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Optimal monitoring strategy for endangered short-lived butterflies

Master's thesis of sciences in evolutionary Biology and Conservation

by

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Abstract

All studies in the domain of species conservation require an accurate estimation of population size. A frequently used method to assess butterfly population is the so-called "Mark-Recapture" method. It is the only method that provides absolute estimates of population size along with demographic parameters. However, this method is time consuming and marking generate a risk of damaging individuals. To avoid these problems, many monitoring programs rely on count-based methods to estimate relative population size. Here, we compared population estimates of a short-lived endangered species (*Maculinea nausithous*) acquired from Mark-Recapture analysis and count-based methods Pollard-Yates, Manly and Zonneveld approach, Royle replicated counts model and distance sampling. We found a highly significant relationship in population estimates. These results increase confidence in the application of count-based methods to assessing the state of multiple short-lived butterflies' species. Advantages and inconvenient of each method are discussed to provide efficient monitoring guidelines.

Keywords: population monitoring, threatened species, transect counts, Lepidopteres, Dusky Large Blue, Switzerland

Résumé

Toutes études dans le domaine de la conservation d'espèces exigent des estimations précises de taille de population. Une méthode fréquemment utilisée pour déterminer la taille de population de papillon est la méthode connue sous le nom de « Marquage-Recapture ». C'est la seule méthode fournissant des estimations absolues de taille de population ainsi que des paramètres démographiques. Cependant, cette méthode prend beaucoup de temps et le marquage induit un risque d'endommager des individus. Pour éviter ces problèmes, nombreux suivis d'espèce se basent sur des méthodes de comptages pour estimer des tailles relatives de population. Ici, nous avons comparé les estimations de taille de population d'une espèce menacées à vie courte (*Maculinea nausithous*) acquis par Marquage-Recapture et par les méthodes basées comptages Pollard-Yates, Manly and Zonneveld approach, Royle replicated counts model et distance sampling. Nous avons trouvé un rapport très significatif entre les estimations des tailles de population. Ces résultats augmentent la confiance en l'application des méthodes basées comptages pour évaluer l'état de nombreuses espèces de papillons à courte durée de vie. Les avantages et inconvénients de chaque méthode sont discutés pour fournir les directives efficaces en matière de suivi de telles espèces.

Mots-clefs: suivi d'espèce, espèces menacées, comptage sur transect, Lépidoptères, Azuré des paluds, Suisse

Introduction

With the present extinction crisis, estimation of biodiversity has become of fundamental importance in ecology and conservation. To prioritize areas for conservation, biologists and managers need information on species diversity and abundance in threatened habitats. The resources available for such inventories remain severely limited, increasing the need to develop speedier approaches to estimate the status of target habitat (Kerr et al. 2000). Moreover, conservative estimates suggest that 50-90% of the existing insect species on Earth have still to be discovered, thus creating an important challenge to scientists to monitor change in insect diversity. One solution is the use of selected indicator taxa as proxies for the biodiversity of a habitat in the hope that, by successfully conserving reasonable numbers of the indicator taxon, a large proportion of local biodiversity can also be saved (Landres et al. 1988, Tardif and DesGranges 1998). Butterflies are often the only group for which precise measures of change can be obtained. Indeed, monitoring butterflies has the advantage that it provides adequate information of variation for many terrestrial invertebrates groups and that surveys can be accomplished worldwide by a large numbers of amateur and professional lepidopterists (Thomas 2005). Butterflies are also used as reliable indicators of environmental variation, with changes in distribution and abundance being related to landscape, habitat and climate change (Parmesan et al. 1999, Asher et al. 2001, Fox et al. 2001, Roy et al. 2001, Thomas et al. 2004) In Switzerland, where the landscape is particularly fragmented, many studies have set up species and diversity monitoring protocols (Gonseth et al. 2007, Kery and Plattner 2007).
In order to measure changes in ecosystems, precise estimation of long term trends in abundance are essential. These measurements have the important task to detect the tendencies of populations while taking into account natural fluctuations. Until now, diverse methods have been used to estimate butterfly population size. They are briefly presented here.

A. Mark-Recapture (MR)

Mark-Recapture (MR) is a frequently used method for rare butterflies (Gall 1984, Bergman 2001, Baguette and Schtickzelle 2003). MR studies involve capturing and marking individuals within a population (Maes et al. 2006) and using individual capture histories (series of 100101) to estimate demographic parameters based upon well-developed statistical methods (Schwarz and Arnason 1996, White and Burnham 1999, Williams et al. 2002). Traditionally used methods for butterflies are based on the assumptions that populations are “open” and thus subject to births and immigrations as well as deaths and emigrations.

The major advantage of MR is that it is the only method that provides absolute estimates of population size along with several demographic parameters. However, MR has some disadvantages that render its large-scale application difficult. First, capturing and marking individuals is time consuming and often prohibitively expensive when not simply impossible (as for canopy inhabiting species). Second, it may harm or kill butterflies (Murphy 1987) or change their behaviours (and thus their probability of recapture) (Singer and Wedlake 1981).

To avoid these problems, many monitoring programs rely on count-based methods to estimate population size. Butterfly counts are often based on transect. In this case, one or more fixed transects crossing a butterfly’s habitat are set up, and observers inspect these transects frequently during the butterfly’s flight season, counting the number of individuals observed on each occasion. For delicate species such as butterflies, the ability to estimate population from such visual counts is valuable because they are easier and cheaper to conduct, and they do not require a delicate handling of

individuals. Count-based methods estimates are thought to be particularly well-suited for rare or endangered species of butterflies, where monitoring population trends is invaluable, and the cost of damaging individuals is elevated (Singer and Wedlake 1981, Murphy 1987, Mattoni et al. 2001). Several methods have thus been developed to derive population sizes from transect counts (Table 1).

B. Pollard-Yates index (PY)

The basic butterfly count-based method is called the Pollard walk (or Pollard-Yates counts) (Pollard 1977, Seidl 1999, Mattoni et al. 2001, Schultz and Hammond 2003, Pellet et al. 2007). The counts are used to calculate an annual index of population abundance. This index is the sum of the mean weekly counts to build an index for the flight season (Pollard and Yates 1993). This method assumes that the proportion of individuals detected is constant in space (sites) and time (years). Some studies have confirmed that Pollard-Yates indices correlate with population size (Thomas 1983, Haddad et al. 2008), but others underlined sources of possible bias (Harker and Shreeve 2008).

