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Compilation and illustration of statistical methods for the analysis of state and trends in populations and species level biodiversity

Deliverable 12 of EuMon's Work Package 2.2

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Policy Summary

Distribution and population size are the two criteria accepted for the reporting of member states on the status of the Annex species of the Birds and Habitats Directives to the European Commission. Deliverable 12 provides an illustrated compilation of methods to quantify state and trends of the distribution and population size of a species. The suggested methods include the estimation of distribution with presence-absence data and the estimation of population size with relative abundance data for large-scale surveys as well as the estimation of population size with capture-mark-recapture sampling for small-scale ones. All three classes of methods are exemplified by the case studies of the EuMon partners on birds, butterflies, and orchids, described in a uniform format. Special focus is given to dealing with the problems of spatial variation and imperfect detection, which are the key issues in species monitoring. Only few monitoring schemes can apply exhaustive sampling in which all the potential sites where a species may occur are surveyed within the area of interest. In the remaining cases, when a small fraction of the area has to be selected for sampling, a random or systematic selection of sampling sites or their post-stratification during the data analysis is recommended. Similarly, total count, in which all individuals are detected, is hardly ever possible. The recorded value of a parameter monitored (distribution or population size) is typically the product of its true value and the detection probability. Thus unless imperfect detection is accounted for, any changes in the recorded value may not necessarily reflect the true changes in the parameter that monitoring scheme is intended to document, but instead they may be due to variation in detection probability.

I. Background and Objectives

Numerous research papers and literature surveys exist on how to optimise field sampling designs to monitor biodiversity trends in space and times. However, actual practices do not fully take profit from recent methodological advances. They even rarely meet optimal sampling designs because of different constraints, such as minimizing complexity to maximize volunteer involvement or not interrupting long lasting time series of data, the collection of which started with non-optimal sampling designs. Ongoing practices in biodiversity monitoring are characterised by EuMon's survey on biodiversity monitoring schemes in Europe (<http://eumon.ckff.si/monitoring/>; cf. Deliverables 8 and 9).

The goal of the present Deliverable is to provide an illustrated compilation of methods to quantify state and trends of biodiversity at population and species levels. For that, we focus on identifying methods that meet both the reality of biodiversity monitoring i.e. used sampling designs actually applied at a wide scale in Europe (cf. Deliverable 17) and methodological recommendations for sampling design and statistical analysis (see Deliverable 2 for details). Applications of those chosen methods are illustrated using datasets available from EuMon research partners (Appendices 1–3), in order to provide guidance on how monitoring designs could be implemented in practice.

The EuMon activity has been launched under the 2010's target of the Convention of Biological Diversity (Balmford 2005a,b), and is funded by the European Commission, partly for the evaluation and support of the Birds and Habitats Directives. Therefore, we illustrate statistical methods for biodiversity monitoring that allow quantifying state and trend in species distribution and population size at the spatial scale ranging from a single site and to the whole country or even biogeographical region, with a specific focus on the Birds and

Habitats Directives species. Distribution and population size are the two criteria accepted for the reporting of member states on the Birds and Habitats Directives to the European Commission (see its note *Assessment, monitoring and reporting of conservation status – Preparing the 2001-2007 report under Article 17 of the Habitats Directive*; DocHab-04-03-03 rev.3 at http://forum.europa.eu.int/Public/irc/env/monnat/library?l=/reporting_framework). They also correspond to the species level headline of biodiversity indicators recommended to the Commission by SEBI2010 (<http://org.eea.europa.eu/news/Ann1148473248/sebi.pdf>) and the European Environment Agency (http://reports.eea.europa.eu/eea_report_2006_5/en).

Our conclusions are relevant to EU environmental policy, particularly in evaluating the suitability of available biodiversity monitoring data to assess the progress towards the stop of the biodiversity decline by 2010 at the level of each single member state. In addition, our illustrated, practical methodological recommendations should be of help for institutions and individuals designing and coordinating biodiversity monitoring schemes.

II. Compilation of statistical methods

Deliverable 2 (Recommendations for survey design and data analysis) provided a compilation of general concepts and methods for designing and analysing monitoring data. Case studies developed in the present Deliverable were chosen to illustrate the good practices listed and explained in Deliverable 2. In brief, these good practices are characterised by the following choices. Firstly, the goal of the monitoring must be clearly defined, as it will determine (i) the biological parameters and models to be monitored, (ii) the sampling design of the monitoring, and (iii) the context for interpretation and use of monitoring results. Secondly, according to the monitoring goal, a biological parameter to be measured is chosen (cf. Appendix 1 in Deliverable 2). For our further considerations we focus on distribution and population size (i.e., abundance) and their variations in space and time. Monitoring of other biological parameters is beyond the scope of the present Deliverable and environmental policy issues that the DoW of EuMon addresses. Thirdly, the choice of the sampling design will determine the representativity of monitoring data. In other words, the sampling design will determine to which extent monitoring results can be extrapolated to a larger geographic area than actually sampled, or to what extent they are representative of temporal changes that actually occurred throughout the monitoring period. Components of an ideal sampling design to ensure representative data are (i) exhaustive, random, or systematic choice of sampling sites or post-stratification to transform a non-representative into a representative design by weighting samples, (ii) stratification of samples if the sampling effort varies in space or time, (iii) sampling following an experimental design if the monitoring goal is to quantify the impact of known causes of change (e.g. management regime), and (iv) replication of samples to account for measurement error, as e.g. correction for imperfect detection of individuals or species during sampling.

The case studies presented in details in Appendices 1–3 illustrate how these general principles of monitoring design translate into specific characteristics of sampling design, statistical analyses and results interpretations. The methodologies covered by the case studies include the estimation of state and trend in species distribution with presence-absence data (section III) and the estimation of state and trend of the population size of a species with relative abundance data (section IV). Both approaches are considered optimal for their purposes (cf. Appendix 1 in Deliverable 2). In addition, we describe case studies dealing with the estimation of state and trend of the population size of a species with CMR (capture-mark-recapture) data (section V). This last solution is the best for its purpose from a purely

methodological point of view, but hardly applicable in large-scale monitoring due to high cost and labour requirements. However, CMR may be suitable for intensive local studies, e.g. targeting endangered populations, especially because their results provide additional information on population structure and demography, which makes it possible to move from just recording trend in population size to understanding of the underlying processes and their causes. For all three classes of methods we present case studies on birds, butterflies and orchids (Table 1), which are the most popular taxonomic groups among animals and plants monitored in Europe (cf. Deliverables 5 and 8). The aim of such a selection of case studies is to demonstrate that despite issues which are specific to particular groups of organisms, e.g. field data collection, they all share common properties as far as sampling design requirements and models of data analysis are concerned.

All the case studies are described using a uniform format in order to highlight both their common features as well as methodological differences among them. The emphasis is on methodological aspects of the case studies, such as characteristics of the sampling design and the data used, statistical methods applied for the analysis, field and analytical skills required to conduct the study, and potential methodological refinements. Special focus is given to the issue of measurement error within the parts devoted to the sampling design and data characteristics. Measurement error is the imprecision due to the fact that replication of observations does not yield identical values because of uncontrolled variation in the sampling process. Sources of this variation include e.g. differences in hour of the day, meteorological conditions, differences among observers, etc. The measurement error can thus be minimized by minimizing differences in sampling conditions among visits to sampling sites (e.g. sampling is implemented at the same hour of the day by the same observer).

Table 1. Compilation of the case studies presented in Appendices 1–3 of Deliverable 12.

Methodological approach	Taxonomic group		
	Birds	Butterflies	Orchids
Estimating state and trend of distribution of a species with presence-absence data (Appendix 1)	Case study 1 Distribution dynamics of a common bird, the magpie, in France (MNHN)	Case study 2 Presence-absence patterns in metapopulations of <i>Maculinea</i> butterflies (UJAG)	Case study 3 Distribution of orchids in Britain and Estonia (ESTAGUN)
Estimating state and trend of population size of a species with relative abundance data (Appendix 2)	Case study 4 Trends of common birds in France (MNHN)	Case study 5 Abundance patterns in metapopulations of <i>Maculinea</i> butterflies (UJAG)	Case study 6 Populations of the <i>Cypripedium calceolus</i> orchid in Estonia (ESTAGUN)
Estimating state and trend of population size of a species with CMR data (Appendix 3)	Case study 7 Several populations of common birds in France (MNHN)	Case study 8 Population size of Lepidoptera (UJAG)	Case study 9 Orchid populations in Estonia (ESTAGUN)

III. Estimating state and trend of distribution of a species with presence-absence data

Estimating the distribution of a species involves recording its presence or absence on sites surveyed. The detection of a species indeed indicates its presence, if only species misidentifications are avoided, which may require certain field skills. However, non-detection is not necessarily equivalent to the absence of a species, because it may go undetected when present (MacKenzie et al. 2002). Thus, the estimates of distribution ranges of species monitored may be expected to be negatively biased, unless imperfect detection is properly dealt with as exemplified by the case studies (Appendix 1).

Another problem is the variation of occurrence in space. Only few monitoring schemes can apply exhaustive sampling in which all the potential sites where a species may occur are surveyed within the area of interest. Such a situation is typically only possible in the case of small-scale monitoring of specialist species with narrow and well known habitat requirements (e.g. *Maculinea* butterflies; see the Case study 2). Otherwise, a small fraction of the area has to be selected for sampling, and the selection of sampling sites must be done in a way that allows inference of the results to the entire area of interest (Thompson 1992; Yoccoz et al. 2001; Pollock et al. 2002).

IV. Estimating state and trend of population size of a species with relative abundance data

Just like in the case of presence-absence (or precisely speaking detection-nondetection) data (see section III), the relative abundance data are also affected by imperfect detection. Here, however, it is the imperfect detection of individuals that matters. Great majority of the abundance estimators (reviews in Seber 1982; Lancia et al. 1994) can be expressed as count statistics divided by detection probabilities: $\hat{N} = C / \hat{p}$. Without accounting for detection probability count statistics do not provide information about actual population size, and can serve at most as relative indices of abundance. However, since detection probabilities are likely to be variable in time and/or space, these indices should not be used directly to infer trends in population sizes or their spatial patterns. The problem may be overcome through assuming a certain pattern in detection probabilities or calibrating the indices with methods that account for detection probabilities (e.g. CMR), which can be regarded as their indirect estimation with independent data. Among the case studies described in Appendix 2 the former approach has been used in the Case study 4 on common birds (where random pattern in detection probabilities among sites, years, and species is assumed) as well as the Case study 6 on orchids (where equal detection probability for ramets and genets is implicitly assumed). The latter one has been adopted in the Case study 5 on *Maculinea* butterflies.

The problem of spatial variation in abundance and its effect on representativity of sampling sites is in principle the same as in the case of presence-absence patterns (see section III).

V. Estimating state and trend of population size of a species with CMR data

In capture-mark-recapture methods (CMR; alternative names include mark-release-recapture, MRR, and capture-recapture, CRC) capture probability, which is conceptually equivalent to detection probability, is directly estimated from the data. Consequently, in survey planning it is no longer accounting for imperfect detection that poses the difficulty, but instead the efforts should be focused on ensuring that assumptions of particular CMR models are met. The most standard assumptions are those of (1) permanent marking; (2) equal capture probability; (3) spatial and demographic closure of population. The first assumption, implying that marks are not lost or overlooked in subsequent samplings, is relatively easy to meet for most organisms if proper marking techniques are used and sampling is done carefully enough. Thus its consideration is important for field methodology, but not for the statistical analysis of CMR data. The other two assumptions are more difficult to fulfil since they depend not only on the properties of the survey, but also on characteristics of populations investigated. However, advances in CMR theory (review in Schwarz & Seber 1999) made available a wide selection of models that allow relaxing these assumptions. The case studies described in Appendix 3 present applications of various CMR models for estimation of population size and other demographic parameters.

VI. Conclusions and complementary considerations

Both theoretical considerations and the case studies presented within this Deliverable have underlined the importance of imperfect detection for estimating species occurrence and abundance, regardless whether it is manifested in the form of species detection probability in the case of presence-absence data (section III), individual detection probability for count data (section IV), or individual capture probability in CMR methods (section V). In any species monitoring the recorded value is the product of the true value of a parameter (occurrence or abundance) and the corresponding detection probability: $C = N * p$ (note that this equation is just a rephrasing of the one introduced in section IV). The crucial implication of the above is that any changes in the recorded value may not necessarily reflect the true changes in the parameter that monitoring is intended to document, but instead they may be due to variation in detection probability.

The standard way of dealing with the problem of imperfect detection, and the one followed in most of the case studies, is the estimation of the detection probability so that observed values can be corrected for it to produce estimates of true parameter values. However, it is worth mentioning that there are some alternative solutions, i.e. maximising p , standardising methods so that p is hold constant, or using variables that correlate with p and are easy to measure (Caughley 1977; Seber 1982; Lancia et al. 1994). The total count in which $p = 1$ is hardly ever possible, however as long as p is close to 1 its variation remains small in relation to true parameter changes and the resulting bias can be neglected. The decisive drawback of this approach is that maximising p typically comes at a greatly increased cost of survey as it can only be achieved through an enormous intensity of field sampling, usage of expensive equipment etc. With constant p observed values become indices of occurrence or abundance. They do not provide information about the state of the parameters, which is sometimes essential, e.g. for management decision, but their use allows to assess trends in occurrence or abundance in an unbiased way. Furthermore, if the assumption of constant p is met then absolute values of the parameters can be estimated with additional data available, e.g. the

number of individuals removed from a population in change-in-ratio methods (CIR, for details see Seber 1982; Skalski & Millspaugh 2006). The use of predictor variables for p is highly context specific and therefore will not be covered in detail here. The most popular method in this class is distance-sampling (Burnham et al. 1980).

