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Novel grid-based population estimates correlate with actual population sizes of the marsh fritillary (*Euphydryas aurinia*), while transect and larvae counts are less reliable

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Abstract

1. Established butterfly survey methods that are useful for monitoring species that are widely distributed and numerous may be less accurate for more rare species. We therefore need new monitoring approaches.
2. We describe a plot-based survey method, where butterflies or larvae nests are counted within 1-ha grid cells. The aim was to compare this grid method with more traditional transect counts and evaluate both methods in relation to high-quality capture–mark–release (CMR) population estimates (reflecting the 'true' population). We do this using data from a large population of the marsh fritillary butterfly in Sweden. Moreover, we followed the overall population trend from 2017 to 2021 for both adult butterflies and larvae.
3. Results showed a higher detection probability using the grid method compared with transect counts, which for adult butterflies seem to be explained by time effort. Moreover, grid surveys of adult butterflies showed a clear significant relationship with the estimated 'true' population size from CMR, while transect counts did not. For larvae, both methods showed significant relationships with the estimated adult population size, but the grid method found 5.7 times more larvae. The overall population fluctuated significantly across years. In years with low densities, the transect method largely failed to detect the species.
4. The grid method seems more reliable for detecting the marsh fritillary and for estimating its population size, and thus, tracking the population trend. We propose this novel method to be integrated into surveys and monitoring of biodiversity, especially when focusing on rare habitat specialists that are normally underrepresented in monitoring based on volunteer counts.

KEYWORDS
butterfly monitoring, capture–mark–release, population trends, survey methods

INTRODUCTION

Insects are declining rapidly across the globe due to human activities, for example, changes in land use and climate change (Chapin III et al., 1998; Forester & Machlis, 1996; Newbold et al., 2015; Sala et al., 2000; Wagner, 2020). The status of butterflies is no exception; reports from all over Europe indicate that butterfly populations are declining rapidly (Franzén & Johannesson, 2007; Maes & van Dyck, 2001; van Dyck et al., 2008; van Swaay et al., 2010; van Swaay et al., 2016; Warren et al., 2021). To halt this trend, defining conservation plans to protect threatened species is crucial, with monitoring programmes being an important tool to assess the status and population trends (Kral-O'Brien et al., 2021; Pereira et al., 2013). There are standardised methods for monitoring species diversity already in place (e.g., the UK Butterfly Monitoring Program; van Swaay et al., 2008). The established monitoring methods that have been proven useful for monitoring species that are widely distributed and numerous may be less accurate for rare species. To gain reliable population data for these species, we not only need to better target their specific habitat but also choose methods that capture their appearance within habitat patches. Selecting a method to monitor rare target species is not a simple task, and it seems that with each method there is a compromise (Haddad et al., 2008; Nowicki et al., 2008).

Method selection is certainly a crucial part of any study to ensure the gathering of rigorous data (Kral et al., 2018). However, the choice of methodology is often limited by several factors, such as time, resources, common practice, etc. Thus, there is a need to identify and compare different methods to make monitoring more efficient without compromising the quality of the data collected. Some of the most common methods to monitor butterflies are transect counts, such as the Pollard walk (Collier et al., 2006; Pollard, 1977; Pollard & Yates, 1993; Riva et al., 2020; Royer et al., 1998; Taron & Ries, 2015), capture–mark–release (CMR, Hanski et al., 2000; Taron & Ries, 2015; Zimmermann et al., 2011) and, for certain species, egg counts (Maes et al., 2004; Vries et al., 2011) and larval surveys (Bergen et al., 2020; Hula et al., 2004; Ojanen et al., 2013). Transect counts have become popular largely as they are more cost-effective and practical than some other methods (Nowicki et al., 2008). Still, they have been criticised for imperfect detection (Isaac et al., 2011; Pellet et al., 2012; Shuey & Szymanski, 2010) and they may underestimate population densities (Harker & Shreeve, 2008; Isaac et al., 2011). While capture–mark–release usually provides highly accurate population data for estimating population size and detection probabilities (and provides more detailed information on, for example, dispersal and demography than other methods), it is invasive (due to the physical handling of the butterflies) as well as time-consuming and by that costly (Haddad et al., 2008). There are different methods for sampling immature life stages, such as larvae (e.g., timed surveys, Ojanen et al., 2013; complete area searches, Konvička et al., 2005; transect counts, Konvička et al., 2003; Smee, Smyth, et al., 2010). With the right method, the detection probability is high; however, the information it can provide on the status of a population may be more limited compared with other methods (Nowicki et al., 2008).