C. Manly and Zonneveld index (MZ)

Another count-based method that is becoming increasingly popular was first developed by Manly (1974) and later modified by Zonneveld (1991). This method is called the Manly-Zonneveld (MZ) approach and relies on a simple population dynamics model that describes the time course of abundance of adult insects for species emerging in discrete generations. The qualitative characteristics of the model depend on one dimensionless parameter only, namely the product of the death rate and a dispersion measure for the symmetric emergence distribution (Zonneveld 1991). Assuming constant adult mortality over the season, no generations overlap, no net migration and logistically distributed emergence times (all a priori reasonable assumptions for butterfly populations), it permits to estimate four population parameters (total population index [N], the day of peak emergence [μ], the spread of emergence time [β] and the butterfly's death rate [α]).

D. Royle replicated counts

Recently, Royle (2004) developed a method for assessing population abundance for spatially replicated counts. Originally developed for bird survey, this approach is adequate for many monitoring programs in which populations are surveyed repeatedly. This method is based on binomial mixture models which allows estimating and modelling abundance and detection probability from count data (Dodd and Dorazio 2004, Royle 2004). This class of models enables detectability-corrected abundance estimates in the absence of individual identification. The principal condition of these models is the temporal replication of counts at a number of sample locations. Because this modelling assumes that the population is demographically closed between replicated counts (ie. no births, no deaths, no immigrants and no emigrants), repeated butterfly counts within a single day may be viewed as independent realizations of a binomial random variable with parameters N_i (local butterfly abundance) and p_i (individual detection probability) (Kery et al. 2005). Another interesting functionality with this method is that both parameters (N_i, p_i) may be modelled as functions of covariates to increase precision or to investigate covariate relationship.

E. Distance sampling

The last method that we investigate is distance sampling (Buckland et al. 2001). The central concept is that individual detection decreases with distance from a transect (Brown and Boyce 1998). The detection function is a mathematical model to describe the probability of detecting a butterfly given its distance from the transect line (Buckland et al. 1993). This approach permits adjustments for differences in detectability among sites (e.g. vegetation structure, visibility…). By accounting for the proportion of individuals present but not detected, Distance sampling estimates the true density of individuals in the surveyed area. This method will provide unbiased estimates of absolute density for each site surveyed if the following key assumptions are met (Buckland et al. 1993):

- Transects are located in areas in which butterfly densities is uniform (homogenous habitat)
- The distances from the line are accurately recorded (at least in categories)
- All butterflies on the survey line are detected
- The butterflies are detected at their initial location, or, if there is undetected movement prior to detection, it is random and relatively slow relative to the speed of the observer

An advantage of this method is that the resulting site-density can easily be converted to absolute population abundance. Distance sampling also provides the variance of parameter estimates.

Table 1 Commonly used methods to estimates absolute (method A and E) and relative (methods B to D) butterfly abundance and their potential demographic parameters produced.

Methods	Estimates produced	Examples
A. Mark-Recapture	o Absolute estimates of daily and total population sizes o Apparent daily survival (ϕ) o Daily catchability (p) o Recruitment (p_{ent}) o Daily number of births (B_i)	(Watt et al. 1977) (Schwarz and Arnason 1996) (Baguette and Schtickzelle 2003) (Haddad et al. 2008)
B. Pollard-Yates index	o Annual index of population abundance (sum of weekly average count)	(Pollard and Yates 1993) (Schultz and Hammond 2003) (Collier et al. 2008) (Haddad et al. 2008) (Pellet et al. 2007)
C. Manly-Zonneveld index	o Total population index o Day of peak emergence (μ) o Spread of emergence time (β) o Death rate (α)	(Zonneveld 1991) (Mattoni et al. 2001) (Gross et al. 2007) (Haddad et al. 2008)
D. Royle replicated counts	o Total population index o Individual detection probability (p_i)	(Royle 2004) (Kery et al. 2005)
E. Distance sampling	o Effective survey width (esw) o Daily site-density	(Buckland et al. 1993) (Brown and Boyce 1998) (Powell et al. 2007)

Pollard-Yates index, Manly-Zonneveld index and Royle replicated counts do not estimate absolute population size, but provide a relative population abundance estimate. Choosing the optimal strategy for monitoring species is influenced by financial, time and field limitations, ecological characteristics of the species and ease of implementing the method. Because of its efficiency, practicality on broad scale and adequacy for fragmented landscapes, ecologists and

conservation biologists frequently apply count-based approaches to estimate the relative population size and to monitor population variations (Pollard 1977, Moss and Pollard 1993, Mattoni et al. 2001). Even despite their common utilisation, few studies have tried to demonstrate a relationship between such relative measures of abundance and absolute population size (Thomas 1983, Krauss et al. 2004, Collier et al. 2008, Haddad et al. 2008).

The main goal of the present study is to assess the suitability of various count-based methods to estimate population size in short-lived butterflies. Population size estimates acquired from MR analysis and the count-based methods Pollard-Yates, Manly and Zonneveld approach, Royle Replicated Counts model and distance sampling are compared. In addition, time consumption of the different methods and their potential impact on threatened species is also discussed.

Material and Methods

Study species and study area

The organism being studied is the Dusky Large Blue (*Maculinea nausithous*) (Fig. 1), a short-lived endangered species typical of fens and wet meadows in central Europe (mostly Molinion and Filipendulion). This species is present on the red list of threatened species of Switzerland and its status is considered as very endangered (Gonseth 1994). Furthermore, this species also integrates the national conservation plan of priority species of diurnal butterflies (Rhopalocera and Hesperiidae) of Switzerland (Swiss Butterfly Conservation). Concerning its life history traits, the larvae first feed on Great Burnet (*Sanguisorba officinalis*) and then prey on *Myrmica rubra* broods. Adults are sedentary and have a life expectancy that hardly exceeds five days (LSPN (Ligue Suisse pour la Protection de la Nature). 1999-2004). The flight season typically lasts from June to August depending on altitude and region. The five European species of *Maculinea* have been diminishing in numbers and are highly endangered with local extinctions in numerous countries (Wynhoff 1998, Munguira and Martin 1999). Thus having precise estimates of the population abundance is crucial to the continuation of conservation programs.

Fig. 1 Dusky Large Blue (*Maculinea nausithous*) on Great Burnet (*Sanguisorba officinalis*) (Picture David Parietti).

