



Demographic analysis and population models in ecology, evolution and conservation: a transversal approach with case studies

L'anàlisi demogràfica i els models poblacionals en ecologia, evolució i conservació: un enfoc transversal amb casos d'estudi

Albert Fernàndez Chacón



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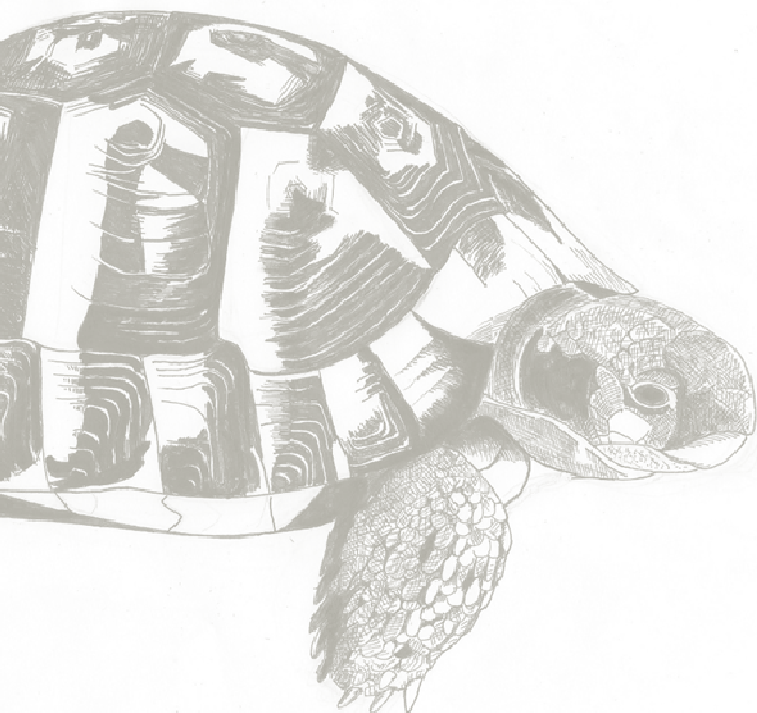
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approach with case studies

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evolució i conservació: un enfoc transversal amb casos
d'estudi.

Memòria presentada per Albert Fernández Chacón per optar
al grau de doctor per la Universitat de Barcelona.

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Juny de 2013

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A tots aquells que m'heu acompanyat fins aquí

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General introduction

The study of populations in ecology

Ecology is primarily interested in the processes that make the state of biological systems change over time and space (Krebs 2001, Kéry and Schaub 2011) and seeks to understand the mechanisms responsible for the dynamics of these biological systems by making inferences across different scales of organization, from groups of individuals or populations to a collection of communities or metacommunities (Begon et al. 1986).

A population is a group of individuals of the same species occupying a defined area during a specific time (Begon et al. 1986). Real-world populations are open to individual gains and losses and their size and structure changes depending on the number of individuals that are added to and removed from the population during a given time period. Birth and immigration constitute gains of individuals into the populations, whereas death and emigration constitute the losses; when gains exceed losses, the population will grow, and in the reverse situation, the population will decline or become extinct (Lande and Orzack 1988, Sinclair et al. 2009).

Population ecology is the branch of ecology that focuses on the study of populations as fundamental biological units and analyzes changes in population characteristics (size, structure) in space and time, which are the cumulative result of multiple individual processes (birth, deaths, immigration and emigration) (Begon et al. 1996, Sutherland 1996). The study of population dynamics spans from single populations to population networks or metapopulations (Hanski 1998). Increasing levels of organization (communities, metacommunities) are all large-sized versions of the same population concept and can be described by analogous state variables (variables quantifying the current state of the system, such as abundance or occupancy) and vital rates (the parameters that govern changes in the state variables such as survival, fecundity, recruitment or dispersal). Therefore, by studying biological systems that are nested within higher

scales of organization and by dealing with quantitative descriptors that can be applied across all levels of ecological integrity, population ecology provides the best framework for the scientific study and management of populations, metapopulations and communities, linking fundamental research in ecology with more applied disciplines such as conservation biology and wildlife management (Morris and Doak 2002, Weddell 2002, Mills 2007, Sinclair et al. 2009).

Population ecology and biodiversity conservation

Humans affect living resources either directly, via interactions such as hunting or fishing, or indirectly, by modifying the local and global environments. Since the second half of the 20th century, the general increase in population growth and resource consumption has accelerated biodiversity loss worldwide due to the spread of environmental problems such as overexploitation of natural resources, pollution, habitat destruction, and introduced organisms, raising the rate of species' extinction well above background levels and causing what has been described as the 6th mass extinction event in the history of Earth (Leakey and Lewin 1995, Thomas et al. 2004, Burney and Flannery 2005, Mills 2007).

Until recently, living resources were only valued in economic terms, following a utilitarian vision of biodiversity, and conservation was largely limited to harvesting regulations of game species, despite many non-game species provide services that are valued by humans such as decomposition, pollination, pest control and the production of substances of medical use (Grifo and Rosenthal 1997, Weddell 2002, Mills 2007). Enhanced by the late 20th century biodiversity crisis, the conservation and management of living resources shifted from a utilitarian to a preservationist point of view where such resources, regardless of their economic value, should be protected, giving rise to the crisis-oriented discipline of conservation biology (Soulé 1985, 1991, Weddell 2002).

Conservation biology is a synthetic discipline that addresses the dynamics and problems of anthropogenic perturbed species, communities and ecosystems (Soulé 1985). The underlying goal of all conservation efforts is the protection of biodiversity and the success of such efforts requires a previous understanding of

the individual components (i.e. populations) that make up a community or ecosystem (Soulé 1985, Morris and Doak 2002). Thereby, resource managers need scientific information on which to base their decisions about conservation (informed management actions by scientific evidences), making scientific research and resource management interrelated ongoing processes rather than independent entities (Soulé 1985, 1991, Morris and Doak 2002, Weddell 2002, Mills 2007). Conservation biology makes questions about the real world (e.g. How many individuals are there? Is survival high? Is the population likely to become extinct?) that require quantitative answers (i.e. population sizes, survival rates, extinction probabilities) and the discipline of population ecology provides an ideal framework to answer these questions via the analysis and modelling of demographic data (Williams et al. 2002). The use of longitudinal data obtained by monitoring species or marked individuals through time allows the estimation of state variables important for the conservation of populations such as site occupancy or local abundance as well as the underlying parameters (survival, fecundity, dispersal, extinction and colonization) responsible of state changes and such population-based knowledge is also of high value for conservation efforts aimed at higher levels of ecological integrity such as metapopulations or communities (Dorazio et al. 2010, Kéry and Schaub 2011).

Population analysis: from field observations to process predictions

The monitoring of a biological system is needed to improve the biological understanding on which management actions can be based (Nichols and Williams 2006). Thus, monitoring programs are a key component of the large process of conservation-oriented science and management and the collection of field data is the first step to produce estimates of system status and other variables (system vital rates) that can be compared against model-based predictions for the purpose of learning (MacKenzie et al. 2006, Nichols and Williams 2006). In population studies, mechanistic hypotheses frequently concern the vitals rates (e.g. survival, fecundity, immigration/emigration) responsible for changes in a state variable of interest (e.g. population size). The main objective is to understand how populations or communities respond to a variety of factors (i.e. predation/poaching, habitat/climatic changes, pollution, disease, etc...), and to do

so, we have to discriminate between competing hypothesis about the relevance of different causal factors to system dynamics, with the ultimate goal of being able to predict the magnitude of the state variable in the next time step given its previous magnitude and knowledge of the causal factors operating between times t and $t+1$ (Williams et al. 2002).

Overall, population analyses have 3 fundamental goals: i) to directly estimate rate parameters or state variables, ii) to model predictor-response relationships between rate parameters and causal factors and iii) to predict the magnitude of state variables at $t+1$ given conditions at t . To achieve these goals, population analyses mostly rely on data collected during observational studies because free ranging populations are usually not subjected to experimental manipulation and in some situations (e.g. research on threatened species), to carry out such experiments would be unacceptable. However, a problem of observational studies involving populations is that in most practical situations, some state variables and dynamic states are not observable because the detection of individuals is imperfect (Seber 1982, Lebreton et al. 1992, Williams et al. 2002). Therefore, because our field data are always a combination resulting from ecological and observation processes, inferences on the state of the system and its dynamics must be made taking into account imperfect detection (MacKenzie et al. 2002, 2003, Royle et al. 2005, Kéry and Schaub 2011).

Population analyses provide useful tools to understand the behaviour of ecological systems under conditions that cannot be directly observed, via the modelling of field data and the incorporation of detection bias (Pradel et al. 1997a, Pradel 2005, MacKenzie et al. 2009, Gimenez et al. 2012). A model is an abstract representation of a system that can be used to predict system behaviour under specified conditions. Normally, the type of modelling conducted in population analyses involve translating our ideas about how a natural system works into a set of mathematical equations that contain predefined parameters that symbolize the key processes of that system (Nichols 2001, Williams et al. 2002). Both ecological and observational processes are integrated in the model structure by means of different rate parameters, and competing hypothesis can be formulated by means of competing mathematical models (Kendall 2001, Nichols

2001). The exercise of model selection involves fitting a set of candidate models to the same set of data and formally determine which model (and hence which hypothesis) has a greater support given the data in hand (i.e. the most parsimonious model). The finally retained model will be the most useful to make predictions about system behaviour and usually the type of model required to conduct simulation exercises. This is done by giving certain values to the model variables and performing calculations under a wide range of scenarios, which is of tremendous value in research on pest species and rare or endangered species as it does not require any risky experimental manipulation of the population(s) under study.

Toolbox for population analysis

Many analytical tools are available to achieve the fundamental goals of the analysis of population data. This has been a field of intense research over the past 20 years, with many advances in the statistical analysis of observational data gathered using capture-recapture techniques or by means of presence-absence surveys (see below). Such advances allow a vast array of biologically interesting parameters to be estimated and, basically, the choice of which analytical tool to use depends on the type of question(s) we want to answer. However, because resources in research and conservation are usually limited and individual records are often few, incomplete or both, the optimization of sampling efforts and the type of data available will usually condition the quantitative variables of interests and the type of analysis conducted respectively.

Capture-recapture models

The interest in individual flows (gains and losses) is central in population ecology and has driven the development of empirical approaches to measure them (Lebreton et al. 2009). One key approach is the capture-recapture method which uses repeated observations of marked individuals to provide insights into population mechanisms. Under this approach, demographic information is generated by following individuals through time, so individuals need to be identified at each sampling occasion and traditionally this has been achieved by

marking them using permanent artificial tags, such as the metallic rings used in the study of bird populations. However, capture-recapture techniques are more diverse and do not always require individuals to be physically captured and marked using artificial tags; in fact, individual identification may rely on natural tags (e.g., scars, dorsal fin shape, spots, etc.) or the collection of samples such as hair or faeces, which are processed in order to identify different genotypes corresponding to different individuals (Caniglia et al. 2012). Camera trapping and genetic sampling are examples of non-invasive techniques that have been applied to the demographic study of animals such as large carnivores (Karanth 1995, Royle and Nichols 2009) or marine mammals (Langtimm and Beck 2004, Mackey and Durban 2008). Problems such as tag loss or unwanted negative effects of tags on animals can be completely avoided using non-invasive techniques. However, if animals can only be identified and/or followed using artificial tags, tag loss may be prevented by double-tagging the animals, and the use of small transmitters or marks that can be read from the distance (e.g. PVC rings in colonial seabirds) may help to reduce capture stress on the individuals by capturing them only once and following them through time by means of visual encounters or by radio-tracking techniques (Minta and Mangel 1989, Devillard and Bray 2009).

Under a standard capture-recapture study, as described in Lebreton et al (1992), data collected in the field are eventually summarized into individual encounter histories for further analysis. A typical encounter history consists in a row of numbers which contain information on whether the individual was captured or not at each sampling occasion. The simplest way to codify this information is to use a binary code with "1" meaning that the individual was captured at this occasion and "0" meaning that the individual was not captured. Basically, the fact that an individual is encountered (1) or not (0) in a given occasion is the product of two probabilities: the probability that the animal survives to this occasion (Φ_i) and the probability that, given it is alive, it is captured at this occasion (p_i). In this sense, individual encounter histories in a capture-recapture dataset can be seen as multiple sequences of probabilistic events that permit to obtain maximum likelihood estimates of the parameters Φ_i and p_i .

Originally, capture-recapture programs were designed to estimate population size (Seber 1982, Minta and Mangel 1989) with interest on the processes causing individual flows gradually increasing until the primary objective shifted from population size to the underlying parameters responsible of population change (Lebreton et al. 1992, Clobert et al. 2001, Morris and Doak 2002). In parallel, this shift initiated a wide diversification of capture-recapture models for estimating demographic parameters under imperfect detection of individuals, allowing reliable estimates of basic parameters responsible of individual flows, such as survival, and providing an important source of information on the individual groupings (age-classes or life stages) present in the populations and their associated demographic rates (Lebreton et al. 2009, Gimenez et al. 2012).

Most population studies interested in the processes involving survival patterns in wild populations use the Cormack-Jolly-Seber model (CJS) as a departure model in the analysis of capture-recapture data because they allow year-specific estimates of survival and recapture probabilities (Lebreton et al. 1992). Survival is “apparent” because under this approach the fate of the individuals that are not encountered in the area where sampling is conducted is usually unknown and mortality processes are confounded with permanent emigration from the population. CJS models make assumptions such as independence of fates and identity of rates among individuals, which need to be tested prior to model construction by means of Goodness of fit tests evaluating heterogeneities in survival and recapture probabilities (Pradel et al. 1997, Choquet et al. 2009). Usually time dependence or constancy in apparent survival estimates are tested under a CJS approach, but this modelling scheme also permits to test group effects, since it allows to split the data in permanent groups (individual covariates such as male/female) and defining age classes, with their survival and capture probabilities. Much literature relies on CJS models to test the effect of external environmental variables (temperature, habitat quality, rainfall, food availability, predation) and intrinsic factors (sex, age, density, disease) on local survival (Cezilly et al. 1996, Barbraud et al. 1999, Hakkarainen et al. 2002, Barbraud and Weimerskirch 2003) and also to study more specific processes such as senescence (Jorgenson and Festa-Bianchet 1997, Toïgo et al. 2007) or retrospective

assessments of management effects on the survival of threatened populations (Bertolero et al. 2007, Tuberville et al. 2008).

Encounter histories are not restricted to be a row of 1's and 0's and if more information about the marked individuals is gathered during sampling, such individual characteristics may be codified as different "states" using different numbers (1, 2, 3...) or letters (A,B,C) in the encounter histories. Such "multistate" encounter histories form the basis of the analysis using *multistate* capture-recapture models, a further step in the study of open animal populations (Lebreton and Pradel 2002, Lebreton et al. 2009). Multistate models were originally developed to study movement rates of individuals within a metapopulation (Multisites) (Hestbeck et al. 1991, Spendelov et al. 1995) so "states" corresponded to the set of geographic locations that individuals could occupy during each sampling occasion (site). However, the potential of multistate models was soon found to be greater than the potential of *unistate* CJS and this concept was later expanded to other "dynamic" states, such as breeding states (breeder, non-breeder) or combination of geographic location and breeding status (e.g. breeding at site A). In contrast to CJS models that only allow estimation of survival and recapture probabilities, multistate models allow the estimation of a third parameter, the transition probability, or movement rate among different states and the sequence of probabilistic events in a multistate encounter history is then defined by survival, transition and recapture parameters. Survival and transition probabilities are usually modelled independently assuming a 1st order Markovian process; the animal first survives in the state s occupied at time i and then moves to occupy a state r at time $i+1$.

Although multistate models are data demanding and the inclusion of a third parameter may increase their complexity compared to CJS models, important questions about movement and life history traits can be addressed with these models through estimates of transition probabilities, offering a common framework for the simultaneous study of many different biological processes (Lebreton et al. 2009). The identification of states as geographic location permits to study dispersal processes, which are of primary interest in the metapopulation theory (Hanski 1999). The study of dispersal using multistate models allows to

answer key biological questions such as when does the dispersal takes place, why do individuals disperse, and which are the cost/benefit ratios of dispersal in the population (Clobert et al. 2001). Asymmetrical transition probabilities between geographic states may be good indicators of differences in habitat quality or site-specific environmental conditions. Using multistate models, lowered survival rates have been detected at some sites affected by disturbances (Cam et al. 2004a, Lyet et al. 2009), and this has been linked to a post-disturbance dispersal response (Cam et al. 2004a). Multistate models permit to test the effects of multiple causal factors (population size, distance between sites and changes in environmental conditions) on dispersal processes and this methodology has extensively been applied in studies on colonial birds such as Roseate terns (Spendelov et al. 1995) Canada geese (Hestbeck et al. 1991), Black-headed gulls (Grosbois and Tavecchia 2003), and great cormorants (Hénaux et al. 2007).

