

# A simplified mark–release–recapture protocol to improve the cost effectiveness of repeated population size quantification

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## Abstract

1. Obtaining an accurate quantification of population size is often of prime importance in ecology and conservation biology (e.g. population viability analysis, a basic step for assessing species and population status in a given area and guiding effective conservation). When obtaining a reliable quantification of absolute (vs. relative) population size is required, Mark–Release–Recapture (MRR) is a method of choice for many organisms. This is a highly reliable but costly procedure in terms of time and potential impact on species and sites. Consequently, less costly alternatives are highly desirable for conservation and population ecologists.
2. We present here a simplified MRR protocol to mitigate this cost of repeated MRR sampling with little compromise on the quality of the population size estimation. Using one of the largest existing butterfly MRR databases, collected on two fritillary species over a period of 20 years and >20 populations in Belgium, we assessed the possibility to reduce the effort of collecting MRR data while keeping accurate quantification of total population size. By downsampling from the full datasets and calculating a range of demographic census metrics, we specifically investigated whether marking individuals is necessary, and whether the number of sampling sessions can be reduced.
3. We found that (1) counting individuals is not enough: some individual marking, even in a simplistic way to differentiate newly recorded from previously seen individuals, is essential for estimating population size. (2) A simple linear conversion function (number of “missed” individuals for each marked one) can be used to compute population size from the number of individuals marked over a small number of MRR sampling sessions. (3) Parameterizing this function is system specific, because it depends on detectability of individuals, but only requires an initial effort of traditional high-effort MRR in a few populations encompassing the expected range of population size, combined with previous knowledge on the species about potential factors affecting detectability.
4. Our simplified MRR protocol should allow scientists to obtain absolute population size estimates almost as good as with traditional high-effort MRR, but at a cost lowered in both the marking procedure and the intensity of field visits.

## KEYWORDS

bog fritillary butterfly, *Boloria aquilonaris*, *Boloria eunomia*, Capture–Mark–Recapture, catch effort, cranberry fritillary butterfly, long-term monitoring, MARK software, sampling efforts

## 1 | INTRODUCTION

Quantifying and understanding the distribution and abundance of organisms represents the ultimate subject matter of ecology (Krebs, 1972). The number of individuals (i.e. population size) is a fundamental demographic unit of a population (Van Dyke, 2008; Williams, Nichols, & Conroy, 2002). Obtaining an accurate estimation of population size is thus a basic step to assess species and population status and trends in a given area and to guide effective conservation (Sutherland, 1996). As it is most often impossible to inventory or census all the individuals in a given population (Preston, 1979), estimation methods have to be used (Williams et al., 2002). Mark–Release–Recapture (MRR, also known as Capture–Mark–Recapture, CMR) is a standard, broadly used procedure to obtain estimates of absolute population size while overcoming the problem of imperfect detection (i.e. not all individuals can be recorded). It is employed for a wide range of taxa, for example, for small mammals (Lindenmayer, Lacy, & Viggers, 1998), birds (Morrison, Bolger, & Sillett, 2004), amphibians (Arnold, Anderson, Sorenson, & Emery, 2002) and butterflies (Schtickzelle, Le Boulengé, & Baguette, 2002). There is ample evidence that MRR gives reliable estimates (Grimm, Gruber, & Henle, 2014; Haddad, Hudgens, Damiani, Gross, & Kuefler, 2007; Nowicki, Settele, Henry, & Woyciechowski, 2008; Williams et al., 2002) as long as some basic assumptions are respected: mainly, unique and permanent markings, no effect of marking on behaviour and homogeneity among individuals from the same group in terms of capture probability, survival rate and birth rate (i.e. groups with different values can exist, such as males vs. females, but homogeneity must exist within groups); models relaxing some of these assumptions exist but are often tailored to specific cases (Lindberg, 2012). Guidelines, common designs, and statistical models are broadly available (e.g. Cooch & White, 2017; Lindberg, 2012; Sandercock, 2006), and software is now widespread to analyse MRR data (see Bunge, 2013 for a review), such as the widely used `MARK` program (White & Burnham, 1999), `MARKED` (Laake, Johnson, & Conn, 2013), `SPACECAP` (Gopalaswamy et al., 2012) and others.

Alternative methods exist to estimate (relative) abundance, which include area or time-limited census methods, point counts and transect walks (see Douwes, 1970; Thomas, 2005; van Strien et al., 1997; van Swaay, Nowicki, Settele, & van Strien, 2008 for a description of those methods). They are less time-consuming, may generate less negative impact on individuals and habitats (e.g. Gross, Kalendra, Hudgens, & Haddad, 2007; Nowicki et al., 2008) and can be more easily used for entire species' communities or a large spatiotemporal scales (Collier, MacCay, & Bekendorff, 2008; van Swaay & van Strien, 2005). However, these methods provide only indices of relative abundance (Nowicki et al., 2008); they cannot, by definition, derive estimates of absolute population sizes because this requires estimating (1) the detectability of individuals to be able to quantify the fraction of the population that remains unseen (e.g. Clobert, 1995) and (2) some measure of lifetime expectancy to quantify the rate of turnover of individuals and associated probability of multiple counting (e.g. Nowicki et al., 2005). Species action plans or large scale monitoring schemes try to overcome such limitations by a high level of standardization in

the count protocol. This can be very successful to produce global population trends, but requires assuming constant detectability among the conditions to be compared (species, sites, time series, etc.). Believing abundance indices from count methods are automatically reliable estimates of absolute population size is misleading. This was for example illustrated in the Mitchell's satyr butterfly (Shuey & Szymanski, 2010) with no correlation found between daily population size obtained by MRR and abundance estimated from transect walks (but see Thomas, 1983). Distance sampling is another count method (see Buckland, Anderson, Burnham, & Laake, 2005 for a description) that allows assessing detectability (as a function of the distance to the observer) to evaluate population density. Isaac et al. (2011) compared results obtained with transect counts and distance sampling applied to butterflies and found that population density estimates were highly correlated. However, we found no evidence that it can be used to estimate absolute population size, except for the sand dune lizard where counts yield consistent population size estimates with MRR (Kacolis, Berkunsky, & Williams, 2009). Mark–Release–Recapture therefore remains the method of choice to estimate absolute population size when this is required.

Methods of analysing MRR work particularly well for univoltine insects with clear spatial (discrete habitat patches) and temporal (non-overlapping generations) population boundaries, characterizing many habitat specialist and rare butterflies (Ehrlich & Hanski, 2004). However, even in this case, MRR is time-consuming and laborious, with costs increasing sharply with the number of populations, generations and years to monitor (Field, Tyre, Possingham, & Lubow, 2005). Mark–Release–Recapture protocols can also have potential negative impacts on the viability and recapture frequency of individuals due to their manipulation/handling and possible associated physical damage (e.g. Singer & Wedlake, 1981; Morton 1982; Gall 1984). Finally, intensive repeated visits to study sites can affect the habitats, for example, through vegetation trampling, disturbing elusive animals, or even facilitating invasive species and diseases (Ruiz & Carlton, 2003). Alternative individual marking techniques limiting potential negative impacts (e.g. using individual identification based on the combination of camera traps, body marks or DNA fingerprints as the mark to recognize individuals), regularly employed with birds and mammals, can hardly be transposed to insects. Therefore, MRR implementation remains limited in nature reserves, fragile ecosystems and endangered species with a limited number of populations and individuals.

So, although butterflies in particular, and other insects in general, are considered as good indicators for which estimates of population size might be of high interest, we did not find evidence in the literature that the existing alternative methods to MRR can provide reliable estimates of absolute population size (contrary to relative abundance index). Consequently, there is a need to develop less expensive and less time-consuming methods than traditional high-effort MRR that could still allow for a rigorous estimation of population size when this is needed. Here, "high-effort MRR" is to be understood as MRR with unique marks for individuals, and an intensity (number and timing of sampling sessions) that is large enough to provide reliable estimates of demographic parameters; what this represents in practice depends on

the study species and system, and more specifically of the recapture rate, the key to estimate detectability and use it to correct estimates of survival and population size (Cooch & White, 2017).