In 2008, we surveyed twelve *Maculinea nausithous* populations in western Switzerland (Table 2). Fixed transect routes were selected so that they passed through areas of high quality butterfly habitat (all populations were more or less casually surveyed on previous years by different observers). Survey routes were between 314 and 1'696 m in length. Every populations was visited at random times between 10:00 and 17:00 (BST) every 2-3 days (weather permitting) and transects were walked at a constant and slow pace (accordingly to Pollard, 1977). We used two persons on all surveys, one to watch (DP for capture and mark during MR transects), and an assistant to record data on protocol sheets. Surveys started before the first butterflies emerged (first butterfly seen on June 9th) and were ended when no butterflies were detected for 2 consecutive visits (last individual seen on August 16th). Duration of each survey was recorded to compare for time consumption of the different methods.

Table 2 Location of the 12 study population and basic survey data.

Populations	Swiss coordinates	Latitude Longitude	Transect length	Count sessions	Mean number of butterflies counted per count session	MR sessions	Mean number of butterflies marked per MR session
Rogivue 1	558449 / 157491	46°34'2.66"N 6°53'48.10"E	314 m	15	19.1	15	6.1
Rogivue 2	558155 / 157606	46°34'6.32"N 6°53'34.26"E	559 m	12	8.3	12	2.7
Beveret	573505 / 156122	46°33'21.10"N 7° 5'35.33"E	1'696 m	18	27.6	18	8.3
Lussy Nord	558760 / 155081	46°32'44.70"N 6°54'3.48"E	776 m	10	3.1	10	1
Lussy Sud	558754 / 154629	46°32'30.03"N 6°54'3.33"E	1'257 m	13	12.1	13	5.8
Chesaux 1	541940 / 182365	46°47'23.71"N 6°40'41.61"E	728 m	18	17.8	18	5.4
Chesaux 2	542516 / 182669	46°47'33.74"N 6°41'8.66"E	203 m	14	5.1	15	2.2
Chesaux 3	543178 / 183054	46°47'46.41"N 6°41'39.67"E	985 m	17	31.1	17	9.5
Chabrey 1	565126 / 198527	46°56'12.89"N 6°58'50.35"E	728 m	18	4.1	18	1.1
Chabrey 2	565028 / 198513	46°56'12.44"N 6°58'45.71"E	659 m	17	13.9	17	3.7
Champmartin 1	566055 / 199206	46°56'35.07"N 6°59'34.09"E	854 m	16	11.2	16	3.4
Champmartin 2	565985/ 199597	46°56'47.70"N 6°59'30.66"E	838 m	13	3.3	14	0.9

A. Mark-Recapture data collection and analysis

During MR surveys, individual were netted and numbered with a thin point permanent pen on the underside of the hind wing and immediately released afterwards. For each (re)capture, the following information were collected: number, sex, size (small, medium or large), wing-wear (1-5 scale (Watt et al. 1977)) and location was indicated on 1:5'000 aerial photographs. In such cases where the number could be seen from a distance, butterflies were not physically recaptured. In total, 183 MR surveys were accomplish and 797 butterflies were numbered, of which 266 (33%) were recaptured more than once.

Demographic parameters were estimated from individual capture histories (history 100101 indicates that an individual was captured at sampling occasions 1, 4 and 6) basing on generalisations of Constrained Linear Models (CLM)

(Lebreton et al. 1992, Schtickzelle et al. 2003). Basically, there are two types of CLM for live recapture data: Cormack-Jolly-Seber type (CJS) and Jolly-Seber type (JS) models. We used the POPAN formulation of the JS approach (Schwarz and Arnason 1996) as incorporated in MARK, v. 5.0 to estimate demographic parameters for our 12 populations. *POPAN* estimates three primary parameters; apparent daily survival (Φ), catchability (p) and recruitment (p_{ent} a probability of entering the population combining both births and immigration). Derived parameters are; daily number of births (B_i), daily population size (N_i) and total population (N_{tot} the total number of butterflies – caught or uncaught – in the population). Model parameters are estimated through maximum likelihood. We compared a set of a priori defined models (Table 3) and ranked them in a decreasing AICc weights order (the higher the *AICc* weights the better rank the model received) (Akaike 1973, Burnham et al. 1995). If more than one model converged, Mark model averaging procedure was used to estimate parameters. Model 1 assumed constant daily survival, constant catchability and constant recruitement. It thus read $\phi(.)$ $p(.)$ $pent(.)$ $N(.)$. Subsequent models (2 to 8) were based on combinations of constant and session-specific parameters (t).

For the count-based methods (Pollard-Yates index, Manly-Zonneveld index, Royle replicated counts index and distance sampling), butterflies observed from the survey route were recorded. Site- and sampling covariates were also collected for each survey. In total, 343 transect surveys were done, during which 2'525 butterflies were observed.

B. Pollard-Yates index

This method requires only the count of individual that flew within 10 meters of the observer (strict limits on observation area and condition) during Pollard walk surveys (Pollard 1977). Calculation of the annual index of population abundance is done without the need of any software (sum of the mean weekly counts) (Pollard and Yates 1993).

C. Manly-Zonneveld index

For this method we collected a time series of counts that we effectuated according to the same directives of Pollard-Yates counts (Pollard and Yates 1993). Counts should cover the entire flight period and should be evenly spaced in time (3, 2, 8, 26, 28, 21, 16, 17, 15, 4, 3, 2, 1, 0, 0 is a time series of counts for a small population). We used the online computer program Insect Count Analyser (INCA) (available at http://www.urbanwildlands.org/INCA). This program estimates the total population index (N), the day of peak emergence (μ), the spread of emergence time (β) and the butterfly's death rate (α). In addition to the estimated parameters, the INCA also provides the standard deviation that indicates the magnitude of the uncertainty and a coefficient of variation that gives an idea about the reliability of the estimate. INCA permits the use of prior information on the death rate if the program fails to find unambiguous estimates for all parameters.

D. Royle replicated counts

This method uses counts that are replicated in space and time. To apply this method, we walked each transect back and forth (on the same day after morning emergences (Elferrich 1963, Thomas 1984, Thomas and Lewington 1991, Elferrich 1998), thus respecting the close population assumption). We used the online computer program Presence 2.2 (http://www.mbr-pwrc.usgs.gov/software/doc/presence/presence.html) for this method. Parameters were modelled as function of site- and sampling covariate to increase precision and investigate covariate relationship. Site covariates

were: transect length, amount of precipitation between two visits and food-plant density, and sampling covariate were temperature, wind speed and sunning. Because program Presence could not estimate parameters from each of our populations independently (less than 20 replicated counts), we pooled all the data together (thus obtaining 2 vectors of back and forth counts) to obtain global estimates. From the estimated (global) detection probability, a total population size index was calculated for the day of peak flight activity in each population as: $N_i = n_i/p$, where N is the abundance index for population i, n_i is the maximum number of individual counted in population i and p is the global detection probability.