Multistate modelling with the definition of breeding states such as “non-breeder”, “pre-breeder” and “breeder”, permits investigations on key demographic processes, such as recruitment and life history tradeoffs, such as the cost of reproduction. However, in most capture-recapture studies, non-breeders are usually unobservable because only the breeding population is sampled, making it difficult to study processes where non-breeding individuals are involved. An interesting feature of multistate models is that they permit to estimate survival and transition probabilities from unobservable states by setting to zero the recapture probabilities of individuals that are in a state that is not observable after first capture, solving the problem of studying processes involving unobservable individuals (Kendall and Nichols 2002, Jenouvrier et al. 2008). Before the consolidation of multistate models, questions about recruitment or reproductive costs were addressed using unistate models, without a unified approach (Clobert et al. 1994, Pradel 1996, Schwarz and Arnason 2000, Tavecchia et al. 2001). By considering states that combine geographic location and breeding status, multistate models permit to study dispersal and recruitment processes simultaneously (Lebreton et al. 2003) and examine the factors determining recruitment into a colony while checking for differences in dispersal patterns between pre-breeders and breeders (Crespin et al. 2006, Hénaux et al. 2007). Multistate models considering reproductive states have been applied to examine

the existence of reproductive costs in a wide range of species including sheep (Tavecchia et al. 2005), Weddel seals (Hadley et al. 2007), storm petrels (Sanz-Aguilar et al. 2008) and meadow voles (Nichols et al. 1994).

Multistate models make the assumption that the state of the encountered individuals is always ascertained, but sometimes we are uncertain about the state in which an animal is found upon capture. In general terms, uncertainty may affect sex assignment, reproductive state or the geographic location of the individual, so one should refer to "events" rather than states to define the field observations (ex: "sitting on an egg", "feeding in a nearby field", or "not observed"). An extension of multistate models with uncertainty in state assignment are the *multievent* models (Pradel 2005). In the multievent approach, both "ones and zeros" are informative and reflect observed events (encountered or not), allowing all encounters of unknown state to be used, including missing or incomplete records. The observed events are the result of different processes linked to different underlying states. For instance, a zero in the encounter history (event "not encountered") may correspond to several processes such as capture failure, temporary emigration out of the study area or the death of the animal (Péron et al. 2010, Sanz-Aguilar et al. 2011a). Field records are codified as events, while states are only included in the model definition, conditioning the probability of any possible event. The definition of unobservable states becomes much more flexible under the multievent framework because the number of states no longer needs to be identical as the number of events and additional states can be added to the model and linked to event "0". This is especially useful in the investigation of processes such as temporal emigration which is modelled under the multievent framework by letting individuals move to an unknown location or "ghost site" that can be explicitly defined as a new state with associated transition probabilities (chapter 3). Another application of the addition of "extra" unobservable states in multievent models is the modelling of recapture heterogeneity. In many studies involving large numbers of marked individuals it is easy to detect heterogeneities in recapture because the more data we have the more likely it is to detect different trap responses in the individual encounter histories. By creating extra states reflecting different "trap" states, and allowing individuals to move between such

states, multievent models are able to correct such heterogeneities and provide more robust estimates of the vital rates of interest (Pradel and Sanz-Aguilar 2012).

Multievent models are the most recent incorporation into the capture-recapture toolbox and provide a general framework for both unistate and multistate models, being also a useful tool to examine hidden processes (e.g. reproductive skipping or influence of past states on transition probabilities; Gimenez et al. 2012) making use of both complete and incomplete records. Despite multievent models are at a higher level of complexity and have seen relatively low implementation compared to other capture-recapture modelling approaches, they have proven very useful for studies aimed at distinguishing capture failures from temporary emigration out of the study area (Sanz-Aguilar et al. 2011a) and have dealt successfully with capture heterogeneity in open populations (Crespin et al. 2008) and uncertainty in state assignment (Genovart et al. 2012).

Occupancy models

Ecological studies often attempt to understand patterns of distribution and abundance of species across the landscape (Andrewartha and Birch 1954), but sometimes such state variables are costly to measure or estimate and it may be more appropriate to use less information-rich but more easy to measure (and less expensive) state variables such as occupancy (MacKenzie et al. 2006, Kéry and Schaub 2011). The study of occupancy simply consists in determining the presence of one or more species in sampling units and sampling programs aimed to obtain a rate of site occupancy (Ψ) or proportion of occupied sites within a study area depart from a situation in which several spatial units are visited by researchers in order to record the presence or absence of a single or several species of interest. The size of the sampling unit can be defined naturally (island, pond, forest fragment) or arbitrarily (plot, transect) and while surveying a sampling site, researchers typically spend their time trying to find individuals or evidence of the presence of the species of interest within the spatial unit, either directly or indirectly. The result of such surveys is a list of sites that are “occupied” (where the species has been detected) and sites that are “unoccupied”

(where the species has not been detected). Contrary to capture-recapture sampling, here the resulting encounter histories are associated to the sampling sites, which constitute our study populations, and not to individually marked animals of a particular population.

The main problem of presence-absence, or more correctly, detection-non detection surveys, is that some places where the species is present but no evidence of it has been collected are erroneously classified as unoccupied (wrong zeros), generating “false absences” in the field data (MacKenzie et al. 2002). Most of the time, the chance to detect a species in a site may be influenced by the environmental conditions during the realization of the survey and by the cryptic nature of the species themselves. The main advantage of occupancy models is that they do not overlook this situation and allow obtaining estimates of occupancy taking into account a probability of species detection, which is analogous to the recapture probability p in the capture-recapture framework. As in capture-recapture analysis, each detection history is a mathematical statement defined using model parameters associated to both ecological (occupancy) and observational processes (detection) and maximum likelihood techniques are used to estimate such parameters (MacKenzie et al. 2006).

Occupancy models designed to analyse data collected during a single sampling season are known as single season occupancy models (MacKenzie et al. 2002, 2006). These models permit to obtain estimates of site-occupancy and species’ detectability thanks to a “Robust design” sampling scheme (Pollock 1982), in which surveys are conducted during a primary time period or season by means of repeated visits to the sites or secondary sampling sessions separated by short time intervals. Occupancy estimates are associated to the primary sampling sessions, so they are season-specific and may be related to site characteristics but not allowed to vary over time (they are “static”), whereas detectability is survey-specific and allowed to show variation over time and among sites. By extending this sampling scheme to multiple seasons or years, we can make inferences about the processes involved in the changes of occupancy over time. These changes are determined by local extinction and colonization rates that can be explicitly included as additional parameters in the model structure and modelled in the light

of different biological hypotheses. These models are known as multi-season occupancy models (MacKenzie et al. 2003) and are especially useful for the study of metapopulation dynamics (Hanski 1998). A recent extension of occupancy models goes beyond simply determining the presence or absence of species in spatial grids and focus on the “state” in which a species is found at a site (Nichols et al. 2007, MacKenzie et al. 2009). Occupancy “states” can be defined using extra information collected in the field about the recorded species such as evidences of reproduction or high/low density of individuals in a patch. Multistate occupancy models are a generalization of both single (static) and multiseason (dynamic) occupancy models in which the occupancy status of the sampling units moves within a finite set of states that go beyond simplistic presence-absence formulations, allowing a clearer understanding of the dynamic processes governing a population system by using spatial information on the species’ activity or relative abundance collected across sites (Martin et al. 2009, 2010).

Many research fields require reliable information on occupancy and seek to predict species occurrence for both fundamental and applied reasons. Single season occupancy models are especially useful for disentangling species-habitat relationships that may be interesting for species niche studies and such knowledge can be applied to predict future occurrence of the species or the most suitable areas for reintroduction projects (Guisan and Thuiller 2005, Price et al. 2011, Breck et al. 2012, Barber-Meyer et al. 2013). Because the study of occupancy involves collection of data over several sites, the sampling design provides a natural framework for the study of metapopulation dynamics. Using multiseason occupancy models, patch occupancy dynamics, or the rate of change in occupancy over time, can be described by vital rates such as local extinction and colonization probabilities, coming closer to the prime metapopulation model (Levins 1969). By extending the classical metapopulation models to account for imperfect detection of species, multiseason occupancy models permit to robustly address important questions about metapopulation dynamics, such as area-extinction relationships, the effects of patch isolation on colonization or trends in extinction/colonization over time, with important implications for the study and conservation of species inhabiting habitat fragments (Ferraz et al. 2007, Van Strien et al. 2011). The lower costs compared to capture-recapture sampling and the flexible modelling tools

available makes occupancy a more appropriate quantitative variable than abundance to describe the status and fluctuation of animal populations across large geographic areas. Occupancy is an important state variable for biodiversity monitoring and of primary interest in large-scale monitoring programs aimed at multiple species of butterflies (see chapter 4), amphibians (Weir et al. 2009) or birds (Mattsson and Marshall 2009). In recent years, the development of multistate occupancy models permits to address finer questions on habitat-occupancy relationships (MacKenzie et al. 2011) and has revealed promising applications in the conservation and management of flagship species (Martin et al. 2009, 2010), which represents a methodological improvement in the use of rather simple data on species' records collected over extended areas with minimum cost and impact on the sampled populations.

Population viability analysis

Capture-recapture and occupancy models are useful tools to estimate key vital rates and to examine the factors affecting population dynamics in space and time. However, the way these vital rates and its variation translate into population viability is an important question in more applied situations involving the management of plant and animal populations (Caswell and Fujiwara 2004, Mills 2007). Viable populations are those that have a low chance of going extinct before a specified future time (Morris and Doak 2002) and the quantification of viability may be achieved by means of population projections or simulation exercises that allow the calculation of future population sizes, population growth rates (λ) and quasi-extinction probabilities.

Population viability analysis (PVA) is an analytical tool that uses population data and models to estimate the probability that a population will persist for a specified time into the future, with emphasis on the quantification of quasi-extinction probability (Beissinger and Westphal 1998, Mills 2007). Quasi-extinction probability reflects the likelihood that the population falls below a quasi-extinction threshold set as the minimum number of individuals (often females) below which the population is critically imperilled and functionally extinct (Morris and Doak 2002, Mills 2007). PVAs may be performed by means

of the analysis of time-series of abundance (count-based PVAs) or by means of matrix population modelling using information on vital rates (Demographic PVAs). Census data is usually more available than information on vital rates, so count-based PVAs may be *a priori* more easily performed than the more data-hungry demographic PVAs. However, from a conservation point of view, demographic PVAs may be more useful for the evaluation of different management actions on the recovery of small, declining populations and conservation practitioners may use demographic PVAs to understand long-term effects of changing demographic rates on lambda (Morris and Doak 2002).

Demographic PVAs rely on matrix population models to predict population size at time $t+1$ from information on vital rates of individuals at time t (Caswell 2001, Beissinger et al. 2008). To conduct a population projection, a population matrix containing the different stages of the population and their vital rates must be constructed. Vital rates values, such as survival rates, are obtained by means of capture-recapture analysis and incorporated into the cells of the matrix, together with other stage-specific values such as fecundity. Once the matrix is filled, it can be projected through time by multiplying it by a vector of elements containing the number of individuals in each stage or age class of the population (Caswell 2001, Mills 2007). Such population projections can be deterministic, if the vital rates have always the same value, or stochastic, if these values are allowed to change over time. Deterministic population projections may be used to obtain the proportion of individuals at each stage of the population when the stable age distribution (SAD) is reached and mean values of population growth rate, as well as the quantification of the life stage mostly contributing to population growth (the one with the highest reproductive value). However, in real-world populations, vital rates are unlikely to remain constant over time, so adding stochasticity (both demographic and environmental) into matrix population models allows more realistic projections and this can be achieved by giving to the vital rates values that at each time step are taken from distributions based on mean rate values and process variance (Morris and Doak 2002, Mills 2007). These values may be also deliberately changed in order to quantify the relative importance of different vital rates and management actions on population persistence. Such exercises are known as sensitivity analyses, when absolute

changes in both vital rate and lambda values are evaluated or elasticity analysis when the evaluation concerns proportional changes in lambda given proportional changes in a vital rate (Caswell 2001, Naujokaitis-Lewis et al. 2009, Chirakkal and Gerber 2010). Sensitivities and elasticities of stage-specific survival and fertility rates provide managers with guidelines on the relative contributions of various life-history stages to long-term population growth (Mills 2007).

Demographic PVAs have been applied to forecast population response to environmental change, providing quasi-extinction likelihoods under different scenarios for species inhabiting vulnerable areas due to global change agents such as climate warming (Jenouvrier et al. 2009, Hunter et al. 2010) or fire (Sanz-Aguilar et al. 2011b), and to evaluate the future outcome of management actions on population fate (Doak et al. 1994, Fernández-Olalla et al. 2012). This is also useful to evaluate the conservation status of poorly known species, contrasting the effects of demographic vs. environmental stochasticity on population persistence (Fujiwara and Caswell 2001, Oro et al. 2004b). In all cases, the use of PVA provides answers of high conservation value on the consequences of particular management actions or future environmental conditions and such simulations are nowadays an essential tool for conservation biologists. However, the goal of PVAs is not to give a precise answer about the date of extinction of a population but to enable a more informed decision about long-term conservation, by comparing risk of extinction associated with different future scenarios.

Objectives

Thesis aims and outline

Throughout this thesis I have moved between the basic and applied ecological science with the aim to explore the applications of both classical and recently developed analytical tools for the study of population dynamics at different scales on different animal taxa (reptiles, fish, birds and insects) showing a variety of life history traits and conservation status. This thesis is divided in 4 chapters or case studies, each of them representing different analytical approaches (figure 1) and different biological questions (see below), ordered following increasing levels of ecological complexity, from studies on discrete and isolated populations to studies on multiple species living in population networks.

To carry out this thesis, field data were provided by different researchers through collaborations with several institutions and organisations. For three consecutive years (2009-2011), I participated in the collection of capture-recapture data on Mediterranean tortoise (*Testudo hermanni*; Chapter 1) and Audouin's gull (*Larus audouinii*; Chapter 3) at the Ebro Delta Natural Park (Tarragona, Spain); these species have been monitored at this site for more than two decades, allowing to base my analyses in the long-term datasets available both at my home institution (IMEDEA, CISC-UIB) and those provided by Dr. Albert Bertolero Badenes (IRTA) and the people responsible of the monitoring of Audouin's gull at the different Spanish colonies of the species (Balearic Government, Doñana Biological Station and Picampall association), which coauthor the study presented in chapter 3. Dr. Alfredo G. Nicieza, professor at the University of Oviedo, provided the capture-recapture data on brown trout analysed in chapter 2 and the collaboration with Dr. Constantí Stefanescu, coordinator of the Catalan Butterfly Monitoring Scheme (CBMS) provided the detection-non detection data for the analyses of butterflies in chapter 4. A general outline of each chapter is as follows.

In chapter 1, with the aim to conduct a robust conservation diagnosis, I studied the effects of climatic variability on the survival and ultimately on population growth and persistence of the Mediterranean tortoise, an endangered reptile species in Spain and potentially vulnerable to rapid climatic shifts. To achieve this objective, I first analysed a high quality capture-recapture dataset on the tortoise population found in the Ebro delta Natural Park by means of CJS models to obtain age-dependent survival estimates and to assess the relationship between survival and meteorological variables. Then, I constructed an age-structured matrix population model to perform a demographic PVA and I projected the study population under 3 future climatic scenarios for the 21st century, repeating this exercise for 10 additional tortoise populations found across the geographic distribution of the species. To my knowledge, this is the first attempt to model population responses to climate change over the entire geographic distribution of a species of reptile.

In chapter 2, I expanded the modelling of demographic rates to several discrete populations and groups of individuals within populations using multistate models. I analysed a 6-year capture-recapture dataset from a system of three discrete brown trout populations inhabiting small streams in the Picos de Europa National Park in Northern Spain to investigate whether stream habitat characteristics or temperature were determining spatial differences in individual survival and growth. In this case, multistate models, by treating size class as a dynamic state, allowed to obtain estimates of individual survival, growth and maturation probabilities for the three study sites, obtaining contrasting patterns of growth between streams and also evidences of size-dependent survival at all but the smallest stream, where mortality was not associated to the size-state of the individual but seemed to be more influenced by winter severity.

In chapter 3 I focused on the study of the dispersal process by applying multievent models to a large multistate capture-recapture dataset collected in 4 breeding colonies of Audouin's gull in the Western Mediterranean. The practical difficulties to get information on immigration and emigration have made dispersal a largely ignored process in most population studies, despite its relevance for population dynamics and metapopulation persistence. In this case, I took

advantage of the multievent approach to examine unobservable processes such as temporal emigration and solve problems with recapture heterogeneity, which is common in datasets containing many individual encounter histories. I was also able to decompose the dispersal process into their fidelity and settlement components to investigate the mechanisms involved in fidelity and settlement decisions. Using this approach, site-fidelity could be estimated and compared among sites and hypothesis regarding increasing trends in departure from the largest colonies could be evaluated. Settlement estimates provided insights about the destination sites of dispersers, revealing movements to other sites out of the study area. In this chapter, I performed a post-hoc analysis of settlement that had never been attempted before given the novelty of the software developed for the construction of multievent models. This post-hoc analysis revealed that, within the study area, settlement decisions were ruled primarily by population size, with dispersers using the density of conspecifics as an informative cue for habitat selection.