Throughout this Deliverable we focused primarily on the accuracy of species monitoring methods, but the issue of precision is equally important for survey planning. If monitoring is to fulfil its aims then its results should allow detecting trends of *a priori* defined magnitude. The Scientific Working Group of the Habitats Committee at DG Environment of the European Commission has suggested the following thresholds, among its criteria for assessing favourable conservation status of species of the Birds and Habitats Directives Annexes:

- (i) trend in range: 1% annual decline OR 5 % annual decline in favourable reference range;
- (ii) trend in population: 1% annual decline OR 10% annual decline in favourable reference population OR population structure deviating from normal.

Obviously the statistical power to detect trends of a certain magnitude strongly depends on spatial (the number of sites sampled per year) and temporal coverage (the number of years). Nevertheless, it is also a function of temporal variance of the parameters investigated, which is an exclusive property of monitored population and not of its survey (e.g. large mammal populations tend to be more stable than those of insects). Additional difficulty lies in distinguishing between real trends and cyclic fluctuations or density-dependent regulation. The issue of statistical power of monitoring schemes will be elaborated in detail within EuMon's Work Package 5.

VII. References

This section provides cited references other than references for the case studies developed in this Deliverable, which are provided in the Appendices at the beginning of each case study.

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Appendix 1. Case studies documenting state and trend of distribution of a species with presence-absence data

Case study 1. Distribution dynamics of a common bird, the magpie, in France (MNHN)

Source reference(s):	
Chiron F., Lee A. & Julliard R. (2008). Effects of landscape urbanization on magpie occupancy dynamics in France. <i>Landscape Ecology</i> , 23: 527-538	
Rationale:	
Objective(s):	The goal of this study was to quantify changes in distribution and habitat use of the black-billed magpie during the breeding period.
Biological model:	The black-billed magpie <i>Pica pica</i> is a common, medium-sized passerine bird, widely-distributed in the Western Palearctic.
Context:	In France, the black-billed magpie is expanding: it colonises new sites, mainly in urban areas, within its current distribution range. The present study aims at demonstrating and quantifying differences in distribution dynamics of the magpie among major habitat types. Two specificities of this study are using a volunteer-based, wide-range monitoring scheme addressing not only the black-billed magpie but also all common bird species in the country (i.e. Breeding Bird Survey), and adjusting parameters for distribution dynamics for spatial variations in detection probability.
Sampling design:	
Spatial coverage:	Country (France).
Temporal coverage:	5 years (2001-2005).
Season:	Spring (April - mid-June).
Sampling sites:	There are 827 2x2 km squares, based on Lambert grid (geographic projection). Random choice of square was conducted after stratification for observer presence, i.e. observers provided a locality name, and a square was randomly chosen within 10 km from this locality. There are 10 sampling points per square; points are chosen by observers, at least 300-m apart from each other to prevent double-counting, and their distribution is expected to be representative of habitat diversity in the square.

Sampling duration:	5 minutes at each sampling point.
Within-year frequency of sampling:	2 visits per year (before and after 8 May, with 4-6 weeks between counting sessions).
Among-year frequency of sampling:	All squares were sampled each year, but there are some missing data (i.e. new squares were started and some squares were quitted during the study period). On average, a square was monitored for 2.6 years.
Protocol minimizing measurement error:	Visits to points of a given square are made by the same observer, on the same date (± 7 days) and the same hour (± 15 min).
Detailed information on the sampling design can be found in the Protocol of the French Breeding Bird Survey (<i>Suivi Temporel des Oiseaux Communs EPS</i> ; http://eumon.ckff.si/monitoring/monitor_show_wp23-2.php?sid=2&mid=2).	
Data characteristics:	
Sampling technique:	Counting individuals contacted (visually or auditively) during each visit to fixed sampling points.
Data type:	Counts of individuals per visit per sampling point. To document distribution, counts of individuals were converted to presence (at least one individual) and absence (no individual) data. Information in within-year replicates of presence/absence measure (i.e. the 2 annual visits) was not used. Data were pooled per sampling point per year (i.e. if at least one individual was detected during one or two visits, the magpie was considered present; otherwise it was considered absent).
Measurement error:	The main source of measurement error expected when documenting distribution dynamics with presence/absence data is due to imperfect detection of individuals at sampling sites. When no individual was detected, it can mean that no individual was present (in this case, measurement was exact) or that individuals were present but that they were not detected by the observer (in this case, there is an error of measurement). To control for this confounding effect of detection probability, a specific statistical design must be used so that independent replicates allow estimation of detection probability. Here, the 10 sampling points per square were considered as independent (spatial) replicates of the measure of the magpie presence/absence per square.

Statistical analysis:

Parameter for annual state of distribution is square occupancy probability on year t , noted ψ_t . Parameter for measurement error (also called noise parameter) is detection probability per square, for year t , noted p_t . Three parameters characterised distribution dynamics: (i) square extinction probability from year t to year $t+1$, noted ε_t , that is the probability that an occupied square on year t becomes vacant on year $t+1$; (ii) square colonization probability from year t to year $t+1$, noted γ_t , that is the probability that an occupied square on year $t+1$, was colonised between year t and year $t+1$; and (iii) temporal rate of change in occupancy probability from year $t-1$ to year t , noted λ_{t-1} , that is the fraction of increase ($\lambda_{t-1} > 1$) or decrease ($\lambda_{t-1} < 1$) in occupancy rate. In other terms, it quantifies the temporal change in local distribution, i.e. expansion ($\lambda_{t-1} > 1$) or contraction ($\lambda_{t-1} < 1$) within the species range.

Statistical method was capture-mark-recapture modelling adapted to presence-absence data per square to model state and trend parameters while adjusting for imperfect detection. Specifically, model was adapted for a Pollock's Robust Design (Pollock 1982), i.e. with two nested time-scale sampling levels to separate the biological process of interest (presence-absence of magpies) from the noise process (imperfect detection). The primary sampling level was the year, with visits to squares to document presence/absence on each year. The secondary (nested) sampling level was spatial replicates per year: the 10 point counts per square were used as replicates of presence/absence measurement per square per year.

A constraining assumption of this approach is that, within a year, there was no change in distribution of magpies. In statistical terms, square occupancy by magpies must not change among secondary sampling points, the distribution being considered as 'closed' (if they were present, they were present at all sampling points, and if they were absent, they were absent at all sampling points on the two visits). Since magpies are territorial during the sampling period, it could be reasonably assumed that magpie occupancy did not change within years. In practices, a raw detection history for one square is presented as:

1100001000 0000000000 0001001001

where '1' denotes detection and '0' no detection. It indicates that, for this square, magpies were detected in years 1 and 3, not in year 2. And within years, they were detected at sampling points 1, 2 and 7 in year 1, and points 4, 7 and 10 in year 3.

A critical assumption when applying such models is that of parameter homogeneity. That is: detection probability is the same, within years, at all sampling points in occupied squares, and occupancy, extinction and colonisation probabilities are the same at all sampling squares per year. These assumptions are unrealistic (i.e. parameters are heterogeneous) since: (i) some sampling points are in habitats unsuitable for magpies, (ii) some squares are in geographic regions/habitats where the species tend to increase or decrease, whereas the distribution is stable in other squares.

To increase both statistical reliability of parameters estimates and biological meaning of distribution parameters, stratification of sampling squares can be taken into account when parameterising statistical models. Stratification used here is habitat type (to distinguish occupancy rate and dynamics among habitats). These habitat variables are included as explanatory variables in the statistical model to explain major sources of heterogeneity in parameter values among squares, or within squares among sampling points.

Several habitat variables were used. First, observers attributed habitat per sampling point to one of four habitat categories: farmland, semi-natural, urban and other (including wetlands and bare rock). Square level habitat was the habitat present at more than 50% of sampling points in the square. Second, trend in artificial habitat coverage was extracted from a national survey of land cover in 1992 and 2002 (named TERUTI), where the variable ‘Proportion of Artificial Land’(PAL) quantified the proportion of land covered by urban habitat and human settlements in both years. Indeed, grids for TERUTI and BBS did not match exactly, and PAL values in BBS squares were interpolated with a kriging model from PAL values in TERUTI squares. Habitat variables are not detailed here since general principles for the analysis and interpretation of results are the same whatever the habitat variables are.

Procedure for model selection was based on information criteria (AIC). The software used was MARK 4.3 (White & Burnham 1999).

Skills required:

The present field data type (point counts) requires that the observer is able to identify visually and audively the species under study. Actually, monitoring data used here were collected by volunteers. The present statistical method requires basic knowledge of database management, statistical tests (interpretation of major effects, interactions, and significance level) and model selection principles.

Results:

Detection probability varied among habitat types (Fig. 1). This illustrates the importance of accounting for spatial variation in detection probability when inferring distribution from presence-absence data. In this study case, the aim is to quantify how artificiality of habitat influences magpie occurrence. Since detection probability also varied with artificiality of habitat, the biological question was critically confounded by measurement error. Two alternative scenarios were confounded: are magpies more ‘frequent’ at artificial sites because they are more easily detected in this habitat, or because they are actually more frequent in this habitat? Using a statistical framework that allows separating distribution parameter from detection probability (e.g. as developed here) is necessary to obtain unbiased estimates of distribution parameters.

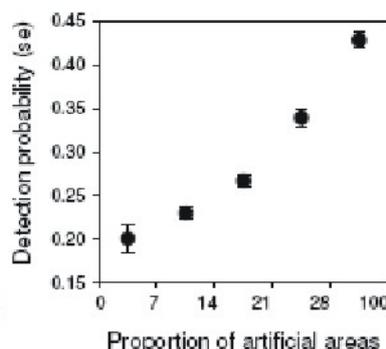


Fig. 1. Effect of human-induced habitat artificiality on the detection probability of black-billed magpie per sampling point (French Breeding Bird Survey).

Nonetheless, it should be noted that in the present case study, detection probabilities per square were high in all habitat types: $p_{\text{semi-natural}} = 0.92 \pm 0.1$, $p_{\text{farmland}} = 0.96 \pm 0.1$, and $p_{\text{human settlement}} = 1 \pm 0.2$. Therefore, naive estimates of occupancy rate were very close from an unbiased occupancy rate (difference in occupancy rate: 0.02 in semi-natural habitats, 0 in farmland, 0.05 in human settlements). Occupancy rate increases with increasing proportion of artificial areas in farmland and semi-natural habitats (that is, the interaction between the effect of proportion of artificial areas and habitat type is significant). In squares dominated by human settlements, the magpie is present in all squares. Averaged across all habitats, and during the 2001-2005 study period, occupancy probability did not change. However, it changed for some habitat types. Local extinction probability decreased with the increase of artificial habitat coverage between 1992 and 2002 (Fig. 2). Local colonisation probability depended on habitat type, and increased with the proportion of artificial areas. That is, the more artificial the habitat is and becomes, the more magpies are likely to establish, and the more this establishment is durable.

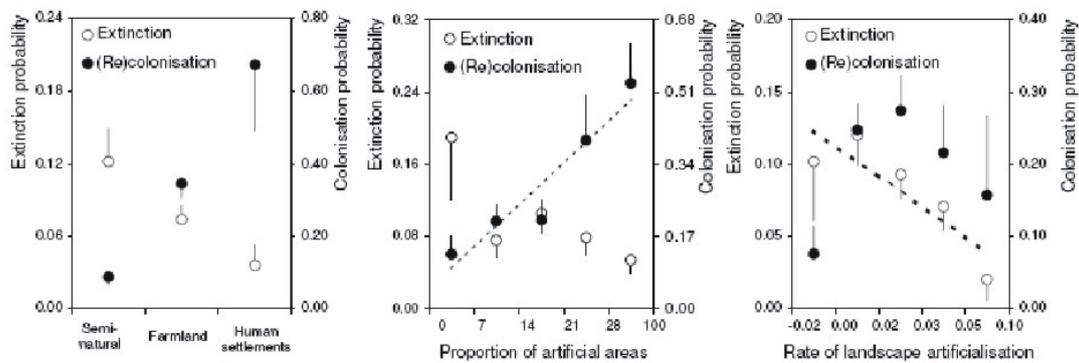


Fig. 2. Relationships between habitat type, proportion of artificial areas and rate of landscape artificialisation (between 1992 and 2002) and extinction and colonisation probabilities for the black-billed magpie at the square level (French Breeding Bird Survey).

Between 2001-2005, occupancy rate increased (i.e. net colonization; Fig. 3) in recently transformed, artificial areas, and decreased in less artificial areas and areas where artificial habitats tended to decrease. This may reflect a change in optimal habitat for the black-billed magpie, the species diminishing in rural areas, and increasing in urbanized areas.

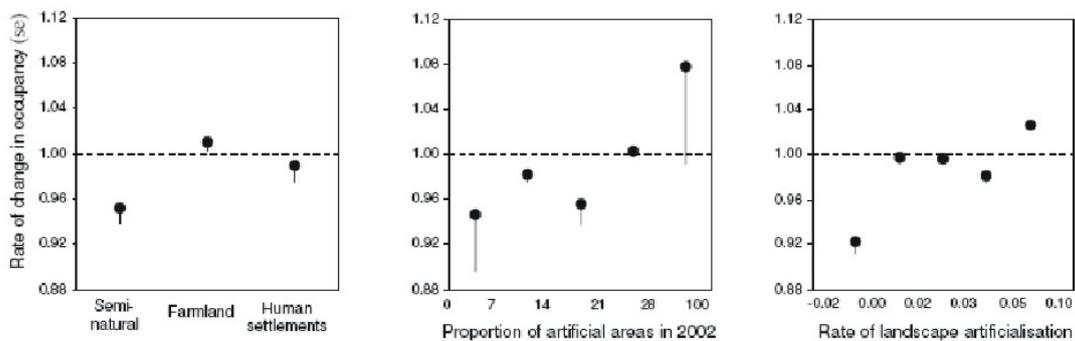


Fig. 3. Rate of change in square occupancy by the black-billed magpie in relation to habitat type, proportion of artificial areas and rate of landscape artificialisation (between 1992 and 2002; French Breeding Bird Survey).