E. Distance sampling

Data-gathering for distance sampling is done just by recording the perpendicular distance of each observed individuals from the transect centreline at the time of original detection. For this method, we used the online software package Distance 5.0 (http://www.ruwpa.st-and.ac.uk/distance/). The software estimates the site effective survey width (or *esw*, the distance from the transect line out to which the number of butterflies unseen equals the numbers seen beyond that distance) (Buckland et al., 1993). We calculated Akaike's information criterion (*AICc*) for each model to aid in model selection (Akaike 1973, Burnham et al. 1995). In the analysis of the detection function distance data in 1 meter intervals were used and we truncated the distance at 6 meters to delete the outliers as recommended by Buckland et al., (1993). The effective survey width was used to estimate site density. The estimate of density, D, from distance sampling is $D = n/L*2*esw$, where n is the maximal number of butterflies observed during transects for a site and L is the transect's length. Resulting density estimates could then easily be converted to maximum population abundance (this was done by multiplying the density estimates by the visited surface area). We thus calculated maximum population abundance $N = DLW$, where W is the transect width covered. Distance sampling also provides the calculation of the variance of parameter estimates.

Finally, population estimates generated by Mark-Recapture, Pollard-Yates index, Manly-Zonneveld index, Royle replicated counts index and maximum population abundance derived from distance sampling were compared with Pearson's correlation to test for any significant relationship. Ranking of population size issued from Mark-Recapture was compared with the ranking issued from the other methods. Furthermore, time consumption of each method was also examined with the average fieldwork (in minutes) as well as categorisation of the time to analyse the data.

Results

A. Mark-Recapture

Even though the number of marked and recaptured individuals was relatively high, most of the models did not converge with program Mark (Table 3). The model with constant apparent survival, constant catchability, variable recruitment and constant total population size $\phi(.)p(.)p_{ent}(t)N(.)$ largely outperformed the other tested models. Because of no model convergence or incoherent estimates, we had no estimates issued from MR data for 3 of our 12 populations (Lussy Nord, Chesaux 2 and Champmartin 2). For Lussy Sud's population, two models mainly converged: the just above cited model as well as the model $\phi(.)\ p\ (t)\ p_{ent}\ (t)\ N\ (.)$.

Table 3 Model selection with program Mark on MR data. The model with the highest AICc weights is $\phi(.)\ p(.)\ p_{ent}(t)\ N(.)$ where ϕ is the apparent survival, p the catchability, p_{ent} the recruitment (probability of entering the population combining births and immigration) and N the total population size. No estimates could be deduced from Lussy Nord, Chesaux 2 and Champmartin 2 data. Two models mainly converged on Lussy Sud's data.

Populations	Rogivue 1	Rogivue 2	Beveret	Lussy Nord	Lussy Sud	Chesaux 1	Chesaux 2	Chesaux 3	Chabrey 1	Chabrey 2	Champmartin 1	Champmartin 2	Mean of AICc weights	Model rank
Number of marked individual	91	32	149	10	75	97	33	161	19	63	54	13		
Recapture fraction	0.40	0.34	0.38	0	0.24	0.32	0.30	0.30	0.42	0.51	0.35	0.38		
Models														
(1) $\phi(.)\ p(.)\ p_{ent}(.)\ N(.)$	**	**	**	*	**	**	**	**	**	*	**	**	-	-
(2) $\phi(.)\ p(.)\ p_{ent}(t)\ N(.)$	1	1	1	**	0.61	1	**	1	1	1	1	**	0.96	1
(3) $\phi(.)\ p(t)\ p_{ent}(.)\ N(.)$	*	*	*	**	*	*	*	*	**	*	*	**	-	-
(4) $\phi(.)\ p(t)\ p_{ent}(t)\ N(.)$	**	**	0	**	0.29	0	**	0	0	0	**	**	0.05	3
(5) $\phi(t)\ p(.)\ p_{ent}(.)\ N(.)$	*	*	*	**	*	*	**	**	**	**	**	**	-	-
(6) $\phi(t)\ p(.)\ p_{ent}(t)\ N(.)$	**	**	**	**	0.1	**	**	**	**	**	**	**	0.1	2
(7) $\phi(t)\ p(t)\ p_{ent}(.)\ N(.)$	*	*	*	**	**	*	*	*	*	*	*	**	-	-
(8) $\phi(t)\ p(t)\ p_{ent}(t)\ N(.)$	**	**	**	**	0	**	**	**	**	**	**	**	0	4

* : Model did not converge

** : Model converged but produced incoherent estimates

Model estimated survival indicated that *Maculinea nausithous* has an average daily survival rate of 77%, but that this value ranges from 67% to 83% between populations. Capture probability was likewise variable, but was on average of 46% ±9, meaning that on each occasion, we caught approximately half of the individuals on the wing. Recruitment (birth and immigration) was on average 6.8% on each day. Total population size (± SE) ranged from 35 ± 7 individuals (Chabrey 1) to 413 ± 44 individuals at Chesaux 3.

Table 4 Parameter estimates with program Mark from Mark-Recapture data and their standard error (SE). ϕ is the apparent survival, p the daily catchability, p_{ent} the recruitment (probability of entering the population combining births and immigration) and N the total population size.

Populations	ϕ (SE)	p (SE)	p_{ent} (SE)	N (SE)
Rogivue 1	0.81 (0.03)	0.41 (0.06)	0.068 (0.04)	183 (19.81)
Rogivue 2	0.81 (0.04)	0.34 (0.10)	0.086 (0.06)	78 (17.96)
Beveret	0.77 (0.02)	0.43 (0.06)	0.056 (0.02)	314 (28.86)
Lussy Nord**	-	-	-	-
Lussy Sud*	0.79 (0.10)	0.30 (0.15)	0.098 (0.09)	218 (43.68)
Chesaux 1	0.67 (0.03)	0.71 (0.09)	0.058 (0.02)	205 (21.48)
Chesaux 2**	-	-	-	-
Chesaux 3	0.75 (0.02)	0.42 (0.06)	0.061 (0.02)	413 (43.87)
Chabrey 1	0.76 (0.07)	0.57 (0.15)	0.059 (0.06)	35 (7.27)
Chabrey 2	0.83 (0.03)	0.34 (0.06)	0.061 (0.04)	128 (16.87)
Champmartin 1	0.73 (0.04)	0.65 (0.10)	0.067 (0.03)	103 (13.09)
Champmartin 2**	-	-	-	-
Mean	0.77 (0.04)	0.46 (0.09)	0.068 (0.04)	-

* : Model averaging was used to produce estimates

** : Model did not converge or produced incoherent estimates

B. Pollard-Yates index

Pollard-Yates annual index of population abundance varied between 5.5 and 104.7. The smallest index is associated with Lussy Nord and the largest with Beveret. This method does not provide any estimate of incertitude.