In chapter 4, I expanded the study of spatially structured populations to multiple insect species and used multi-season occupancy models to obtain reliable species' extinction and colonization estimates and to assess the effects of habitat and environmental features of the local patch and surrounding landscape on extinction-colonization dynamics. More specifically, I applied a set of 60 candidate models to detection-nondetection data on 73 butterfly species sampled under the Catalan Butterfly Monitoring Scheme CBMS, a network of monitoring sites in North Eastern Spain and the oldest and most extended butterfly monitoring program in Southern Europe, with the aim to make a diagnosis of the status of this rich butterfly community and the causal factors impacting their metapopulation dynamics in space and time. A first result was to obtain species-specific extinction and colonization rates that, when compared between species' categories of dispersal and habitat specialization, revealed some influences of the species' traits on these parameters. The analysis of model results for each species' allowed inferences on the main factors conditioning population turnover across species and among species' groups, providing useful scientific information for the development of conservation plans aimed at both particular species and entire communities.

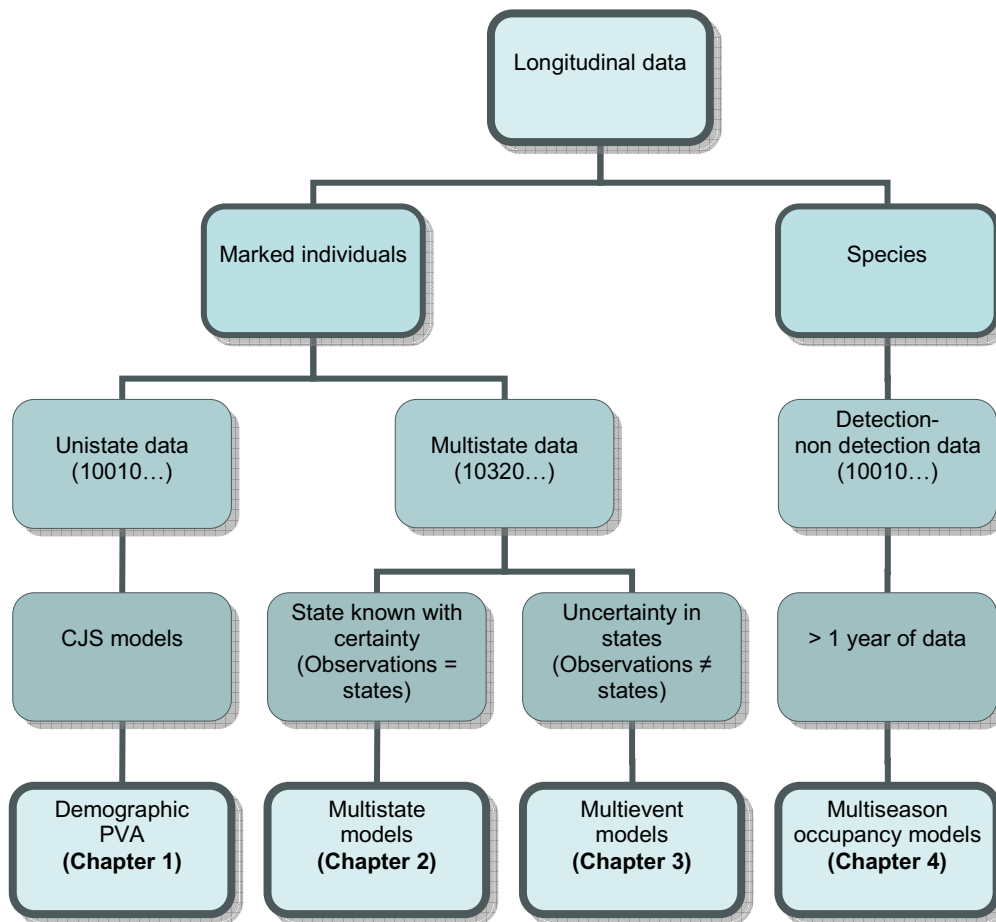


Figure 1. Diagram showing the process and criteria followed in the selection of the different analytical tools used in this thesis and the chapters where these tools have been applied.

Resum de les publicacions

Article 1. Heterogeneïtat espacial en els efectes del canvi climàtic sobre les dinàmiques poblacionals d'una tortuga mediterrània.

Resum:

Les variacions climàtiques poden augmentar el risc d'extinció de les poblacions, especialment d'aquelles que ja es veuen afectades per factors antròpics. La nostra capacitat de predicció de les conseqüències del canvi climàtic en espècies amenaçades és bastant limitada degut a l'escàs coneixement dels efectes que la variabilitat climàtica té en les dinàmiques poblacionals i la incertesa de les projeccions climàtiques, les quals varien en funció de la regió de la Terra que estiguem considerant.

En aquest estudi es varen analitzar dades d'un programa de seguiment a llarg termini (1988-2009) de tortuga mediterrània (*Testudo hermannii*) amb l'objectiu d'avaluar les conseqüències dels canvis en temperatura i precipitació pronosticades per la regió Mediterrània en la demografia d'una espècie de vida llarga amb poca capacitat de dispersió i sotmesa a un gran nombre d'ameneses. L'aplicació de models uniestat per l'anàlisi de dades de captura-recaptura d'individus marcats d'una població de tortugues del Delta de l'Ebre (Catalunya) ens va permetre avaluar l'efecte de la variabilitat climàtica local en la supervivència per edats. La pluja d'hivern va resultar el millor predictor de la mortalitat anual de juvenils i immadurs, mentre que la supervivència adulta es va mantenir alta i constant durant tot el període d'estudi. A continuació, utilitzant sèries temporals de precipitació obtingudes *ad hoc* per mitjà de simulacions climàtiques regionals per aquesta i 10 altres localitats mediterrànies amb presència de tortugues, es va fer un exercici de projecció d'aquestes poblacions sota 3 escenaris futurs de precipitació (humit, sec i intermedi) fent servir models matricials de poblacions amb estocasticitat ambiental.

El resultat mostren que un canvi cap a un clima més àrid tindria conseqüències negatives per a la persistència de les poblacions, causant una greu

mortalitat de juvenils i augmentant el risc d'extinció local degut a una davallada en reclutament. Encara que aquests processos varien segons la població i l'escenari climàtic considerat, els resultats obtinguts indiquen que si la mortalitat lligada a causes antròpiques (ex: caça furtiva, incendis, fragmentació de l'hàbitat) no desapareix, les variacions climàtiques pronosticades augmentaran els riscos d'extinció de l'espècie a gran part de la seva àrea de distribució actual.

Paraules clau: projeccions climàtiques, demografia, risc d'extinció, matrius poblacionals, precipitació, supervivència, *Testudo hermanni*.

Article 2. Poblacions veïnes, dinàmiques oposades: patrons de supervivència i creixement de la truita comuna (*Salmo trutta*) en rierols de muntanya.

Resum:

L'estudi de la dinàmica de les poblacions animals es recolza en el seguiment en el temps d'individus marcats per tal de desentranyar els factors que influencien trets d'història de vida com els patrons de creixement i supervivència. Els salmònids residents en ambients fluvials estacionals són models d'estudi ideals per dur a terme aquest tipus d'investigacions, però degut a que molts estudis es centren en poblacions o estadis vitals concrets, i a més la detecció dels individus és imperfecta, el nostre coneixement sobre els patrons de supervivència i creixement en salmònids i les causes de la seva variació és encara incomplet.

En aquest estudi es va analitzar una base de dades de captura-recaptura de truita comuna (*Salmo trutta*) obtinguda per mitjà del seguiment d'individus marcats durant un període de 6 anys (1996-2001) en un sistema de 3 rierols de muntanya aïllats al parc nacional de Picos de Europa (Astúries). Les característiques de cada rierol (ex: elevació, composició faunística i llargària) diferencien a cada població de truites, tot i compartir un mateix paisatge protegit on la pesca està prohibida. Les dades van ser analitzades per mitjà de models multiestat per tal d'obtenir estimes fiables de les taxes de supervivència i creixement individual corregides per la probabilitat de recaptura, i també per testar hipòtesis biològiques concretes sobre aquests processos vitals.

La selecció de models revelà una supervivència variable en el temps i entre poblacions. En tots els rierols es va trobar un efecte de la mida corporal en la supervivència dels individus, excepte en el rierol més petit on tampoc es detectà depredació ni presència d'un recurs tròfic important: el cranc de riu. En aquest rierol, un 88% de la variació temporal en supervivència va ser explicada per les variacions en la temperatura de l'aigua durant els mesos d'hivern, i a més, el peixos mostraren unes taxes de maduració baixes. La resta de poblacions, en rierols més grans, varen presentar taxes de maduració idèntiques entre sí i significativament majors que les del rierol més petit.

Els nostres resultats suggereixen que les diferents condicions ambientals de cadascun dels rierols influencien de manera directa les taxes de supervivència i creixement locals, fent que poblacions veïnes mostrin dinàmiques totalment oposades. Aquesta recerca posa de manifest la necessitat de dur a terme estudis en múltiples poblacions i estadis vitals com a prerequisit en la recerca de les causes de variació en els trets d'història de vida i també per a una correcta gestió de poblacions discretes de truita comuna.

Paraules clau: models multiestat, *Salmo trutta*, hàbitat fluvial, maduració, mortalitat dependent de la mida, severitat de l'hivern, E-SURGE.

Article 3. Quan quedar-se, quan dispersar i cap a on anar: patrons de supervivència i dispersió en una població d'aus marines estructurada en l'espai.

Resum:

La dispersió és un procés clau per a les dinàmiques de poblacions estructurades en l'espai (tant a escala local com a escala metapoblacional), de manera que entendre els mecanismes que regulen el moviment d'individus en l'espai i en el temps és important tant des d'una perspectiva ecològica com evolutiva.

En aquest estudi es va analitzar, per primera vegada, una base de dades de captura-recaptura recollides a llarg termini (1992-2009) en quatre poblacions locals o colònies reproductores d'una au marina de vida llarga, la gavina corsa (*Larus audouinii*), que en conjunt sumen prop del 90% de la població mundial de l'espècie. Aquestes colònies mostren diferències ecològiques i demogràfiques que permeten estudiar la influència de diferents factors potencialment involucrats en els patrons de dispersió reproductora a una escala temporal i espacial grans. L'ús de models multievent, una eina recent en l'anàlisi de dades de captura-recaptura, ens va permetre obtenir estimes separades de probabilitats d'emigració i assentament, creant un marc analític ideal per a testar diferents hipòtesis biològiques per a cada pas del procés de dispersió.

Els resultats obtinguts revelaren que la fidelitat a la colònia de cria era l'estratègia més comuna entre els individus reproductors, amb taxes d'emigració molt baixes a totes les colònies excepte la més petita i amb pitjor qualitat d'hàbitat. No obstant això, la dispersió reproductora augmentà all llarg del període d'estudi a les dues colònies més grans com a resposta a pertorbacions ecològiques severes. Els individus en dispersió varen assentar-se en colònies de cria diferents, segons el seu origen, triant preferentment com a destí les colònies amb major mida poblacional abans que les colònies més properes o aquelles amb major èxit reproductor o àrea de plataforma continental (un indicador de la disponibilitat d'aliment). Els nostres resultats indiquen que una colònia reproductora no és abandonada fins que tenen lloc una sèrie de pertorbacions acumulades en el temps; un cop iniciada la dispersió, els individus es dirigeixen cap aquelles colònies més densament poblades, fent servir la mida poblacional com a indicador de la qualitat de la colònia de destí per a l'assentament.

Article 4. Determinants de les dinàmiques d'extinció i colonització en papallones mediterrànies: el paper del paisatge, el clima i el tipus d'hàbitat local.

Resum:

Moltes espècies presenten avui en dia poblacions fragmentades que es troben ocupant reductes d'hàbitat natural immersos en paisatges fortament humanitzats. La persistència d'aquesta xarxa de fragments poblacionals requereix d'un equilibri entre processos d'extinció i colonització els quals s'assumeix que depenen principalment de l'àrea i grau aïllament dels respectius fragments d'hàbitat, tot i que la contribució d'altres factors com les característiques de l'hàbitat dins i fora del fragment (matriu de paisatge), els trets propis de cada espècie (capacitat de dispersió, grau d'especialització) o la variabilitat climàtica local ha estat poques vegades avaluada de manera simultània.

La identificació de variables ambientals associades a l'ocupació de fragments d'hàbitat i el recanvi poblacional pot resultar especialment útil per als esforços de conservació de múltiples espècies sota l'actual escenari de canvi global. No obstant això, per a una estimació robusta de les taxes d'ocupació i paràmetres relacionats, s'ha de tenir en compte l'error de detecció, un problema sovint ignorat que pot donar lloc a estimes esbiaixades i conclusions equivocades sobre les dinàmiques poblacionals.

En aquest estudi es mostren evidències empíriques directes sobre els efectes de diferents variables ambientals en les taxes d'extinció i colonització d'una rica comunitat de papallones del Mediterrani occidental. L'anàlisi es recolza en una base de dades de 17 anys composta per dades de detecció-no detecció d'espècies recollides en 26 transectes distribuïts per Catalunya i Balears. Per mitjà de models d'ocupació, que tenen en compte la detectabilitat de les espècies, es varen obtenir estimes robustes de les probabilitats d'extinció i colonització locals per a cada espècie i es varen comprovar els efectes potencials de diferents variables externes com l'àrea d'hàbitat favorable i la variabilitat topogràfica dins el transecte, la permeabilitat del paisatge al voltant del transecte i la variabilitat temporal en aridesa local.

El resultat demostren l'existència d'un patró general a nivell de totes les espècies on la composició de l'hàbitat i la permeabilitat del paisatge destaquen com a millors predictors de les dinàmiques d'ocupació, per damunt de la topografia i l'aridesa local. Una major àrea d'hàbitat favorable dins el transecte redueix fortament el risc d'extinció local i per a un gran nombre d'espècies, tant una major quantitat d'hàbitat com una major permeabilitat del paisatge augmenta les taxes de colonització locals. Un altre resultat destacable és que l'augment en la variabilitat topogràfica redueix el risc d'extinció d'espècies amb poca capacitat de dispersió, les quals també mostren taxes de colonització significativament més baixes. Les prediccions dels models indiquen una major sensibilitat de la comunitat de papallones estudiada a canvis deterministes en les característiques de l'hàbitat que a canvis estocàstics en els patrons meteorològics, amb algunes relacions clarament influenciades pels trets biològics propis de cada espècie.

Paraules clau: Punt calent de biodiversitat, Precipitació efectiva, Lepidòpters, Programa de seguiment, Dinàmiques d'ocupació, PRESENCE, Heterogeneïtat espacial, aliances d'espècies.

Director's report

Report of the directors of the Ph.D. Thesis in reference to its derived publications and the student's contribution to them

Dr. Daniel Oro de Rivas, Professor of Research at CSIC and Director of the Biodiversity and Conservation Department at IMEDEA (CSIC-UIB), Esporles, Mallorca, Spain, as PhD supervisor
and,

Dr. Meritxell Genovart Millet, member of the research group PEG (Population Ecology Group) at IMEDEA (CSIC-UIB), as co-supervisor
of the Ph.D. Thesis authored by Mr. Albert Fernández Chacón entitled *Demographic analysis and population models in ecology, evolution and conservation: a transversal approach with case studies*.

INFORM

That the results and conclusions achieved in the research developed by Mr. Albert Fernández-Chacón as part of his Ph.D. Thesis have been organised in 4 chapters which correspond to 2 publications and 2 manuscripts (one of them in second review round and the other ready to be submitted). Following, the list of publications and manuscripts is shown, indicating the journal impact factor IF (according to SCI of ISI Web of Knowledge, Journal Citation Report-2011) as well as the median impact factor of the main subject categories and the position of the journal within the corresponding category.

1. Fernández-Chacón, A., Bertolero, A., Amengual, A., Tavecchia, G., Homar, V., Oro, D. 2011. Spatial heterogeneity in the effects of climate change on the population dynamics of a Mediterranean tortoise. *Global Change Biology* 17: 3075–3088. Impact Factor: 6.862. This journal is reported in the subject 'Ecology' and its median impact factor is 2.393, being the 14th of 259 journals in the subject area (Q1).
2. Fernández-Chacón, A., Genovart, M., Álvarez, D., Cano, J.M., Ojanguren, A.F., Rodríguez-Múñoz, R., Nicieza, A.G. Neighbouring populations, opposite dynamics: survival and growth patterns of brown trout *Salmo trutta* in mountain streams. To be submitted to the *Journal of Animal Ecology*. Impact Factor: 4.937. This journal is reported in the subject "Ecology" and its median impact factor is 2.393, being the 30th of 259 journals in the subject area (Q1).
3. Fernández-Chacón, A.; Genovart, M.; Pradel, R.; Tavecchia, G.; Bertolero, A.; Piccardo, J.; Forero, M.G.; Afán, I.; Muntaner, J.; Oro, D. 2013. When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured population of a long-lived seabird. *Ecography* (in press). DOI: 10.1111/j.1600-0587.2013.00246.x. Impact Factor: 4.188. This journal is reported in the subject "Ecology" and its median impact factor is 2.393, being the 39th of 259 journals in the subject area (Q1).

4. Fernández-Chacón, A.; Stefanescu, C.; Genovart, M.; Nichols, J.D.; Hines, J.E.; Páramo, F.; Turco, M.; Oro, D. Determinants of extinction-colonization dynamics in Mediterranean butterflies: the role of landscape, climate and local habitat features. 2nd round of review in the Journal of Animal Ecology. Impact Factor: 4.937. This journal is reported in the subject "Ecology" and its median impact factor is 2.393, being the 30th of 259 journals in the subject area (Q1).

and CERTIFY

that Mr. Albert Fernández-Chacón contribution has been very active, as it is demonstrated by his first co-authoring of all the manuscripts that conform this Ph.D. Thesis. Concretely, his participation included the following tasks:

- Definition of the objectives and focus of the research and its derived manuscripts.
- Experimental design and fieldwork, statistical analysis and ecological modelling:
 - Capture-recapture modelling
 - Multi-event models
 - Occupancy models
 - Stochastic population models
- Results compilation and data analysis and interpretation.
- Tables and Figures design and preparation.
- Main writing of the manuscripts, and contact person for the reviewing and editing process.