In this paper, we focus on a methodology to develop a reduced effort MRR sampling protocol providing estimates of population size that are almost as accurate but with a much lower cost. It implies to count the number of different individuals, discriminating already counted individuals via a simple marking, and to apply a conversion function to transform it into a population size estimate. The need to first calibrate the conversion function makes the protocol most useful for studies implying repeated quantification of population size. We illustrate and test it using one of the largest MRR databases existing for butterflies: it contains 150 independent MRR datasets among which 115 were used for the present analysis with around 24,000 marked individuals and 41,500 (re)captures (Appendix S1), collected yearly over two decades in a series of Belgian populations of two butterfly species, the bog fritillary *Boloria eunomia* and the cranberry fritillary *Boloria aquilonaris*. In particular, we investigate the following questions: (1) Is marking of individuals necessary? (2) Can the marking be simplified into a single generic mark used for all the captured individuals instead of a unique identifier, simply to distinguish previously marked and unmarked individuals? (3) Can the sampling effort be reduced while maintaining the estimates for population size as reliable as with high-effort MRR? (4) Can a general conversion function be used in different contexts and/or for different species and how to estimate its parameters?

## 2 | MATERIALS AND METHODS

### 2.1 | Study species and landscapes

The bog fritillary *B. eunomia* (Esper, 1799) and the cranberry fritillary *B. aquilonaris* (Stichel, 1908) are specialist species of wet meadows and peat bogs. Their distribution in Belgium is restricted to the south of the country, and both species are considered as vulnerable in Belgium (Fichefet et al., 2008), but of least concern in Europe (van Swaay et al., 2011). We studied 15 populations of *B. eunomia* and 14 populations of *B. aquilonaris*, over the 1992–2012 period; not every population was sampled every year however.

The two species were sampled by MRR: habitat patches were regularly visited (every 4 days on average), weather permitting, during the flight period (May–June for *B. eunomia*, June–July for *B. aquilonaris*) and butterflies were netted and marked with an individual code on the underside of the left hindwing using a permanent pen. Sampling routes were kept fixed and their lengths adjusted to the area of every habitat patch to keep catch effort homogeneous. For each (re)capture, the following information was recorded: individual code, first capture vs. recapture, sex, date and location (habitat patch). This protocol was similar for the two species and kept constant for all populations over the years. Sites supporting *B. aquilonaris* populations were classified as “open” (large bogs without tree edges) vs. “closed” (bogs surrounded by tree edges). To reduce error rate and ensure the highest possible quality to our MRR data, the marking protocol has been optimized and MRR data extensively

checked (Schtickzelle, 2003). First, individual codes were formed with signs and figures that were highly reading error proof even if some parts of the signs are lost (e.g. when a portion of the wing was damaged). Second, the capture histories (sequences of capture records for each individual) were checked for inconsistencies in sex, location or timestamp (e.g. an individual cannot change sex or be recaptured before being marked).

For both species, dispersal events between populations were very rare, so we could assume that population size is not biased by dispersal events. Furthermore, each dataset (i.e. MRR data collected on one specific population and specific year) is statistically independent from all the others because they share extremely few data and very few individuals were recorded in more than one population. Accordingly, every dataset was analysed separately, and could be regarded as one independent data point in subsequent statistical analyses.

### 2.2 | Reference population size

The total population size, #Ntot, corresponding to the total number of different butterflies present in a given population in a given year (i.e. over the whole yearly adult generation), was estimated using Jolly–Seber (JS) models, as implemented in the POPAN analysis in MARK software (White & Burnham, 1999). Based on capture histories of the different individuals recorded in a population, the probability of an individual to be (re)captured (a measure of detectability) is estimated, and subsequently used to correct estimates of survival, birth rates, daily and total (seasonal) population size (Cooch & White, 2017). For each dataset, we computed #Ntot, its standard error and 95% confidence interval following the methodology and its implementation for butterflies' MRR datasets as initially described in Schtckzelle et al. (2002).

### 2.3 | Calculation of abundance metrics

A series of abundance metrics were computed for each MRR dataset separately:

- #C, the total number of captured (i.e. marked) individuals;
- #CR, the total number of (re)capture records;
- #CRmax, the maximum number of (re)capture records on any single capture session;
- #Cadj, the adjusted versions of #C according to sampling effort (see below);
- #CRadj, the adjusted versions of #CR according to sampling effort (see below).

#CR and #CRmax are proxies for simple counts that do not distinguish previously counted from newly seen individuals. #C and #CR being sums over all sampling sessions of the dataset, they are likely to increase with the sampling effort (i.e. the number of MRR sampling sessions, #Sampling). We therefore computed #Cadj and #CRadj as adjusted versions of the #C and #CR abundance metrics by dividing them by an inflation factor IF. IF is assumed to sigmoidally

increase with the sampling effort from 0 to a maximum value of 1 in the high-effort MRR dataset; it was therefore computed according to the following equation:

$$\text{logit (IF)} = a + b \times \text{\#Sampling.}$$

The two parameters,  $a$  and  $b$ , were estimated by logistic regression of IF according to  $\text{\#Sampling}$  (PROC GENMOD in SAS 9.4, www.sas.com) on the pool of MRR datasets containing at least six sampling sessions and 25 marked butterflies (i.e. 59 datasets for *B. eunomia*, 25 and 28 datasets for *B. aquilonaris* in closed and open sites respectively). For each dataset, we computed the values of  $\text{\#C}$  and  $\text{\#CR}$  that would have been obtained if the population was sampled for a certain number of sessions, from three to the real number of sessions. This was performed by downsampling the MRR data to keep (re)captures recorded on a subset of samplings sessions, as regularly spaced during the flight season as possible. In practice, we first determined the mean length of the flight season for each of the species, which was 28 days for *B. eunomia* and 25 for *B. aquilonaris*. We then split the flight season into time intervals of equal length, whose mid-points were the target dates for downsampling. Finally, (re)captures recorded on the sampling date closest to each mid-point was retained.  $\text{\#C}$  was then computed as the total number of different butterflies recorded at least once in these samplings days, and  $\text{\#CR}$  as the total number of (re)captures. Dividing  $\text{\#C}$  (or  $\text{\#CR}$ ) by the real value observed in the full dataset gave the observed data point, that is, the value of IF, expressing the proportion of individuals that would have been marked if sampling had been restricted to that specific number of sessions.

## 2.4 | Statistical analysis of the power of abundance metrics as population size predictors

The five abundance metrics described above ( $\text{\#C}$ ,  $\text{\#Cadj}$ ,  $\text{\#CR}$ ,  $\text{\#CRadj}$  and  $\text{\#CRmax}$ ) were individually used in a linear model to explain variations in  $\text{\#Ntot}$  among the datasets. No intercept term was included because a zero population size is expected when no MRR data are recorded; this also helps avoiding problems where the intercept, hence  $\text{\#Ntot}$  predicted at small  $\text{\#C}$ , is estimated as a negative value given the best line fit is constrained by data points at large  $\text{\#C}$  (more information about forcing zero intercept is given in Appendix S2). The slope was estimated via weighed linear regression (PROC GENMOD in SAS 9.4). For *B. aquilonaris*, two variants of the model were fitted, one with a different slope for closed and open sites, and one with a single slope for all sites. The weight of each observation was  $1/\text{cv\_Ntot}$ , with  $\text{cv\_Ntot}$  being the coefficient of variation associated to the estimate of  $\text{\#Ntot}$  from the original MRR datasets. The rationale for using such a weighed regression is that the relative uncertainty in the estimation of  $\text{\#Ntot}$  from the MRR data was different for each dataset, according to the amount of information it contained (linked to the number of marked individuals and overall frequency of recapture observed for that population that year).