Table 5 Pollard-Yates annual index of population abundance for our 12 study populations.

Populations	Pollard-Yates index
Rogivue 1	54
Rogivue 2	20.3
Beveret	104.7
Lussy Nord	5.5
Lussy Sud	33.8
Chesaux 1	60.5
Chesaux 2	15.5
Chesaux 3	97.5
Chabrey 1	10.7
Chabrey 2	36.6
Champmartin 1	36.3
Champmartin 2	7.8

C. Manly and Zonneveld index

Program INCA generated estimates of total population index (N), death rate (α), day of peak emergence (μ), and spread of emergence time (β) and their uncertainty (SD and CV) for only 4 of our 12 populations (Table 6). Using prior information on the death rate derived from the population with the lowest CV (Rogivue 1), we were able to produce estimates (without their uncertainty) for four supplementary populations. INCA could not generate estimates for the last four populations in spite of using prior information. Total population index (± SD) varied between 29 (Rogivue 2) and 166 (± 63) (Beveret). Death rate varied between 20% and 26% per day (mean 22%), day of peak emergence between

the 13th of June and the 25th of July (2 phenological periods) and spread of emergence time (μ) between 2.1 and 4.6 days.

Table 6 Manly-Zonneveld parameter estimates (total population index (*N*), death rate (α), day of peak emergence (μ) and spread of emergence time (β)) and their standard error for our 12 studied populations.

Populations	N (SD)	α (SD)	μ (SD)	β (SD)
Rogivue 1	70 (19)	0.200 (0.05)	169 (1)	2.7 (0.5)
Rogivue 2[a]	29	0.202	166	2.1
Beveret	166 (63)	0.235 (0.09)	173 (1)	3.9 (0.5)
Lussy Nord[b]	-	-	-	-
Lussy Sud[a]	58	0.200	162	3.6
Chesaux 1	109 (102)	0.262 (0.24)	201 (3)	4.6 (1.0)
Chesaux 2[b]	-	-	-	-
Chesaux 3[a]	129	0.203	202	4.1
Chabrey 1[b]	-	-	-	-
Chabrey 2	70 (37)	0.264 (0.14)	204 (2)	3.2 (0.7)
Champmartin 1[a]	50	0.202	204	3.3
Champmartin 2[b]	-	-	-	-
Mean	-	0.221 (0.13)	-	-

[a] = need of prior information

[b] = could not produce estimates

D. Royle replicated counts

The model with detection probability depending on temperature and constant average abundance across sites ($p(temperature + temperature^2)\ \lambda\ (.)$) outperformed the other tested models (Table 7). Detection probability was thus best modelled in function of the sampling covariate temperature.

Table 7 Model selection with program Presence on all data pooled together. The model with the highest AIC was $p(temp + temp^2)\ \lambda(.)$ where p is the detection probability and λ the average abundance.
Tested site covariates were: transect length, amount of precipitation between two visits (precipitation) and food-plant density, and sampling covariate were temperature and wind speed.

Models	AIC	deltaAIC
(1) $p(temperature + temperature^2)\ \lambda(.)$	2886	0
(2) $p(temperature)\ \lambda(.)$	2890	4
(3) $p(.)\ \lambda(.)$	2950	60
(4) $p(sunning)\ \lambda(.)$	2954	68
(5) $p(wind\ speed)\ \lambda(.)$	2996	110
(6) $p(.)\ \lambda(food\text{-}plant\ density)$	3780	894
(7) $p(.)\ \lambda(precipitation)$	6553	3667
(8) $p(.)\ \lambda(transect\ length)$	*	*

* : Model did not converge

Individual detectability (± SE) was estimated as 72% (± 2%). Total population index (± SE) calculated at peak flight activity ranged from 8 (0.2) (Champmartin 2) to 64 (1.8) (Beveret), what was largely inferior as the total population size issued from Mark-Recapture.

Table 8 Individual detectability and total population indices estimated with Royle replicated counts method.

Populations	Detectability (SE)	Royle replicated counts total population index (SE)
Rogivue 1	0.72 (0.02)	42 (1.2)
Rogivue 2		21(0.6)
Beveret		64 (1.8)
Lussy Nord		10 (0.3)
Lussy Sud		28 (0.8)
Chesaux 1		42 (1.2)
Chesaux 2		11 (0.3)
Chesaux 3		56 (1.6)
Chabrey 1		11 (0.3)
Chabrey 2		32 (0.9)
Champmartin 1		20 (0.6)
Champmartin 2		8 (0.2)

E. Distance sampling

Effective survey width (*esw*) varied between 1.61 (Chabrey 1) and 3.44 m (Chabrey 2). The calculated site density varied between 1.2 (Champmartin 2) and 16.9 butterflies per hectare (Rogivue 1). Maximum population abundance (± SE) varied between 12 (± 4) (Champmartin 2) and 148 (± 11) (Beveret).

Table 9 Distance sampling parameter estimates (Effective survey width (*esw*), site density and maximum population abundance derived form distance sampling) and their standard error (se) for our 12 studied populations.

Populations	*esw* (SE)	Density (SE) (individual/ha)	Maximum population abundance (SE)
Rogivue 1	2.82 (0.13)	16.9 (2.1)	64 (8)
Rogivue 2	3.03 (0.23)	4.4 (0.4)	30 (2)
Beveret	1.95 (0.13)	7.3 (0.5)	148 (11)
Lussy Nord	1.62 (0.22)	2.8 (0.4)	26 (4)
Lussy Sud	2.76 (0.35)	2.8 (0.5)	44 (6)
Chesaux 1	1.9 (0.19)	10.8 (1.2)	95 (11)
Chesaux 2	2.29 (0.18)	8.6 (0.7)	21 (2)
Chesaux 3	1.74 (0.13)	11.7 (0.9)	138 (11)
Chabrey 1	1.61 (0.21)	3.4 (0.5)	30 (5)
Chabrey 2	3.44 (0.41)	5.1 (0.7)	40 (5)
Champmartin 1	2.37 (0.59)	4 (1.3)	41 (13)
Champmartin 2	3.06 (0.79)	1.2 (0.4)	12 (4)