Finally, we certify that any of the co-authors of the manuscripts detailed above has used, neither is going to use, implicitly or explicitly, the information produced and presented with the purpose of elaborating another Ph.D. Thesis.

Esporles, 21 May 2013

Dr. Daniel Oro

Dr. Meritxell Genovart

Chapter 1

Spatial heterogeneity in the effects of climate change on the population dynamics of a Mediterranean tortoise

Albert Fernández-Chacón, Albert Bertolero, Giacomo Tavecchia, Arnau Amengual, Victor Homar, Daniel Oro (2011). *Global Change Biology* 17, 3075–3088.

Photo credit: Albert Bertolero Badenes



Spatial heterogeneity in the effects of climate change on the population dynamics of a Mediterranean tortoise

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Abstract

Climatic shifts may increase the extinction risk of populations, especially when they are already suffering from other anthropogenic impacts. Our ability to predict the consequences of climate change on endangered species is limited by our scarce knowledge of the effects of climate variability on the population dynamics of most organisms and by the uncertainty of climate projections, which depend strongly on the region of the earth being considered. In this study, we analysed a long-term monitoring programme (1988–2009) of Hermann's tortoise (*Testudo hermanni*) aimed at evaluating the consequences of the drastic changes in temperature and precipitation patterns predicted for the Mediterranean region on the demography of a long-lived species with low dispersal capability and already suffering a large number of threats. Capture–recapture modelling of a population in the Ebro Delta (NE Spain) allowed us to assess the effect of climate variability on the survival of tortoises. Winter rainfall was found to be the major driver of juvenile and immature survival, whereas that of adults remained high and constant across the study. Furthermore, local climate series obtained ad hoc from regional climate simulations, for this and 10 additional Mediterranean locations where tortoises occurred, provided us with reliable future climate forecasts, which were used to simulate the fate of these populations under three precipitation scenarios (mean, wet and dry) using stochastic population modelling. We show that a shift to a more arid climate would have negative consequences for population persistence, enhancing juvenile mortality and increasing quasiextinction risk because of a decrease in recruitment. These processes varied depending on the population and the climate scenario we considered, but our results suggest that unless other human-induced causes of mortality are suppressed (e.g. poaching, fire, habitat fragmentation), climate variability will increase extinction risk within most of the species' current range.

Keywords: climate projections, demography, extinction risk, population matrices, precipitation, survival, *Testudo hermanni*

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Introduction

Climate change, manifested through global warming and changes in the distribution, amount and frequency of precipitation, is a major cause of concern worldwide as its impacts on all ecosystems are becoming increasingly apparent (IPCC, 2007; Parmesan and Yohe 2003). Observational evidence indicates that the average temperature of the globe has increased by about 0.74°C over the last four decades, and that this trend is inducing some ecological responses such as changes in phenology, shifts in species distribution and changes in community composition (Walther et al. 2002; McCarty, 2001; Parmesan and Yohe, 2003; Root et al. 2003).

Ecological responses to climate change are mediated by local rather than by global changes in temperature and precipitation patterns. The spatial heterogeneity of climatic conditions across a species range calls for examining responses at the population level when studying species' responses to climate change (Wolf et al. 2010; Grosbois et al. 2006). Local changes have a direct impact on demographic rates (Saether et al. 2000; Sillett et al. 2000; Forchhammer et al. 1998; Coulson et al. 2001; Jenouvrier et al. 2005), modifying local population dynamics and resulting population-specific responses across the geographic range of a species (McCarty, 2001). The species' inherent ability to withstand climatic shifts determines the type of responses displayed and thus the vulnerability of its populations to local environmental changes; species with low dispersal capability and with populations occurring in fragmented habitats will be unlikely to adapt to rapid environmental changes by shifting their geographic distribution and colonizing new suitable areas in different altitudes or latitudes (Root & Schneider 2006, Loss et al. 2010, Foufopoulos et al. 2011). Hence their persistence will depend strongly on the degree of variation in local conditions, with potentially higher extinction risks in areas already suffering population declines due to non-climatic stressors and where important changes in climate are predicted (Sala et al. 2000, McCarty 2001, Walther et al. 2002, Parmesan & Yohe 2003, Foufopoulos et al. 2011).

As a consequence, it is essential to forecast the future responses of natural systems to changes in the climatic conditions in order to implement mitigation strategies aimed at increasing or maintaining the resilience of organisms to such

changes (Hannah et al. 2002, Coenen et al. 2008, Hagerman et al. 2010, Hansen et al. 2010). Long-term datasets of populations occurring in relatively undisturbed areas enable us to correlate life-history parameters and population trends to climate variability without the confusing effects of other stressors in the underlying climatic trend (Parmesan and Yohe, 2003). However, these datasets are rare and many studies that investigate the regional consequences of climate change on the biota rely on species-specific climatic envelopes to forecast species distributions under future climatic scenarios (Rebello et al. 2010) rather than forecasting population responses to projected regional climate changes (but see (Jenouvrier et al. 2009; Wolf et al. 2010)).

Reptiles have recently been considered a vulnerable taxonomic group, given that important population declines have been detected worldwide and that climate change is suspected to be one of the drivers of this global trend (Gibbons et al. 2000). Among reptiles, land tortoises (family Testudinidae) are likely to be the most vulnerable, given their low dispersal capabilities, their occurrence in fragmented habitats and that most species are already threatened (26 of the 32 evaluated species; IUCN 2010). These features should be particularly important in arid and semi-arid ecosystems such as the Mediterranean region. Sala et al. (2000) classified the Mediterranean basin as one of the regions where the consequences of climate change will be more pronounced, forecasting dramatic losses in biodiversity. Indeed, recent observations reveal a surface warming trend of 0.25 to 0.35°C per decade over the last 40 years and a decrease in annual precipitation amounts between 5-20% for the same period, and these trends are expected to continue in the future (IPCC, 2007), in addition to a higher frequency of drought events and heat waves (Piervitali et al. 1997). Rainfall patterns are more difficult to predict than temperature due to the local variability imposed by topography, distance from the sea and land use (Gao et al. 2006), but precipitation is likely to increase its seasonal character, and occur in the form of intense events (Sánchez et al. 2004). These predicted trends will contribute to a general increase in aridity over the entire Mediterranean region (Christensen et al. 2007).

Here we examine the effects of climate variability on the population dynamics of Hermann's tortoise (*Testudo hermanni*), a threatened reptile species endemic to the Mediterranean region, in order to forecast the population responses to the regional climate changes predicted for this area. Hermann's tortoise occurs

throughout the entire European Mediterranean region. Factors such as habitat destruction, illegal collection for the pet trade, use of pesticides, forest fires, and increase in predation pressure are generally thought to be responsible for the decline of Hermann's tortoises (Hailey, 2000; Stubbs et al. 1985; Stubbs and Swingland, 1985; Guyot and Clobert, 1997; Matache et al. 2006; Cheylan, 2001; Rozyłowicz and Dobre, 2009). Nevertheless, the role of climatic variability (which may be additive to the other drivers of population decline) in the population dynamics of tortoises and other reptiles remains poorly understood (but see Converse et al. 2005, Chamaillé-Jammes et al. 2006), and to our knowledge there is no information on the magnitude of the demographic responses to future regional climate changes in any ectothermic vertebrate. To shed some light upon the matter, we begin by assessing the correlation between local climate variability and survival rates using data from a long-term monitored population in the Ebro Delta (western Mediterranean) inhabiting a semi-arid environment and lacking anthropogenic disturbances. Then we will build stochastic population models to investigate the consequences of future climate variability for the whole geographical range of the species distribution. Instead of using general circulation models, which cannot resolve regional particularities of climate (Tabor & Williams 2010), here we use a set of regional climate simulations for the 21st century and derive local series using an empirical calibration method that improves climate projections by accounting for local relevant factors for the study populations, allowing us to make more realistic predictions of their quasi-extinction probabilities under several possible future climate scenarios.

Materials and methods

Study area and population

This study was carried out at Punta de la Banya reserve, a protected area located in the Ebro Delta Natural Park (NE Spain, 40° 37'N, 00°35'E, Fig.1). Punta de la Banya is a flat sandy peninsula covering 2514 ha, connected to the mainland by a long, narrow natural isthmus. Its legal protection and relative isolation from the

mainland guarantee a lack of human disturbances, fire events and, most of the time, intrusions of terrestrial predators into the area (for more details see Bertolero *et al.*, 2007a, b). The area lies within the thermo-Mediterranean climatic zone, with more than a third of the annual precipitation being registered in autumn. Meteorological data collected in the Park (see below) show a mean daily temperature of 16.8°C and a mean annual rainfall of 474.7 mm; these values are within the range of a semi-arid ecosystem (Quézel & Barbero 1982).

As part of a local conservation effort aimed at Hermann's tortoises, 44 individuals were released in the southern portion of the reserve between 1987 and 1988, with a second batch of 22 individuals released between 1997 and 1998 (see Bertolero 2002, Bertolero *et al.* 2007b). Prior to the first release, the punta de la Banya lacked any established population of Hermann's tortoise although the area lies within the historical range of the species (Bertolero & Martínez-Vilalta 1994). Reintroduced individuals were a mixture of adults and subadults from captive populations in different Spanish localities but all belonging to the western subspecies *T. h. hermanni*. All released tortoises were marked individually with notches in the carapace (see Bertolero *et al.* 2007b for more details). Reproduction was recorded soon after the first release (Bertolero, 2002; Bertolero *et al.* 2007a).

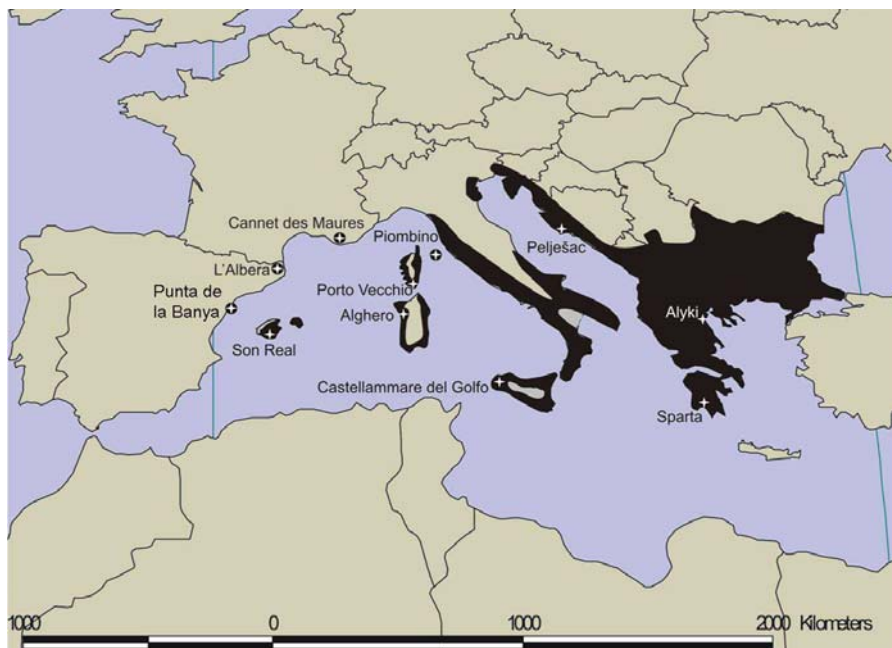


Fig. 1 Present-day geographic distribution of the Hermann's tortoise and location of the populations mentioned in this study.

Capture-recapture data

Our capture-recapture monitoring was focused on those tortoises born in the wild at Punta de la Banya reserve (descendants of reintroduced adults). Tortoises were visually encountered by walking across the release area and its surroundings. Tracks left on the sand and the hearing of tortoise's movement through the bush helped in our search. One person (A. Bertolero) was involved in the surveys 85% of the days, whereas in the remaining 15%, surveys were performed by that person accompanied by 1 to 7 observers (mean: 2.0, SD: 0.1). When first encountered, tortoises were marked with notches in the carapace for future recognition and their age was estimated by carapace size and by counting the number of growth rings in the scutes, following Bertolero *et al.* (2005). Thanks to the annual monitoring of the population, those individuals showing deteriorated notches or those in their growth stages were re-marked to avoid tag loss or future misidentification of doubtful animals.

The first wild-born tortoises were detected in autumn 1988, but capture-recapture sampling did not start until 1991. Since then, continuous annual monitoring has resulted in a 19-year long capture-recapture dataset (1991-2009). Tortoises were captured or recaptured each year from April to June, a period of negligible length when compared to the between-captures interval (see Lebreton *et al.* 1992), which ensures mortality to be more likely outside the sampling months. Here we only included those individuals born in the wild since 1988, because they were the only known-age individuals, which allowed us to include age classes in the survival analysis. Most wild born individuals (77%) were first encountered at age 0 and 1 (tortoises within their first and second years of life), but some of them were first encountered several years after birth. Individuals were sorted according to their age at first marking into 14 different groups (from age 0 to age 13, the oldest age at which one animal was first encountered). Considering that the first individuals were born in autumn 1988, a wild animal first caught in spring 1991 could be either 0, 1 or 2 years old, and since our dataset goes from 1991 to 2009, the maximum possible age attained by a monitored tortoise was 20 years. Thus, our age-at-first-marking groups were

combined with the time since marking to build 20 age classes for survival analysis.

Local weather data

We obtained local meteorological records from 1991 to 2009 taken at the Ecomuseum Meteorological Station located in Deltebre, 17 km away from the study area. To test the effects of climate on tortoise survival, we used monthly values of temperature and accumulated rainfall. We were interested in year-round weather data, excluding the sampling months (April to June) for correlating the observed weather with the survival probabilities estimated for each year. Weather during hibernation (November to February), post-hibernation (March), and summer months (July to September) may have consequences for the survival of tortoises (Converse *et al.* 2005; Díaz-Paniagua *et al.* 2001). In our analysis we used the following environmental covariates: winter rainfall (total rainfall from November to February), summer rainfall (total rainfall from July to September), March rainfall (total rainfall in March), winter temperature (average minimum temperature from November to February), and summer temperature (average maximum temperature from July to September). Rainfall was supposed to be a biologically relevant covariate for our study species as it determines water and food availability, leading us to the prediction of a positive relationship between rainfall and tortoise's survival. More specifically, dry winters would be detrimental for Hermann's tortoise's survival by inducing mortality through dehydration during hibernation (Gregory 1982) and through a reduction in the amount of food availability in the following spring. March rainfall maybe critical for recovering hydration level after hibernation, whereas summer drought may increase tortoise's mortality by desiccation and starvation (Peterson 1994). We did not consider rainfall during late spring (April-June) as a covariate because this period overlapped with sampling and survival was estimated out of the sampling months; the fact that these months corresponded to both the end and beginning of two consecutive annual intervals makes the effect of late spring rainfall on survival difficult to assess since it may affect simultaneously the survival estimated at both intervals. In terms of temperature we expected that the coldest days would have the largest potential to reduce the survival of overwintering

tortoises, so we used minimum temperatures to check our prediction of a positive relationship between winter temperature and survival. In summer, the highest temperatures would have the largest potential to reduce survival, so we used maximum temperatures to check for a potential negative relationship between summer temperature and survival.

Capture-recapture modelling

Our capture-recapture dataset was analysed using Cormack-Jolly-Seber (CJS) and related models to obtain separate estimates of both survival and recapture probabilities (Lebreton *et al.* 1992). This approach does not differentiate mortality from permanent emigration, so that the obtained survival estimates must be referred to as local or apparent survival rates. However, in our long term monitoring programme, individuals that have not been detected in a previous year (due to dispersal to less surveyed sites; see figure 1 in Bertolero *et al.* 2007b) may be recaptured in subsequent sampling occasions the following years, so a continuous monitoring allowed us to control for dispersal within the study area and obtain local survival rates that may be really close to real survival rates.

Prior to the modelling of our capture-recapture data, a Goodness-Of-Fit (GOF) test was performed using program U-CARE (Choquet *et al.* 2005) to make sure that the data followed the CJS model assumptions (Lebreton *et al.* 1992). Due to a high capture effort in the field (nearly all adult individuals were captured and/or recaptured each year, see Bertolero 2002) and the low dispersal rates of tortoises, we expected a low proportion of transients (individuals caught once but never recaptured again).