Potential refinements and developments:

Firstly, how to obtain a distribution map from occupancy probability analysis? One method can be to use kriging interpolation methods that account for habitat-dependency of occupancy probability (named co-kriging). Raw data are the occupancy probability per sampling square and land cover layers containing information on the habitat. The interpolation process allows generating predictions of occupancy probability for squares not sampled. Output is a map of expected occupancy rate, at the geographical scale of interest, and accounts for results of occupancy probability determinants and spatial autocorrelation in occupancy.

Secondly, sampling points (within squares) could have been stratified per habitat type. In the present study case, sampling squares were attributed to habitat types according to the habitat description by observers at each sampling point. This assumes that detection probability is the same at all sampling points per habitat type. To further lower heterogeneity in detection probability among sampling points, habitat type could have been taken into account at the sampling point level instead of the sampling square level.

Thirdly, to distinguish occupancy rates and dynamics between core and margins of the species range, squares could have been stratified per geographic area. If squares are stratified as inside, at the margin, or out of the known species range, then all parameters documenting distribution dynamics (local occupancy rate, extinction probability, colonisation probability) provide a full characterisation of distribution expansion/contraction inside and outside the species range core.

Finally, in the present study, data were collected during the breeding period. Thus, only distribution dynamics of populations on breeding grounds is documented. Non-breeding dynamics may also be of interest for management purposes. A separate survey could be run with a sampling design adapted to the non-breeding period. Analysing data with the same procedure and statistical models as during the breeding season then would identify differences in distribution dynamics and habitat use between the non-breeding and the breeding period.

Case study 2. Presence-absence patterns in metapopulations of *Maculinea* butterflies (UJAG)

Source reference(s):	
<p>Nowicki P., Pepkowska A., Kudlek J., Skórka P., Witek M. & Woyciechowski M. (2005) Landscape scale research in butterfly population ecology – <i>Maculinea</i> case study. In: Settele J, Kuhn E & Thomas JA (eds) <i>Studies in the Ecology and Conservation of Butterflies in Europe</i>. Vol. 2. Pensoft Publishers, Sofia – Moscow, pp 140-143</p> <p>Nowicki P., Pepkowska A., Kudlek, J., Skórka P., Witek M., Settele J. & Woyciechowski M. (2007) From metapopulation theory to conservation recommendations: lessons from spatial occurrence and abundance patterns of <i>Maculinea</i> butterflies. <i>Biological Conservation</i>, 140: 119-129.</p>	
Rationale:	
Objective(s):	The goal of the study was to identify factors affecting presence-absence patterns of <i>Maculinea</i> butterflies.
Biological model:	Three species of the genus <i>Maculinea</i> (<i>M. alcon</i> , <i>M. nausithous</i> and <i>M. teleius</i>) are highly specialised butterflies, requiring specific foodplants and specific <i>Myrmica</i> ant hosts (myrmecophily).
Context:	Classic metapopulation theory, which has become a paradigm in large-scale butterfly studies, assumes relatively frequent population extinctions and colonisations on local habitat patches (Hanski 1994). However, one may expect <i>Maculinea</i> not to be particularly prone to exist in classic metapopulations, because of their ecological characteristics: stability of local populations and low individual mobility. In the present study it is tested how well <i>Maculinea</i> fit in the theoretical framework of classic metapopulation theory.
Sampling design:	
Spatial coverage:	Wet meadow complex covering 7 x 5 km section of the Vistula river valley, west of the city of Kraków.
Temporal coverage:	5 years (2003–planned till 2007).
Season:	Summer (late July – early September).
Sampling sites:	Exhaustive selection of all known patches of <i>Sanguisorba officinalis</i> (foodplant of <i>M. nausithous</i> and <i>M. teleius</i> ; n = 61, total area = 211 ha, range: 0.005–33 ha) and <i>Gentiana pneumonanthe</i> (foodplant of <i>M. alcon</i> ; n = 18, total area = 8 ha, range: 0.001–3 ha) that were intensively mapped in 2001–2002 with GPS.

Sampling duration:	Precisely 1 or 2 hours per patch depending on their area in the case of adult survey of <i>M. nausithous</i> and <i>M. teleius</i> and unspecified (depending on the number of eggs recorded), but roughly similar in the case of egg survey of <i>M.alcon</i> .
Within-year frequency of sampling:	2 visits per year on consecutive days in the time of peak occurrence of flying adults (<i>M. nausithous</i> and <i>M. teleius</i>) or 1 visit per year after the end of adult flight period, i.e. when all the eggs have been oviposited and their shells remain conspicuous on foodplants (<i>M.alcon</i>).
Among-year frequency of sampling:	All patches are sampled each year.
Protocol minimizing measurement error:	All the patches on which no butterflies or their eggs are detected through the standard sampling as described above are subsequently sampled again several times.
Data characteristics:	
Sampling technique:	Counting individuals captured in entomological nets (<i>M. nausithous</i> and <i>M. teleius</i>) or eggs recorded (<i>M.alcon</i>) along 2-m wide transects on larger patches (>0.25 ha) or on entire area of smaller ones.
Data type:	Capture frequencies, i.e. numbers of individuals captured per time unit (<i>M. nausithous</i> and <i>M. teleius</i>) or egg densities, i.e. their numbers per sampled area (<i>M.alcon</i>). To document distribution, counts were converted to presence (at least one individual) and absence (no individual) data.
Measurement error:	Since there were very few patches on which the species investigated were not recorded within the standard sampling and, what is more important, on none (!) of such patches the species were found during the subsequent repeated sampling, it is believed that detection rate in the study has reached 1, and thus the detection-non-detection data collected in fact represent true presence-absence.
Statistical analysis:	
Using GIS software ArcView 3.2 and Idrisi 2.0 values of several environmental and spatial parameters were derived for all the foodplant patches and used as predictors in models of occupancy of the three <i>Maculinea</i> species. These predictor parameters included foodplant abundance, vegetation height, moving regime, distance from buildings (measure of potential anthropogenic pressure) as well as patch area, connectivity and indices of internal fragmentation (edge proportion and patch compactness). The effect of habitat parameters on presence-absence patterns of the three <i>Maculinea</i> species were tested with multiple logistic regression models, applying forward stepwise variable selection procedure. With a clear deficit of permanently unoccupied patches, those on which a given species was absent in at least one of the first two years of the study were treated as zeros.	

Skills required:

It is required that the observer is able to identify visually all three species investigated, which can be easily learned within less than one hour as successfully tested on volunteers with absolutely no previous experience in recognising butterflies. The analysis requires basic knowledge of statistical testing.

Results:

Occupancy rates were very high (consistently > 75%) for all three species investigated. For *M. nausithous* and *M. teleius* the occupancy was almost complete and no patches remained permanently unoccupied, which is atypical for classic metapopulations. For the above reason only few colonisations of patches unoccupied in the previous year could have been observed, and local population extinctions were similarly infrequent. Interestingly, no such events were noted for *M.alcon* despite the highest potential chances of occurring, which implies that populations of this species are particularly stable. The only factor significantly affecting the occurrence of *M. teleius* was foodplant patch area, with the few patches temporarily lacking the species being all extremely small (< 0.1 ha). For *M. nausithous* and *M.alcon* additional significant effect of patch connectivity was detected; in both cases smaller and more isolated patches had lower probability of occupancy. The pattern that such patches are more likely to experience population extinctions as well as less likely to become colonised is explicitly assumed in the classic metapopulation theory.

Potential refinements and developments:

The above results have been based on the first two years of the study and all the unoccupied patches have been treated as a single class. With much more data gathered after the end of the study it should be possible to distinguish between patches temporarily unoccupied due to decreased likelihood of colonisation – the effect of patch isolation is expected here, and those that suffer from increased rate of population extinctions as an effect of small patch area.

Case study 3. Distribution of orchids in Britain and Estonia (ESTAGUN)

Source reference(s):	
Kull T. & Hutchings M. (2006) A comparative analysis of decline in the distribution ranges of orchid species in Estonia and the United Kingdom. <i>Biological Conservation</i> , 129, 31-39	
Rationale:	
Objective(s):	The goal of the present study was to conduct a comparative analysis of decline in the distribution ranges of species of orchids for two European regions, namely the United Kingdom in western Europe, and Estonia in NE Europe.
Biological model:	Orchids are among the best monitored plants in many countries due to the activity of many volunteers taking an interest in these plants. With complicated life-history, different traits could influence the distribution decline. To determine whether the extent to which the ranges had altered depended on the environmental preferences of different species, Ellenberg indicator values were tabulated for as many of the species as possible.
Context:	The availability of detailed records of changes in the distribution of species over time (results of mapping programs) provides opportunities for comparative analyses of declines in ranges both within and between ecological and taxonomic groupings, and between geographical areas.
Sampling design:	
Spatial coverage:	Country (Estonia and the United Kingdom).
Temporal coverage:	1921-2004.
Sampling sites:	In both countries the presence of orchid species has been recorded on maps in grid squares corresponding to 100 km ² . Decline for each species in each country was measured as the change in the number of grid squares occupied in the national plant atlas databases between the two survey periods (1930–1969 and 1987–1999 in the UK; 1921–1970 and 1971–2004 in Estonia).
Data characteristics:	
Sampling technique:	Detecting presence/absence of a species in a grid square.
Data type:	Species recorded or not recorded in a square in a certain time period.
Measurement error:	The main sources of measurement error could be the insufficient knowledge of species, misidentification, or underestimation of possible localities inside the square visited.

Statistical analysis:

The following Ellenberg indicator variables were used:

- (i) light preference, ranging from 1 (tolerant of full shade) to 9 (found in completely unshaded conditions);
- (ii) temperature, ranging from 1 (cold-tolerant) to 9 (tolerant of extremely warm conditions);
- (iii) continentality, ranging from 1 (euoceanic) to 9 (eucontinental);
- (iv) soil wetness, ranging from 1 (tolerant of very dry soils) to 12 (plants growing beneath water);
- (v) soil reaction, ranging from 1 (highly acidic) to 9 (highly calcareous);
- (vi) nitrogen demand, ranging from 1 (soils extremely nitrogen-deficient) to 9 (soils extremely rich in nitrogen).

In addition, the species were categorized according to the habitat type in which they occur most commonly: woodlands (w), calcareous grassland (c) or wet grassland (wg). Flora Europaea (<http://rbg-web2.rbge.org.uk/FE/fe.html>) was used to categorise species for the following biotic variables: mean height of inflorescence (species were categorised as short (<30 cm) or tall (>30 cm)), and type of underground organ (rhizomes or tubers). Information from the literature was used to categorise species as either clonal or non-clonal, and both published and unpublished estimates of life span were used to classify species as either short-lived (defined as those in which genet half-life is <3 years) or long-lived (those in which genet half-life is >3 years).

Statistical analysis to determine the influence of different parameters on species decline was carried out using the SAS GLM procedure. The decline was estimated as the relation between the number of occupied squares in the first and the second period. It means that number recorded in the first period was adopted as the independent variable, whereas the number in the second period was treated as the dependent variable. The effect of covariates was studied using interactions with the number at the first period. Factors were tested via stepwise selection. The numbers of occupied squares in these countries were clearly different and therefore centred values for both periods (i.e. the differences between the actual number of occupied squares for each species, and the mean number for all species in the same country) were used in the analysis of the shared data (see Results).

Skills required:

The present field data type requires that the observer is able to identify the species. The present statistical method requires basic knowledge of database management and statistical tests.

Results:

Declines in the ranges of orchid species in UK and Estonia were significantly different. In the UK, there was a mean (\pm SD) decline of $49.7 \pm 22.0\%$ (range 14 – 100%) in the range of all orchid species over the 30-year period between the ends of the two survey periods.

Table 2. Analysis of parameters having significant impact on decline in range of orchid species in the UK, in Estonia, and in both countries together. The dependent variable was the number of grid cells occupied by species at the second survey. Start – number of grid cells in the first time period; c calcareous grassland; w – forest; wg – wet grassland and mires.

Parameter	Estimate	Standard error	<i>t</i> -value	<i>P</i>
UK				
Intercept	-29.68	16.29	-1.82	0.078
Start	0.899	0.129	6.94	<0.001
Start*Habitat c vs w	0.028	0.046	0.60	0.552
Start*Habitat c vs wg	-0.175	0.060	-2.93	0.006
Start*Habitat w vs wg	-0.203	0.057	-3.54	0.001
Start*life-span (long)	0.174	0.046	3.78	0.001
Start*plant height (short)	-0.206	0.057	-3.63	0.001
Start*soil wetness	-0.036	0.015	-2.37	0.024
Estonia				
Intercept	-5.509	2.740	-2.01	0.056
Start	0.610	0.079	7.70	<0.001
Start*Habitat c vs w	-0.063	0.039	-1.64	0.114
Start*Habitat c vs wg	0.148	0.037	3.95	0.001
Start*Habitat w vs wg	0.211	0.034	6.11	<0.001
Start*life-span (long)	-0.121	0.030	-3.99	0.001
Start*light	0.033	0.010	3.45	0.002
Both countries together				
Intercept	-14.36	9.319	-1.54	0.131
Start*Habitat c vs w	-0.048	0.075	-0.65	0.521
Start*Habitat c vs wg	-0.291	0.063	-4.64	<0.001
Start*Habitat w vs wg	-0.243	0.074	-3.26	0.002
Start*life-span (long)	0.227	0.057	3.98	<0.001
Start*soil pH	0.044	0.016	2.69	0.010
Start*soil fertility (N demand)	0.039	0.019	2.07	0.045

In comparison, the mean decline in the distribution of orchid species in Estonia over the 34-years between the ends of the two survey periods was $25.0 \pm 16.0\%$. Percentage decline in the range of rarer species was more variable, and in many cases larger. Percentage decline in the thirty species common to both the UK and Estonia was significantly correlated ($r = 0.46$, $P = 0.01$) (Fig. 4).