The relative predictive power of the different models (5 for *B. eunomia*, 10 for *B. aquilonaris*) was compared on three criteria: (Criterion 1)  $R^2$  and the  $\text{AIC}_c$  value of the model, expressing the fit/complexity

ratio based on the absolute prediction error  $|\text{\#Ntot} - \text{\#Ntot\_predicted}|$ ; (Criterion 2) the average over all datasets of the relative prediction error, computed as  $|\text{\#Ntot} - \text{\#Ntot\_predicted}|/\text{\#Ntot}$ , expressing prediction error in % instead of absolute magnitude; and (Criterion 3) the proportion of datasets for which  $\text{\#Ntot\_predicted}$  fell within the 95% confidence interval of  $\text{\#Ntot}$ . The rationale to use these criteria is to obtain a more complete picture of the prediction power of each model (beyond merely goodness of fit), with quantitative measures that consider especially population size, since obviously a given error of, let's say, 10 individuals would be far more significant if  $\text{\#Ntot}$  was 30 than if it was 1,000 individuals.

## 3 | RESULTS

### 3.1 | Data summary

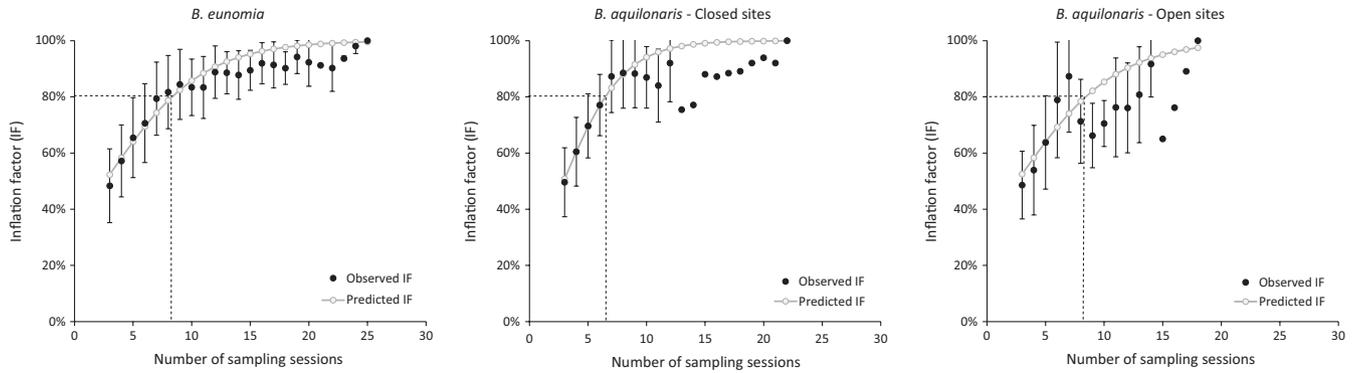
The 63 MRR datasets for *B. eunomia* and 52 for *B. aquilonaris* total to 13,246 and 10,851 marked individuals, 26,973 and 14,489 (re) captures respectively. Reliable estimates of the reference population size ( $\text{\#Ntot}$ ) could be obtained using Jolly–Seber demographic models from 61 and 36 of these datasets for the two species respectively.  $\text{\#Ntot}$  ranged from 14 to 1,553 individuals ( $M = 359$ ) for *B. eunomia* and from 53 to 2,482 individuals ( $M = 702$ ) for *B. aquilonaris*. In these datasets providing a  $\text{\#Ntot}$  estimate, the number of sampling sessions ( $\text{\#Sampling}$ ) per dataset (one species, one population, 1 year) ranged from 6 to 35 ( $M = 12.6$ ) for *B. eunomia* and from 7 to 22 ( $M = 10.2$ ) for *B. aquilonaris*. More details on demographic metrics for all datasets are provided in Appendix S1.

### 3.2 | Inflation factor: How many sampling sessions do we need?

By downscaling datasets and plotting the inflation of marked individuals with sampling intensity, we found that the slope of the saturation curve (inflation factor, IF) differed between the two species as well as between the open and closed sites for *B. aquilonaris* (Figure 1). Nonetheless, for both species about 80% of the population was already marked by 6–8 sampling sessions during the flight season.

### 3.3 | Models for predicting population size

Among the tested metrics and models for estimating the total population size ( $\text{\#Ntot}$ ),  $\text{\#Cadj}$  performed best for *B. eunomia*, while a model considering site type (open vs. closed) and  $\text{\#C}$  performed best for *B. aquilonaris* (Table 1). For the two species, any of the metrics for estimating the total population size ( $\text{\#Ntot}$ ) could seemingly explain a high proportion of the variation in  $\text{\#Ntot}$  among datasets ( $R^2 = 71\%–98\%$ , Table 1). However, there were striking differences in predictive performance when assessing the different models in terms of prediction error: abundance metrics that are based on marked individuals ( $\text{\#C}$  and  $\text{\#Cadj}$ ) had low error with respect to the estimated  $\text{\#Ntot}$  (18%–19% for both species), whereas metrics that are based on counts only ( $\text{\#CR}$ ,  $\text{\#CRadj}$  and  $\text{\#CRmax}$ ) yielded double or nearly double error values for



**FIGURE 1** Inflation factor IF estimated as a sigmoidally increasing function of the number of sampling sessions; IF represents the proportion of the marked individuals in the full Mark–Release–Recapture dataset that would have been marked if sampling had been restricted to that specific number of sessions. This figure illustrates this for (a) *Boloria eunomia*, (b) *Boloria aquilonaris* in closed sites and (c) *B. aquilonaris* in open sites. Black dots show the observed values ( $M + SD$ ) for the datasets (59, 24 and 28 respectively; see Appendix S1) containing at least three sampling sessions. Grey curves with dots represent the sigmoid regression curve; note that, for each panel, the number of datasets decreases as the number of sampling days increases, which explains why the best fit curves might not always closely match observed data for high values of sampling sessions, containing a comparatively lower amount of data points. The dotted lines indicate the number of sampling sessions necessary to IF = 80% (arbitrary level chosen for illustration)