The large number of age classes considered increased the complexity of model notation, because a given effect can be important for one age class or parameter, but not for others. We chose a model notation similar to the one used in Catchpole *et al.* (2000), in which each modelled parameter was separated by a “/” symbol. The model assuming a full age effect (20 age classes) for the survival probability, Φ , and recapture probability, p , was then denoted $\Phi_0/\dots/\Phi_{19}$, $p_0/\dots/p_{19}$. The subscript indicates the age of the tortoise and the symbol “/.../” indicates that all age-classes in between were modelled separately. To simplify model structure, we grouped the age parameters that had similar values into a

single class: the age classes were denoted by the first and the last age of the class joined by the underscore symbol “_”. For example, a model assuming the same survival for individuals from age 6 to 19 was noted as Φ_{6_19} . The effect of time was denoted in brackets after the parameter as (t); therefore, full age and time interactions were expressed as $\Phi_0(t)/\dots/\Phi_{19}(t)$, $p_0(t)/\dots/p_{19}(t)$. Additivity between parameters was denoted with the symbol “//”, and when parameters were assumed to vary in parallel over time, with no interaction, the notation was $\Phi_0(t)//\dots//\Phi_{19}(t)$, $p_0(t)//\dots//p_{19}(t)$.

Models were built using program M-SURGE (Choquet *et al.* 2004). We began with the modelling of the recapture probability p , considering a first model with full interaction of age and time in both survival and recapture. Once we found the best model for p , we kept this structure to model survival following the same procedure to obtain a consensus model, a parsimonious model for both recapture and survival. Afterwards, climatic covariates were introduced, and the amount of variation in survival explained by the covariate was assessed through an ANODEV test with a Fisher–Snedecor distribution, which compares the deviances of the constant model with the corresponding time-dependent model and the model including the covariate (Skalski *et al.* 1993). Model selection was made following the Akaike Information Criterion (AIC) (Burnham & Anderson 2004). We selected our best model as the one with the lowest AIC value, whereas models that differed in less than 2 values of AIC ($\Delta\text{AIC} < 2$) were considered statistically equivalent.

Climate projections

Climate projections for the 21st century were derived from the output of 13 regional climate models (RCMs) produced in the framework of the ENSEMBLES European project (Hewitt and Griggs, 2004; further information at: <http://ensembles-eu.metoffice.com>). Simulations were run from 1951 to 2100 using the A1B emissions scenario (SRES) forcing, which is a scenario of intermediate emissions that considers a balanced use of fossil and non-fossil fuels. These RCMs operate at 25 km horizontal grid-length spatial resolution, allowing for a more explicit representation of local factors of climate than the most commonly used atmosphere-ocean general circulation models (AOGCMs; Tabor

& Williams 2010). Here we consider a multi-model approach to deal with the uncertainties arising from model error formulations (i.e. the representation of physical processes within RCMs) and also the inaccuracies found in their boundary conditions. Despite the enhanced representation of regional scale processes and geographical settings, RCM outputs still contain inaccuracies in climate representation at local scales. In order to generate data suitable for our analyses, we have applied to each RCM output a quantile-quantile statistical adjustment described in detail by Amengual *et al.* (2011).

In this study, for each tortoise population (see *Population modelling* section), the nearest available weather station within the World Meteorological Organization Global Telecommunication System (WMO GTS) database was used as the climatic historical record for the site. Regarding the future projections, daily-averaged simulated mean temperature and precipitation for each individual model were bilinearly interpolated to the individual sites from the grid points within a radius of 2° (Akima 1978 and 1976). Then, observed monthly mean temperatures and accumulated rainfall from 1980 to 2009 (the most complete historical record) were calculated and used as a baseline in the calibration method. In particular, the statistical calibration approach consists of calculating the changes in the continuous cumulative distribution functions (CDFs) of the monthly mean atmospheric variables between the 30-year simulated baseline period (i.e. 1980-2009) and successive 30-year simulated time slices from 2009 to 2099. These variations are corrected and then transferred to the observed CDFs for the baseline period. Thus, the new calibrated CDFs successfully convey the local climate signal for the subsequent time intervals (Amengual *et al.* 2010). By doing this, we obtained 13 calibrated series of monthly mean temperature and accumulated rainfall spanning from December 2009 to November 2099 for each tortoise population. Since we were mainly interested in November to February precipitation (see *Results*), we calculated yearly total winter rainfall values by adding up the monthly values from November to February. As a result, we obtained a time series of winter rainfall for the period 2009-2099 for each RCM and tortoise population.

To simplify the statistical treatment of the multi-model climatic projections, the ensemble mean together with an upper and lower confidence bound series (wet and dry respectively) were considered in our population models.

These upper and lower bound series were produced by either adding or subtracting the yearly winter intra-RCM standard deviation to or from the corresponding mean value. These three time series are assumed to encompass the set of most likely precipitation scenarios for each tortoise population: the most probable (represented by the ensemble mean), an upper bound (i.e. favourable wet conditions) and a lower bound (i.e. representing very unfavourable dry conditions).

Population modelling

We built a 7-age class Leslie matrix based on the most parsimonious structure found in our population (see *Results*), and considered a life cycle where only animals in the oldest age class were breeding (Fig. 2). Matrix entries for survival and fecundity were extracted from this study and the available literature (see below and Table 3).

Population projections were run using the software ULM (Legendre and Clobert, 1995). We performed a projection for each of the 11 populations of Hermann's tortoises from several Mediterranean sites (see Fig. 7). For each model, we introduced in the population matrix all the demographic data available; adult survival and fecundity rates (clutch size and frequency) were available for Punta de la Banya (this study and Bertolero *et al.* 2007a) and populations in Corsica (Henry *et al.* 1999), Greece (Willemsen and Hailey, 2001) and mainland France (Guyot, 1996), whereas for the remaining sites, we used adult survival and fecundity rates averaged from those available in the literature for several populations, excluding the one at Punta de la Banya, because here the common environmental and anthropogenic threats for tortoises were absent (Table 3). Juvenile survival rates were defined as a function of the local precipitation scenarios predicted for each locality as found in our survival analysis (see *Results*).

The initial number of female tortoises was known only for Punta de la Banya (28 adult females in 1988). For the other ten populations, we started each projection considering an initial number of 200 females (a relatively optimistic

scenario without strong demographic stochasticity), assuming an initial stable age distribution (SAD) as in Punta de la Banya (see *Results*). We considered that a population was not viable when the number of females decreased to 10% of the initial number, so we set the quasi-extinction threshold at $n=20$ females.

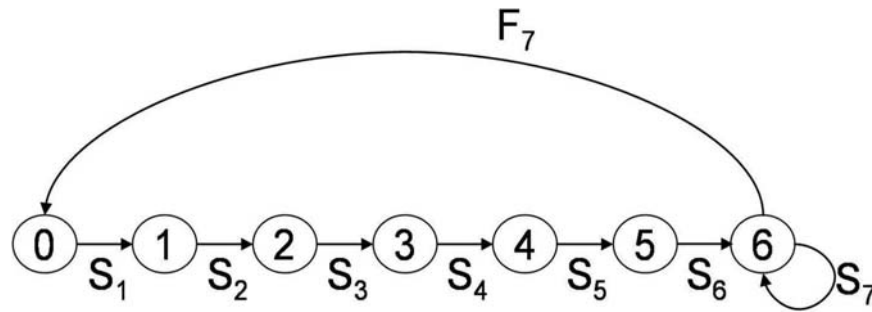


Fig. 2 Life cycle with prebreeding census for the Hermann's tortoise population occurring at Punta de la Banya reserve. Our capture period overlapped with mating and egg-laying, but hatching occurred a few months later; therefore, the number of female offspring present in the population the following year (F_7) was the product of the number of eggs laid per female (or mean clutch size, CS), the mean number of clutches laid by adult female in each season (or clutch frequency, CF), the sex ratio of the offspring (assumed to be $sr = 0.5$) and a survival rate of hatchlings from September to April (s_0), which was assumed to be the same as the survival of the first age class (s_1).

We began by a deterministic population projection for Punta de la Banya and ran this simulation for 111 time steps (from 1988 to 2099). By doing so, we were able to calculate the SAD in our study area and the time needed for the population to reach it. We then performed a population projection introducing environmental stochasticity into both adult survival and fecundity parameters by means of probabilistic distributions (Beta and Gaussian respectively; Samaranayaka & Fletcher 2010). Juvenile survival was defined as a function of winter rainfall. To simulate population growth between 1988 and 2009, we used the actual local winter rainfall values recorded during this period, whereas from 2010 onwards we used sequences of winter rainfall for the 3 future scenarios obtained from RCMs covering the study area. To obtain mean population growth rates, population sizes and quasi-extinction probabilities, we ran 1000 Monte Carlo simulations for each scenario. By running simulations for the period

1988-2009, we were able to assess whether the obtained mean population size in 2009 was close to the size estimated for that year using capture-recapture techniques. Stochastic population projections conducted for the other 10 Mediterranean localities were run from 2010 to 2099 in the same way. Since these populations are subjected to many disturbances (pollution, habitat destruction, poaching, predation and fire events), environmental stochasticity was assumed to have only negative effects on adult survival and fecundity.

Table 1 Demographic rates (mean \pm SE) reported from several populations of Hermann's tortoise that were used in the population modelling.

Population	Adult survival	Clutch size	Clutch frequency
Punta de la Banya (Ebro Delta, Spain)	$0.97 \pm 0.01^*$	$2.71 \pm 0.19^\dagger$	$1.38 \pm 0.16^\dagger$
Porto-Vecchio (Corsica, France)	$0.95 \pm 0.02^\ddagger$	$4.01 \pm 0.19^\dagger$	$1.67 \pm 0.17^\dagger$
Maures (France)	$0.92 \pm 0.02^\S$	$2.64 \pm 0.20^{**}$	$1.4 \pm 0.1^\ddagger^\ddagger$
Alyki (Greece)	$0.91 \pm 0.02^\P$	$3.60 \pm 1.50^\dagger^\dagger$	$1.90 \pm 0.50^\dagger^\dagger$
Sparta (Greece)	$0.80 \pm 0.03^\S^\S$	–	–
Litochoron (Greece)	–	$4.10 \pm 1.10^\dagger^\dagger$	$2.40 \pm 0.80^\dagger^\dagger$
Deskati (Greece)	–	$6.00 \pm 0.60^\dagger^\dagger$	$2.40 \pm 0.80^\dagger^\dagger$
Average values $^\P^\P$	0.90 ± 0.06	3.84 ± 1.22	1.95 ± 0.45

Complete data on adult survival and fecundity was only available for Punta de la Banya, Porto-Vecchio, Maures and Alyki populations. For the remaining sites (Sparta, Albera, Son Real, Alghero, Castellammare del Golfo, Piombino and Peljesac peninsula) we used averaged values for survival and fecundity when one or both rates were unknown. Litochoron and Deskati populations were not modelled but provided complementary clutch size and frequency values that were used to calculate average fecundity rates. References: *This study, † Bertolero et al. (2007a), ‡ Henry et al. (1999), § Guyot (1996), ¶ recalculated from Hailey (2000), ** Longepierre et al. (2003), $^\dagger^\dagger$ Hailey and Loumbourdis (1988), $^\ddagger^\ddagger$ Fertard (1992), $^\S^\S$ Willemsen & Hailey (2001).

$^\P^\P$ The average is calculated using data from all populations, excluding Punta de la Banya.

Results

Recapture and survival probabilities

Our data set comprised 255 encounter histories, with 19 capture occasions and 14 age-at-first-marking (called “age” hereafter) groups. Significant trap-dependence

and transient effects were detected by directional tests (*Z*-tests, see Choquet *et al.* 2005) in some of the age-groups, but the overall goodness-of-fit statistic indicated that our model assuming time-dependent parameters on each age-group described the data adequately ($\chi^2=162.15$, $p= 0.94$).

Model building began with the modelling of recapture probability (Table 1). We simplified the structure of the departure model and increased model parsimony when recapture probability was allowed to vary only with age (model 15 vs. model 16), but we finally obtained the best model structure when an additive effect of age and time was considered (model 16 vs. model 13). Survival was modelled following the same criteria: we also found an additive effect of age and time on survival, but model selection revealed the existence of only seven age classes in survival. The factorial 'time' effect describing the year-to-year variation in survival was then replaced by the climate covariates (temperature and rainfall) to assess their relationship to survival. Winter rainfall (November to February) was the best-supported environmental covariate. The ANODEV test showed a higher positive effect of winter rainfall on the survival of younger age classes than on older ones, with no rainfall effects on the survival of the oldest age class (aged 6 years and older). We kept survival for the oldest age class constant and left an additive effect between age and rainfall on the survival of the younger age classes (model 1): this was selected as the most parsimonious model, with a model weight of almost 90%. The model that was finally selected showed that recapture probability remained high most of the years and increased with age (Fig. 3a and 3b respectively). Survival showed a gradual increase from 0.39 (95% CI: 0.22-0.59) for 0y-old to 0.97 (95% CI: 0.95-0.98) for ≥ 6 y-old tortoises (Table 2). Winter rainfall had a significant positive effect on survival of juveniles and immatures (Pearson correlation coefficient (95% CI) = 0.568 (0.120-0.824), $p = 0.017$). The lower survival rates of the younger age classes fluctuated according to local winter rainfall, with increased survival in wetter years (Fig. 4a and 4b), whereas in older age classes we found a less pronounced variability in survival, which became constant in the oldest age class.

Table 2 Ranking of models performed in the survival capture-recapture analysis for Hermann's tortoise at Punta de la Banya (Ebro Delta), showing the models structure for survival (Φ), recapture (p), number of parameters (np), deviance (DEV) and AIC values for each one.

Model	Φ	p	np	DEV	AIC	ΔAIC	ω_i
1	$\Phi_0(\text{winter rain})//\dots//\Phi_5(\text{winter rain})/\Phi_{6_19}$	$p_0(t)//\dots//p_{19}(t)$	45	1618.16	1708.16	0	0.876
2	$\Phi_0(\text{winter rain})//\dots//\Phi_{6_19}(\text{winter rain})$	$p_0(t)//\dots//p_{19}(t)$	45	1622.11	1712.11	3.950	0.122
3	$\Phi_0(t)//\dots//\Phi_{6_19}(t)$	$p_0(t)//\dots//p_{19}(t)$	61	1599.66	1721.66	13.503	0.001
4	$\Phi_0(t)//\dots//\Phi_{7_19}(t)$	$p_0(t)//\dots//p_{19}(t)$	62	1598.10	1722.10	13.940	0.001
5	$\Phi_0(t)//\dots//\Phi_{8_19}(t)$	$p_0(t)//\dots//p_{19}(t)$	63	1597.86	1723.86	15.703	0.000
6	$\Phi_0(t)//\dots//\Phi_{19}(t)$	$p_0(t)//\dots//p_{19}(t)$	73	1578.71	1724.71	16.548	0.000
7	$\Phi_0(t)//\dots//\Phi_4(t)//\Phi_{5_19}(t)$	$p_0(t)//\dots//p_{19}(t)$	60	1607.70	1727.70	19.542	0.000
8	$\Phi_0(\text{summer temp})//\dots//\Phi_5(\text{summer temp})/\Phi_{6_19}$	$p_0(t)//\dots//p_{19}(t)$	45	1642.87	1732.87	24.714	0.000
9	$\Phi_0(\text{summer rain})//\dots//\Phi_5(\text{summer rain})/\Phi_{6_19}$	$p_0(t)//\dots//p_{19}(t)$	44	1647.31	1735.31	27.150	0.000
10	$\Phi_0/\dots//\Phi_{6_19}$	$p_0(t)//\dots//p_{19}(t)$	44	1647.32	1735.32	27.160	0.000
11	$\Phi_0(\text{winter temp})//\dots//\Phi_5(\text{winter temp})/\Phi_{6_19}$	$p_0(t)//\dots//p_{19}(t)$	45	1646.28	1736.28	28.124	0.000
12	$\Phi_0(\text{march rain})//\dots//\Phi_5(\text{march rain})/\Phi_{6_19}$	$p_0(t)//\dots//p_{19}(t)$	45	1646.50	1736.50	28.347	0.000
13	$\Phi_0/\dots//\Phi_{19}$	$p_0(t)//\dots//p_{19}(t)$	56	1632.62	1744.62	36.464	0.000
14	$\Phi_0(t)/\dots//\Phi_{19}(t)$	$p_0(t)//\dots//p_{19}(t)$	55	1752.56	1862.56	154.401	0.000
15	$\Phi_0(t)/\dots//\Phi_{19}(t)$	$p_0(t)//\dots//p_{6_19}(t)$	42	1798.56	1882.56	174.401	0.000
16	$\Phi_0(t)/\dots//\Phi_{19}(t)$	$p_0/\dots//p_{19}$	38	1824.24	1900.24	192.076	0.000
17	$\Phi_0(t)/\dots//\Phi_{19}(t)$	$p_0(t)/\dots//p_{19}(t)$	35	1873.92	1943.92	235.761	0.000

ΔAIC is the difference in Akaike information criterion (AIC) value when comparing the current model with the selected best model. Akaike weight (ω_i) is the probability that a model is the best model of the set discounting parsimony

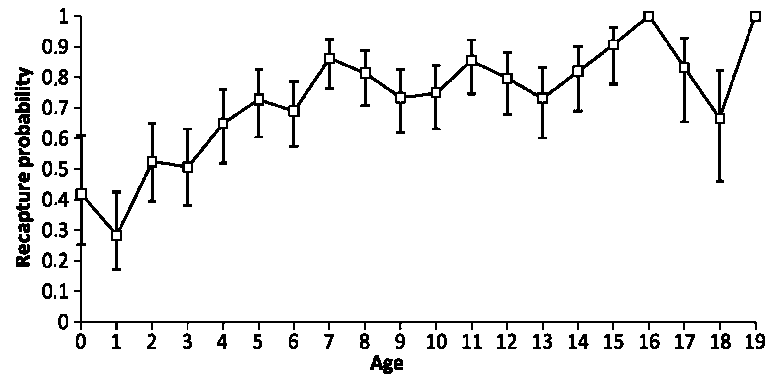


Fig. 3 Age-related recapture probabilities of tortoises at Punta de la Banya, drawn from the outputs of model 16.