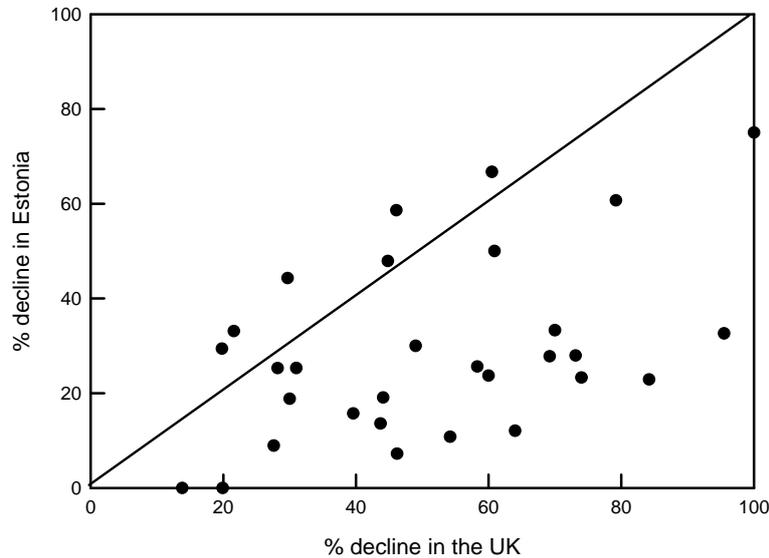


Fig. 4. A comparison of the percentage change in distribution range of the thirty species of orchid common to the UK and Estonia. The diagonal line indicates equal percentage change in distribution range in the two countries. Points above and below the line indicate more decline in Estonia and in the UK respectively.

Parameters that were significantly correlated with species decline were habitat, and species life-span. On average, species of wet grasslands declined by little more than half as much as species characteristic of calcareous grassland and woodland (Table 2). Short-lived species declined more than long-lived ones.

Potential refinements and developments:

Mapping projects are time and effort consuming. However, the shorter is the time period during which we get data on distribution of a number of species, the better are the possibilities to analyse them. Thus, the mapping projects should store the data in a way that would enable to analyse them using different time periods, and as a result to provide conclusions about the dynamics of the monitored species. Concerning spatial scale grid squares could be smaller than 10x10 km to enable better correlation between species distribution and habitat changes. Alternatively, one can use the smaller grids in addition to the larger ones.

Appendix 2. Case studies documenting state and trend of population size of a species with relative abundance data

Case study 4. Trends of common birds in France (MNHN)

Source reference(s):	
Julliard R., Jiguet F. & Couvet D. (2004) Common birds facing global changes: what makes a species at risk? <i>Global Change Biology</i> , 10, 148-154	
Rationale:	
Objective(s):	The goal of this study was to quantify temporal trends in relative abundance for a large set of common birds, at a national scale, and to test if some species characteristics could explain inter-specific differences in trends.
Biological model:	National population growth rate is derived from standardized counts of individuals for the 77 most detected and/or captured bird species in France, mostly passerine. The full list of monitored species can be found at http://www.mnhn.fr/mnhn/crbpo/r%E9sultats_etat_populations.htm#resultat , or in schemes' description in the DaEuMon survey.
Context:	<p>Biodiversity is affected by climate change and human-induced modifications of natural ecosystems. These general, widely accepted results come from independent, repeated analyses of monitoring datasets. The present study is one of those studies that quantify decline in relative abundance for common animal species, and that link species trends to putative global change mechanisms through correlations between species characteristics and trends.</p> <p>In practice, this study is composed of two analytical parts: (1) estimation of annual population growth rates per species from standardized counts of individuals (monitoring data) and (2) testing if variations in estimated growth rates can be explained by inter-specific differences. Candidate variables to explain these differences across species are latitudinal distribution, habitat specialisation, hunting status, migrating strategy, and body mass.</p> <p>The present study is also a good illustration of how data from rather different schemes and sampling techniques can be combined into a single analysis (relevant for illustrating purposes in Deliverables 16 and 18). Indeed, the number of individuals counted at French Breeding Bird Survey (FBBS) plots and captured at French Constant Effort (Bird Ringing) Sites (FCES) were analysed in a single statistical model, thus producing a national estimate of population growth rate per species, averaged over sites and sampling techniques. Both data type could be combined since, for both methods, the unit of count is the number of individuals of a given species at a given site in a given year.</p>

Sampling design:	
This study uses the data from two different schemes of bird relative abundance monitoring (FBBS and FCES). Note that, although FBBS is the same scheme as the one presented for the distribution dynamics of the black-billed magpie (Appendix 1, Case study 1), the sampling design presented here is slightly different. FBBS protocol changed in 2001, and data analysed here come from the original sampling design applied before 2001, i.e. before the randomisation of the selection of monitoring sites.	
Spatial coverage:	Country (France).
Temporal coverage:	12 years (1989-2001).
Season:	FBBS: April to mid-June; FCES: mid-May to mid-July.
Sampling sites:	<p>No sampling design was applied for the choice of sites to be monitored, i.e. locations of groups of count points (i.e. FBBS sites) or ringing stations (i.e. FCES), were freely chosen by observers. Thus, there is no formal measure taken to secure that sampling sites are representative at a national scale (see e.g. Link & Sauer 1998 for a similar practice).</p> <p>There were 134 groups of 10-15 fixed FBBS sampling points, at least 200-m apart from each other to prevent double-counting as well as 53 ringing FCES stations, with 12-50 12-m mist-nets each, with density of 3-4 mist-nets/ha. Captured birds were marked with an individually numbered ring, thus preventing double-counting.</p>
Sampling duration:	FBBS: 5 minutes at each FBBS sampling point; FCES: half a day to one day for ringing stations (duration is constant across years for a given site).
Within-year frequency of sampling:	FBBS: 1 visit per year; FCES: 3-5 sessions per year.
Among-year frequency of sampling:	All squares were sampled each year, but there are some missing data (i.e. new squares were started and some squares were quitted during the study period). On average, groups of count points (FBBS) were monitored over 6 years, and FCES ringing stations over 5 years.
Protocol minimizing measurement error:	In the case of FBBS visits to a given group of point counts were made by the same observer, on the same date (± 7 days) and the same hour of the day (± 15 min) each year. In the case of FCES mist-net numbers and locations, number, date, and duration of capture sessions were fixed within ringing stations.

Data characteristics:	
Sampling technique:	<p>FBBS: counting individuals contacted (visually or audiotively) during each visit to fixed sampling points.</p> <p>FCES: counting adult individuals captured per capture session at a ringing site per species.</p>
Data type:	<p>FBBS: counts of individuals per group of count points (i.e. site) per year per species.</p> <p>FCES: count of adult individuals captured per ringing station (i.e. site) per year per species.</p> <p>Information on within-year replicates of numbers of individuals captured (i.e. 3 to 5 annual capture sessions) was not used. Data were summed per permanent plot (i.e. local set of count points or ringing station) per year.</p>
Measurement error:	<p>Both counts of individuals by visual/auditive contacts and by capture are biased by imperfect detection, i.e. only a fraction of individuals present during the study period are contacted/captured. However, this source of measurement error was not accounted for in the analysis, assuming that variations in detection probability across sites, years, and species was random, thus just lowering the precision of our results without inducing any bias.</p>
Statistical analysis:	
<p>Parameter for state of population size is the number of individuals counted per year. Since not all individuals present per year are detected or captured (i.e. detection probability < 1 and capture probability < 1), and since detection/capture probabilities are much influenced by site characteristics (such as observer characteristics, habitat structure, date, etc.), raw values cannot be used as measures of actual population size. Indeed, analyses such as the one presented here do not provide any estimate of actual population size (but see discussion hereafter).</p> <p>Parameter for trend in population size is the growth rate of number of contacted individuals. If one can assume that site specificities influencing detection probability are constant through time, then after accounting for site effects in the statistical analysis, the slope for the linear effect of year (taken as continuous numerical value) directly estimates instantaneous growth rate of number of contacted individuals per species, averaged over sites and years.</p> <p>The first step of the analysis is estimating the average population growth rate per species. A log-linear model (also named Poisson regression model) is used, with count of individuals per year per site as dependent variable (assumed to follow a Poisson's distribution), a log-link function, and the additive effects of site (qualitative variable) and year (quantitative, linear variable) as independent variables (see section 5 of Deliverable 2 for a general discussion of this method). Given the log-link function, the estimate of the slope for the linear effect of year is actually the estimate of the instantaneous growth rate of the number of contacts/captures.</p>	

The second step of the analysis is testing for species characteristics that discriminate differences in population size trend among species. Estimates of instantaneous growth rate per species are supposed to be normally distributed. Thus, they can be analysed by classical ANOVA model, where instantaneous growth rate per species is the dependent variable, and different species characteristics are tested as potential explaining variables. Each variable was tested alone (Type I error) or in presence of the other variables (Type III error). These species characteristics were defined *a priori* and based on results of independent studies on the major determinants of population growth rate (references in the original article). Five characteristics were tested: (i) hunting status (i.e. categorical variable, hunted or not); (ii) migratory status (i.e. categorical variable, long-distance migrant, short- distance or partial migrant, and sedentary); (iii) average latitude of the French breeding distribution; (iv) body mass; and (v) an index of habitat specialization, i.e. the coefficient of variation of the number of individuals counted in the different habitat types. Habitat types were defined *a priori*. Observers had to attribute each sampling point to one of the five following habitat categories: forest, scrub, marshland, farmland and human settlement (see Julliard et al. 2006 for a recent development of this habitat specialization concept).

Precision of estimates of instantaneous growth rate are likely to vary across species. Precision depends on the number of counts per species (i.e. sample size), thus the less common the species, the less precise the estimate. A solution is to weigh species estimates by the inverse of their standard error in the analysis (i.e. weighed ANOVA). Also, inter-annual variations in abundance can vary greatly among species. The higher these erratic, inter-annual variations, the lower the reliability of the average growth rate, which is estimated by assuming a constant, linear temporal trend during the whole study period. To account for significant residual temporal variation beyond the trend, standard errors of growth rate estimates were multiplied by an inflation factor, and then were used to compute weights for the weighed ANOVA.

Skills required:

The present field data types require that the observer is able to identify visually and auditively the species under study (FBBS) or that he/she has the appropriate technical training for implementing ringing studies (FCES). Actually, monitoring data used here were collected by volunteers. The present statistical method requires basic knowledge of statistical tests (interpretation of major effects, interactions, and significance levels). Log-linear and ANOVA models can be built with any statistical analysis package. The TRIM software has been specifically developed for implementing log-linear regression analysis of monitoring data to estimate trends in relative abundance indices (Pannekoek & van Strien 2001).

Results:

Estimates and results presented hereafter rely on 260,000 birds counted and 42,000 birds ringed. On average, common French birds decreased in abundance by 1.3% per year (average slope: -0.013 ± 0.001), that is a 14% decline between 1989 and 2001. This approach also revealed that the collared dove *Streptopelia decaocto*, a species expanding throughout Europe since the 1950s, is still increasing in France, with an annual growth rate of $+0.077 \pm 0.007$. Updated estimates of growth rate per common bird species in France can be downloaded at http://www.mnhn.fr/mnhn/crbpo/r%E9sultats_etat_populations.htm.

Two species characteristics significantly explained among-species variations in annual growth rate: latitudinal distribution (Fig. 5) and habitat specialization (Fig. 6). These effects are interpreted as correlative evidences of the impact of climate change – the more northern is the distribution, the stronger the decline (see also Jiguet et al. 2006), and habitat change – the more specialized the species, the stronger its decline (see also Jullard et al. 2006) on population size trends of common bird species.

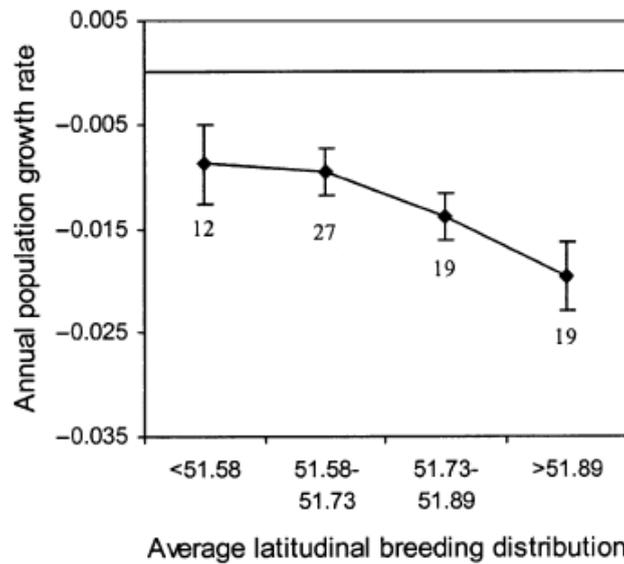


Fig. 5. The effect of average latitudinal breeding distribution of common birds on their population decline (i.e. negative annual growth rate). Data from the French Breeding Bird Survey and the French Constant Effort (Bird Ringing) Sites for 77 species, during the period 1989-2001. Numbers below the curve indicate the number of species per class.