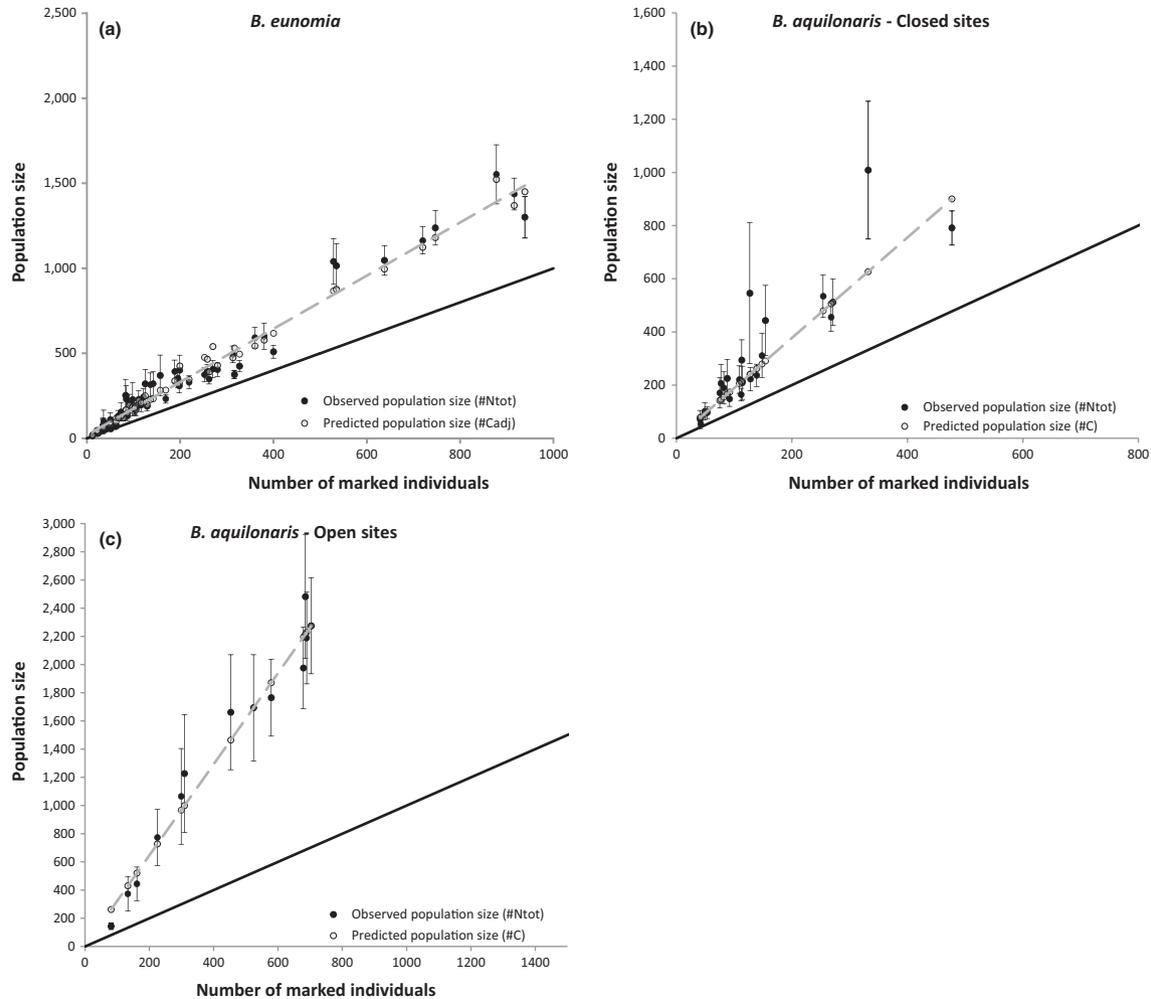
**TABLE 1** Fit and predictive power of the different models tested (5 for *Boloria eunomia*, 10 for *Boloria aquilonaris*) to predict population size (#Ntot) from the following demographic metrics: #C = total number of marked individuals; #CR = total number of (re)captures; #CRmax = maximum number of (re)captures on a single day; #Cadj = adjusted version of #C according to sampling effort (number of MRR sampling sessions); #CRadj = adjusted versions of #CR according to sampling effort; type = site configuration (open vs. closed), for *B. aquilonaris* only. See text for details on how these metrics were estimated. Prediction error is reported both as mean relative prediction error, computed as  $|\#N_{tot} - \#N_{tot\_predicted}| / \#N_{tot}$ , and as the proportion of datasets for which the prediction was classified as correct, that is, when #Ntot\_predicted fell within the 95% confidence interval of the observed #Ntot estimate

| Species               | Demographic metric | Model fit         |                         |                    | Model selection  |                    | Prediction error            |  |
|-----------------------|--------------------|-------------------|-------------------------|--------------------|------------------|--------------------|-----------------------------|--|
|                       |                    | No. of parameters | Residual sum of squares | R <sup>2</sup> (%) | AIC <sub>c</sub> | Δ AIC <sub>c</sub> | Mean  prediction error  (%) | Proportion of datasets with correct prediction (%) |
| <i>B. eunomia</i>     | <b>#Cadj</b>       | <b>2</b>          | <b>3,949,213</b>        | <b>98</b>          | <b>679.98</b>    | <b>0.00</b>        | <b>18.4</b>                 | <b>62</b>  |
|                       | #C                 | 2                 | 4,568,310               | 97                 | 688.86           | 8.88               | 18.8                        | 54   |
|                       | #CRadj             | 2                 | 23,266,000              | 86                 | 788.16           | 108.18             | 35.2                        | 38   |
|                       | #CR                | 2                 | 27,870,228              | 83                 | 799.17           | 119.19             | 37.7                        | 26   |
|                       | #CRmax             | 2                 | 30,870,246              | 81                 | 805.41           | 125.43             | 35.7                        | 31   |
| <i>B. aquilonaris</i> | <b>Type*#C</b>     | <b>3</b>          | <b>4,705,355</b>        | <b>98</b>          | <b>430.85</b>    | <b>0.00</b>        | <b>17.5</b>                 | <b>78</b>  |
|                       | Type*#Cadj         | 3                 | 5,873,174               | 97                 | 438.84           | 7.99               | 19.4                        | 75   |
|                       | Type*#CRadj        | 3                 | 7,019,273               | 96                 | 445.25           | 14.40              | 28.5                        | 61   |
|                       | Type*#CR           | 3                 | 10,639,577              | 95                 | 460.23           | 29.38              | 28.6                        | 47   |
|                       | #Cadj              | 2                 | 13,650,636              | 93                 | 466.81           | 35.96              | 36.0                        | 53   |
|                       | Type*#CRmax        | 3                 | 15,444,905              | 92                 | 473.64           | 42.79              | 33.5                        | 56   |
|                       | #C                 | 2                 | 19,534,423              | 90                 | 479.71           | 48.86              | 37.1                        | 53   |
|                       | #CRadj             | 2                 | 35,292,646              | 82                 | 501.00           | 70.15              | 59.9                        | 39   |
|                       | #CRmax             | 2                 | 47,519,807              | 76                 | 511.71           | 80.86              | 71.2                        | 33   |
|                       | #CR                | 2                 | 56,142,692              | 71                 | 517.72           | 86.87              | 55.5                        | 36   |

In bold are the selected models based on the AIC<sub>c</sub> criterion.

both species. Better performance was reflected also by substantially lower AIC<sub>c</sub> values for models containing #Cadj and #C compared to all other models. For *B. eunomia*, it was evident also when we considered

the proportion of (downsampled) datasets included in the 95% CI of #Ntot: 62% and 54% the models considering #C and #Cadj were included in the 95% CI, compared to 26%–38% for the other models



**FIGURE 2** Total population size as estimated on original Mark–Release–Recapture data (#Ntot with its 95% confidence interval; black dots) and as predicted with the best model (grey dots and grey dashed lines) for (a) *Boloria eunomia*, (b) *Boloria aquilonaris* in closed sites and (c) *B. aquilonaris* in open sites, as a function of the number of marked individuals (#C). The solid black line indicates the 1:1 line, that is, the ideal case where every existing individual would have been marked (detectability = 100%), to illustrate the differences between the three cases in the proportion of missed individuals, reflected in how the slope of the linear regression differs from this ideal case

(Table 1). For *B. aquilonaris*, the difference was less profound, but still, any model with marked individuals performed better compared to the same model/metric with unmarked individuals (counts).

### 3.4 | Calculating the conversion function: How many individuals are missed per marked or observed one?

Plotting the predicted population size according to the number of marked individuals illustrates that the “conversion function” (“marked to real”) differed between the two species and between the two site types for *B. aquilonaris* (Figure 2). The slope of the function was 1.49 for *B. eunomia*, meaning that for any two marked butterflies, circa 1 individual was “missed” in the population. For *B. aquilonaris*, the slope of the relation was significantly higher for open (3.23) compared to closed sites (1.89), meaning that for every marked individual, either circa 2 or 1 individuals were missed in open vs. closed sites.