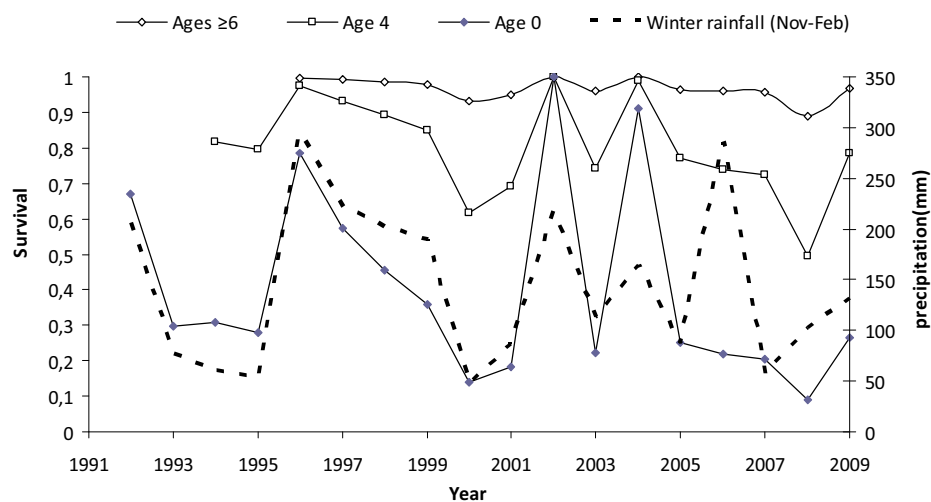


Fig. 4 Yearly fluctuations in survival (only mean values are shown) for ages 0, 4 and ≥ 6 at Punta de la Banya, taken from the survival time-varying model (see model 3 in Table 2). The dotted line shows the total winter rainfall (November to February) recorded at the Ebro Delta each year of the study period.

Climate projections

The winter (November to February) rainfall series predicted by the RCM's reveal high spatial variability among geographical locations of Hermann's tortoise throughout the Mediterranean (Fig. 5), owing to the strong modulation that local factors produce on the absolute accumulations (Lionello *et al.* 2006). The Spanish sites show the lowest rainfall amounts, with annual winter values barely exceeding 200 mm, whereas French and Italian sites reach 300 to 400 mm per winter. The unique series for Pelješac exceeds a mean of 600 mm observed winter rainfall, arguably because of its surrounding rugged terrain.

The dry, mean and wet scenarios projected by the multi-model ensemble of RCMs depict a variety of future evolutions with regard to the winter rainfall resource for Hermann's tortoise populations. Easternmost sites tend to show diminishing amounts over the century for the three scenarios, with Sparta and Castellammare being the most severely affected locations with losses of up to 30% at the end of the century. In other areas such as Punta de la Banya, Son Real and Alghero, none of the winter precipitation scenarios are projected to have significant changes over the considered periods, meaning that, for the Spanish sites, future winter precipitation amounts are expected to continue being the lowest among the range of Mediterranean locations analysed here. Additionally, note the large uncertainty sites like Maures, Porto-Vecchio and Piombino display, with both increasing and decreasing amounts for the wet and dry scenarios, respectively.

Table 3 Survival estimates for Hermann's tortoise at Punta de la Banya for each age; 95% confident intervals (in brackets) and SE are given. Results shown are from model 10 (see Table 2).

Age	Survival	SE
0	0.39 [0.22–0.59]	0.10
1	0.45 [0.31–0.60]	0.08
2	0.77 [0.59–0.89]	0.08
3	0.68 [0.53–0.80]	0.07
4	0.86 [0.70–0.94]	0.06
5	0.88 [0.76–0.95]	0.05
6	0.97 [0.95–0.98]	0.01

Population projections

The deterministic population projection for Punta de la Banya yielded a population growth rate (λ) of 1.045 for the first 21 years (period 1988-2009), and a λ of 1.021 when projected for the whole time horizon (1988-2099). The population reached a stable age distribution after 21 years, with 43% of the individuals belonging to the oldest age class (Fig. 6). Under environmental stochasticity, Monte Carlo simulations yielded a mean population growth rate of 1.035 (SE: 0.0001) for the period 1988-2009. The predicted number of female tortoises after 21 years of simulation was 58.5 ± 0.1 , meaning a total population size of 117 individuals that year, assuming a 1:1 sex ratio; this value was slightly

lower than the population size estimated (182 tortoises [95% CI: 105-265]; Albert Bertolero, unpublished data) but within the 95% confidence interval for this estimate. Projections for the 21st century (2010-2099) showed a positive trend under future mean and wet scenarios, with mean population growth rates higher than 1, whereas a negative trend was obtained when projecting the population under a dry scenario (Table 4, Figs. 7 and 8). Under this scenario, the population would reach the quasi-extinction threshold after 82 years (Table 4, Fig. 9).

The stochastic population projections performed for the other ten Mediterranean populations yielded mean population growth rates ≥ 1 for the mean and wet scenarios, whereas below 1 growth rates and negative population trends were detected in some populations when considering dry scenarios (Albera and Son Real in Spain and Alyki in Greece; Table 4, Figs. 7 and 8). Under a dry scenario and starting from a population size of 200 females, the quasi-extinction threshold was reached after 31 years in Son Real, 35 years in Albera and 62 years in Alyki (Table 4, Fig. 9).

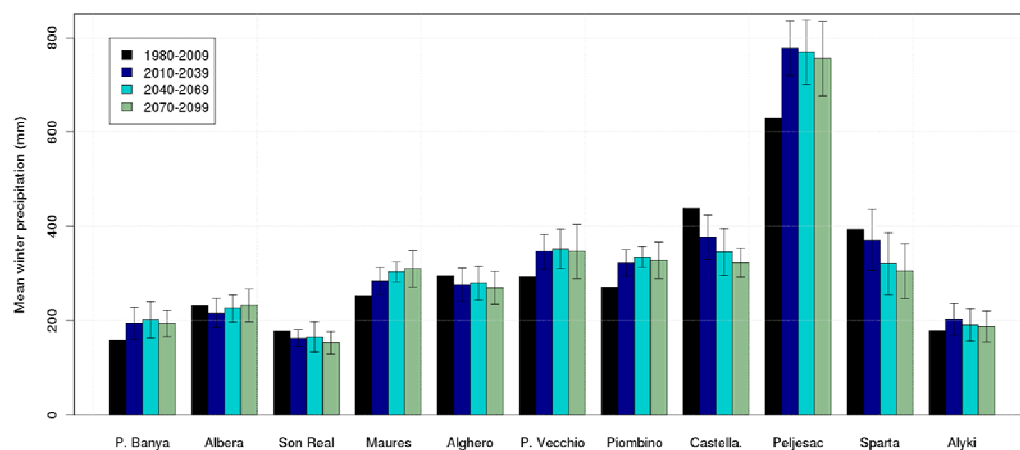


Fig. 5 Mean winter accumulated precipitation for 30 year periods spanning over present (1980-2009), early (2010-2039), mid (2040-2069) and late (2070-2099) 21st century. “Present” values correspond to the nearest available SYNOP station to the 11 Hermann’s tortoise population locations. Projected values result from the multimodel mean and vertical bars denote the intermodel standard deviation which define the mean, dry and wet scenarios used throughout the text. Note the west-east order of the sites for easier interpretation.

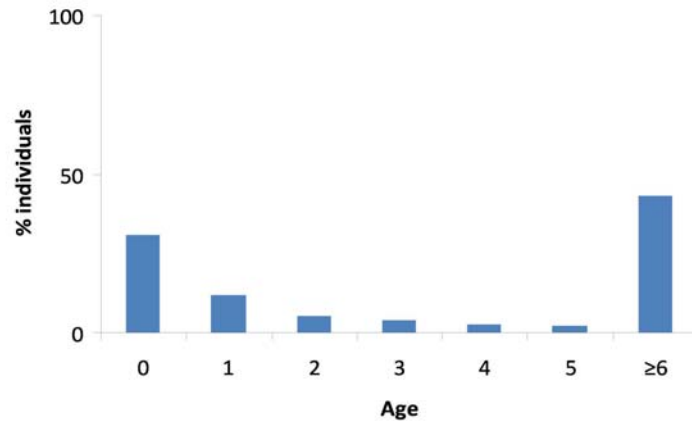


Fig. 6 Proportions of individuals when stable age distribution is reached in our study population of Hermann's tortoises.

Discussion

To our knowledge, this is the first study to assess the effects of climatic covariates on survival of Hermann's tortoise and the first to forecast population responses under regional climate change scenarios for any species of reptile (but see Hawkes *et al.* 2007). By obtaining robust estimates of demographic parameters and reliable regional climate projections, we were able to assess the consequences of predicted climate on the fate of several populations across the whole biogeographic range of the species. For Hermann's tortoises, winter rainfall was the main driver of juvenile and immature survival in populations that were free from other disturbances (natural and anthropogenic) and a potential increase in arid conditions would be detrimental to population persistence, especially for those also suffering from non-climatic stressors. These results support the predictions that climate change will have negative consequences for Mediterranean biodiversity (Sala *et al.* 2000, Araujo *et al.* 2006), and highlight the need to consider the effects of climate change, as well as other stressors, on population dynamics when implementing management efforts aimed at threatened species, especially for those with low dispersal capabilities.

The capture-recapture modelling conducted in our study allowed us to obtain robust age-related survival estimates, including juvenile and immature survival rates that are seldom recorded due to the low detectability of young individuals (Doak *et al.* 1994, Hailey 2000, Tuberville *et al.* 2008; but see

Congdon *et al.* 1994, Keller *et al.* 1998,(Henry *et al.* 1999). Pike *et al.* (2008) suggested that juvenile survival in reptiles may be often underestimated in capture-recapture analysis if offspring disperse from the study area. However, in our case, bias seems unlikely given that annual recapture rates were always higher than 40% and that we have observed most juveniles staying in the surveyed area through the monitoring of the colonization process (Bertolero 2002 and unpublished data). On the other hand, our mean juvenile survival (from 0 to 5 years old) was 0.64, which is close to that estimated by Pike *et al.* (2008) for juvenile turtles (0.65). Survival was found to increase with age, whereas the climate signal decreased. The oldest tortoises showed a high and invariable survival, whereas that of juveniles and immatures was much lower and influenced by climate (winter rainfall). These findings are typical life history traits of long-lived species such as chelonians (Stearns 1976): in these organisms, population dynamics are most sensitive to changes in adult survival, whereas changes in juvenile and immature survival have less impact on these dynamics (Heppel, 1998; Shine and Iverson, 1995; Doak *et al.* 1994). In these species, juveniles and immatures may be less buffered against environmental stochasticity than adults, but in most situations population persistence seems ensured given the high and constant survival recorded for adults; however, these life history traits may also constraint the ability of tortoise's populations to respond to chronic disturbances (see Congdon *et al.* 1994). Mean adult survival in our study population (0.97) was considerably higher than that recorded in most other populations (ranging from 0.60 to 0.96, Bertolero *et al.* 2007b). This was probably due to the lack of human disturbances, fire events and low predation rates in Punta de la Banya.

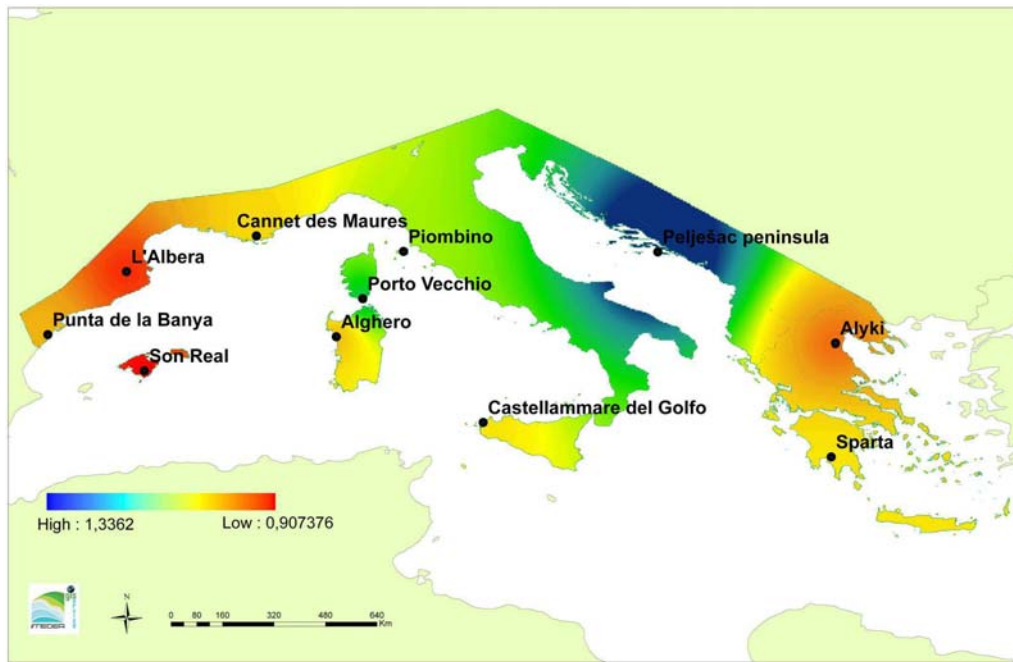


Fig. 7 Map showing the location of the populations selected for this study and the range of population growth projected under a dry precipitation scenario for the 21st century across the geographic distribution of the Hermann's tortoise. The colour shading of the figure emphasises the variation in population growth rates (λ) among the 11 populations under a dry scenario. For regions lying between two known populations, where no information was available, lambda values for the tortoise populations (if any) found there were interpolated using the inverse distance weighted (IDW) interpolation technique implemented in software ArcGis 9.3 ESRI.

Table 4 Mean population growth rates (λ and SE in parenthesis) obtained under three future climate scenarios (dry, mean and wet) for the 11 populations considered.

Population	Scenario			Time to reach $P_{q0(90)}=1$
	Mean	Wet	Dry	
Punta de la Banya	1.055 (0.00004)	1.146 (0.00006)	0.985 (0.00018)	89
Albera	1.092 (0.00012)	1.229 (0.00014)	0.925 (0.00011)	35
Son Real	1.014 (0.00011)	1.133 (0.00013)	0.907 (0.00011)	31
Maures	1.158 (0.00005)	1.237 (0.00004)	1.018 (0.00005)	–
Alghero	1.212 (0.00014)	1.306 (0.00015)	1.002 (0.00011)	–
Porto-Vecchio	1.295 (0.00006)	1.360 (0.0005)	1.131 (0.00006)	–
Piombino	1.240 (0.00014)	1.319 (0.00015)	1.065 (0.00012)	–
Castellamare	1.305 (0.00015)	1.351 (0.00015)	1.026 (0.00012)	–
Peljesac	1.356 (0.00015)	1.359 (0.00015)	1.336 (0.00015)	–
Sparta	1.208 (0.00011)	1.287 (0.00015)	1.026 (0.00011)	–
Alyki	1.066 (0.00011)	1.180 (0.00015)	0.952 (0.00006)	62

In bold, mean growth rates for populations predicted to reach a quasiextinction probability ($P_{q0(90)}$) of 1 within a time horizon of 90 years. Expected times (in years) to quasiextinction are also given.

Our climate signal on juvenile and immature survival was driven by precipitation rather than by temperature, with decreased survival in dry winters. These results are congruent with recent findings that point to drought rather than global warming as the main threat for reptiles and amphibians inhabiting semi-arid environments (Araujo *et al.* 2006). Nevertheless warming is still the main cause of species extinction in lizards (Sinervo *et al.* 2010) and tropical ectotherms (Deutsch *et al.* 2008). In temperate areas, low temperatures trigger hibernation in reptiles (Shine, 2005), which allows them to survive during the coldest months of the year. Thanks to this strategy, chelonian species living in high latitudes are able to withstand very low winter temperatures. Indeed, some turtle species even tolerate freezing without major consequences (Constanzo *et al.* 1995) and lower winter temperatures have been correlated with higher survival in North American box turtles (Converse *et al.* 2005). On the other hand, precipitation regimes determine water and food supplies and a shortage in these vital resources might have serious consequences for tortoises and their hydration, ranging from poorer body condition to lower survival and fecundity rates (Gregory 1982, Henen 1997, Henen *et al.* 1998). Given the low humidity retention of the sandy soils found in our study area, dehydration may be contributing to increase juvenile and immature mortality in dry years. Another plausible explanation for lower survival among younger age classes in dry years would be the decrease of available fresh vegetation after hibernation, causing higher mortality due to food scarcity.