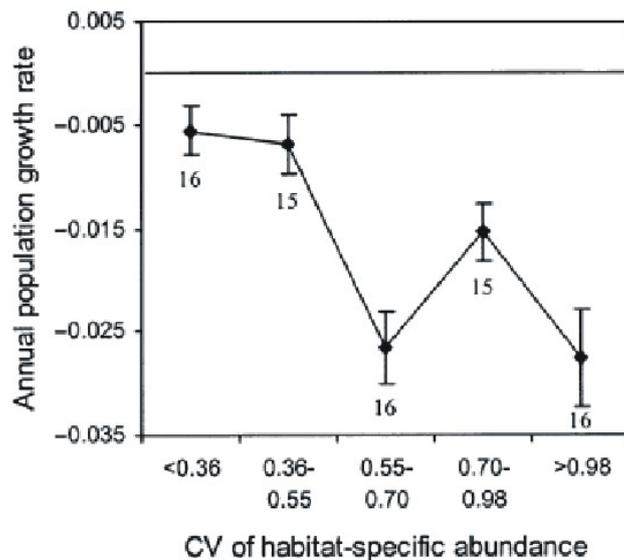


Fig. 6. The effect of habitat specialization of common birds on their population decline (i.e. negative annual growth rate). Index for habitat specialization per species is the coefficient of variation of the number of individuals counted in the different habitats (5 categories). Numbers below the curve indicate the number of species per class.

Potential refinements and developments:

By accounting for measurement error, the relative abundance index can be transformed into population size estimates. As justified in the previous part 'Data type and statistical unit', the number of individuals counted (FBBS) or captured (FCES) is an index of relative abundance. If one needs estimates of actual population size, these indices of relative abundance need to be adjusted for detection (FBBS) or capture (FCES) probability, i.e. the major sources of measurement error. Methods for adjusting for detection probability are reviewed, e.g., in Thompson (2002), Bart et al. (2004), Kissling & Garton (2006), and methods for adjusting for capture probability are reviewed in, e.g., Pollock et al. (2002) and Amstrup et al. (2005).

How to account for spatial variations in trend? As stressed in Deliverable 2, a common problem when drawing general conclusions on state and trends at a national or international scale is how to account for trend variations in space? To test for spatial variation, it corresponds to grouping sampling sites per habitats or per regions and testing for an interaction between the linear effect of year and the effect of sites groups. If the interaction is significant, then growth rate is different across regions or habitats. In this case, the average of growth rate should be computed after post-stratifying data according to region area or habitat coverage (or other weights according to monitoring goals and design; cf. discussion of weights and post-stratification in Deliverable 16) so that the global estimate can be considered as representative at a national scale.

Case study 5. Abundance patterns in metapopulations of *Maculinea* butterflies (UJAG)

Source reference(s):	
<p>Nowicki P., Pepkowska A., Kudlek J., Skórka P., Witek M. & Woyciechowski M. (2005) Landscape scale research in butterfly population ecology – <i>Maculinea</i> case study. In: Settele J, Kuhn E & Thomas JA (eds) <i>Studies in the Ecology and Conservation of Butterflies in Europe</i>. Vol. 2. Pensoft Publishers, Sofia – Moscow, pp 140-143</p> <p>Nowicki P., Pepkowska A., Kudlek, J., Skórka P., Witek M., Settele J. & Woyciechowski M. (2007) From metapopulation theory to conservation recommendations: lessons from spatial occurrence and abundance patterns of <i>Maculinea</i> butterflies. <i>Biological Conservation</i>, 140: 119-129.</p>	
Rationale:	
Objective(s):	The goal of the study was to investigate abundance patterns of <i>Maculinea</i> butterflies in relation to the characteristics of their foodplant patches.
Biological model:	Three species of the genus <i>Maculinea</i> (<i>M.alcon</i> , <i>M.nausithous</i> and <i>M.teleius</i>) are highly specialised butterflies, requiring specific foodplants and specific <i>Myrmica</i> ant hosts (myrmecophily).
Context:	<i>Maculinea</i> butterflies are endangered in many regions of Europe due to habitat loss and fragmentation. However, in the Kraków region, southern Poland, the three species live sympatrically in large to very large metapopulations. The study focused on assessing the relative importance of factors reflecting habitat quality of <i>Maculinea</i> foodplant patches as well as spatial characteristics of these patches for local population densities.
Sampling design:	
Spatial coverage:	Wet meadow complex covering 7 x 5 km section of the Vistula river valley, west of the city of Kraków.
Temporal coverage:	5 years (2003–planned till 2007).
Season:	Summer (late July – early September).
Sampling sites:	Exhaustive selection of all known patches of <i>Sanguisorba officinalis</i> (foodplant of <i>M.nausithous</i> and <i>M.teleius</i> ; n = 61, total area = 211 ha, range: 0.005–33 ha) and <i>Gentiana pneumonanthe</i> (foodplant of <i>M.alcon</i> ; n = 18, total area = 8 ha, range: 0.001–3 ha) that were intensively mapped in 2001–2002 with GPS.
Sampling duration:	Precisely 1 or 2 hours per patch depending on their area in the case of adult survey of <i>M.nausithous</i> and <i>M.teleius</i> and unspecified (depending on the number of eggs recorded), but roughly similar in the case of egg survey of <i>M.alcon</i> .

Within-year frequency of sampling:	2 visits per year on consecutive days in the time of peak occurrence of flying adults (<i>M. nausithous</i> and <i>M. teleius</i>) or 1 visit per year after the end of adult flight period, i.e. when all the eggs have been oviposited and their shells remain conspicuous on foodplants (<i>M. alcon</i>).
Among-year frequency of sampling:	All patches are sampled each year.
Protocol minimizing measurement error:	<p><i>M. nausithous</i> and <i>M. teleius</i> adult sampling has been conducted in fine weather ($> 20^{\circ}$ C, sunny) in which butterfly activity, and thus their catchability, is little affected by ambient conditions. Time of day, tested in four 2-hour periods between 9:00 and 17:00, had no significant effect on capture frequencies (ANOVA: $F_{3,216} = 1.35$, $P = 0.2594$). Participants of the survey ($n = 13$) were selected from among people with medium capture efficiency and did not differ significantly in this respect (ANOVA: $F_{12,89} = 0.92$, $P = 0.5350$ in 2003; $F_{12,25} = 1.11$, $P = 0.3931$ in 2004).</p> <p>In the case of <i>M. alcon</i> detectability of its eggs is believed to be (almost) perfect as suggested by earlier studies; the eggs are white and relatively large, and thus quite conspicuous on <i>Gentiana pneumonanthe</i>. The detectability of gentian plants is also very high, consistently well above 95% as tested by double observer method.</p>
Data characteristics:	
Sampling technique:	Counting individuals captured in entomological nets (<i>M. nausithous</i> and <i>M. teleius</i>) or eggs recorded (<i>M. alcon</i>) along 2-m wide transects on larger patches (> 0.25 ha) or on entire area of smaller ones.
Data type:	Capture frequencies, i.e. numbers of individuals captured per time unit (<i>M. nausithous</i> and <i>M. teleius</i>) or egg densities, i.e. their numbers per sampled area (<i>M. alcon</i>). To document abundance the data were converted to densities, based on the linear relationship between butterfly densities and their capture frequencies ($R^2 = 0.61$) tested and parameterised on patches intensively investigated with CMR method (cf. Appendix 3, Case study 8) or average fecundity, i.e. number of eggs oviposited per average female ($\bar{x} = 150$, the variation is unknown but apparently low).
Measurement error:	There are two main sources of measurement error in the present study. The first comprises temporal variation in capture frequencies of <i>M. nausithous</i> and <i>M. teleius</i> on any given patch as well as spatial variation in densities of <i>M. alcon</i> eggs. The former is rather low as proved by the fact that capture frequencies recorded in the two consecutive days were highly concordant. Spatial variation of <i>M. alcon</i> egg densities is higher due to their clumped distribution, however increasing sample size to >10 basic sampling units (10-m long transect sections) enabled to reduce measurement error to $< 30\%$. In the case of total count of eggs on entire patches this source of error did not exist. The second source of variation is the conversion of relative abundance data to densities as explained above, the precision of which is not 100%.

Statistical analysis:

Prior to proper analyses of the early data (2003–2004) it was necessary to check for possible spatial autocorrelations between local populations of the three *Maculinea* species with Mantel tests (Mantel 1967) and analysis of semivariograms (Johnston 1998). Testing was carried out for spatial autocorrelations in local population densities, calculated as average values for the two years of the study ($D_i = \text{avg.}\{D_{it}, D_{it+1}\}$), as well as in their relative year-to-year changes (D_{it+1}/D_{it}); only populations present in both years were included. Since neither method provided any evidence for any spatial autocorrelations (Mantel test r always well below 0.10) all the local populations were treated as independent demographic units in the subsequent analysis.

The effect of habitat parameters (see statistical analysis in Appendix 1, Case study 2) on local densities of the three *Maculinea* species were tested with multiple linear regression models, applying forward stepwise variable selection procedure. *Maculinea* densities and several predictor parameters were logarithmically transformed in order to achieve normal distributions.

Skills required:

It is required that the observer is able to identify visually all three species investigated, which can be easily learned within less than one hour as successfully tested on volunteers with absolutely no previous experience in recognising butterflies. The analysis requires basic knowledge of statistical testing.

Results:

The overall metapopulation size of *M. teleius* was estimated at almost 150 thousand individuals in 2003, decreasing by about one third in 2004 (Fig. 7). In the case of *M. nausithous* and *M. alcon* there was only small year-to-year difference in metapopulation size estimates, which remained at the level of ca. 50 thousand individuals and slightly over 500 individuals respectively.

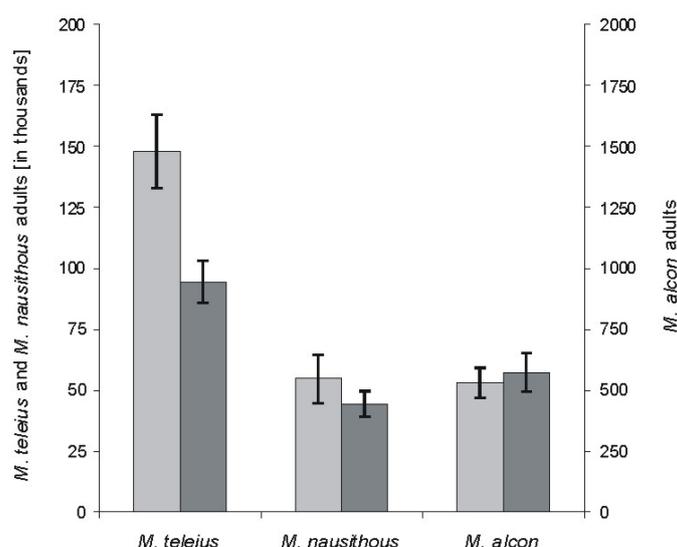


Fig. 7. Metapopulation sizes ($\hat{N} \pm \text{SE}$) of three *Maculinea* species in the Kraków region in 2003 (light bars) and 2004 (dark bars).

Population densities of *M. teleius* and *M. nausithous* were strongly negatively affected by patch area. Secondary, but still significant, positive effects of internal patch fragmentation were found for both species. Patch area and its fragmentation appeared to have together relatively good predictive power ($R^2 = 0.54$ and $R^2 = 0.79$ respectively). *M. alcon* densities predominantly depended on *G. pneumonanthe* foodplant abundance; however a positive effect of internal patch fragmentation could also be traced ($R^2 = 0.55$).

The maximum year-to-year increase in population density, assumed to be a good approximation of basic reproductive rate R_0 , was 4.3 for *M. teleius* as well as *M. nausithous*, and 3.0 for *M. alcon*. Analysing observed relative year-to-year changes against initial densities suggested the existence of density dependence of population trends, at least in the case of the two former species (Fig. 8). In the case of *M. alcon* the procedure was not attempted due to inadequate sample size and the fact that year-to-year changes in population density of this species were very small, often within the confidence limits of yearly estimates.

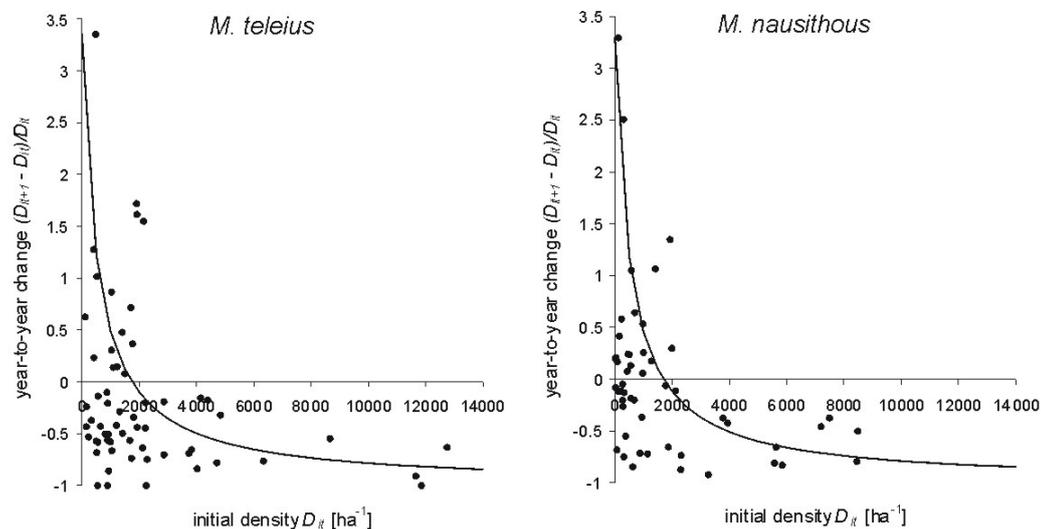


Fig. 8. Relative changes in *Maculinea* population densities between 2003 and 2004 in relation to densities recorded in 2003. The curve fitted was $D_{it+1} = rxD_{it} / (x + rD_{it})$, where D_{it} is population density on patch i in 2003, and D_{it+1} is its density in 2004. For *M. teleius*: $r = 4.35$, $x = 2271$ ($R^2 = 0.22$); for *M. nausithous*: $r = 4.30$, $x = 2212$ ($R^2 = 0.38$).

Potential refinements and developments:

After the end of the study, when five-year time series will become available, the magnitude of effects of density dependence and environmental variation (e.g. weather patterns) on local population trends will be evaluated. Apart from this, it will be tested whether smaller populations experience greater annual fluctuations of their size as it can be expected theoretically.