A potential compromise between the required effort and data generated could be achieved through a fourth method—a plot-based survey. In plot-based surveys, entire plots (e.g., a whole patch or other predetermined areas) are searched for butterflies for a set amount of time (Grill et al., 2005; Hardersen & Corezzola, 2014; Kral, 2018; Levanoni et al., 2011; Marini et al., 2009; Taron & Ries, 2015). As the whole plot is zig-zagged through, it might not have the same issues with poor species detection and underestimations of species abundance (Kadlec et al., 2012) as fixed transects. Moreover, it can be less time-consuming and costly than CMR while still documenting the spatial distribution of butterflies without handling them. Knowledge of the spatial distribution of a species can provide crucial information as to how a species utilises a habitat and can identify possible hotspots, for example, areas important for reproduction (Lewis & Hurford, 1997). While the method of plot-based surveys has not yet been standardised, it has good potential to be (Hardersen & Corezzola, 2014).

In this study, we describe a novel plot-based grid survey method, with 1-ha grid cells distributed over the habitat. In some respects, our grid survey is similar to some transect methods described in other studies, where several shorter segments together form one long trail, covering large parts of the habitat within a plot (Bergman & Jansson, 2012; Thomas, 1983). The main difference is that our method is more flexible in respect to where surveyors spend most of their time during one visit.

The aim of this study was to compare the grid survey method with more traditional transect counts and evaluate both methods in relation to high-quality capture–mark–release (CMR) population estimates (reflecting the 'true' population size). We do this based on records of adult butterflies and larvae nests from a relatively large population of the marsh fritillary butterfly on Gotland, Sweden.

METHODS

Study species

The marsh fritillary butterfly (*Euphydryas aurinia*) is found in Europe, western and central Asia, and North Africa. Within its range, the species is typically found in damp meadows, wet heathland and other open habitats with a mosaic of vegetation types. Due to its drastic decline during the last century, the marsh fritillary is regarded as endangered (EN) or vulnerable (VU) in most of its European range (JNCC, 2021), and it is listed on Annex 2 of the Habitats Directive as a species of conservation concern in Europe. The main threats to the marsh fritillary include habitat loss and fragmentation, changes in land management practices, and climate change (e.g., Hula et al., 2004; Johansson et al., 2020; Schtickzelle et al., 2005). Given its conservation status, effective monitoring and management of marsh fritillary populations are critical for its long-term survival.

The marsh fritillary is univoltine, with adults flying from late May to late June in Sweden. Females mate once and lay large egg batches (50–500 eggs/batch) on the leaves of the host plant *Succisa pratensis*.

In other parts of its distribution, the marsh fritillary also utilises other host plants (e.g., Singer et al., 2002), which seems to co-vary with the phylogenetics of the species (Korb et al., 2016). After hatching, the larvae spin a silken nest around the host plant. Larvae feed and bask gregariously on the host plant during sunny days until they reach the fourth instar in September, when they enter diapause in a collective conspicuous nest (larvae nest). The larvae become active again in early spring and resume feeding and basking together. They become more solitary at the end of the fifth instar, when their food requirements increase. In total, the larvae undergo six instars.

Study site

The study was conducted in a 27.7-ha area close to Slite on the island of Gotland in the Baltic Sea (Figure 1a), Sweden (midpoint of the area: 57°43.2′ N 18°42.0′ E). In the study area, the species occurs in wet parts of unfertilized calcareous wet grasslands that in most places remain naturally open due to the poor soil and slow accumulation of humus (Eliasson, 2008). To identify potential habitat for the marsh fritillary in the study landscape, we mapped the distribution of the host plant *Succisa pratensis* throughout the landscape and combined it with high-resolution land cover data (Swedish land cover data, CadasterENV) and tree cover information from laser radar data (LiDAR). Potential habitat was defined as all open grasslands with occurrence of the host plant (Johansson et al., 2019).

Survey methods

In this study, we used three different survey methods for the adult marsh fritillary: (1) capture–mark–release (CMR), (2) transect counts and (3) a plot-based grid survey. CMR was conducted during the flight season spanning from late May to late June 2017 and 2019–2021. In 2020, all three survey methods were conducted simultaneously. Surveys were conducted between 8 AM and 6 PM, provided there was no persistent precipitation and the temperature was at least 17°C.

CMR was conducted daily during the entire flight season for the four years (>20 days each year), 2017 and 2019–2021, provided that the weather requirements were being met. The observer walked slowly in a zigzag pattern covering the whole habitat and butterflies were caught using a fine net. All butterflies were individually marked with a waterproof permanent marker (Staedtler felt-tip pen). GPS position of each individual was recorded in the field using ArcGIS and the app Collector. The CMR survey covered all identified habitat of 27.7 ha (Figure 1b).

