



Survey precision moderates the relationship between population size and stability



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ABSTRACT

Positive relationship between size of local populations and their stability is a central concept in conservation biology, utilised in its tools including metapopulation models and population viability analysis, although most empirical studies found this relationship rather weak. In the present study I evaluated the impact of the precision of population estimates on the strength of the relationship between population sizes, or patch areas used as their proxy, and the extent of their temporal variability. Based on the data provided by 13-year monitoring of three species of *Maculinea* (= *Phengaris*) butterflies, I quantified the variability of their population time-series with the coefficients of variation (CVs), using both their overall temporal variances as well as the variances corrected for sampling variance, which reflects the precision (sampling error) of seasonal population size estimates. The extent of population variability, expressed with the CVs uncorrected for sampling variance, correlated negatively with both population size and habitat patch area, but these relationships were relatively weak, especially in *M. teleius* and *M. nausithous* ($R^2 \sim 0.1$). However, sampling error increased considerably with population size and patch area, due to smaller fractions of individuals being sampled. Consequently, in the case of the CVs based on the variances corrected for sampling variance, the negative correlations with population size and patch area were substantially stronger (R^2 reaching 0.3–0.6). My results highlight the advantage of monitoring methods that allow quantifying sampling error, which is essential for assessing species extinction risk.

1. Introduction

Analysing population time-series is a key issue in applied ecology and conservation biology (Caughley, 1994; Keith et al., 2015). Detecting substantial declines in population size allows identifying species or (at local scale) populations that should be of conservation concern as they may be likely to face extinctions in near future (Stanton, 2014; Keith et al., 2015). In turn, in the case of populations without a significant negative trend the extent of population size fluctuations, typically expressed with their coefficient of variation (CV hereafter), becomes of prime importance (Lundberg et al., 2000). Such an index of population size variability serves as an inverse measure of population stability, which directly translates into population viability. Less stable, i.e. more fluctuating populations are more vulnerable to extinctions due to stochastic processes (Pimm et al., 1988; Lande, 1993; Caughley, 1994). Their risk of extinction would be further increased if strong negative Allee effects act in years when populations reach low numbers (Courchamp et al., 1999, 2008). Besides, local population fluctuations indirectly affect the numbers of dispersers through positive density-dependence of emigration that have been documented in many organisms (Byers, 2000; Matthysen, 2005; Nowicki and Vrabec, 2011),

thus influencing metapopulation persistence (Nachman, 2000; Hovestadt and Poethke, 2006).

Positive relationship between local population size, or habitat patch area used as its proxy, and population stability constitutes one of central concepts in conservation biology, and it is utilised in its popular tools such as metapopulation models and population viability analysis (Boyce, 1992; Hanski, 1999). The validity of this concept is supported with several theoretical arguments. Higher number of individuals makes population dynamics less sensitive to demographic stochasticity as well as to Allee effects at low densities (Pimm et al., 1988; Courchamp et al., 1999). In addition, larger populations typically occupy larger habitat fragments, which due to their greater spatial extent tend to be more heterogeneous, and habitat heterogeneity was proven to enhance population stability (Kindvall, 1996; Oliver et al., 2010). Finally, small habitat patch area translates into higher emigration rate and higher number of immigrations relative to the number of local residents (Hambäck and Englund, 2005; Englund and Hambäck, 2007 and references therein). Consequently, while the dynamics of large populations is predominantly shaped by intrinsic processes, small populations may occasionally be destabilised by high losses of emigrants or influxes of immigrants.

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Quite a few empirical studies documented the negative relationship between population size and temporal population variability (Watt, 1964; Karr, 1982; Thomas et al., 1994; Oliver et al., 2010, 2012; Franzen et al., 2013). However, the effects of population size reported in these studies, although significant (usually thanks of extremely large sample sizes of population monitoring data), were not particularly strong and sometimes less eminent than those of other factors investigated, such as population location within species distribution ranges (central vs. marginal), climatic parameters, or habitat composition (Thomas et al., 1994; Oliver et al., 2010, 2012). Such an outcome is likely to stem from the fact that the aforementioned studies used relative abundance indices, namely counts along transects or on sampling plots, of unknown precision.

Relative abundance indices rely on the assumption that a small fraction of individuals that are sampled remains constant for consecutive surveys of a given population. As long as this assumption is met, relative abundance indices may serve as unbiased indices of temporal changes in population size even if the population size itself remains unknown (Seber, 1982; Lancia et al., 1994). However, since the proportion of individuals sampled is not estimated, the precision of relative abundance indices cannot be quantified (Seber, 1982; Williams et al., 2002). This is a key deficiency for analysing population size variability, or precisely speaking variability of population size estimates. Overall variability of population size estimates inevitably derives not only from genuine population fluctuations but also from the estimate precision, i.e. sampling error (Link and Nichols, 1994; Hovestadt and Nowicki, 2008). To illustrate this principle with an extreme example it is worth noting that even if a population remains perfectly stable within a given period, its estimates will fluctuate among seasons. What is worse, the sampling error is likely to vary among surveyed populations, as it depends negatively on the proportion of individuals sampled, which in turn is influenced by several factors, including those that may affect population stability itself. In particular, one may predict that the estimates of larger populations are typically less precise (i.e. subject to larger sampling errors), because they are based on a smaller proportion of recorded individuals.