Case study 6. Populations of the *Cypripedium calceolus* orchid in Estonia (ESTAGUN)

Source reference(s):	
Kull T. (1995) Genet and ramet dynamics of <i>Cypripedium calceolus</i> in different habitats. <i>Abstracta Botanica</i> , 19, 95-104	
Rationale:	
Objective(s):	The aim was to estimate the relative importance of ramet and genet dynamics for population performance of <i>Cypripedium calceolus</i> using permanent plot monitoring data.
Biological model:	The dynamics of the population size within an area of a clonal plant such as <i>C. calceolus</i> could be a result of different processes. Population changes include changes in the numbers of genets (generative reproduction and death of clones) and changes in the sizes of genets (vegetative reproduction and death of ramets).
Context:	Monitoring data for <i>C. calceolus</i> , a flagship species of biodiversity conservation and a Natura 2000 species, exist in several European countries.
Sampling design:	
Spatial coverage:	Country (Estonia).
Temporal coverage:	1978-1994.
Season:	Spring (May - mid-June).
Sampling sites:	The five populations monitored were located in different plant communities in western and central Estonia. In each population, all clones on a fixed permanent plot were mapped and the number of ramets of each clone was counted every year. Plot size differed in different populations due to the spatial pattern.
Within-year frequency of sampling:	One visit per year.
Among-year frequency of sampling:	All squares were sampled each year.
Data characteristics:	
Sampling technique:	Counting clones and shoots on permanent plots.
Data type:	Counts of ramets and genets per visit per sampling point.

Statistical analysis:

The number of ramets of a clone was chosen as the size variable for the projection matrix analysis of the population dynamics. The following size classes were used: 0 = no ramets, 1 = 1-2 ramets, 2 = 3-5 ramets, 3 = 6-10 ramets, 4 = 11-15 ramets, 5 = over 16 ramets in the clone. Size rather than age has often been used in this type of investigations. The standard projection matrix model was used; this summarizes the transition probabilities from one size class to another in time steps equal to one year. The model used has the following form in the matrix notation:

$$n(t+1) = A * n(t) ,$$

where $n(t)$ is a column vector describing the clonal size structure of the population at time t , and A is a square matrix of the associated transition frequencies.

The transition matrices were built for three different models :

Model 1 assumes that new ramets may arise only vegetatively, and all clones that disappear are considered to be dormant. Accordingly, dormancy may last for a long time. Consequently the number of clones (dormant plus growing) is constant. The sum of elements in each column of the transition matrix is equal to 1.

Model 2 assumes that new ramets may arise only vegetatively, but that dormancy may last one season at most. In contrast to Model 1, the transition 0-0 has the zero value, and the other elements of the first column have normalized values to give the sum equal to 1. All other elements in the matrix are equal to those of Model 1.

Model 3 assumes that clones may disappear and appear, without distinguishing between growth from seed and growth from dormant rhizome. In contrast to Models 1 and 2, the transition matrices omit the first (0) row and the first (0) column. Therefore, column sums may become smaller than 1. The appearance of new clones (the information about this was contained in the 0-column) is described by adding the frequencies of appearance to the corresponding diagonal elements of the transition matrix.

There was not enough data to build a model which could consider both death and dormancy of the clones as different states.

The mean matrices for each population, computed over all the years of the study, were used. The annual matrices were not used because of the low number of clones in the populations.

For technical reasons, the transition frequencies equal to zero were replaced by the value 0.01. It enables one to get values in the transition matrix for the columns where all values were initially zero (e.g., the right columns of the transition matrices for swamp forest and wooded meadow site). The influence of this technical detail on the calculated matrix parameters and other results is negligible.

Eigenvectors and eigenvalues were calculated for the mean matrices.

The sensitivity (s_{ij}) and elasticity (e_{ij}) coefficients were calculated according to the formula:

$$s_{ij} = v_i w_j / \langle w, v \rangle ,$$

where v and w are respectively the left and right eigenvectors of the matrix A and $\langle w, v \rangle$ is their scalar product, and:

$$e_{ij} = a_{ij} / \lambda * s_{ij} ,$$

where a_{ij} is an element of matrix A and λ is its dominant eigenvalue.

Population growth rate (λ) was also calculated from the data of the first and the last year of the population monitoring, assuming that populations are in equilibrium. In that case:

$$n(t+1) = \lambda * n(t) ,$$

where $n(t)$ is population size in the year t . From the above equation we get:

$$\lambda^k = n(t+k) / n(t) ,$$

where k is the length of the period (expressed in years).

Skills required:

The present field data type requires that the observer is able to identify the species.

The present statistical method requires basic knowledge of statistical analysis.

Results:

The population structures according to genet size are considerably different between the studied populations, the wooded meadow population being one extreme with the highest proportion of small clones and the spruce forest population being the other extreme with the highest proportion of large clones (Fig. 9).

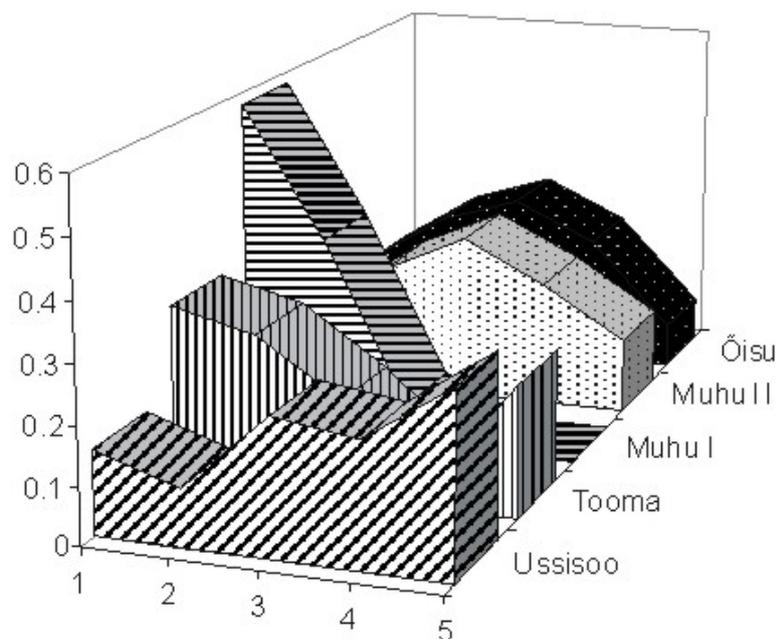


Fig. 9. The population structures in the calculated equilibrium for five populations of *C. calceolus*. The following size classes were used: 0 = no ramets, 1 = 1-2 ramets, 2 = 3-5 ramets, 3 = 6-10 ramets, 4 = 11-15 ramets, 5 = over 16 ramets in the clone.

On the basis of the observed transition frequencies, the corresponding transition matrices with transition probability values were built according to the assumptions of the three models used. The eigenvalues of the transition matrices, as compared to the λ values calculated directly using the exponential growth equation, are presented in Table 3.

Table 3. λ values for the studied *Cypripedium calceolus* populations calculated for both genets and ramets.

Population	Genets		Ramets
	Eigenvalue λ (model 3)	Growth rate λ (calculated)	Growth rate λ (calculated)
Spruce forest	1.010	1.015	1.067
Drained forest	0.998	0.992	1.044
Wooded meadow	1.032	1.031	1.000
Pine forest	1.000	1.000	1.041
Swamp forest	0.986	1.036	1.222
Maximum difference	0.046	0.044	0.222

According to the assumptions used in Models 1 and 2 $\lambda=1$. The λ values calculated from the matrix model (Model 3) are very close to the values obtained from the exponential growth equation, except for the swamp forest population.

The equilibrium structures (right eigenvectors of the transition matrices) of the populations were calculated by the three different models. Regardless of the exclusion of mortality in Models 1 and 2, all three models lead to relatively similar equilibrium structures (stable states) in the size-classes 1-5. The values for the size class 0 according to Model 1 are the maximum estimates of frequencies of dormant clones, the highest being 8 % for the wooded meadow population.

Potential refinements and developments:

In the monitoring of rare species the low number of sites may be a limiting factor for analyses. All European data pooled together may help to solve the problem.

In clonal plant species (i.e. most perennials) genet and ramet dynamics should be monitored separately as they both affect genetic diversity.

Appendix 3. Case studies documenting state and trend of population size of a species with CMR data

Case study 7. Several populations of common birds in France (MNHN)

Source reference(s):	
Julliard R. (2004) Estimating the contribution of survival and recruitment to large scale population dynamics. <i>Animal Biodiversity and Conservation</i> , 27, 417-426	
Rationale:	
Objective(s):	The goal of this study was to link temporal variations in population growth rate to variations in survival and recruitment for four common bird species at a national scale. The challenge tackled here is to identify how demographic mechanisms drive national population growth rate per species, that is the respective role of entries (recruitment events, i.e. the appearance of new reproducers) into or exits (deaths) out of the ‘national population’, and compensation between the two mechanisms.
Biological model:	National population growth rate is derived from standardized counts of individuals for the 4 most captured bird species in France within the French Breeding Bird Survey (FBBS), and French Constant Effort (Bird Ringing) Sites (FCES) schemes. Species analysed are blackcap <i>Sylvia atricapilla</i> , blackbird <i>Turdus merula</i> , chiffchaff <i>Phylloscopus collybita</i> , and reed warbler <i>Acrocephalus scirpaceus</i> . They are all insectivores during the breeding season, small to medium-sized species. The three first ones are sedentary or short-distance/partial migrants, and the last one is a long-distance migrant.
Context:	<p>Global changes impact biodiversity at large spatial scale. This translates, for instance, in population dynamics of different species being synchronized over very large geographic (international) areas. Large-scale, coordinated monitoring schemes are thus ideal candidates for providing appropriate data to quantify and to explore determinants of these large-scale temporal trends in population sizes. The present study illustrates how data from national schemes concurrently monitoring relative abundance, survival and recruitment for common animal species can be combined to understand drivers of changes in ‘national population sizes’.</p> <p>In practice, this study is composed of two analytical parts: (1) estimation of annual population growth rates per species from standardized counts of individuals (i.e. exactly the same analysis as in Appendix 2, Case study 4), (2) correlating annual survival and recruitment rates per species, estimated from standardized capture/recapture follow-up of individuals, with annual estimates of annual growth rates.</p>

	<p>Indeed, it is not exactly the recruitment rate that was analysed but the seniority rate, i.e. the complement to one of recruitment rate (<i>sensu</i> Pradel 1996). This is a good illustration of how data from different schemes, sampling techniques and statistical analyses can be combined to gain complementary understanding of mechanisms driving changes in population size (relevant for illustrating purposes in Deliverables 16 and 18).</p> <p>It should be noted that actual population sizes per species could have been estimated easily from CMR data with appropriate CMR models (i.e. closed population models; e.g. review in Pollock et al. 2002; Amstrup et al. 2005) and post-stratification of data to extrapolate estimates to the national scale. But such an approach should be avoided for three reasons. The first one is that when monitoring temporal trends in population size, we are more interested in estimates of annual population growth rate than estimates of annual population sizes. Apart from this, CMR estimators of population growth rate are more robust to violation of application assumptions than CMR estimators of population size (e.g. Nichols et al. 2000; Nichols & Hines 2002; Rotella & Hines 2005). Finally, for the present study, data to document population growth rates must be different from the data that serve to estimate survival and recruitment rates. This is required so that observed correlations actually quantify correlated biological processes and not just sampling correlation of estimators (due to comparison of different parameters that were estimated with the same dataset).</p>
Sampling design:	
This study uses the data from two different schemes of bird relative abundance monitoring (FBBS and FCES).	
Spatial coverage:	Country (France).
Temporal coverage:	12 years (1989-2001).
Season:	FBBS: April to mid-June; FCES: mid-May to mid-July.
Sampling sites:	<p>No sampling design was applied for the choice of sites to be monitored, i.e. locations of groups of count points (i.e. FBBS sites) or ringing stations (i.e. FCES), were freely chosen by observers. Thus, there is no formal measure taken to secure that sampling sites are representative at a national scale (see e.g. Link & Sauer 1998 for a similar practice).</p> <p>There were 134 groups of 10-15 fixed FBBS sampling points, at least 200-m apart from each other to prevent double-counting as well as 53 ringing FCES stations, with 12-50 12-m mist-nets each, with density of 3-4 mist-nets/ha. Captured birds were marked with an individually numbered ring. For each site only species with at least 5 adults captured and 1 adult recaptured were included (FCES).</p>
Sampling duration:	FBBS: 5 minutes at each FBBS sampling point; FCES: half a day to one day for ringing stations (duration is constant across years for a given site).

Within-year frequency of sampling:	For FBBS, 1 visit per year; for FCES, 3-5 sessions per year.
Among-year frequency of sampling:	All squares were sampled each year, but there are some missing data (i.e. new squares were started and some squares were quitted during the study period). On average, FCES and FBBS sites were monitored over 8 years.
Protocol minimizing measurement error:	For FBBS, visits to a given group of point counts were made by the same observer, on the same date (± 7 days), and the same hour of the day (± 15 min) each year; for FCES, mist-net numbers and locations, number, date and duration of capture sessions were fixed within ringing stations.
Data characteristics:	
Sampling technique:	FBBS: counting individuals contacted (visually or auditive) during each visit to fixed sampling points. FCES: capturing and marking of adult individuals per capture session per ringing site per species.
Data type:	FBBS: counts of individuals per group of count points (i.e. site) per year per species. FCES: capture history (i.e. capture or no capture) per adult individual per ringing site for all years per species. Information on within-year replicates of capture events (i.e. 3-5 annual capture sessions) was used for helping estimation of capture probability per site per year per species (for computational convergence problems). The mean number of within-year recaptures was used as a proxy for capture probability modelling.
Measurement error:	Counts of individuals by visual/auditive contacts (FBBS) are biased by imperfect detection, i.e. only a fraction of individuals present during the study period are contacted/captured. However, this source of measurement error was not accounted for in the analysis, assuming that variations in detection probability across sites, years and species was random, thus just lowering the precision of our results without inducing any bias. The main source of measurement error expected when documenting demographic rates with presence/absence of individuals (FCES) is due to imperfect capture probability of individuals at sampling sites. When an individual was not captured, it can mean that it was not present (either it had died or was not recruited yet; in this case, measurement was exact) or that it was present but not captured. CMR statistical models are designed to adjust estimates of parameters of interest (here, survival and recruitment rates) for this confounding effect of capture probability (review in Pollock et al. 2002; Amstrup et al. 2005). To estimate capture and recapture probabilities, which need to be and are assumed to be identical, there is need to have replicated attempts of capture of individuals. In the present analysis, temporal replication is used to estimate capture probability with the data limited to the FCES sites that were monitored for at least 3 consecutive years.