Both transect counts and grid surveys were conducted simultaneously on six separate occasions between 5 June and 18 June 2020. Using the experience from CMR conducted in 2017 and 2019, this time period was selected as it would cover the population peak of the study species (Johansson et al., 2022). During transect counts, a total of 20 fixed transects distributed across 20 one-hectare grid cells within the 27.7 ha of identified habitat of the study species were surveyed (Figure 1b). For each grid cell, on average, five transects were randomly placed across the cell, and we chose the transects that had the highest cover of suitable habitat. Transect length was 100 m and adult butterflies of the study species were recorded within 5 m from the observer (to both sides, forward and upwards), equalling transect width to 10 m. Time required per transect was set to a maximum of 15 min, in accordance with the guidelines from the Swedish Butterfly Monitoring Scheme (Pettersson, 2012).

During grid surveys, the same 20 one-hectare grids were surveyed (Figure 1b). Each grid overlapped with one respective transect. The observer walked slowly through 1-ha grid at a time, covering all habitats present in each respective grid. Time required per grid was set to a maximum of 30 min, depending on the amount of habitat

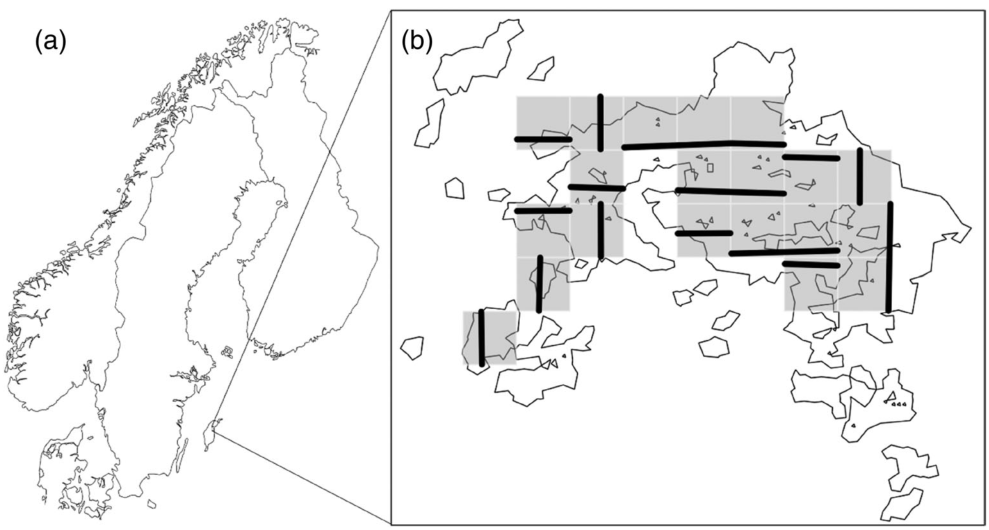

FIGURE 1 The (a) study area on the island of Gotland in the Baltic Sea where the marsh fritillary was recorded across its (b) habitat (white polygons) using different survey methods along 20 transects (black lines) and in 20 ha grid cells (grey squares).

within each respective grid. In total, six experienced observers conducted both the transect survey and the grid survey. Both methods were always carried out on the same day, and we randomly altered the order for each visit.

For the larvae nests, we used three survey methods: (1) total counts, (2) transect counts and (3) grid survey. Total counts were conducted yearly in the first to second week of September in 2017–2021. In 2020, all survey methods were conducted simultaneously. GPS position of each larvae nest was recorded in the field using ArcGIS and the app Collector. The larvae surveys were done by five skilled lepidopterologists, with a deep understanding of the marsh fritillary habitat in the study area. All team members participated in an intensive half-day training session before starting the surveys. The method proved to be straightforward following the training, with minimal risk of observer bias.

During total counts, all identified habitat of 27.7 ha were surveyed (Figure 1b). The observer walked slowly in a zigzag pattern covering the whole habitat and larvae nests were registered as one observation per nest.

In 2020, transect counts of larvae nests were conducted in the same 20 transects used for the inventory of adult butterflies (Figure 1b). The observer walked slowly through one transect at a time, covering the whole width and length (10×100 m) of each transect. Simultaneously in 2020, the 20 one-hectare grid cells from the inventory of adult butterflies were surveyed for larvae nests. The observer walked slowly through 1-ha grid at a time, covering all habitats present in each respective grid. Maximum time required per transect/grid was the same as in the adult surveys (i.e., 15 and 30 min).

Statistical analysis

We used a Kruskal–Wallis test to compare the average detection probability (Kéry & Plattner, 2007), which is the proportion of visits where the species was found, between the transect method and the grid method. We also used the same test to compare the mean time (in minutes) to detection between the two survey methods. Based on the average detection probability, we then calculated the cumulative detection probability for each method from one to six visits and over the time spent searching for the species. Moreover, we correlated the detection probability (for the transect method and the grid method separately) with the habitat area and the estimated population size from CMR (see below) using Spearman rank correlations. The detection probability, when using the transect method for counting larvae nests, was defined as the proportion of transects in which nests were found, among those grid cells where nests were present.