Method comparisons

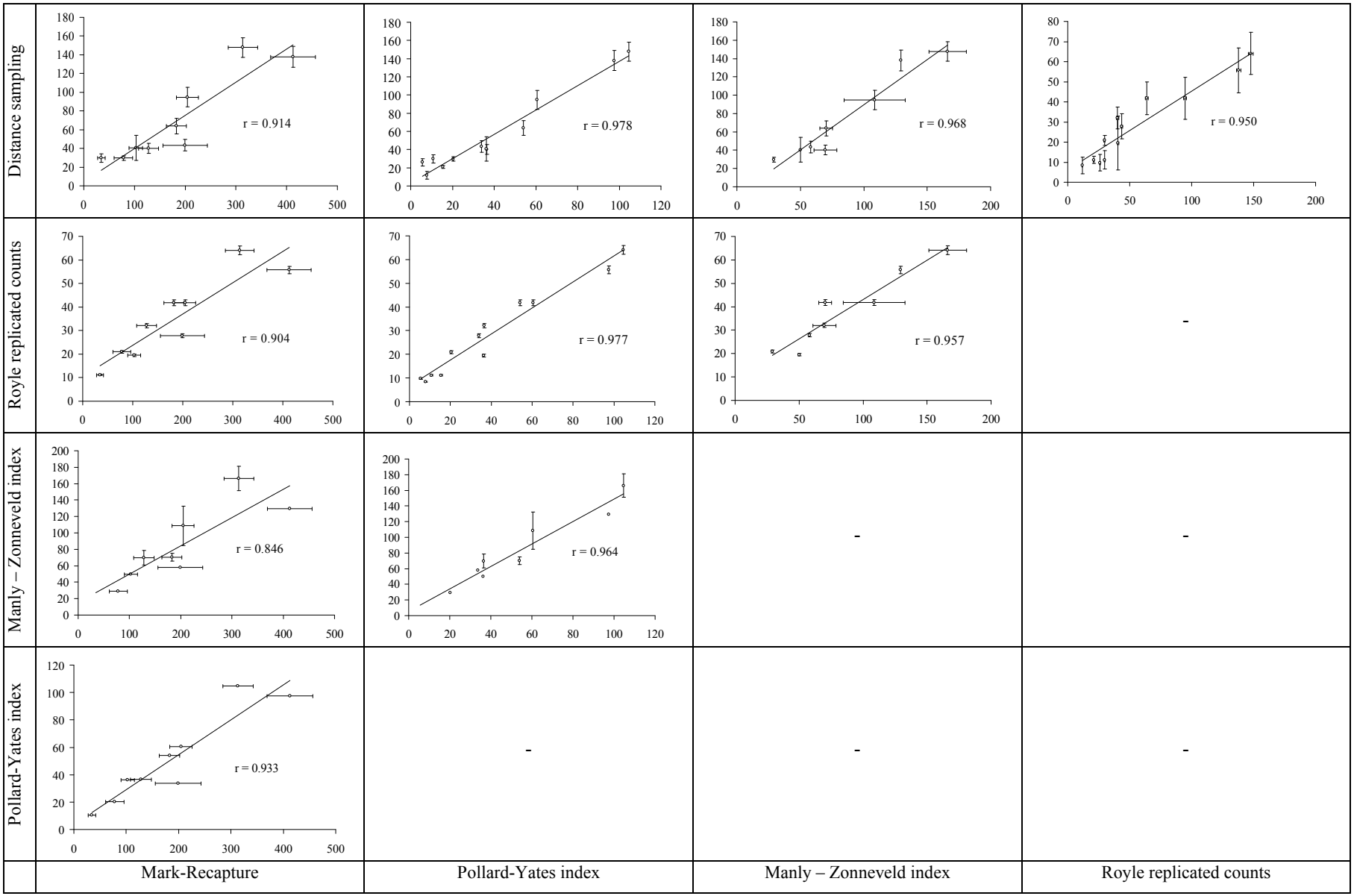
Pearson's correlation coefficient (r) for pairwise relationships between MR population estimates, population indices (Pollard-Yates Counts, Manly and Zonneveld, Royle replicated counts) and maximum population abundance derived from distance sampling were very high and varied between 0.846 and 0.978.

Pollard-Yates indices (r = 0.933) were more closely correlated with Mark-Recapture population estimates than were Manly and Zonneveld indices (r = 0.846), Royle replicated counts indices (r = 0.904) and maximum population abundance derived from distance sampling (r = 0.914) (Figure 1).

When population indices and population abundance were compared between them, Royle replicated counts indices and maximum population abundance derived from distance sampling were the indices that best correlate with Pollard-Yates indices (r = 0.977 and r = 0.978 respectively)

Estimates that best correlated with Manly and Zonnveld's indices were Royle replicated counts indices (r = 0.957) and maximum population abundance derived from distance sampling (r = 0.968). Concerning Royle Replicated Counts indices and maximum population abundance derived from distance sampling they both best correlated with Pollard-Yates indices (r = 0.977 and r = 0.978 respectively).

Fig. 2 Comparison between Mark-Recapture population estimates, population indices (Pollard-Yates, Manly and Zonneveld index and Royle replicated counts) and maximum population abundance derived from distance sampling. r is Pearson's correlation coefficient.



Ranking of population size issued from Mark-Recapture (Table 10) showed that Chesaux 3 was the largest and Chabrey 1 the smallest population (without having estimates for 3 populations). Ranking's with the other 4 count-based methods showed that Beveret was considered as the largest population and different populations were designed as the smallest (for example Lussy Nord for Pollard-Yates index). On the whole, the ranking issued from the count-based method was near from the ranking issued from Mark-Recapture.

Pollard-Yates index, Royle replicated counts and distance sampling had the advantage of having been able to produce estimates for the 12 populations and thus allowed the ranking of all of them.

Table 10 Ranking of population size issued from Mark-Recapture and comparison with the ranking issued from the other methods.