Statistical analysis:

Parameter for state of population size is the number of individuals counted per year (from FBBS data). Since not all individuals present per year are detected or captured (i.e. detection probability < 1 and capture probability < 1), and since detection/capture probabilities are much influenced by various factors (e.g. observer characteristics, habitat structure, date, etc.), raw values cannot be used as measures of actual population size. Indeed, analyses such as the one presented here do not provide any estimate of actual population size.

Parameter for the trend in population size is the growth rate of number of contacted individuals. If one can assume that site specificities influencing detection probability are constant through time, then after accounting for site effects in the statistical analysis, slopes for the effects of years directly estimate the annual growth rate of the number of contacted individuals per species averaged over sites.

The first part of the analysis was the estimation of the annual population growth rate per species. A log-linear model was used, with count of individuals per year per site as dependent variable (assumed to follow a Poisson's distribution), a log-link function, and the additive effects of site (qualitative variable) and year (qualitative variable) as independent variables (see section 5 of Deliverable 2 for a general discussion). Since we are interested in explaining among-year variations in annual growth rate, a categorical year effect was used here instead of the continuous linear year effect used in the Case study 4 (Appendix 2). Given the log-link function, slopes for year effects are estimates of annual growth rate of the number of contacts.

The second part of the analysis was correlating annual survival and recruitment probabilities with annual growth rates to identify demographic mechanisms driving changes in population size. CMR histories, analysed with CMR models, allowed estimations of three parameters: (i) recapture probability in year t , noted p_t , that is the probability that an individual present at a given site was captured on year t ; (ii) survival probability from year t to year $t+1$, noted ϕ_t , that is the probability that an individual present in year t was still alive and present at the monitored site on year $t+1$; and (iii) seniority probability from year t to year $t-1$, noted γ_t , that is the probability that an individual present in year t was already alive and present at the monitored site in year $t-1$. Theoretical relationships among these parameters and with the annual multiplication rate (i.e. exponential of the population growth rate) and the usual definition of recruitment (i.e. the *per capita* recruitment rate, in other words the number of new reproducing individuals produced per reproducing individual per year) are fully detailed in the original study.

A simple CMR model, i.e. Cormack-Jolly-Seber model, was applied to capture histories with years in the chronological order (i.e. classical survival analysis) or in reverse-time chronological order (i.e. recruitment analysis; Pradel 1996). Models that were built included the following independent variables: (i) site effect, year effect and mean number of capture per individual per year (i.e. a proxy for capture efficiency per site and year) for modelling annual recapture probability parameters; (ii) year effect and effect of annual multiplication rate for modelling survival probability parameters; and (iii) year effect, effect of survival probability (estimates) and effect of annual multiplication rate (estimates) for modelling seniority probability parameters.

Model selection procedure was based on Akaike's Information Criteria (AIC). The software applied was SURGE 5 (White & Burnham 1999). Strength of correlations between survival, recruitment and population growth rates were quantified by changes in deviance for the different nested models defined above.

Skills required:

The present field data types require that the observer is able to identify visually and auditively the species under study (FBBS) or that he/she has the appropriate technical training for implementing ringing studies (FCES). Actually, monitoring data used here were collected by volunteers. The present statistical method requires basic knowledge of statistical tests, as well as some expertise in CMR modelling and model comparisons. Log-linear models can be built with any statistical analysis package. The TRIM software has been specifically developed for implementing log-linear regression analysis of monitoring data to estimate trends in relative abundance indices (Pannekoek & van Strien 2001). CMR models can be built with different freeware such as SURGE or MARK

Results:

The results rely on CMR histories of 6272 blackcaps, 3446 blackbirds, 3205 reed warblers and 2722 chiffchaffs. Annual fluctuations of relative abundances of the studied species are available at: http://www.mnhn.fr/mnhn/crbpo/r%20E9sultats_etat_populations.htm#resultat.

Much of among-site and among-year variation in recapture probability was accounted for when modelling recapture probability with the proxy for capture efficiency (i.e. the average number of within-year recaptures per site per year per species). This modelling for recapture probability was used in all subsequent CMR models.

Survival and seniority rates exhibited significant among-year variations (Fig. 10). Among-year variation was on average 1.5 times higher for survival than for seniority rates (variation being computed as the difference in deviance between models with or without year-dependency; Table 2 in the original reference).

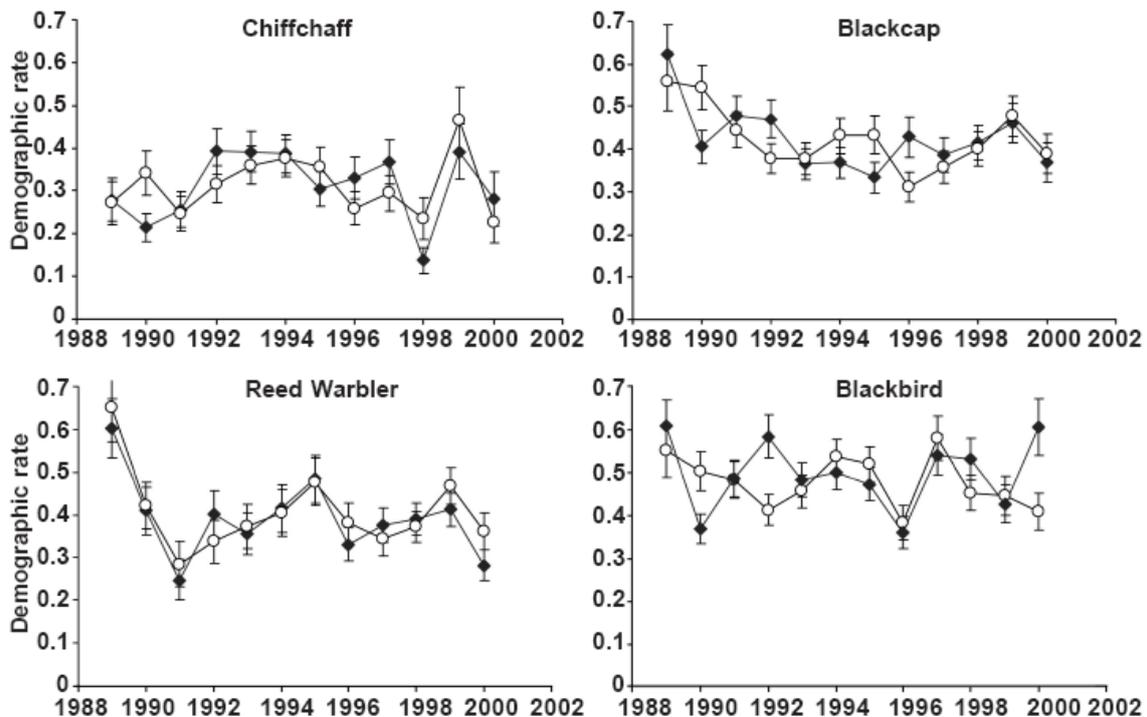


Fig. 10. Temporal variation in survival (black diamonds) and seniority (open circles) for four common passerines: vertical bars \pm 1 SE.

For blackcaps and chiffchaffs, survival was strongly positively correlated to population growth rate. Seniority was negatively correlated to population growth rate and positively to survival. This suggests that annual national population growth rate was determined concomitantly by variations in survival and recruitment. For reed warblers, survival, seniority, and population growth rate were all positively correlated. This suggests that population is strongly regulated (the level of recruitment is dependent on the level of survival), with recruitment variation compensating (sometimes partially only) for survival variation. For blackbirds, only survival was positively correlated to population growth rate. This suggests that annual national population growth rate was on average more determined by survival, but in some years recruitment had a major importance.

Potential refinements and developments:

The question is how to estimate population sizes, population growth rates, and survival/recruitment rates with CMR data only (i.e. without using independent data from counts of individuals). Actually, estimating all population dynamics parameters with CMR models would be ideal since all parameters of interest (state and trend of population size) would be adjusted for spatio-temporal variations in capture/recapture probabilities. However, if population growth rates and survival/recruitment rates are to be compared, they should come from independent datasets. This is rarely achievable since, usually, only one national CMR dataset exists per major taxonomic group. One solution is to make two subsets of data (with random or systematic attribution of CMR monitoring sites to each), and to use one subset for estimating national annual population growth rates, whereas the other subset for estimating demographic rates. Also see the refinements suggested for the Case study 4 (Appendix 2), which are mostly relevant here as well

Case study 8. Population size of Lepidoptera (UJAG)

Source reference(s):	
Nowicki P., Richter A., Glinka U., Holzschuh A., Toelke U., Henle K., Woyciechowski M. & Settele J. (2005) Less input same output: simplified approach for population size assessment in Lepidoptera. <i>Population Ecology</i> , 47, 203-212	
Rationale:	
Objective(s):	The goal of the study was to develop simplified methods of seasonal population size assessment in Lepidoptera.
Biological model:	Lepidoptera comprise butterflies, moths and burnet moths. The important feature of this organism group is that their adult life span is considerably shorter than the time of adult occurrence (flight period). In other words, the individuals belonging to one generation, which together constitute population size, are not all present at any single moment of time. This phenomenon of temporarily fragmented populations is also present in many other invertebrate groups and therefore the general approach of this study is relevant for them as well even though specific results (e.g. model parameter values) may differ.
Context:	<p>Transect counts and capture-mark-recapture sampling are two standard methods for estimating population size in Lepidoptera (Gall 1985; New 1991; Warren 1992). The former method is cheap and time-efficient, yet less reliable as it normally yields only relative indices of abundance and thus CMR studies are still necessary to calibrate them. What is more important, transect counts can provide, at most, the estimates of snapshot (usually daily) population sizes, but they do not deal with the turnover of individuals within season. Consequently, one cannot estimate the seasonal population size, i.e. the number of individuals occurring in one generation, which is of prime interest in most population studies.</p> <p>On the other hand, CMR methods yield estimates of not only daily numbers of individuals, but also of their turnover, and hence, if properly planned, they enable the calculation of seasonal population size. Unfortunately, high costs involved in capturing individuals throughout the entire flight period prohibit their wide use in large-scale research. Hence the idea was to elaborate a simplified design for sampling Lepidoptera populations that would considerably reduce the amount of labour invested, but retain the accuracy of traditional CMR. For this purpose we investigated the relationship between peak and seasonal population sizes and how it is affected by adult life span and their flight period length.</p>
Sampling design:	
Spatial coverage:	15 local populations of six Lepidoptera species in Germany, Poland and Czech Republic.

Temporal coverage:	Although some populations were sampled for more than one year all the seasonal data sets were treated as independent units.
Season:	Summer (June – September).
Sampling sites:	Entire sites of local populations (0.2–11.4 ha) were sampled.
Sampling duration:	Sampling intensity ranged from every day to every third day (with sporadic longer breaks), which depending on flight period length corresponded to approx. 15–40 sampling days. On any given day the sampling lasted for a minimum of 1 hour (this time limit is of no importance <i>per se</i> , but instead each sampling session has to last long enough to ensure that adequate proportion of individuals are captured). In several cases there were three or four capture sessions per day, but these data had to be pooled daily for the purpose of consistency of the analysis.
Protocol minimizing measurement error:	Out of a larger sample of available data sets only those in which: (i) sampling covered the entire flight period, (ii) populations were effectively spatially closed, and (iii) recapture rates were high enough to provide reasonably precise estimates of population parameters, were used in the analysis ($n = 23$).
Data characteristics:	
Sampling technique:	Standard CMR. Captured individuals are uniquely marked, optimally with consecutive numbers written with water-proof fine-tipped markers on the underside of their hind wings.
Data type:	Individual capture histories, in which '1' denotes capture and '0' no capture during a particular sampling day (compare statistical analysis in Appendix 1, Case study 1). Combined together for all individuals captured at least once in a given population they created matrices with rows representing individuals, and columns representing sampling days.
Measurement error:	Capturing an individual is a random event depending on capture probability p , which may be either constant in time and equal for all individuals or affected by time variation, heterogeneity between individuals, 'behavioural' (or 'trap') response (p changes once an individual has been captured), or any possible combination of the above phenomena (Otis et al. 1978). With large enough numbers of individuals captured and several capture sessions per day all the phenomena can be detected and their effect on measurement error can be quantified, e.g. using Pollock's Robust Design model (Pollock 1982). With only one session per day it is possible to account for time variation, but not for heterogeneity and behavioural response. However, in Lepidoptera the predominant source of heterogeneity are inter-sexual differences, which may be removed by analysing both sexes separately, while the behavioural response typically does not occur unless individuals are improperly handled at capture.