To estimate local population sizes in the 20 one-hectare grid cells used for comparison of survey methods in 2020, we used Craig's population estimator (Craig, 1953) and CMR data from each hectare grid cell (Kindvall et al., 2022). Craig's model is quite simple and only considers the number of captured individuals and the total number of captures within the grid cell to estimate the population size. We used this approach as we were unable to fit the more advanced Jolly–Seber–Schwarz–Arnason model (see below) for individual grid cells (as the number of individuals was too few in most grid cells). However, Craig's model most often gives similar results as more advanced models (Drag et al., 2011; Ranius, 2001).

To analyse the relationship between the estimated population size in a grid cell and the number of butterflies found in the same grid during one visit, using the transect method or the grid method, we used a generalised linear mixed-effects model with a negative binomial distribution (over-dispersed count data). Explanatory variables were estimated population size (Craig's estimate), survey method (a factor with two levels: transect or grid). We also included the interaction between population size and survey method. We included grid identity and surveyor identity as random effects to account for multiple visits in each grid and inter-observer variability. The model was built based on AIC, and the final best model was the one with the lowest AIC.

To analyse the relationship between the estimated imago population size in a grid cell and the number of larvae found in the same grid, using the transect method or the grid method, we used a generalised linear mixed-effects model with a negative binomial distribution (over-dispersed count data). Explanatory variables were estimated population size, survey method (a factor with two levels: transect or grid) and their interaction. Grid identity was included as random effect.

To estimate the yearly total population size for the entire study area (Figure 1), we used capture–mark–release (CMR) data from each year and Jolly–Seber–Schwarz–Arnason models for open populations (Schwarz & Arnason, 1996). In these models, survival probabilities were time-dependent (i.e., they were allowed to vary over the season when the model was fitted to the data), which is likely, for example, because of vanishing food supply (this also improved the model based on the AIC, compared with constant probabilities). However, to reach model convergence, we had to keep capture probabilities and recruitment probabilities constant (Johansson et al., 2022). We also calculated the relationship between the yearly adult population size and the yearly number of larvae nests in the entire study area. Moreover, based on yearly transect counts of larvae nests, we calculated detection probability for each year (2017–2021) and correlated it with the total number of nests found in the entire study area using Spearman rank correlation.

RESULTS

Detection probability

The number of visits during which the marsh fritillary was found (among the six visits during the flight period in 2020) ranged from 3 to 6 for the transect method among the 20 grid cells, while the corresponding numbers were 4–6 for the grid method. The detection probability (i.e., the proportion of visits where the species was found) was significantly higher than that found using the grid method

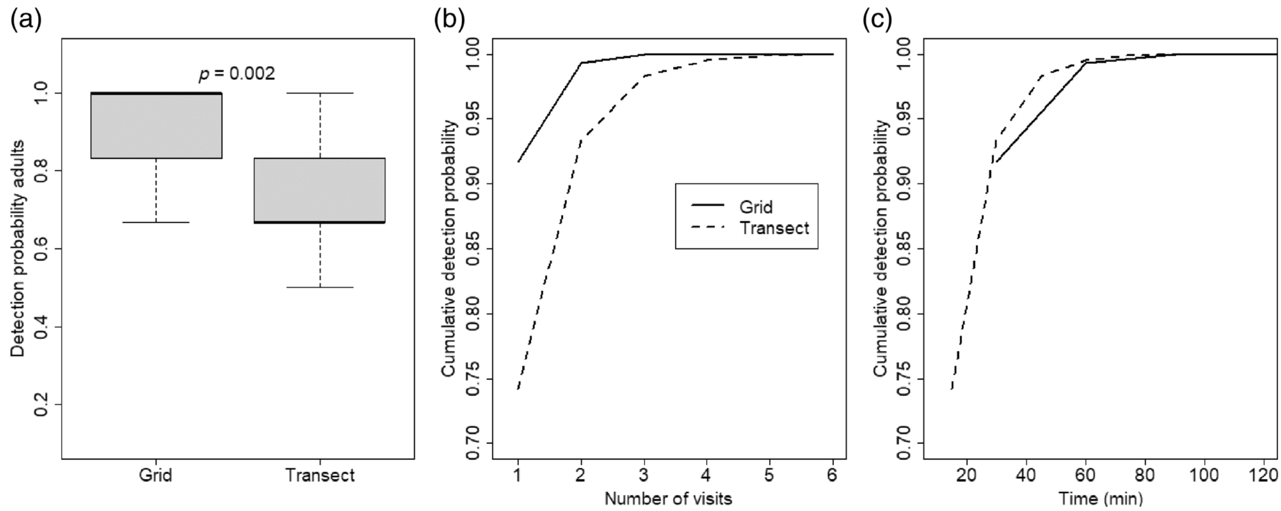

FIGURE 2 The (a) detection probability, that is, the proportion of visits where the adult marsh fritillary was found (among the six visits) using the grid and transect methods in the 20 grids cells used for comparison of methods (see Figure 1), the (b) cumulative detection probability after one to six visits based on the mean detection probability from each method and the (c) corresponding cumulative detection probability over survey time. The statistical difference in (a) was tested with a Kruskal–Wallis rank test.