At the level of overall geographic distribution of Hermann's tortoises, we detected some signs of population decrease and quasi-extinction events when considering dry projection scenarios for the 21st century. Those populations located at the Western and Easternmost edges of the species' range might suffer the worst consequences of a shift to a more arid climate. Dry-scenario precipitation regimes expected for these areas may lead to a continuous reduction in juvenile survival that these populations seem unable to withstand for a long period of time despite the high and constant survival displayed by adults. These negative population trends would result from a chronic deficit in recruitment, also enhanced out of our study area by the lowered fecundity rates caused by negative environmental stochasticity. Recruitment of non-breeders may be critical to ensure population persistence in long-lived species (Votier *et al.* 2008). Low

levels of recruitment due to harvesting of old juveniles in the snapping turtle *Chelydra serpentina* have been found to be unsustainable (Congdon *et al.* 1994), highlighting the limited capability of turtles to withstand continuous increases in mortality on this life stage. Previous studies on Hermann's tortoises in mainland France have also documented population decreases with low adult mortality (Henry *et al.* 1999; Stubbs and Swingland, 1985) and these trends could be attributed to extremely low levels of recruitment caused by high levels of nest predation (95 % nest predation in Maures; Stubbs & Swingland 1985). Strikingly, we predicted the quasi-extinction of our study population in the long term, providing evidence that even the best habitats are not necessarily safer from the consequences of regional climate changes (Pounds *et al.* 1999). However, compared to other tortoise populations in Spain, our study population reached the quasi-extinction threshold much later when projected under a future dry scenario for the next 90 years, a result otherwise consistent with the expected more deleterious impact of local climate change on populations already suffering from other sources of mortality (McCarty 2001, Walther *et al.* 2002). Population decline elsewhere was also enhanced by the additive negative environmental stochasticity of mortality factors (e.g. poaching, fire, habitat fragmentation) that are absent in Punta de la Banya reserve. These non-climatic disturbances were worked into our population models by considering a negative effect of environmental stochasticity on adult survival and fecundity, but we were unable to introduce an effect of these sources of mortality on the estimation of juvenile or immature survival, since these rates were defined as a function of rainfall. Therefore, our projections should be considered very conservative, since we did not take into account many potential sources of egg, juvenile and immature mortality such as predation or anthropogenic habitat destruction, to which these life stages are especially sensitive (Stubbs & Swingland 1985, Hailey 2000). We also ignored the role of density dependence in our projections due to the lack of information on the carrying capacity for each tortoise population, as well as the important effects of demographic stochasticity in small and fragmented populations (Sanz-Aguilar *et al.* 2010). Projections for populations with more demographic data available (i.e. Maures, Porto-Vecchio, Alyki) were probably more reliable, although still conservative since the effects of non-climatic disturbances, density dependence and its interactions were not fully worked into

the population modelling. However, our population projections are based on local future scenarios generated from the outputs of 13 RCMs developed for each location, and this approach provides more reliable forecasts of future local conditions than previous approaches based on Global Circulation Models (Tabor & Williams 2010) or the application of a single RCM (e.g Wolf *et al.* 2010). Therefore, despite the limitations of our population modelling, the mean growth rates and quasi-extinction risks reported here should provide insights as to the potential impact that spatially heterogeneous climate change may have on several isolated populations of Hermann's tortoise across the species' entire geographic range.

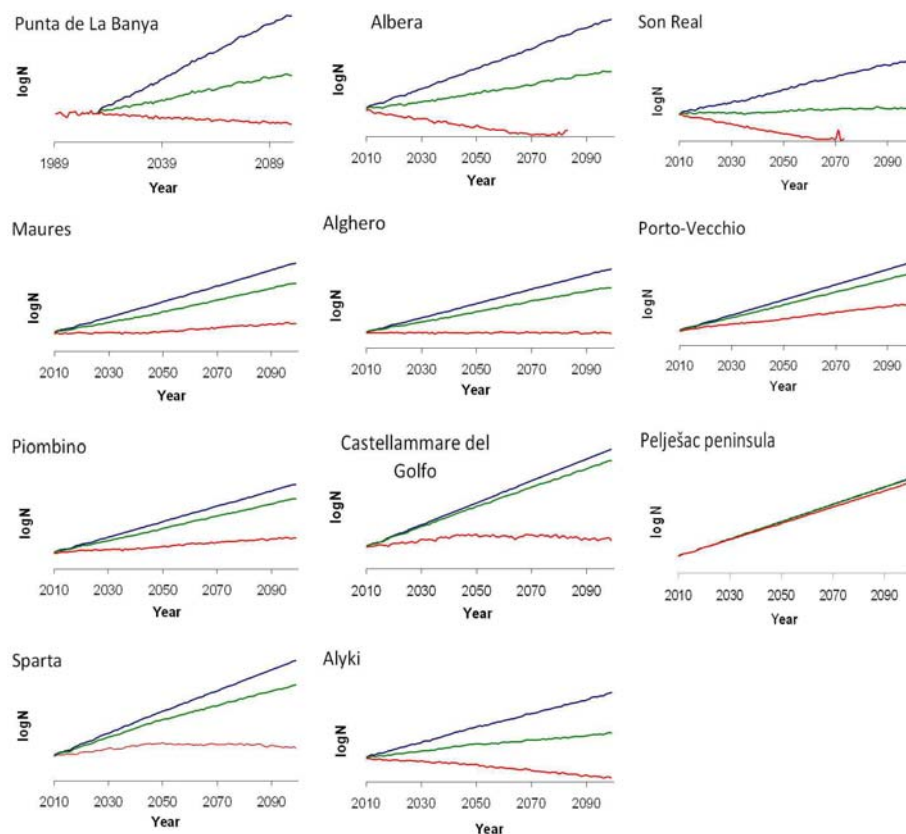


Fig. 8 Population trajectories projected under future dry (in red), mean (in green) and wet (in blue) scenarios for each Mediterranean population of Hermann's tortoises considered. Only the mean trajectory for all the Monte Carlo runs performed are shown. Y-axis numbers are not shown because simulation results are log-scaled and departing from an initial (theoretical) population size of 200 females. Trajectories do not stabilize at any carrying capacity because no density dependence was considered in our population modelling. Note that simulations for Punta de la Banya included the retrospective model of the population dynamics for the period 1988-2009.

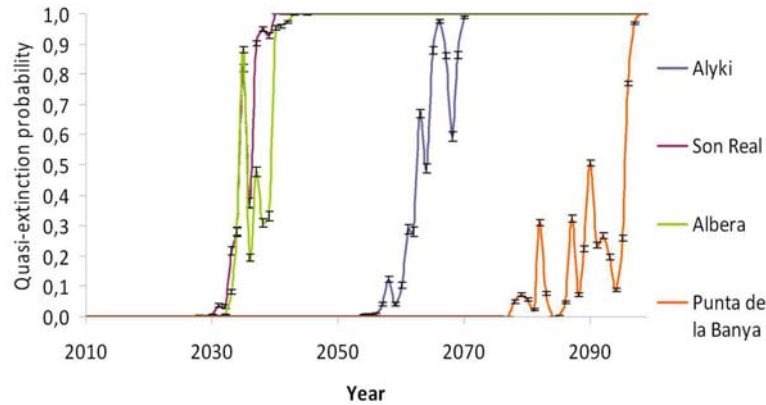


Fig. 9 Quasiextinction probabilities, with corresponding standard errors (bars), obtained for the next 90 years when projecting the Alyki, Son Real, Albera and Punta de la Banya populations under a dry scenario.

Conclusions

This study is a first assessment of the effects of climate change on Hermann's tortoise's demography and population persistence. Our main goals have been to determine the role that climate variability plays in the population dynamics of Hermann's tortoise and the negative consequences that a shift to a more arid climate in the Mediterranean would have for the species, ranging from lowered population growth rates to local extinction events. Our findings are expected to be useful for wildlife managers working with the species and should contribute to design climate-smart conservation efforts. Conservation in the 21st century requires integrating climate change in conservation plans and implementing climate adaptation strategies, especially for those systems already suffering the impacts of multiple non-climatic stressors (Hagerman *et al.* 2010, Hansen *et al.* 2010). Hermann's tortoise is threatened by a great diversity of factors, all related to human activities either directly, such as poaching and habitat destruction, or indirectly, such as increasing predator abundance and changes in landscape configuration. Management efforts focused on the elimination or reduction of these causes of mortality at all life stages (e.g. increasing protection, habitat management) are likely to increase the resilience of the species to future environmental changes in the Mediterranean region. However, as we have seen for our study population, even when human-driven mortality is suppressed and

effective protection is reached, populations might continue decreasing at some areas due to local climatic trends. In these cases, a climate change-integrated conservation strategy (Hannah *et al.* 2002, Heller & Zavaleta 2009) should be applied, primarily focused on enhancing reserve expansion and connection as a way to facilitate range shifts, and increasing genetic diversity as a way to allow for local adaptation to future environmental changes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

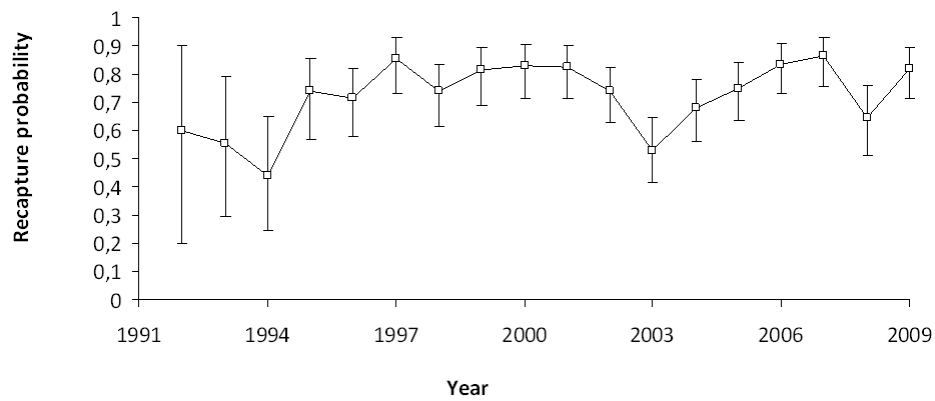


Fig S1 Variability in the recapture probability of tortoises at Punta de la Banya during the study period (1992-2009). For each year, mean values and corresponding standard errors (bars) are given.

Chapter 2

Neighbouring populations, opposite dynamics: survival and growth patterns of brown trout (*Salmo trutta*) in mountain streams.

Albert Fernández-Chacón, Meritxell Genovart, David Álvarez, José M. Cano, Alfredo F. Ojanguren, Rolando Rodríguez-Muñoz, Alfredo G. Nicieza. *Journal of Animal Ecology* (to be submitted).

Photo credit: Alfredo G. Nicieza



Neighbouring populations, opposite dynamics: survival and growth patterns of brown trout (*Salmo trutta*) in mountain streams.

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Summary

1. By following individually marked animals over time, investigations on animal population dynamics attempt to disentangle the factors influencing key life-history components, such as individual growth and survival. Stream-dwelling salmonids, that permanently occupy seasonal freshwater environments, are excellent subjects for such investigations, but because individual detection is usually imperfect and most studies are focussed on specific life stages or restricted to single locations, our knowledge on survival and growth patterns in salmonid fishes and the causes of their variation is still incomplete.
2. Here we analysed a capture-recapture dataset of brown trout (*Salmo trutta*) collected in a system of 3 isolated mountain streams monitored during a 6-year period (1996-2001) in Northern Spain. Local environmental features (e.g. elevation, associated fauna and stream size) differ among trout populations despite all sharing a common protected landscape where no fishing is allowed. Data were analysed under a multistate modelling framework to obtain reliable estimates of both survival and individual growth rates and to assess meaningful biological hypotheses about factors affecting these vital processes.
3. Model selection revealed that local survival rates fluctuated from year to year and differed among sites. Survival was size-dependent at all but the smallest stream, which also lacked crustacean prey, other fish species and avian predators. At this stream, winter severity explained 88% of the temporal variation in survival and fish were less likely to reach the size of sexual maturity. At the remaining larger streams, local fish shared identical growth patterns and showed significantly higher maturation rates, compared to the smallest stream.
4. Our results suggests that local stream environment strongly affects individual survival and growth rates, making neighbouring populations to exhibit opposite dynamics. These findings highlight the need to conduct

studies at multiple populations and life stages as a prerequisite for ecological investigations aimed at the causes of variation in life history parameters and also for the correct management of discrete brown trout populations.

Keywords: multistate models, *Salmo trutta*, stream habitat, maturation, size-dependent mortality, winter severity, E-SURGE.

Introduction

Age or size-dependent survival and individual growth patterns are important life history traits that have a strong impact on individual fitness and have influenced the evolution of different life history strategies (Stearns 1992; Hutchings 1993). Growth patterns are especially important in organisms showing indeterminate growth, such as ectothermic animals in which many fitness-related aspects also scale with body size (Hutchings 1993; Wesselingh *et al.* 1997; Nicola & Almodóvar 2004). In this case, life history theory predicts that an increase in survival with size favours delayed maturity, whereas environments where survival rates decrease with the size of the individuals favour early maturation, making interpopulation variance in survival and growth rates key factors for explaining variability in life history features among populations (Stearns 1992; Hutchings 1993; Nicola & Almodóvar 2004).

Salmonid fish exhibit complex life histories (with or without marine phase; Klemetsen *et al.* 2003) and strong variability in individual emergence, intra-cohort body size and breeding patterns. To a large extent, that variation seems to reflect the wide-range of environmental conditions that individual fish can experience through their lifetime or throughout the species range (Elliott 1994). In particular, stream-resident (i.e. non-anadromous) salmonids are long-lived, iteroparous and highly territorial organisms and this facilitates repeated sampling of individual fish, making them excellent subjects to conduct longitudinal studies to examine the factors affecting growth and survival patterns and the dynamics of the population (Lobón-Cerviá & Rincón 2004; Carlson, Olsen, & Vollestad 2008).

Individual growth patterns are believed to be influenced by resources such as food (Crisp 1993) and cover (i.e. shelter habitats, in the form of increasing depth and substrate complexity, that provide protection from predators or climatic

extremes; Heggenes et al. 1999, Boss and Richardson 2002), so spatial differences in habitat quality among streams may affect local individual growth rates (Quinn & Peterson 1996; Heggenes *et al.* 1999). Because sexual maturity in fish is mostly determined by body size, individual growth rates directly influence local population structure (and ultimately population growth) by determining the number of recruits incorporating into the local breeding population (Lobón-Cerviá 2007). Moreover, individual growth rates, by determining the size of fish, may also influence individual survival and hence local population size (Conover & Present 1990).

Survival is a key vital rate in the population dynamics of many animal taxa, especially long-lived species (Stearns 1992). In fish, survival is often assumed to increase with size because large individuals have fewer predators than smaller ones and they usually have more reserves and less energetic demands (Quinn & Peterson 1996; Sogard 1997; Garvey, Ostrand, & Wahl 2004; Johnston, Bergeron, & Dodson 2005; Byström *et al.* 2006; Carlson *et al.* 2008). Patterns of improved survival with increasing size have been found for several species of salmonids (e.g. Quinn and Peterson 1996, Pollock et al. 2007), but many studies have also failed to confirm this pattern (see Boss & Richardson, 2002; Carlson et al., 2008), indicating that the direction of size-dependent survival may be more associated to local environmental variation than previously thought (Trexler, Travis, & McManus 1992; Xu, Letcher, & Nislow 2010).

Size-specific mortality may be more apparent during periods of starvation, such as the winter season in temperate regions (Garvey *et al.* 2004). Overwintering costs in ectotherms are often assumed to be lower than in endotherms because declining body temperature reduces energy costs associated to metabolism, but when temperatures decrease below an optimal threshold, survival rates of freshwater fish, and small individuals in particular, can be reduced due to depletion of fat reserves and nutritional stress (Jensen & Johnsen 1999; Garvey *et al.* 2004; Byström *et al.* 2006; Carlson *et al.* 2008).

Most investigations on size-dependent survival treat body size as an individual covariate and thus require continuous observations on individual sizes for each sampling occasion. However, this situation is rarely met in the field due to recapture failure causing missing data, leading to biased survival estimates and misleading conclusions about the dynamics of the population (Williams, Nichols,

& Conroy 2002). As a consequence, the examination of size-dependent survival on stream-resident salmonids requires methods that explicitly account for recapture probability (Pollock *et al.* 2007; Carlson *et al.* 2008; Letcher & Horton 2008; Xu *et al.* 2010).