Statistical analysis:

The capture data were analysed using program MARK (White & Burnham 1999) according to the Cormack-Jolly-Seber type constrained models (Schwarz & Arnason 1996; Schwarz & Seber 1999). The selection of the most appropriate model for each data set was based on Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Hurvich & Tsai 1989). The Cormack-Jolly-Seber approach is based on the assumption that the population is demographically open between capture days. In other words, only a fraction of individuals present on capture day i survives till capture day $i+1$ (survival, $\hat{\phi}_i$), while new individuals enter the population during the same interval (recruitment, \hat{B}_i); in the case of populations of adult Lepidoptera the recruitment represents individuals eclosing from pupae. Therefore, the relationship between daily population sizes on consecutive capture days (\hat{N}_i, \hat{N}_{i+1}) is expressed as:

$$\hat{N}_{i+1} = \hat{N}_i \hat{\phi}_i + \hat{B}_i \quad \text{with} \quad \hat{\phi}_i = \hat{\phi}^{\delta_i}$$

where:

$\hat{\phi}$ is the survival scaled to the basic time unit, i.e daily survival rate;

δ_i is the length of the interval between capture days i and $i+1$, measured in days.

The estimates of daily population sizes and daily survival rate are derived directly from the capture history matrix, whereas recruitment can be estimated through the simple transformation of the above formula ($\hat{B}_i = \hat{N}_{i+1} - \hat{N}_i \hat{\phi}_i$). However, some individuals could eclose and die between consecutive capture days whenever the interval between capture days gets longer than one day ($\delta_i > 1$). Hence, the adjusted estimate of recruitment (\hat{B}_i'), which would account for individuals that die before entering the capture day, was used:

$$\hat{B}_i' = \delta_i \frac{\hat{B}_i}{1 + \hat{\phi} + \hat{\phi}^2 \dots + \hat{\phi}^{\delta_i - 1}} = \frac{\delta_i \hat{B}_i (\hat{\phi} - 1)}{\hat{\phi}^{\delta_i} - 1}$$

For each population the following parameters were defined:

(i) peak population size, i.e. the maximum daily population size: $\hat{N}_{peak} = \max(\hat{N}_i)$

(ii) seasonal population size, i.e. total number of individuals eclosing throughout the season:

$$\hat{N}_{total} = \sum_{i=0}^{k-1} \hat{B}_i'$$

(iii) average adult life span: $e = (1 - \hat{\phi})^{-1} - 0.5$

(iv) flight period length (*FPL*), i.e. the time between the first and the last occurrence of flying adults

(v) daily and seasonal sex ratios.

Skills required:

People involved must be able to identify the species investigated; sex recognition is typically required as well. In addition they must possess basing manual skills to mark the individuals captured. The analysis requires moderate knowledge of CMR theory.

Results:

The fraction of individuals occurring at peak, i.e. $\hat{N}_{peak} : \hat{N}_{total}$ ratio, ranged between 11% and 50%, and was highly variable, with $CV = 0.39$. Even among populations of the same species a larger \hat{N}_{peak} was occasionally followed by a lower \hat{N}_{total} . The implication is that the reliability of transect counts, which in fact use indices of daily population sizes to infer about trends in seasonal population size, is questionable. However, if the $\hat{N}_{peak} : \hat{N}_{total}$ ratio was adjusted for different average life spans among the populations it showed less variation ($CV = 0.30$), and when the flight period was also accounted for, the variation decreased even further ($CV = 0.14$). In fact, the average life span to flight period length ratio explained over 90% of the variance in the fraction of individuals flying at peak (Fig. 11). Therefore seasonal population size can be easily derived if only peak population size, average life span and flight period length have been estimated.

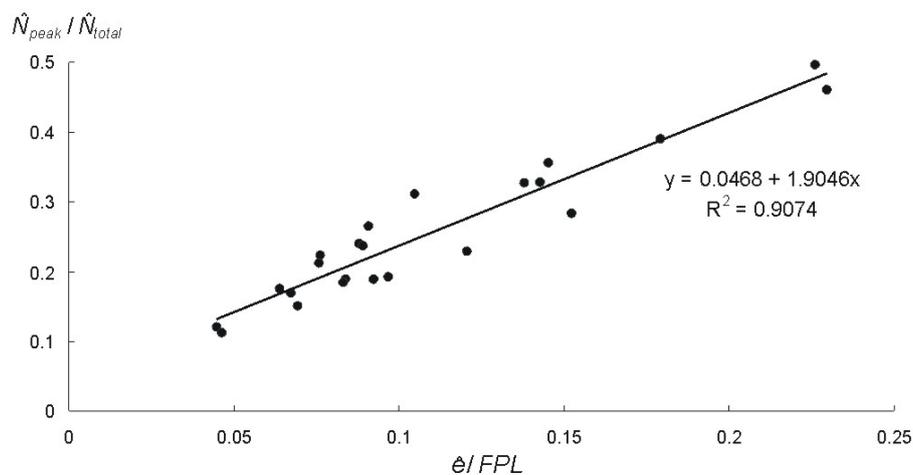


Fig. 11. The proportions of individuals occurring on a peak day vs. the average life span (e) to flight period length (FPL) ratio among the populations surveyed.

The peak sex ratio was never found significantly different from the seasonal one as the 95% confidence intervals of both parameters clearly overlapped in each case. However, such a result did not imply that if sex ratio on a given day was similar to the seasonal one it indicated the peak time. This is because the sex ratio dynamics within the season most often followed a tangensoid curve (type II curve in Fig. 12) rather than a sigmoid one (type I curve in Fig. 12), and as a consequence the period during which daily sex ratios did not differ significantly from the seasonal one was relatively long, usually lasting 2–3 weeks.

Simulating simplified sampling designs by reducing the data sets to a fraction of the original sampling days proved that the peak day can be properly detected if only the mid part of the flight period is sampled with CMR. Estimates of peak population size and average life span are sensitive to the number of capture days, but just five capture days are enough to ensure reasonable precision of these estimates. On the other hand, sampling on every third day as compared to daily one, made no apparent difference to this precision, and thus the former can be recommended for its increased cost efficiency.

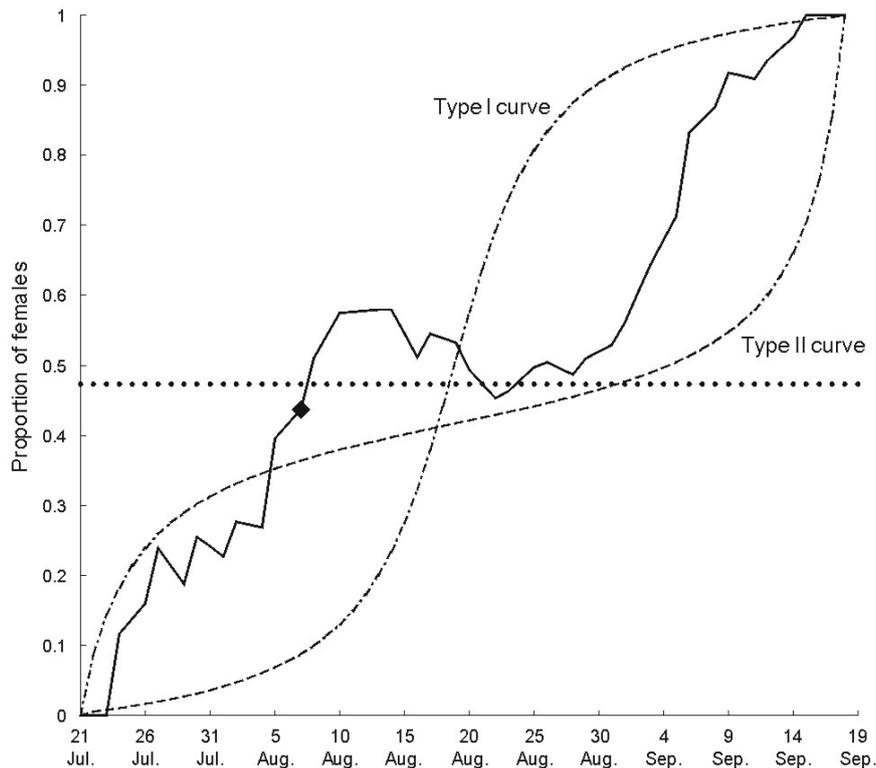


Fig. 12. Seasonal dynamics of the sex ratio (solid line) in the population of *Polyommatus coridon* on the Zappendorf site (Germany) in 1999, as an example of the patterns observed among the populations surveyed. The diamond shows the peak day value, whereas the dotted line represents the seasonal proportion of females. Two hypothetical curves (broken lines) are presented for comparison.

Potential refinements and developments:

The relationship between seasonal population size, peak population size, average life span, and flight period length has been developed on the basis of a limited array of species. The pattern is likely to hold in other Lepidoptera, and possibly some other invertebrates as well, but it should be parameterised through independent empirical research. Caution is needed in the case of species with relatively long-living adults, because (as theoretically predicted by Zonneveld 1991) the relationship between the fraction of individuals flying at peak time and the average life span to flight period length ratio should become non-linear if the latter exceeds 0.2.

Case study 9. Orchid populations in Estonia (ESTAGUN)

Source reference(s):	
Shefferson R.P., Kull T. & Tali K. (2005) Adult whole-plant dormancy induced by stress in long-lived orchids. <i>Ecology</i> , 86, 3099-3104	
Rationale:	
Objective(s):	The aim of the study was to investigate life histories of long-lived perennial orchids <i>Cephalanthera longifolia</i> and <i>Cypripedium calceolus</i> in different populations.
Biological model:	Dormancy is a poorly understood life history phenomenon in which a mature perennial plant fails to sprout any aboveground tissue in one or more growing seasons. It may occur among many plant families, but it generally happens in rare plants with difficult growing requirements, e.g. orchids.
Context:	Changes in population sizes are important in biodiversity conservation, however, phenomenon of dormancy complicates the picture and leads to a severe underestimation of population size. Capture-mark-recapture analysis may help to solve this problem.
Sampling design:	
Spatial coverage:	Estonia.
Temporal coverage:	2002-2004.
Season:	June.
Sampling sites:	Five sites.
Within-year frequency of sampling:	Once per year.
Among-year frequency of sampling:	Every year.
Protocol minimizing measurement error:	Sources of variation that may cause error in census are large differences in phenological development of individual plants.

Data characteristics:	
Sampling technique:	Marking individual plants.
Data type:	Number of marked plants in a population as well as their state and vitality throughout the monitoring period.
Statistical analysis:	
<p>Capture-mark-recapture modelling: An open population capture-mark-recapture analysis was applied to estimate the probabilities of dormancy and apparent survival. To assess spatial, temporal, treatment and species-level variation in these rates, a global model was developed in which apparent survival and resighting varied with group and time (model $\phi_{\text{group}*\text{time}}$, $p_{\text{group}*\text{time}}$, abbreviated as ϕ_{g*t}, p_{g*t}). Groups corresponded to populations and treatments, with three treatments for each of the two populations of <i>Cypripedium</i> and three populations of <i>Cephanthera</i>, which gives a total of 15 groups. Further models incorporated reduced time and group dependence, including species, population, and treatment effects, and all interactions and additive two-parameter relationships through saturation. A total of 145 models were developed, all with design matrices. Resighting histories were modelled for each species-patch combination using program MARK, and maximum likelihood estimation proceeded through the logit-link function (White & Burnham 1999).</p> <p>Model selection: Models were compared through the calculation of AIC_c (corrected Akaike Information Criterion) values, which evaluate a relative level of information loss from the original data set for candidate models (Akaike 1973; Burnham & Anderson 1998). We tested the appropriateness of this approach with the program MARK bootstrap goodness-of-fit test for the global model, using 1000 iterations (White & Burnham 1999), and did not find significant over-dispersion ($\text{deviance}_{\text{expected}} = 2.124 \pm 0.064$ vs. $\text{deviance}_{\text{observed}} = 1.704$, $P = 0.548$). Models were ranked and parsimony was inferred according to differences in AIC_c value relative to the best-fit model (Burnham & Anderson 1998). Further inference was made with Akaike weights, which were determined to examine the likelihood that a particular parameterisation best summarizes the variability in each of the two parameters of interest, i.e. apparent survival (ϕ) and resighting probability (p).</p> <p>Parameter estimation: Final parameter estimates were produced through model averaging in order to reflect model-selection uncertainty (Burnham & Anderson 1998). Standard errors were estimated by the method of moments to propagate dependent random uncertainties (Taylor 1997). Since all individuals were found and monitored each year, resulting in 100% re-detection, we estimated dormancy as the complement to resighting (i.e. $d = 1 - p$; Shefferson et al. 2001). All estimates are presented with ± 1 SE.</p>	
Skills required:	
All stages of development of a species should be recognised. Modelling and statistical expertise should be acquired on a higher level.	

Results:

Cumulative Akaike weights suggested that apparent survival varied most strongly by species (cumulative Akaike weight: $w_{\text{cum}(\text{spc})} = 0.181$). Time was roughly half as strongly supported as species ($w_{\text{cum}(t)} = 0.100$). Model-averaged overall apparent survival was 0.937 ± 0.047 per year for *Cephalanthera longifolia*, and 0.979 ± 0.019 for *Cypripedium calceolus*. In contrast to the apparent survival, dormancy exhibited strong variability among species and populations. Dormancy varied with an additive relationship between population and treatment ($w_{\text{cum}(\text{pop+trt})} = 0.376$) in the best-fit and three equally parsimonious models. The next strongest parameterization, consisting of only population effects, was supported only half as much ($w_{\text{cum}(\text{trt})} = 0.182$). Variation by species was also strongly correlated, but with roughly two-thirds the support of the best-fit parameterization ($w_{\text{cum}(\text{spc})} = 0.281$). Model-averaged overall dormancy was 0.235 ± 0.062 per year for *Cephalanthera longifolia*, and 0.055 ± 0.026 for *Cypripedium calceolus*.

Potential refinements and developments:

Increased frequency of sampling, e.g. sampling twice instead of once a year, should increase the reliability of the results. This may help particularly in the case of species that have asynchronous developmental patterns, for instance perennial plants in which individuals differ in the above-ground shoot formation period or the flowering period.