(mean = 0.92) compared with the transect method (mean = 0.74) based on the Kruskal–Wallis test ($\chi^2 = 10.0$, $p = 0.002$, Figure 2), while the mean time for detection was not significantly different for the two methods ($\chi^2 = 0.22$, $p = 0.64$). There were no correlations between detection probability and habitat area or the estimated population size (based on CMR) for either of the two methods ($p > 0.31$). When counting larvae nests, we found no nests in 5 out of the 20 transects, resulting in a detection probability of 0.75 for the transect method in 2020.

Population estimates

The mean number of butterflies found using the grid method was significantly higher than using the transect method (Table 1, Figure 3). The grid method (average = 8.3 recorded butterflies) resulted in almost four times higher counts than the transect method (average = 2.1). The estimated population size based on CMR (the Craig estimate) was on average 9.46 (SE = 1.27) times larger than the mean number of butterflies seen using the grid method, while it was 49.25 (SE = 9.26) times larger than the mean from the transect method. There was a clear significant relationship between the estimated population size and the number of butterflies found during one visit using the grid-based method, while no such relationship was found for the transect method (Table 1, Figure 3). Model residuals showed no spatial autocorrelation based on Moran I ($p = 0.91$).

In total, we found 295 larvae nests using the grid method (in 2020), and the number of nests ranged from 2 to 32 among the hectare grid cells (mean = 14.8, SE = 1.83). Larvae nests were observed in all surveyed hectare grid cells. The total number of nests found using the transect method was 52 and the number found in individual transects ranged from 0 to 11 (mean = 2.60, SE = 0.70). Larvae nests were observed in 15 out of the 20 surveyed transects.

TABLE 1 The parameter estimates (with standard error) and associated *p*-values for the final model of butterfly counts.

Variable	Estimate (SE)	*p*-value
Intercept	0.73 (0.19)	<0.001
Estimated population size[a]	0.02 (0.09)	0.86
Method (grid)	1.10 (0.13)	<0.001
Est pop size × Method (grid)	0.41 (0.12)	<0.001

[a]The transect method has no significant relationship with estimated population size, while the grid method has a clear relationship (seen in the interaction term, also see Figure 3).

The mean number of larvae found using the grid method was significantly higher than using the transect method (Table 2 and Figure 4). On average, the grid method (average = 14.8 recorded larvae) resulted in 5.7 times higher counts than the transect method (average = 2.6). There was a significant relationship between the estimated population size and the number of larvae found during one visit for both methods (Table 2, Figure 4). The interaction between population size and survey method did not improve the model (based on AIC) and was therefore removed. Model residuals showed no spatial autocorrelation based on Moran I ($p = 0.67$).

Monitoring population trends

The number of unique individuals that were captured during CMR studies was as follows: 1002 (in 2017), 149 (in 2019), 1022 (in 2020) and 1050 in (2021), and the corresponding recapture rates were as follows: 33%, 24%, 22% and 31%. The estimated total population of the marsh fritillary within the study area varied widely between years

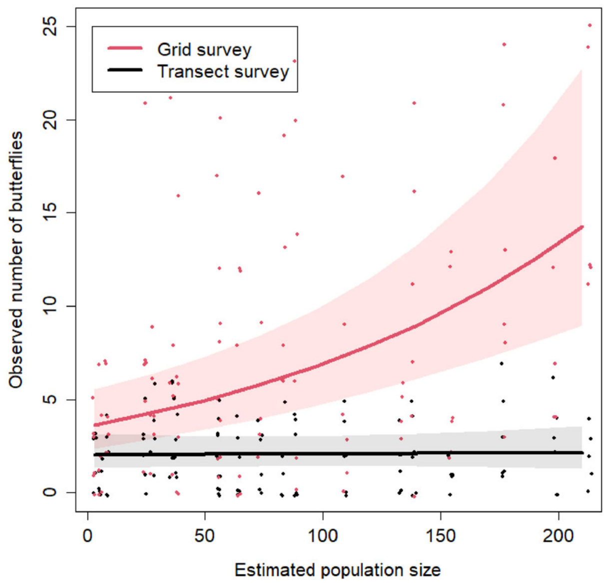

FIGURE 3 The observed number of butterflies in relation to the estimated total population size in a grid cell using the grid or transect method. Lines are model predictions with 95% confidence intervals (shaded areas). Points are the observed data (with a small scatter for better visualisation).