The above problem is true regardless of the survey method. Nevertheless, as long as the sampling error of population size estimates can be quantified, it can also be accounted for in the analyses of population size variability (Hovestadt and Nowicki, 2008). Consequently, the aim of the present study was to test whether accounting for the sampling error of population size estimates may improve the strength of the negative relationship between population size and the extent of its temporal variability. I used the data provided by long-term monitoring of large metapopulations of *Maculinea* (= *Phengaris*) butterflies, conducted using the methods that allow deriving seasonal population size estimates together with their sampling error. This makes it possible to assess the relationship between sizes of local populations and their temporal variability, with as well as without the sampling error of population sizes accounted for, and subsequently to compare the strength of this relationship in both cases.

2. Materials and methods

2.1. Study system

Maculinea are highly specialised grassland butterflies, which require specific foodplants as well as specific host ants of the genus *Myrmica* to complete their life cycle (Thomas, 1984, 1995). Of these two crucial resources host ants are typically wide-spread, but scarce, whereas foodplants are patchily distributed and thus their distribution defines local habitat patches of *Maculinea* butterflies (Anton et al., 2008; Nowicki and Vrabec, 2011). Consequently, *Maculinea* often form classic metapopulations (Nowicki et al., 2007; Dierks and Fischer, 2009).

The study area comprised a wet meadow complex in the Kraków region (50°01' N; 19°54' E), southern Poland, which hosts one of the

largest metapopulations of *M. teleius* and *M. nausitous* in Europe (63 sympatric local populations) as well as a medium-size metapopulation of *M. alcon* (18 local populations) (Nowicki et al., 2007; Kajzer-Bonk et al., 2013). Local population sizes of the two former species range between < 50 to over 10 thousand adults, and the patches of their *Sanguisorba officinalis* foodplants are between 0.02 and 33 ha. In turn, both local populations of *M. alcon* as well as their *Gentiana pneumonanthe* foodplant patches are much smaller, reaching 5–250 individuals and 0.01–3 ha in area (Nowicki et al., 2007).

There is little dispersal among the local populations. The exchange of individuals was estimated with the Virtual Migration model (Hanski et al., 2000) at only 6–7% individuals per season in both *M. teleius* and *M. nausitous* (Nowicki et al., 2014). Although, a similar assessment is not available for *M. alcon*, it may be expected that the exchange of individuals among the populations of this species is even lower, concerning its similar dispersal abilities, but much greater isolation of the habitat patches (typical distances between neighbouring *G. pneumonanthe* patches in the range of 300–700 m vs. 100–300 m in the case of *S. officinalis* patches). Consequently, it is not surprising that local populations of all three species were found to function as independent demographic units with no synchronisation in their year-to-year fluctuations (Nowicki et al., 2007, 2015).

The dynamics of the three focal species in the region do not show any apparent long-term trend (Kajzer-Bonk et al., 2013). Moreover, stochastic extinctions of local populations occur rarely and are restricted to small and highly isolated habitat patches (Nowicki et al., 2007). Except from a complete destruction of few marginally located habitat patches due to urban development in recent years, the system is free from direct human impact, either negative one through deterioration of habitat quality or positive one in form of conservation management.

All the populations of the three *Maculinea* species have been monitored continuously since 2003. Local abundances of *M. alcon* are surveyed through repeated egg counts conducted along 2-metre wide transects at larger patches of *G. pneumonanthe* (> 0.25 ha) or total egg count at smaller ones (Nowicki et al., 2007). The transects are established along the longest axis of each patch, reaching 90–520 m in length, and divided into 10-m sections. The detectability of *M. alcon* eggs is perfect, because they are highly conspicuous and the same is true for the gentians on which they are laid (Maes et al., 2004). The numbers of adult butterflies are estimated assuming 150 eggs per female and 1:1 sex ratio as in Hochberg et al. (1992); in the case of egg counts on transects the results are extrapolated to the total area of the patch (see Appendix S1 for details).

Abundances of *M. teleius* and *M. nausitous* are assessed with the catch-per-time-unit method, tested and parameterised against population size estimates based on intensive mark-recapture sampling in the initial year of the monitoring (see Nowicki et al., 2007 and Appendix S1 for details). The method relies on repeated 1-hour capture sessions conducted during peak occurrence of adult butterflies in late July in order to assess their capture frequencies, which were proven to correlate well with butterfly densities (Nowicki et al., 2007). The latter are subsequently converted into seasonal population sizes following the approach described by Nowicki et al. (2005); (see this reference and Appendix S1 for a detailed description of the method). It is worth pointing out that unlike transect counts traditionally applied in butterfly monitoring, which only offer relative abundance indices (Pollard and Yates, 1993), the monitoring of *Maculinea* butterflies described above provides genuine population size estimates together with their precision measures, which allows quantification of the sampling error (Appendix S1).

2.2. Time-series analysis

In the analysis I used only the time-series of the populations continuously existing for at least 5 years in order to ensure that their length

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