## 4 | DISCUSSION

Because high-effort MRR sampling, as usually performed when estimating population size is the aim, is costly in terms of time and money, and potentially impacts sampled sites and species due to high catch effort, several alternative methods have been developed. Many of these methods involve replacing marking and recapturing individuals by simply counting individuals that are seen. As detailed in the Introduction, these methods may offer good estimates of relative population abundance indices, and they have indeed been used successfully for large surveys, such as butterfly monitoring schemes. However, they are not suitable or designed for quantifying absolute population size, which remains a key for population viability analyses (Morris & Doak, 2002; Pe'er et al., 2013; Schtickzelle & Baguette, 2009) or other estimations of risks to species' populations under (anthropogenic) pressures. Here, we did not aim at comparing MRR with count methods: their objectives are different, and dropping individual identity information

does not make MRR data equal to transect counts because of missing standardization steps, such as the moving box around the experimenter where individuals are counted. We addressed the question of how to reduce the efforts to be invested in MRR without compromising the quality of the population size estimation.

The new finding that clearly arises from our study, performed on one of the largest collections of MRR datasets existing for butterflies, is that it is possible to get a reliable quantification of population size from a simplified MRR protocol via a simple linear conversion function encapsulating all aspects of detectability and rate of turnover of individuals into a slope quantifying the “number of existing (i.e. marked + missed) individuals for each marked one” (Figure 2). Our results indicate three clear specific conclusions: (1) individual marking, even in a simplistic way, is needed for estimating population size; (2) the conversion function can be reliably applied on the number of individuals marked in a limited number of sampling sessions (around 6–8 in our case), largely reducing the overall cost of the sampling; (3) this function is species specific (and potentially also habitat or sex specific) and an initial effort of high-effort MRR in sites covering the range of expected population sizes is needed to parameterize it. Next, we will discuss these conclusions in details, and then provide a methodology for reducing MRR efforts in future studies.

#### 4.1 | To quantify absolute population size, individuals must be marked

On the three cases studied here, the predictive power of models involving marked individuals (captures only) was very good, and largely better than models based on counting the number of observed animals (i.e. captures and recaptures pooled). This confirms that a reliable and precise quantification of population size implies to estimate two parameters: (1) the detectability of individuals, which is known already from a long time as a required quantity to convert number of individuals observed into number of individuals present in the population (e.g. Clobert, 1995; Gross et al., 2007; Isaac et al., 2011; Ry & Schmidt, 2008) and (2) the rate of turnover of individuals, which influences the probability of multiple counts of the same individual. Since detectability may largely vary in space and time, between species and even sexes (e.g. due to the movement behaviour of species; Turlure, Baguette, Stevens, & Maes, 2011), MRR studies used to sample every population of interest with an effort (number of sampling sessions and capture intensity) large enough to estimate it adequately, via the knowledge of the capture histories of the individuals (Schtickzelle et al., 2002). Furthermore, contrary to marking, simply counting the individuals does not prevent from multiple counts of the same individual, whose probability depends on its lifetime. Marking is then necessary to quantify absolute population size, but our results show that it does not imply to record the complete capture history for every individual separately, which requires intensive and repeated MRR with unique individual identifiers. This means that a simplified marking protocol can be used, which can be as simple as a single mark applied to all individuals, greatly simplifying and lightening marking and data recording processes. Moreover, this marking protocol is also suitable

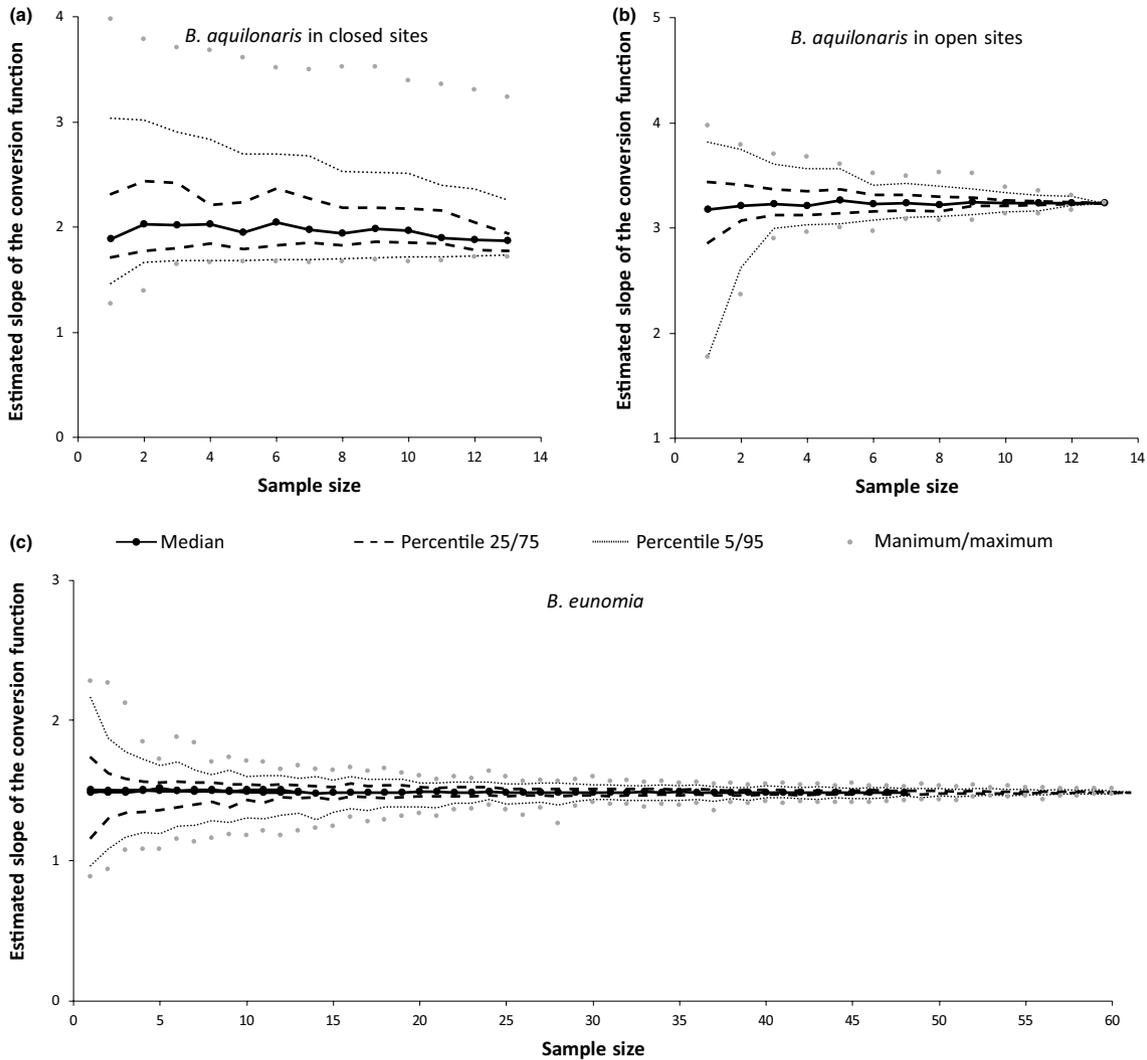
for species too small to allow marking with an individual identifier, such as many of the Lycaenids or Hesperids.

#### 4.2 | The MRR sampling effort can be reduced to a few sampling sessions per population only

Marking is a necessary, but not sufficient, condition to obtain a reliable quantification of population size. A minimal catch effort, in quantity and quality, is needed too in order to obtain a reliable estimate of the number of marked individuals to be translated into population size using the conversion function. In the case of *B. eunomia* and *B. aquilonaris*, the inflation factor curves (Figure 1) indicate that after 6–8 sampling sessions, 60%–80% of the individuals that could be marked with many sampling sessions were already marked. It is important, however, to spread these sampling sessions over the flight season so that every individual present in the population has a chance to be marked. Otherwise, some individuals may be born and die during a “no sampling” period, meaning they cannot be marked or counted, leading to the underestimation of the population size. Notably, sampling frequency is indeed an issue also in systematic monitoring (as shown by, e.g., Schmucki et al., 2016), indicating a need to consider sampling frequency with respect to the anticipated life span and asynchronous emergence of adults and sexes, also when individuals are not marked. In a similar MRR simplification attempt, Nowicki et al. (2005) provided a reduced effort protocol (at least five sampling sessions) based on the conversion of peak daily population size into total population size. It uses a formula containing both the lifetime expectancy (based on recording full capture histories of individually marked butterflies) and the duration of the flight period and has been calibrated on several species. Longcore, Mattoni, Zonneveld, and Bruggeman (2003) also proposed a method that takes life span of individuals into account; based on Zonneveld (1991), it uses the death rate of individuals to correct daily count data.