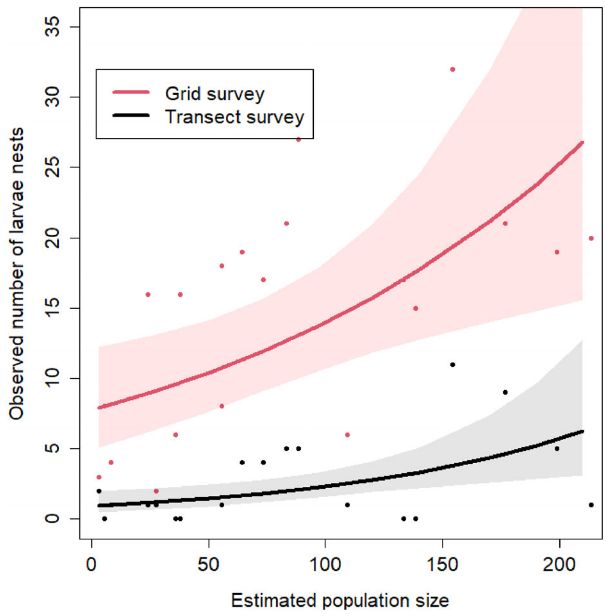

FIGURE 4 The observed number of larvae nests in relation to the estimated total butterfly population size in a grid cell using the grid or transect method. Lines are model predictions with 95% confidence intervals (shaded areas). Points are the observed data.

TABLE 2 The parameter estimates (with standard error) and the associated *p*-values for the final model of larvae nest counts.

Variable	Estimate (SE)	*p*-value
Intercept	1.99 (0.21)	0.45
Estimated population size	0.007 (0.002)	<0.001
Method (grid)	1.79 (0.19)	<0.001

during the five-year study period (2017–2021, Figure 5). The total number of butterflies ranged from 385 to 2772, excluding 2018 when no CMR was conducted, based on the Jolly–Seber–Schwarz–Arnason models for the entire area. The estimated population size in 2020 yielded a butterfly density (100.1 butterflies/ha) similar to the density based on the sum of all Craig's values for the 20 grid cells (112.8 butterflies/ha). The total number of nests ranged from 2 to 346. The number of larvae nests followed the adult population rather well (for the four years we have data on both, Figure 5), constituting roughly 12% of the adult butterflies on average (range = 10.5%–12.7%).

The detection probability, based on larvae nest transect counts, varied between years and was strongly correlated with the total number of nests in the study area, as indicated by the Spearman rank correlation (rho = 1, $p = 0.017$, Figure 6).

DISCUSSION

We found that our plot-based grid method resulted in a higher detection probability and more recorded butterflies and larvae nests compared with transect counts. The grid method also showed a significant relationship with the estimated population size from capture–mark–release for adult butterflies, while the transect counts did not. Based on data over several years, larvae transect count reliability seems to decrease with decreasing population densities. This underlines the importance of method selection when specifically monitoring rare habitat specialist butterflies, such as the marsh fritillary.

Detection probability

The detection probability was higher using the grid method compared with the transect method for both adult butterflies and larvae nests. These results are quite intuitive as grid surveys cover larger areas, and chances of encountering a butterfly or larvae nest when covering a grid are higher than when walking along predetermined transects. For adult butterflies, detectability increased with the number of visits. Already after three visits, the cumulative detection probability was high also for transect counts, and by the fourth visit, any difference in the cumulative detection probability between the two methods was negligible (Figure 2). Both methods had a very similar cumulative probability in relation to total survey time, which suggest that the higher detection probability of adult butterflies using the grid method lies mainly in the longer visits. Hence, the lower detectability of the transect counts could be ameliorated by increasing the survey effort with more and perhaps longer visits (Zonneveld et al., 2003). With fewer than four 15-min visits, however, the risk of observing false absence records (Kéry & Plattner, 2007; Riva et al., 2020) using the transect method was clearly higher than the using the grid method.