Populations	Number of marked butterflies	Mark-Recapture	Pollard-Yates index	Manly-Zonneveld index	Royle replicated counts	Distance sampling
Chesaux 3	161	1	2	2	2	2
Beveret	149	2	1	1	1	1
Lussy Sud	75	3	7	6	6	5
Chesaux 1	97	4	3	3	3	3
Rogivue 1	91	5	4	4	3	4
Chabrey 2	63	6	5	5	5	7
Champmartin 1	54	7	6	7	8	6
Rogivue 2	32	8	8	8	7	9
Chabrey 1	19	9	10	-	9	8
Chesaux 2	33	-	9	-	9	11
Champmartin 2	13	-	11	-	12	12
Lussy Nord	10	-	12	-	11	10

Time consumption for each method (Table 11) showed that Royle replicated counts and Mark-Recapture were both methods that required long fieldwork. Pollard-Yates index, Manly-Zonneveld index and distance sampling were methods which took comparable time on the field. For the time to analyse the data, Mark-Recapture needed very long time and Pollard-Yates index was the method that required at least time.

Table 11 Average time consumption on the field (for surveying a population in minutes) as well as categorisation of the time to analyse the data for the five methods to estimate population abundance.

Time consumption	Mark-Recapture	Pollard-Yates index	Manly-Zonneveld index	Royle replicated counts	Distance sampling
Average time on the field (minutes)	30	23	23	47	23
Time for data analysis	Very long	Very short	Short	Intermediate	Intermediate

Discussion

We evaluate population size estimates acquired from MR analysis and from the count-based methods Pollard-Yates, Manly and Zonneveld approach, Royle replicated counts model and distance sampling. None of the methods performed better across all criteria. Thus, the appropriate choice of sampling approach and analysis depends on the weight allocated to each criterion.

A. Mark-Recapture (MR)

Mark-Recapture has the major advantage of estimating absolute population size along with several demographic parameters. This method is known as being the most rigorous approach to population abundance because it incorporates the greatest amount of information into well-developed statistical methods (Williams et al. 2002). Unfortunately, estimated demographic parameters can be imprecise or even completely nonexistent when only few individuals can be marked (small population, insufficient number of survey or with very mobile species). This was visible in our study; no model converged or incoherent estimates were produced for 3 of our 12 study populations. Lussy Nord, Champmartin 2 and Chesaux 2 are these 3 populations, where only 10, 13 and 33 butterflies were marked respectively (Table 3). *Maculinea nausithous* being regarded as sedentary (adult butterflies feed, mate and rest on the flower heads of the larval food plant (Anton et al. 2007) and a sufficient number of surveys having been carried out, these 3 populations were obviously too small to acquire MR estimates.

When assumptions are met (populations are "open" and thus subject to births and immigrations as well as deaths and emigrations) and enough individuals are marked, MR demographic parameters are reliable and can thus bring precious information. In our study, population Lussy Sud was ranked with MR as the third largest population (Table 10). This population had the smallest daily catchability (p) and the highest recruitment (p_{ent}) (Table 4). The other methods that did not take into account this demographic parameters, have thus wrongly under estimated the size of this population (Table 10). Knowing that variation in detection and survival probabilities due to succession or other environmental change across a flight period is likely for most butterflies, it is thus especially important estimating demographic parameters and their variability (Haddad et al. 2008). Furthermore, MR's demographic parameters are useful to understand population ecology and mechanisms shaping the population dynamics of unfamiliar species. In our case, *Maculinea nausithous* has already been the subject of researches and our MR's demographic parameters, as for example the daily survival rate (ranges from 67 to 83%), were realistic in comparison of what is found in the literature (Nowicki et al. 2005).

In addition to the problem when not enough individuals are marked, MR has also the disadvantage of being a time consuming method and thus often prohibitively expensive. On the field, catching and marking individuals took time and necessitated preliminary training. For the analysis, producing data files and understanding non intuitive programs consumed also time. The last raised problem with MR is the one about handling butterflies. Manipulating butterfly is not without risk, firstly it may harm or even kill butterflies (Murphy 1987) what could be disastrous for rare or endangered species. Secondly, it was shown on the alpine fritillary butterfly, *Boloria acrocnema*, that capturing and marking disrupts flight activity and can generate large positive biases in population size estimates (overestimation by 2 to 4 times the actual population size) (Gall 1984).

To avoid numerous disadvantages that MR can generate when small populations are studied, many monitoring programs rely on count-based methods to estimate population size. The main goal of this study was thus to show if these count-based methods really allow to estimate precisely population size without MR's disadvantages.

B. Pollard-Yates index (PY)

Pollard-Yates annual indices of population abundance proved to be the indices correlating best with our MR population estimates (r = 0.933). This high correlation found on *Maculinea nausithous* is on accord with the results described for other species (e.g., Thomas 1983; Haddad et al. 2008). This excellent result for Pollard-Yates was found although assumptions of this method (proportion of individuals detected is constant in space and time) seemed not totally respected for *Maculinea nausithous.* Indeed, the catchability (p) found with MR results was constant in time but varied between sites (Table 4).

Because of the way this index was calculated, it never failed to produce an index of abundance what was appreciable with small populations. Time consumption was very weak for this method as much for the fieldwork (visual counts) as for the analysis (no software needed). An obvious disadvantage of this approach was the complete absence of demographic parameters and estimates of uncertainty produced.

C. Manly and Zonneveld index (MZ)

Because the program we used (INCA) recommends that the highest count exceeds 15, estimates were produced for only 4 of our 12 study populations (with standard deviation that varied greatly (Table 6)). With the possibility to use prior information on the death rate when the program failed to find unambiguous estimates for all parameters, estimates for 4 supplementary populations could be produced. Thus no information could be produced for our 4 smallest populations (Table 6). In spite of variable value of uncertainty, population indices were well correlated with MR population estimates (r = 0.846). This correlation was the lowest obtained with MR data in comparison with the other count-based methods.

On the other hand, this method had the advantage of producing demographic parameters (day of peak emergence (μ), the spread of emergence time (β) and the butterfly's death rate (α)). Estimates of survival with MR were less variable than INCA estimates of mortality but both values were in the same order of magnitude (Table 4 and 6).

The strong assumptions for this method are not realistic for all butterfly species. Constant adult mortality was possible for *Maculinea nausithous* (best model with MR described survival as constant phi(.)). No generations overlap; this was true because our studied species is univoltine. No net migration; *Maculinea nausithous* is described as a sedentary species (Anton et al. 2007). Last assumption is a logistically distributed emergence times. Daily number of births (B_i) issued from MR had such tendency although this parameter is influenced by weather conditions for *Maculinea nausithous* (data not shown).

Concerning time consumption of the method, fieldwork and time for analysis were short in comparison with other methods.