#### 4.3 | The conversion function must be parameterized with some initial high-effort MRR data

Before it can be used to translate a number of marked individuals into population size, the conversion function must be calibrated with the adequate slope for the study system. This is also true for the inflation factor according to the number of MRR sampling sessions. Indeed, the sampling effort needed to accurately record individuals, mark them or even notice species presence obviously varies greatly from one species to another, and even within a species; this is because detectability varies among not only species but also sexes and contexts. In their simulation study, Archaux, Henry, and Gimenez (2012) showed that a small detectability difference (4%–8%) can lead to the miscalculations of population sizes in 50%–90% of the cases. Detectability can greatly vary between not only species but also sexes and contexts. For instance, Pellet (2008) found detection probabilities ranging from 50% to 77% during transect counts while comparing four butterfly species. This is because individuals hiding in the vegetation or using a perching strategy are probably less easily detected than constantly patrolling ones, or because species can have cryptic coloration. Also, detectability

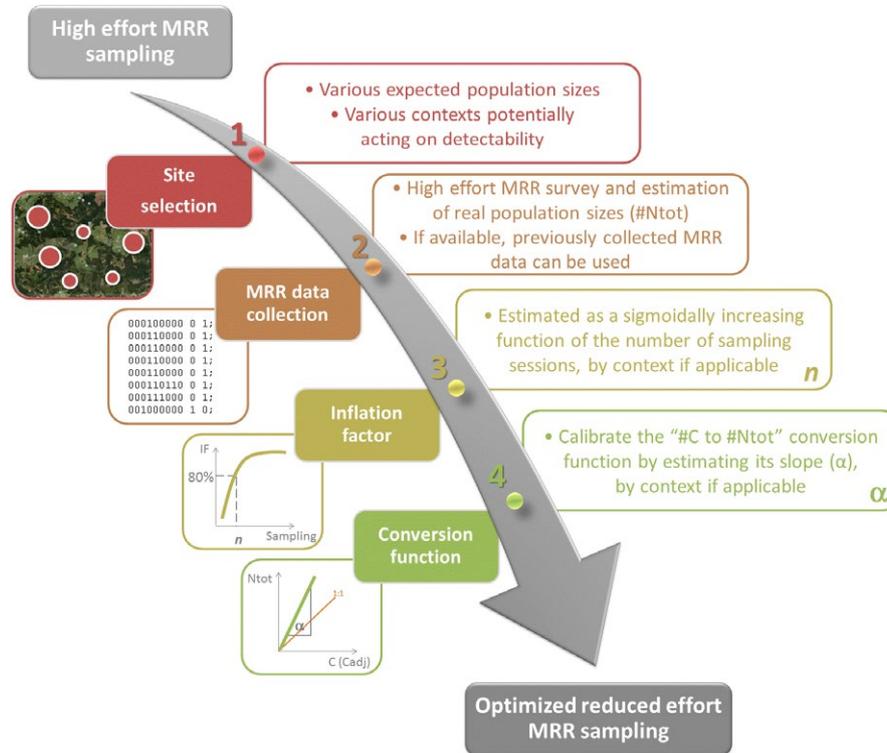


**FIGURE 3** Sensitivity of the estimation of the slope of the conversion function to the sample size (i.e. number of data points from high-effort Mark–Release–Recapture used to estimate the conversion function such as on Figure 2) for (a) *Boloria aquilonaris* in closed sites, (b) *B. aquilonaris* in open sites and (c) *Boloria eunomia*. Displayed are the median (black line), 25%–75% (dashed black lines), 5%–95% (dotted grey line), minimum and maximum (grey dots) of 100 slope estimates, each obtained on a random downsample of the original dataset (as seen on Figure 2) as a function of the sample size. The slope estimation is more variable when the relation is less linear as is the case for *B. aquilonaris* in closed sites (vs. *B. eunomia* and *B. aquilonaris* in open sites). Note that this represents a worst case scenario as we did not control for how the data points were spread along the x-axis (sample size)

was for example assessed at 48% in woodland edges vs. 88% in open fens for the butterfly *Maculinea nausithous* (Pellet et al., 2012).

In our results, the slope of the conversion function, expressing the number of individuals present in the population for every one that was marked, ranged from 1.49 for *B. eunomia* to 3.23 for *B. aquilonaris* in open sites, with an in-between 1.89 for *B. aquilonaris* in closed sites. These can easily be related to behavioural differences: studies of the flight behaviour within habitat indicated a rather tortuous and slow flight in *B. eunomia* vs. rather straight and rapid flight in *B. aquilonaris* (Schtickzelle & Baguette, 2003; Turlure et al., 2011). The behaviour of *B. aquilonaris* in flight, differing between open and closed habitats, also translates into differences in detectability according to site configuration: open areas are often windswept, reinforcing the flight speed of individuals, while closed areas are wind protected by trees.

Fortunately, the conversion function turned out to give estimates of population size very close to those obtained with high-effort MRR even with an extremely simple equation, namely a linear relationship without intercept (Figure 2). This means that it can be parameterized quite easily for the study system with only a few data points, that is, populations for which the real population size has been estimated as precisely as possible using high-effort MRR. These populations chosen for fitting the conversion function should be as much as possible spread over the range of expected population size in the study area to improve the estimation of the slope by linear regression and the ability to check if the linearity assumption holds over that range. Figure 3 illustrates how the estimation of the slopes rapidly stabilizes as the number of data points (#Ntot estimates from high-effort MRR) used to fit the conversion function increases in our three case studies. Such



**FIGURE 4** Schematic representation of the method to design a simplified, reduced effort Mark–Release–Recapture (MRR) sampling scheme to estimate population size. In Step 1, several sites should be carefully selected as hosting populations with a range of different expected size (as represented by circles of various sizes in the map) and contexts. In Step 2, intensive high-effort MRR data are collected on those selected sites and analysed using classical demographic methods to estimate the absolute population size (#Ntot). Those data can of course be complemented by already available (non-)published data. In Step 3, MRR data are used to assess the inflation factor and the minimum number ( $n$ ) of sampling sessions needed to catch a predefined threshold (e.g. at least 80% as illustrated here and on Figure 1) of the possibly marked individuals. In Step 4, the slope  $\alpha$  of conversion function relating #Ntot to the number of marked individuals (#C or #Cadj) can be obtained. Finally, a reduced effort MRR sampling design can be selected, largely reducing the cost of MRR without sacrificing the quality of population size estimates

high-effort MRR datasets are also suitable to estimate how the inflation factor increases with the number of sampling sessions.

#### 4.4 | A simplified MRR protocol

Based on these conclusions, we propose a simple approach to obtain estimates of population size that are almost as good as those yielded by high-effort MRR, but with a much lower sampling intensity. Our proposed simplified MRR is split into four steps (Figure 4). First (Step 1: Site selection), one must identify a few (say, 4–5) sites hosting populations with a range of different expected sizes; if detectability differences are expected, for example, among landscape contexts, this selection should be repeated for each context. Second (Step 2: MRR data collection), high-effort MRR is conducted to obtain precise estimates of population size using classical demographic analyses based on full capture histories of the individuals. Mark–Release–Recapture data previously collected and/or published could be reused here, as we did in this study with *B. eunomia* and *B. aquilonaris*. The third step (Step 3: Inflation factor) involves estimating the inflation factor by downsampling these high-effort MRR datasets. At that stage, it is possible to analyse the impact of the number of sampling sessions and their temporal occurrence so as to determine the optimal MRR

sampling design. Finally (Step 4: Conversion function), one needs to parameterize the conversion function by calibrating its slope using the number of marked individuals and the estimated population size in this set of sites. The linearity assumption can be easily checked (Figure 3) and extra high-effort MRR datasets collected if in doubt about the estimate of the slope. In all four stages, it is important to employ good knowledge of species' biology and behaviour, to consider context-specific effects that could affect these conversion ratios.