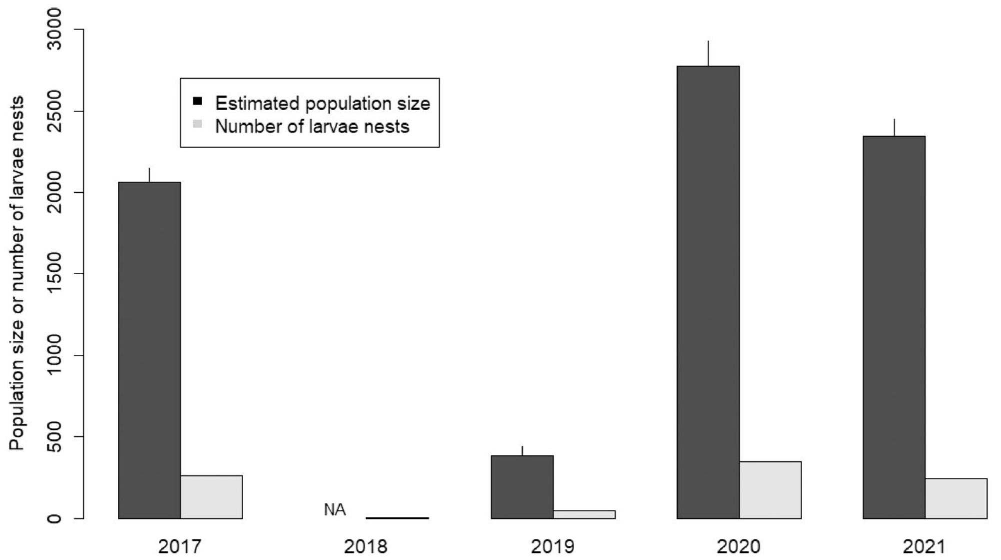

FIGURE 5 The yearly total counts of larvae nests between 2017 and 2021 (grey bars) and the estimated total population size based on capture–mark–recapture data (black bars) for the four years (in 2018 we did not conduct CMR studies). Vertical lines above black bars signify the standard error of the population estimate from the Jolly–Seber–Schwarz–Arnason models.

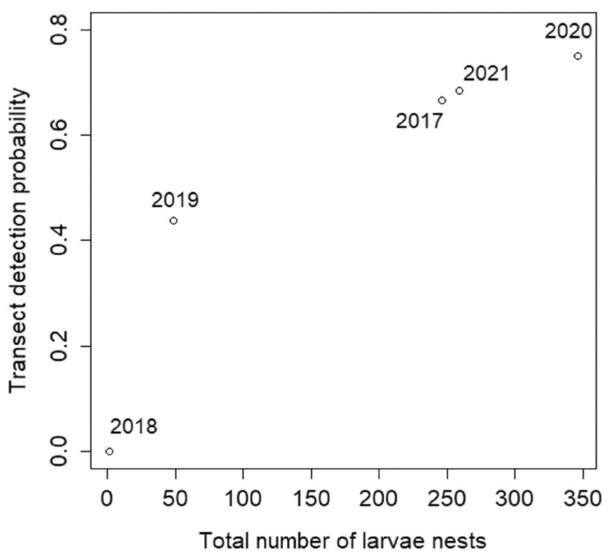

FIGURE 6 The correlation between the total number of larvae nests and the probability of detecting larvae nests when using the transect method for five years (the year is written next to each data point).

Moreover, transect counts of larvae nests resulted in a 25% risk of false absences. The grid method, hence, seem to be more reliable for both adult and larvae when it comes to detecting species occurrence. This is most likely because of its flexibility in where the surveyor spends most of its time, which makes it possible to better target local 'hotspots' for the availability of nectar resources and host plants (which also may vary between years), and vegetational structures that may affect their behaviour (Konvicka et al., 2023). We suggest that the grid method, due to its flexibility, also is less sensitive to species-specific behaviour and appearance (Dennis et al., 2006; Kral-O'Brien et al., 2020; Pellet et al., 2012), for example, in relation to sun exposure (Wittman et al., 2017) and different environmental conditions (Riva et al., 2020) that may affect the probability of species detection in a location at a given time.

It is important to note that our study area contains one of the largest marsh fritillary populations in Sweden. Consequently, butterfly densities are most likely higher compared with other areas where the species occur. Moreover, the butterfly population peaked in 2020 (Figure 5) when this study was conducted. It is therefore likely that we may overestimate the average detection probability, especially for transect counts, which in areas or years of lower population densities most likely is much lower (Kéry & Plattner, 2007).

Population estimates

The grid method resulted in roughly four times more butterflies being recorded than the transect method and showed a clear significant relationship with the estimated 'true' population size, while no such relationship was found for the transect method. The higher number of recorded butterflies is not surprising as the grid method covers a larger area. However, the absence of a relationship between the transect counts and the 'true' population size is unexpected, even though it agrees with Shuey and Szymanski (2010). We think that this, in the same way as for detection probability, is an effect of the flexibility of the grid method compared with the fixed transects. The grid method does not only cover a larger area, but it is also likely to include more variation in the habitat that should better cover potentially aggregated microclimates and floral resources that the butterflies may utilise (Botham et al., 2011; Scherer & Fartmann, 2021). This most likely also applies for many other grassland insects dependent on potentially aggregated floral resources or nesting sites

(Antoine & Forrest, 2021; Szigeti et al., 2016). For larvae, both grid and transect counts showed significant relationship with the 'true' population size. This implies that transect counts could provide useful information on the total population, with less effort than the grid method. However, it is likely that transect counts are less reliable at low densities, and as the number of nests was almost six times lower compared with the grid method, one should still be cautious when interpreting results from transect counts.