D. Royle replicated counts

This study was the first application of Royle replicated counts approach to butterflies. Program Presence was not appropriate for small populations. Indeed, this software could not estimate parameters from each population independently, we had thus to pool all the data together. The index of population size we could calculate for each population was thus based on a global detection probability. Indices correlated well with MR population estimates (r = 0.904) but were largely inferior to the MR population size (Table 7). Estimates of uncertainty were provided but no supplementary demographic parameters were produced. An advantage of this method was that parameters could be

modelled as function of site- and sampling-covariates to increase precision or to investigate covariate relationship. In our case, detection probability was best modelled in function of the temperature. Like many butterflies, *Maculinea nausithous*' activity, and thus its detection probability, is temperature dependent.

This method assumes that the population is demographically closed between replicated counts. This assumption was respected for *Maculinea nausithous* because field surveys (transect back and forth) were effectuated on the same day after morning emergences (Elferrich 1963, Thomas 1984, Thomas and Lewington 1991, Elferrich 1998). Because transects had to be walked back and forth, this method required longer fieldwork in comparison to other methods (Table 10).

E. Distance sampling

Despite Buckland et al. (1993) recommending a practical minimum of about 60 individuals to adequately model a detection function, distance sampling maximum population abundance were highly correlated with MR population estimates (r = 0.914). This abundance corresponds to the population present within the transect, it is thus normal that these values were inferior to MR population estimates.

Distance sampling has the advantage to permit correction for differences in detectability among sites. This was very practical because sites generally differed in habitat structure or visibility. The effective survey widths (*esw*) that were estimated for each population (Table 9) varied considerably and were linked with the type of habitat (Fig 3 and 4).

Fig. 3 Chabrey 1 was a population along a way in a forest. Trees limited the habitat of *Maculinea nausithous* and thus the effective survey width obtained by distance sampling for this population was small (*esw* = 1.61, Table 9) (Picture David Parietti).

Fig. 4 Lussy Sud was a population in wet meadows near a lake. No trees limited the habitat of *Maculinea nausithous* and thus the effective survey width obtained by distance sampling for this population was greater (*esw* =2.76, Table 9) (Picture www.news.admin.ch).

Furthermore, distance sampling let us survey a much larger portion of each site contrary to Pollard-Yates index which limited observations to ≤ 5 meters of the observer (Powell et al. 2007).

For density estimates to be unbiased, four assumptions must be satisfied: (1) transects are located in areas in which butterfly densities is uniform, (2) all butterflies on the survey line are detected, (3) distances from the line are accurately recorded and (4) butterflies are detected at their initial location, or, if there is undetected movement prior to detection, it is at random and relatively slow relative to the speed of the observer. The first assumption was difficult to satisfy because *Maculinea nausithous*' distribution depends on its host plant allocation. Remaining assumptions were met with adequate field training of the observer: in walking at a constant and slow pace (accordingly to Pollard, 1977), in butterfly identification and detection and as well as in estimating distances.

Time consumption was short for the fieldwork and intermediate for the analysis in comparison with the other approaches.

Optimal monitoring strategy

This study showed that demographic parameters issued from Mark-Recapture can increase precision of population size estimates (cf. Lussy Sud's population was wrongly under estimated by the count-based methods (Table 10)). However, these demographic parameters can be imprecise or even completely missing when only few individuals can be marked, what is not practical for monitoring endangered short-lived butterflies.

Even if there was no evidence of capture and marking trauma, such as escape reactions, abnormal dispersal behaviour or increased mortality, we advise to avoid Mark-Recapture for monitoring threatened species. Different results were found on the effect of marking and handling butterflies. It may increase mortality rates (Morton 1984), augment migration rates (Singer and Wedlake 1981) and change activity patterns (Mallet et al. 1987). These effects may vary between species but taking the risk of potentially harming an endangered species can be avoided by using count-based method.

In the present study, we have shown a highly significant relationship in relative abundance and population sizes from Mark-Recapture for *Maculinea nausithous* ($r \geq 0.846$). Consequently, these results increase our confidence in the application of relative abundance measures to assessing the state of multiple short-lived butterfly populations

throughout a landscape. However, each method has its own advantages and inconvenient. For small populations or species with very low capture probability, which is common in rare and threatened species, we recommend avoiding the use of Mark-Recapture, Manly and Zonneveld approach, Royle replicated counts method and distance sampling (based on Buckland's recommendations (Buckland et al. 1993)). Indeed, in such situations, these methods have an important risk not to produce estimates because of the difficulty to acquire sufficient data.

Knowledge on the ecology of a species is very important before choosing a method for monitoring. Species such as *Lasiommata megera*, whose distribution is seasonal, diurnal and temperature related can lead to biases in estimation of abundance with count-based methods ((Harker and Shreeve 2008).
Furthermore, the use of standardized field methods for all monitoring methods is essential to avoid possible biases and obtain reliable estimates.

If little time and/or limited financial means are available, Royle replicated counts method and Mark-Recapture should not be used because they necessitate very long field work.

Pollard-Yates index is really interesting to estimate population size. This method obtains the best correlation coefficient with MR population size estimates and requests minimum time on the field and for the analysis. This method is thus very useful when resources do not permit long fieldwork. The principal inconvenient of this method is the absence of demographic parameter estimates. The study of species whose ecology remains to be discovered is not ideal with this method. For such species, combination of Pollard-Yates index and distance sampling (or Mark-Recapture) can be a solution. In combining both methods, Pollard-Yates indices can be adjusted with estimates of detection probability. Furthermore, adding distance sampling method in monitoring protocols is a negligible increase of work; indeed, it only demands the observer to record the perpendicular distance of each observed individuals.

In this study, total population size index issued from Royle replicated counts and distance sampling maximum population abundance were calculated with the number of individuals seen at peak flight activity. This was possible because we accomplished an intense effort of surveys. If such effort is not possible, we advise to calculate these estimates of population size based on the mean of counts, to avoid the risk of missing the day of peak flight activity. Index based on the mean of counts, such as Pollard-Yates index, should be less variable than index based on a maxima.

Our results are specific to *Maculinea nausithous* but should be applicable on other populations of short-lived butterflies as well. Estimates of population size with count-based method could allow updating measurements of the spatial distribution of species and could be used by park managers. Count-based method could permit the refinement of monitoring protocols for endangered short-lived butterfly species, facilitating repetitive tasks for conservation biologists and park managers. Butterflies comprise the greatest proportion of threatened insects (Haddad et al. 2008). Thus, if a similar relationship between relative abundance and population size can be established for other species of butterflies or other insects, transect count method could be applied across numerous populations so that species can be managed at the landscape level (Collier et al. 2008). Having precise estimates of population size is an essential first step for the conservation of insects and for monitoring biodiversity.

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