a field method making possible the estimation of detection probability of individuals counted on transects. Prospective candidates in this respect include simultaneous count by two observers or the use of two recording bands. Obviously any of the suggested approaches will need rigorous testing of its utility in field conditions and accuracy before it is applied in monitoring programs.

In contrast, it is difficult to imagine any methodological development that would enable transect surveys to effectively deal with the problem of temporal fragmentation in butterfly populations. Instead, future research efforts should be focused on evaluating how variable the longevity of adult butterflies is and consequently how it affects the performance of uncorrected transect survey results. It may be expected that the effect is negligible, i.e., the relative abundance indices derived from transect counts should correlate well with seasonal population sizes, in the case of spatial patterns in abundance of a species. This is because within a particular region (spatial patterns are rarely investigated at a larger scale) all sites are affected by similar weather patterns, presumably resulting in relatively uniform adult life span across the sites. The variation in adult life span among generations is likely to be larger, but still smaller than the typical fluctuations in butterfly population size. The problem becomes crucial in cross-species comparisons since inter-specific differences in longevity are often quite large (Warren, 1992). Therefore we urge against using transect counts to calculate species diversity indexes, e.g., Shannon’s or Simpson’s, as is frequently done nowadays (e.g., Blair and Launer, 1997; Swengel, 1998; Blair, 1999; Kocher and Williams, 2000; Collier et al., 2006).

With all the methodological refinements suggested, we do not call for their immediate implementation in the ongoing butterfly monitoring programs. Several of them have already proved their usefulness in detecting biodiversity trends and at the same time acquired a well-deserved status of a popular “tradition” promoting public involvement in nature conservation (Thomas, 2005). Since they owed their success to well-established sampling protocol, it would be unwise to introduce sudden changes in it. On the other hand, it may be worth attempting the methodological refinements in the programs that have not been doing particularly well so far, and even more so in those that are planned to be launched in the near future. Adopting our recommendations would help to ensure that monitoring results are as unbiased as possible and of measurable precision. This is essential for hypothesis testing—a key component in targeted monitoring, the need of which has recently become eminent (Yoccoz et al., 2001; Nichols and Williams, 2006).

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