Following population trends

We show that the marsh fritillary may fluctuate quite substantially between years, which agrees with earlier results for the species (e.g., Klapwijk et al., 2010; Schtickzelle et al., 2005; Zimmermann et al., 2011), as well as other fritillaries (e.g., Ehrlich et al., 1980; Bergen et al., 2020) and many other grassland insects (e.g., Douwes, 1980; Franzén et al., 2013; Franzén & Nilsson, 2013), for example, due to extreme weather events such as the severe drought in 2018 (Bergen et al., 2020; Johansson et al., 2020; Johansson et al., 2022). Such fluctuations may affect how reliable different survey methods are, and some methods may perform better at high densities. Transect larvae nest counts resulted in a very low detectability when population densities were low (Figure 6), while the grid-based larvae counts showed a relatively stable relation to the total number of adult butterflies over time (Figure 5). Exceptions may, however, occur in years with extreme weather (Johansson et al., 2020), changes in management (Hula et al., 2004) or fluctuating parasitoid pressures (Eliasson & Shaw, 2003; Joyce & Pullin, 2003; Ravenscroft, 2019) when larvae counts may deviate completely from the adult population due to increased larvae mortality. Unfortunately, we did not perform any CMR during the drought year of 2018, but metapopulation patch occupancy suggested that the species was common during the flight period (Johansson et al., 2019) and the number of larvae nests therefore surprisingly few (Figure 5). Hence, extrapolating larvae nest counts to the adult population size the same year can be unreliable (Junker et al., 2021) and, at least some years, the larvae counts will better reflect next year's adult population. Further uncertainty is brought by the observed behaviour that the marsh fritillary occasionally having a biennial life cycle (Eliasson & Shaw, 2003; Ravenscroft, 2021) in accordance with other fritillaries (Eliasson & Shaw, 2003; Wahlberg, 1998), as well as some other grassland insects (Franzén & Nilsson, 2013). Hence, low larvae nest counts do not necessarily have to be the result of a small adult population, and monitoring based solely on larvae nest counts (e.g., Bergen et al., 2020; Ojanen et al., 2013) could therefore lead to false conclusions regarding the population trend. We found only two larvae nests during the 2018 drought, suggesting a massive population crash, in line with the well-studied Glanville fritillary in Finland (Bergen et al., 2020). However, the trend for the adult marsh fritillary was not that drastic (Figure 5), and the species was still relatively common the consecutive year (2019).

CONCLUSION

The novel 1-ha grid survey method showed a high detectability and a strong relationship with the 'true' population size (from capture–mark–release) for the marsh fritillary, while the more traditional transect counts of imago had lower detectability and no significant relationship with CMR estimates. We hence suggest that the grid survey method is a better alternative to follow population trends of the marsh fritillary butterfly. However, this can to some extent be scale dependent, and transect counts may work better for population trends at larger scales (Pollard & Yates, 1993) and for following whole communities. As habitat heterogeneity often affect grassland insect dynamics (Kindvall, 1996), it is important that the area covered each year include appropriate habitat variation (e.g., in ground moisture), to be able to capture potential changes in species distributions between years (e.g., due to weather). This can likely be achieved by adding up transect counts to larger scales, or being more flexible in the way surveyors move at a smaller scale (as the grid method suggested here). For larvae surveys, both methods showed significant relationship with the true population size in 2020. Therefore, larval surveys could be a more cost- and time-effective method compared with adult surveys (as it only requires one visit per location). However, one should be cautious with conclusions regarding population trends in relation to years with, for example, extreme weather. Adult surveys may therefore be necessary. Our approach complements the existing approaches of how landscape structure affects populations in a given habitat and is useful for long-term biodiversity monitoring. We suggest that a new grid-based monitoring approach is widely implemented to monitor rare species and habitat specialists, not picked up by other methods.

AUTHOR CONTRIBUTIONS

Hannah Norman: Writing – original draft; formal analysis; data curation; investigation; project administration. **Demieka Seabrook Säwenfalk:** Writing – original draft; formal analysis; data curation; investigation; project administration. **Oskar Kindvall:** Methodology; writing – original draft; conceptualization; visualization; data curation; investigation; supervision. **Markus Franzén:** Conceptualization; methodology; funding acquisition; writing – review and editing; investigation; supervision. **John Askling:** Conceptualization; methodology; investigation; project administration. **Victor Johansson:** Writing – original draft; writing – review and editing; methodology; supervision; formal analysis; visualization; data curation; investigation; validation.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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