Such a protocol will decrease significantly the cost of MRR studies aiming at estimating precisely the population size by allowing several major simplifications: (1) a simple group marking, even a single mark, can be used; (2) only a few MRR sampling sessions (here 6–8, to be compared to 10–13 on average and up to 35 in our high-effort MRR) are required to get the metric estimate to be converted into population size; (3) initially, a one-shot high-effort MRR campaign must be done to parameterize the conversion function and the inflation factor, but sampling a few populations is enough. Such a decrease in the sampling effort can significantly reduce the costs associated to each demographic survey and/or allow surveying more populations for the same cost. As a practical example, let us imagine one would like to sample all *B. aquilonaris* populations in Belgium (i.e. 54 populations), with on average 1 h of sampling per site by one or two persons

simultaneously between 09.00 and 18.00 hr, and excluding the journey between populations. It would take 36 days (324 hr) in reduced effort MRR (6 sampling sessions) vs. 60 days (540 hr) in a high-effort MRR (10 sampling sessions). Combined via the simple marking of the individuals, which accelerates MRR on the field and data coding, this makes it possible to survey all these 54 populations during the flight period of the species (roughly 5 weeks in Belgium).

Nevertheless, it must be kept in mind that this conclusion holds true for the estimate of population size, but high-effort MRR studies are useful to study other aspects of (meta-) population dynamics. In these cases, the simplified protocol we present here might not be the best solution. For example, to record dispersal events, individual specific (or at least site specific) marking is necessary, and more intense and more frequent MRR sampling sessions mean more movement data with a finer spatiotemporal resolution (Baguette, Clobert, & Schtickzelle, 2011). Another example where our simplified protocol is not adequate is to address questions involving the estimation of vital rates of adults, such as survival or lifetime expectancy (e.g. Vandewoestijne, Schtickzelle, & Baguette, 2008).

## 5 | CONCLUSION

With this study, we add to the existing evidence that counting individuals does not allow to estimate absolute population size because detectability and rate of turnover of individuals remain unknown; individuals need to be marked. Count methods, and the relative abundance indices they provide, are very useful in some contexts, for example, to give the big picture of abundance trend through time (see the many successful examples of butterfly monitoring schemes), but are not aimed at, and cannot be used for, quantifying absolute population size. Obtaining a reliable quantification of absolute population size is still of prime importance in other contexts, for example, quantitative modelling of population viability analysis or definition of IUCN threat status, and MRR is the method of choice for this purpose. We offer here a simple and efficient simplified MRR protocol as a way to reduce its cost and potential impact on species and sites with a limited effect on the reliability of the population size estimate. We believe this protocol, in its approach but not especially its specific details (such as the linearity assumption of the conversion function), can be extended to cases with similar characteristics, that is, mainly aiming at estimating true population size for species (1) with non-overlapping generations and (2) whose populations can be reasonably well delimited in space. Only with these two conditions fulfilled, the estimate of a total size is meaningful for a population because it is finite in time and in space; otherwise, only instantaneous population size is to be estimated, as done for many birds or mammals. However, the generalisation power of our simplified protocol has still to be formally tested on other taxonomic groups.

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## AUTHORS' CONTRIBUTIONS

C.T., M.B. and N.S. designed the study. C.T., M.B. and N.S. performed data collection. C.T. and N.S. performed data analyses; all authors commented, interpreted and participated to the improvement of these analyses. C.T. and N.S. wrote the first draft of the manuscript, and all authors contributed substantially to revisions. All authors read and approved the final version of the paper.

## DATA ACCESSIBILITY

Data are presented in Appendix S1 and archived in Pangaea (<https://pangaea.de>; ref: PDI-15846).

## REFERENCES

- Archaux, F., Henry, P. Y., & Gimenez, O. (2012). When can we ignore the problem of imperfect detection in comparative studies? *Methods in Ecology and Evolution*, 3, 188–194.
- Arnold, T. W., Anderson, M. G., Sorenson, M. D., & Emery, R. B. (2002). Survival and philopatry of female redheads breeding in Southwestern Manitoba. *The Journal of Wildlife Management*, 66, 162–169.
- Baguette, M., Clobert, J., & Schtickzelle, N. (2011). Metapopulation dynamics of the bog fritillary butterfly: Experimental changes in habitat quality induced negative density-dependent dispersal. *Ecography*, 34, 170–176.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., & Laake, J. L. (2005). Distance sampling. In P. Armintage, & T. Colton (Eds.), *Encyclopedia of biostatistics* (pp. 1190–1196). Chichester: John Wiley & Sons, Ltd.
- Bunge, J. A. (2013). A survey of software for fitting capture-recapture models. *Wiley Interdisciplinary Reviews: Computational Statistics*, 5, 114–120.
- Clobert, J. (1995). Capture-recapture and evolutionary ecology: A difficult wedding? *Journal of Applied Statistics*, 22, 989–1008.
- Collier, N., MacCay, D. A., & Bekendorff, K. (2008). Is relative abundance a good estimator of population size? Evidence from fragmented populations of a specialist butterfly (Lepidoptera: Lycaenidae). *Population Ecology*, 50, 17–23.
- Cooch, E. G., & White, G. C. (2017). Program Mark: A gentle introduction. Online Source.
- Douwes, P. (1970). Size of, gain to and loss from a population of adult *Heodes virgaureae* L. (Lep., Lycaenidae). *Insect Systematics & Evolution*, 1, 263–281.

- Ehrlich, P. R., & Hanski, I. (2004). *On the wings of checkerspots. A model system for population biology*. New York, NY: Oxford University Press.
- Fichefet, V., Barbier, Y., Bagnée, J.-Y., Dufrière, M., Goffart, P., Maes, D., & Van Dyck, H. (2008). *Papillons de jour de Wallonie (1985-2007)*. Publication du Groupe de Travail Papillons de jour Lycaena et du Centre de Recherche de la Nature, des Forêts et du Bois (MRW-DGRNE), Gembloux.
- Field, S. A., Tyre, A. J. & Possingham, H. P. (2005). Optimizing allocation of monitoring effort under economic and observational constraints. *Journal of Wildlife Management*, 69, 473–482.
- Gall, L. F. (1984). The effect of capturing and marking on subsequent activity in *Boloria acrocnema* (Lepidoptera: Nymphalidae), with a comparison of different numerical models that estimate population size. *Biological Conservation*, 28, 139–154.
- Gopaldaswamy, A. M., Royle, J. A., Hines, J. E., Singh, P., Jathanna, D., Kumar, N. S., & Karanth, K. U. (2012). Program SPACECAP: Software for estimating animal density using spatially explicit capture-recapture models. *Methods in Ecology and Evolution*, 3, 1067–1072.
- Grimm, A., Gruber, B., & Henle, K. (2014). Reliability of different Mark-Recapture methods for population size estimation tested against reference population sizes constructed from field data. *PLoS ONE*, 9, e98840.
- Gross, K., Kalendra, E. J., Hudgens, B. R., & Haddad, N. M. (2007). Robustness and uncertainty in estimates of butterfly abundance from transects counts. *Population Ecology*, 49, 191–200.
- Haddad, N. M., Hudgens, B. R., Damiani, C., Gross, K., & Kuefler, D. (2007). Determining optimal population monitoring for rare butterflies. *Conservation Biology*, 22, 929–940.
- Isaac, N. J. B., Cruickshanks, K. L., Weddle, A. M., Marcus Rowcliffe, J., Brereton, T. M., Dennis, R. L. H., ... Thomas, C. D. (2011). Distance sampling and the challenge of monitoring butterfly populations. *Methods in Ecology and Evolution*, 2, 585–594.
- Kacoliris, F. P., Berkunsky, I., & Williams, J. D. (2009). Methods for assessing population size in sand dune lizards (*Liolaemus multimaaculatus*). *Herpetologica*, 65, 219–226.
- Krebs, C. J. (1972). *Ecology*. New York, NY: Harper & Row.
- Laake, J. L., Johnson, D. S., & Conn, P. B. (2013). marked: An R package for maximum likelihood and Markov Chain Monte Carlo analysis of capture-recapture data. *Methods in Ecology and Evolution*, 4, 885–890.
- Lindberg, M. S. (2012). A review of designs for capture-mark-recapture studies in discrete time. *Journal of Ornithology*, 152, 355–370.
- Lindenmayer, D. B., Lacy, R. C., & Viggers, K. L. (1998). Modelling survival and capture probabilities of the mountain brushtail possum (*Trichosurus caninus*) in the forests of south-eastern Australia using trap-recapture data. *Journal of Zoology*, 245, 1–13.
- Longcore, T., Mattoni, R., Zonneveld, C., & Bruggeman, J. (2003). Insect Count Analyzer: A tool to assess responses of butterflies to habitat restoration. *Ecological Restoration*, 21, 60–61.
- Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology. Theory and practice of population viability analysis*. Sunderland, MA: Sinauer Associates.
- Morrison, S. A., Bolger, D. T., & Sillett, T. S. (2004). Annual survivorship of the sedentary Rufous-crowned Sparrow (*Aimophila ruficeps*): No detectable effects of edge or rainfall in southern California. *The Auk*, 121, 904–916.
- Morton, A. C. (1982). The effects of marking and capture on recapture frequencies of butterflies. *Oecologia*, 53, 105–110.
- Nowicki, P., Richter, A., Glińska, U., Holzschuh, A., Toelke, U., Henle, K., ... Settele, J. (2005). Less input same output: Simplified approach for population size assessment in Lepidoptera. *Population Ecology*, 47, 203–212.
- Nowicki, P., Settele, J., Henry, P.-Y., & Woyciechowski, M. (2008). Butterfly monitoring methods: The ideal and the real world. *Israel Journal of Ecology and Evolution*, 54, 69–88.
- Pe'er, G., Matsinos, Y. G., Johst, K., Franz, K. W., Turlure, C., Radchuk, V., ... Henle, K. (2013). A protocol for better design, application, and communication of population viability analyses. *Conservation Biology*, 27, 644–656.
- Pellet, J. (2008). Seasonal variation in detectability of butterflies surveyed with Pollard walks. *Journal of Insect Conservation*, 12, 155–162.
- Pellet, J., Bried, J. T., Parietti, D., Gander, A., Heer, P. O., Cherix, D., & Arlettaz, R. (2012). Monitoring butterfly abundance: Beyond Pollard walks. *Plos One*, 7, e41396.
- Preston, F. W. (1979). The invisible birds. *Ecology*, 60, 452–454.
- Ruiz, G. M., & Carlton, J. T. (2003). *Invasive species: Vectors and management strategies*. Chicago, IL: Island Press.
- Ry, M., & Schmidt, B. R. (2008). Imperfect detection and its consequences for monitoring for conservation. *Community Ecology*, 9, 207–216.
- Sandercock, B. K. (2006). Estimation of demographic parameters from live-encounter data: A summary review. *Journal of Wildlife Management*, 70, 1504–1520.
- Schmucki, R., Pe'er, G., Roy, D. B., Stefanescu, C., van Swaay, C. A. M., Oliver, T. H., ... Julliard, R. (2016). A regionally informed abundance index for supporting integrative analyses across butterfly monitoring schemes. *Journal of Applied Ecology*, 53, 501–510.
- Schtickzelle, N. (2003). *Metapopulation dynamics and viability of the bog fritillary butterfly Proclossiana eunomia*. Thesis/Dissertation.
- Schtickzelle, N., & Baguette, M. (2003). Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *Journal of Animal Ecology*, 72, 533–545.
- Schtickzelle, N., & Baguette, M. (2009). (Meta)population viability analysis: A crystal ball for the conservation of endangered butterflies? In J. Settele, T. G. Shreeve, M. Konvicka & H. Van Dyck (Eds.), *Ecology of butterflies in Europe* (pp. 339–352). Cambridge: Cambridge University Press.
- Schtickzelle, N., Le Boulengé, E., & Baguette, M. (2002). Metapopulation dynamics of the bog fritillary butterfly: Demographic processes in a patchy population. *Oikos*, 97, 349–360.
- Shuey, J., & Szymanski, J. (2010). Modified Pollard transects do not predict estimated daily population size for the secretive butterfly, *Neonympha mitchellii mitchellii* French. *Journal of the Lepidopterist's Society*, 66, 221–224.
- Singer, M. C., & Wedlake, P. (1981). Capture does affect probability of recapture in a butterfly species. *Ecological Entomology*, 6, 215–216.
- Sutherland, W. J. (1996). *Ecological census techniques, a handbook*. Cambridge, UK: Cambridge University Press.
- Thomas, J. A. (1983). A quick method of assessing butterfly numbers during survey. *Biological Conservation*, 27, 195–211.
- Thomas, J. A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 339–357.
- Turlure, C., Baguette, M., Stevens, V. M., & Maes, D. (2011). Species- and sex-specific adjustments of movement behavior to landscape heterogeneity in butterflies. *Behavioral Ecology*, 22, 967–975.
- Van Dyke, F. (2008). The conservation of populations: Concept, theory and analysis. In F. Van Dyke (Ed.), *Conservation biology. Foundations, concepts, applications* (pp. 213–242). London: Springer.
- van Strien, A. J., Van De Pavert, R., Moss, D., Yates, T. J., van Swaay, C. A. M., & Vos, P. (1997). The statistical power of two butterfly monitoring schemes to detect trends. *Journal of Applied Ecology*, 34, 817–828.
- van Swaay, C. A. M., Maes, D., Collins, S., Munguira, M. L., Sasic, M., Settele, J., ... Cuttelod, A. (2011). Applying IUCN criteria to invertebrates: How red is the Red List of European butterflies? *Biological Conservation*, 144, 470–478.
- van Swaay, C. A. M., Nowicki, P., Settele, J., & van Strien, A. J. (2008). Butterfly monitoring in Europe: Methods, applications and perspectives. *Biodiversity and Conservation*, 17, 3455–3469.

- van Swaay, C. A. M., & van Strien, A. J. (2005). Using butterfly monitoring data to develop a European grassland butterfly indicator. In E. Kühn, J. A. Thomas, R. Feldman, & J. Settele (Eds.), *Studies on the ecology and conservation of butterflies in Europe* (pp. 106–108). Sofia, Bulgaria: Pensoft Publishers.
- Vandewoestijne, S., Schtickzelle, N., & Baguette, M. (2008). Positive correlation between genetic diversity and fitness in a large, well-connected metapopulation. *BMC Biology*, 6, 46.
- White, G. C., & Burnham, K. P. (1999). Program MARK: Survival estimation from populations of marked animals. *Bird Study*, 46(Supplement), S120–S139.
- Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). *Analysis and management of animal populations: Modeling, estimation and decision making*. San Diego, CA: Academic Press.
- Zonneveld, C. (1991). Estimating death rates from transect counts. *Ecological Entomology*, 16, 115–121.

## SUPPORTING INFORMATION

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