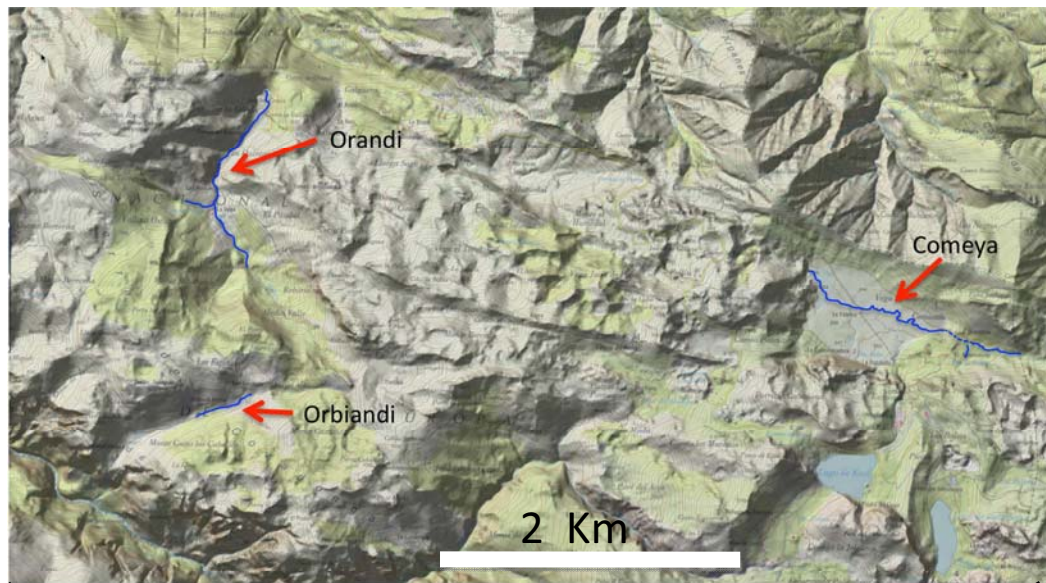
Here we present a 6-year capture-recapture study on brown trout conducted in a system of three mountain streams showing varying degrees of ecological complexity (see below). Data collected on the resident brown trout populations were used to estimate annual survival and individual growth rates by means of multistate modelling (Brownie, Hines, & Nichols 1993; Lebreton & Pradel 2002), a robust analytical tool that allows reliable rate estimates by accounting for individual recapture probabilities. Taking advantage of the information collected over time at the distinct stream populations, multistate models permit to contrast competing hypotheses about the individual processes of survival, growth and maturation across sites and, by treating body size as a discrete “state” rather than a continuous individual covariate, effects of body size on local survival rates can also be evaluated within populations. In summary, in this study we asked for the following questions: 1) are spatiotemporal variation in survival and individual growth rates relevant at the fine scale?, 2) do large individuals consistently survive better than smaller ones, and 3) does water temperature affect overwinter survival of fish? Our main objective was to identify the factors shaping local patterns of growth and survival of fish to improve the understanding of the population ecology of resident brown trout in mountain streams.

Material and methods

STUDY AREA AND ENVIRONMENT

This study was conducted at three mountain streams (Orandi, Orbiandi and Comeya) located within the Picos de Europa National Park in Asturias (Northern Spain, Fig.1), a protected area where no fishing or stocking are allowed. These three streams are “source-sink” watercourses characterized for flowing above ground over a short distance that ranges from few hundred meters (Orbiandi) to 2

km (Comeya) before reaching the sinkhole or the cave where they become subterranean, so the local brown trout populations are closed and do not receive immigrants from other areas in the watershed. Despite proximity, environmental heterogeneity in the system is high and the streams differ in size, elevation, faunal composition and temperature profiles. However, Orandi and Comeya are quite similar in ecological features (Table 1): during the study years, both streams hosted large populations of the freshwater crayfish (*Austropotamobius pallipes*) which seems to be an important energetic resource for trout, especially during the molting period (authors, unpublished). Grey herons (*Ardea cinerea*) were also present in both sites and are considered the main trout predator, as some of the local fish showed beak marks as a result of failed attacks. The Eurasian minnow (*Phoxinus phoxinus*), a smaller fish species, coexisted with brown trout in Comeya, though there was no evidence that minnows could be a significant trophic resource for trout in this stream (authors, unpublished data). In ecological terms, Orbiandi is the most distinctive of these three streams due to the lack of crayfish, avian predators, and other fish species (Table 1). Originally, this stream also lacked any native brown trout population and the individuals found today come from past anthropogenic introductions. Orbiandi is a short, shallow stream that experiences the greatest daily temperature oscillations, and its reduced size, combined with the absence of crustacean prey, can favour more episodes of nutritional stress at this population compared to the other (natural) populations in the system.



Picos de Europa National Park



Fig. 1.: Map of the study area showing the location of the three mountain streams where local brown trout populations were sampled.

Table 1. Elevation, mean December to February water temperature (variation in parenthesis) and ecological features found at the study sites. Brown trout is the only fish species at Orandi and Orbiandi, but co-occurs with the Eurasian minnow in Comeya river. During the study period, large populations of freshwater crayfish and evidences of heron predation were found in Comeya and Orandi, but not in Orbiandi.

Site	Elevation (m. a. s. l.)	Water temperature (degrees Celsius)	Other fish species	Crayfish	Avian predators
Orandi	530-570	8.429 (0.050)	No	Yes	Yes
Orbiandi	734-745	8.354 (0.945)	No	No	No
Comeya	840-860	7.243 (0.165)	Yes	Yes	Yes

DATA COLLECTION

From 1996 to 2001, local brown trout populations were regularly sampled at the study streams during summer (June to September) and winter months (October to March) partially or totally overlapping with the growth and spawning seasons respectively. Each sampling session was completed in several consecutive days in Orandi (2-3 d) and Comeya (5-7 d); because of its reduced size, no more than one day per sampling period was required for Orbiandi. Fish were sampled by electrofishing. We used a high-performance backpack device (EFGI 650; Bretschneider Spezialelektronik, Grüna, Germany) at a pulse frequency of 60 Hz or less to reduce the risk of damage to the fish. After capture, all the fish were anaesthetised with benzocaine, then measured for fork-length (± 0.01 mm) and mass (± 0.1 g), and marked for individual identification. Fish of less than 130 mm in length were individually marked injecting spots of either a biocompatible elastomer (VIE; Visible Implant Fluorescent Elastomer, Northwest Marine Technology Inc., Shaw Island, WA, USA) or alcian blue into caudal, anal, dorsal, pectoral and/or pelvic fins. VIE was available in four different colors, and generally we used combinations of six spot locations or less to generate individual codes. Alcian blue was used when the small size of the fish precluded a stable implant of the VIE marks. Alcian spots were remarked at each recapture event until VIE or Visible Implants Alpha Tags (VI-alpha, Northwest Marine Technology Inc., Shaw Island, WA, USA) could be applied. In general, fish larger than 130 mm were marked with VI-alpha tags.

Fish were classified according to their length in 3 size classes: size 1 (less than 90 mm in length), size 2 (between 90 and 130 mm) and size 3 (more than 130 mm). Because the brown trout in the study area can reach sexual maturity at a size of about 130 mm in length (Mar Toledo, unpublished PhD Thesis), our size classes can reflect also immature (classes 1 and 2) and mature (class 3) life stages. Despite we could not assign an exact age to all sampled fish, size 1 class contained the smallest immature individuals and it was mostly composed of age 0+ or “young of the year” fish (see below).

Data on marked and recaptured brown trout was used to build up a capture-recapture dataset for each site. These datasets contained individual encounter histories showing, for each sampling occasion, whether the fish was encountered (1) or not (0). For this study, we eventually stratified our data by considering the size class of the individual when sampled and re-codified each encounter (1) accordingly as 1, 2 or 3 depending on the size when sampled (a “multistate” codification, see below). To estimate winter mortality and annual growth rates, we kept a single sampling occasion per year using the records from the summer season (June-September), thus generating a multistate dataset with 3 groups (trout populations or streams), 6 capture occasions (summer seasons from 1996 to 2001) and a total of 4,851 encounter histories for statistical analysis.

Data on daily water temperature was collected at each site by using underwater temperature dataloggers (Optic StowAway, Onset Computer Corporation, Bourne, MA, USA), which were attached to stones and distributed along the different sections of each stream giving a record of temperature every 30 minutes. For the aims of this study only water temperature values corresponding to winter (December-March) and spring (April-June) months were used; more specifically, as a measure of winter severity (i.e. an indication of the feeding opportunity during winter time) and post-winter growth conditions, we calculated for each stream the number of days for which mean water temperature reached or exceeded 6°C and the mean water temperature in spring, respectively.

MULTISTATE MODELLING

We analysed our multistate capture-recapture dataset by constructing multistate models in program E-SURGE (Choquet & Nogue 2010), software that allows to define a model pattern to link our field records (events) to the corresponding states through a series of steps based on transition matrices. In our case, capture events 1, 2 and 3 (corresponding to the different individual size classes; see above) were directly linked to states 1 (“young of the year”), 2 (“immature”) and 3 (“mature”). Recorded non-detections (event “0”) can be potentially related to any possible state, including an additional “dead” state (state 4), which is not observable and its corresponding recapture probabilities are structurally zero in our modelling (see appendix 1).

By allowing survivors to move within a finite set of states between capture occasions, multistate models permit to estimate three types of parameters: survival (S), transition (Ψ) and recapture probabilities (p) (Lebreton & Pradel 2002). Transition probabilities (Ψ) are conditional on survival, and in order to obtain separate estimates for each parameter, we took advantage of the process-decomposition tool in E-SURGE and modelled survival and transition processes in a 2-step approach. When modelling transitions, we distinguished only two types of movement between states: growth transitions (transitions from state 1 to state 2) and maturation transitions (transition from state 2 to state 3). Transitions from state 1 to state 3 were not modelled explicitly but estimated as the complement of growth transitions (see appendix 1). Other combinations (i.e. transitions from bigger to smaller size classes) were treated as impossible and set to zero in our modelling. Because state 1 is linked to age 0+ (“young of the year”) and since we only recaptured individuals in states 2 and 3, recapture probabilities in state 1 were always fixed to zero to make parameters identifiable.

GOODNESS OF FIT AND MODEL SELECTION

Prior to the multistate analysis, a Goodness-of-fit (GOF) test was conducted to check if our data met the assumptions of a multistate departure model, the Arnason-Schwarz (AS) model (Pradel, Wintrebert, & Gimenez 2003), which assumes all parameters to be time and state dependent. GOF tests were performed using program U-CARE (Choquet, Lebreton, & Gimenez 2009), that permits to detect sources of lack of fit in our data (i.e. transience or trap dependence effects) and redefine the structure of the departure model to accommodate these heterogeneities. We expected the group (stream) and state (size-class) stratification of our data to account for some of the individual heterogeneity in survival and recapture. In addition, due to the closed nature of our streams and their complete inspection during each sampling season, the proportion of transients (individuals caught once but never recaptured) should be low and reflect true mortality, making our local survival estimates to be very close to real survival rates. In order to scale model deviances and correct for remaining sources of lack of fit, an overdispersion coefficient or \hat{c} (calculated as the sum of chi-square results for each test divided by the total number of degrees of freedom)

was introduced when performing the analyses in E-SURGE. Model selection was based on the Akaike's information criterion corrected for small sample size and overdispersion (QAICc) and we considered as our best model (i.e. the most parsimonious model) the one showing the lowest QAICc value of the set. Models differing in less than 2 points of QAICc ($\Delta\text{QAICc} < 2$) were arbitrarily considered statistically equivalent.

Model construction followed a stepwise approach departing from the general AS model and subsequently reducing the number of estimable parameters to find the most parsimonious structure for survival and transition probabilities. We first modelled group, state and time effects on survival probability by combining constancy (“.”), additivity (“+”) or interaction (“*”) between these effects until the most parsimonious structure for survival was found; then, we kept this structure to model group and time effects on transition probabilities following the same procedure, and finally we constructed less parameterized models by considering different survival and transition dynamics for Orbiandi with respect to the other sites and by removing one or more of the previously modelled effects until a consensus model for both survival and transition probability was found. At this point temperature variables (proportion of optimal winter days and mean spring temperature) were introduced in the consensus model by replacing the factorial time in the survival parameter by the external covariate. The amount of variation explained by the predictor was assessed through an ANODEV test with a Fisher–Snedecor distribution, which compares the deviances of the constant model with the corresponding time-dependent model and the model including the covariate (Skalski, Hoffmann, & Smith 1993).

Results

GOODNESS OF FIT AND MODEL SELECTION

The AS model fitted our data adequately as the global values of the multistate GOF tests performed for each subset of data (study sites) were not significant (Orandi: $\chi^2=17.002$, $df=15$, $p=0.319$; Orbiandi: $\chi^2=30.218$, $df=25$, $p=0.216$; Comeya: $\chi^2=9.803$, $df=10$, $p=0.458$). As expected, we did not detect significant

transient effects at any of the study sites either (p -values of transience test 3G for Orandi, Orbiandi and Comeya respectively = 0.182, 0.189 and 0.301). The overall calculation using the summed chi-square statistics and degrees of freedom for all sites yielded a \hat{c} of 1.140 that was used to scale model deviances in the subsequent analyses.

Model building began with the modeling of survival probability (Table 2), but none of the attempts to remove time, group and state effects and their interaction from the survival parameter improved model parsimony with respect to the departure model (model 1, Table 2), so we kept this initial structure and proceeded with the modeling of transition probabilities (Table 3). Again, we failed to increase parsimony by removing time effects in transition probabilities (model 13 vs. model 14, Table 3). At this point, we kept the structure of model 13 to assess our hypothesis concerning differences in growth patterns between the most distinctive Orbiandi stream and the remaining sites. The model considering identical constant transition probabilities at Orandi and Comeya but different at Orbiandi was the best supported one (model 11 vs. model 13, Table 3). Subsequently, in our search of a consensus model for both survival and transition probabilities, we also checked for different survival structures at Orbiandi with respect to Orandi and Comeya streams (Table 4). Removing state (size class) effects on survival at Orbiandi and keeping only time and state interactions at Orandi and Comeya increased model parsimony substantially (model 21 vs. model 11, Tables 3 and 4), but the removal of time effects at Orbiandi (model 22, Table 4) did not further improved this consensus model. The replacement of time effects on site-dependent survival by the local temperature covariates did not increase model parsimony (model 23 vs. model 21 and model 26 vs. model 21, Table 4), although the proportion of optimal winter days was better supported in the modeling than the mean post-winter temperature (model 23 vs. model 26, Table 4). Finally, we obtained our best model when considering winter severity (proportion of optimal winter days) effects only at Orbiandi, keeping full state and time interactions on survival at the remaining sites (model 20, Table 4), although this structure was statistically equivalent to the consensus model without external covariates (model 21, $\Delta AIC=0.6093$, Table 4). The ANODEV test revealed that the proportion of optimal winter days explained an 88% of the variance in survival at Orbiandi.

Table 2. Model selection step for survival (S) departing from a general model considering group, state and time (t) interactions in the survival parameter. At this step, we always kept the general structure to model growth transitions (Ψ) and recapture probabilities (p). The most parsimonious model for survival at this step is shown in bold.

Model	S	Ψ and P	np	Deviance	QAICc	Δ QAICc
1	general	general	94	13929.701	12410.235	7.877
2	group*state	general	73	14057.827	12479.356	76.998
3	group*t	general	72	14063.486	12482.267	79.909
4	state*t	general	77	14054.011	12484.224	81.867
5	group+t	general	69	14095.018	12503.773	101.415
6	group	general	65	14109.235	12508.051	105.693
7	group+state+t	general	73	14093.070	12510.274	107.916
8	t	general	67	14146.077	12544.463	142.106
9	state+t	general	71	14145.873	12552.484	150.127
10	state	general	67	14167.555	12563.304	160.946

Table 3. Model selection step for growth and maturation transitions ($\Psi_{1\rightarrow 2}$ and $\Psi_{2\rightarrow 3}$), departing from the most parsimonious model for survival found in the previous step. Here, Orandi, Orbiandi and Comeya populations are identified as sites A, B and C, respectively, and such codes are used in the modelling to specify differences in growth and maturation dynamics between sites. The “=” symbol is used in the modelling when identical rates between sites are assumed. The preferred model is shown in bold.

Model	S and p	Transitions		np	Deviance	QAICc	Δ QAICc
		$\Psi_{1\rightarrow 2}$	$\Psi_{2\rightarrow 3}$				
11	Model 1	A=C(.),B(.)	A=C(.),B(.)	78	13961.221	12404.886	2.529
12	Model 1	A(t),B(.),C(t)	A(t),B(.),C(t)	89	13940.363	12409.256	6.898
13	Model 1	group*t	group*t	94	13929.701	12410.235	7.877
14	Model 1	group	group	82	13961.024	12412.945	10.587
15	Model 1	A=C(t),B(.)	A=C(t),B(.)	83	13959.073	12413.294	10.936
16	Model 1	group+t	group+t	81	13963.869	12413.382	11.02
17	Model 1	A=C(t),B(t)	A=C(t),B(t)	89	13948.410	12416.315	13.958
18	Model 1	(.)	(.)	76	13985.419	12422.001	19.64
19	Model 1	t	t	82	13975.976	12426.06	23.703

Table 4. Searching for a consensus model and testing the effect of covariates on survival. At this step, site-dependent survival is modelled explicitly and sites are denoted using A, B and C. *DecMar* refers to the proportion of optimal winter days between December and March, whereas *AprJun* refers to the mean daily water temperature for the April-June period. The most parsimonious model at this step is shown in bold.

Model	<i>S</i>	ψ				
		and <i>p</i>	np	Deviance	QAICc	Δ QAICc
20	A(state*t),C(state*t),B(DecMar)	Model 11	69	13979.404	12402.357	0
21	A(state*t),C(state*t),B(t)	Model 11	70	13977.761	12402.967	0.609
22	A(state*t),C(state*t),B(.)	Model 11	68	13991.610	12411.015	8.658
23	A(state*DecMar),C(state*DecMar),B(DecMar)	Model 11	60	14011.646	12412.221	9.863
24	A(state*t),C(state*t),B(state)	Model 11	70	13989.978	12413.683	11.326
25	A=C(state*t),B(t)	Model 11	60	14044.616	12441.142	38.784
26	A(state*AprJun),C(state*AprJun),B(AprJun)	Model 11	60	14045.325	12441.764	39.406

SURVIVAL, TRANSITION AND RECAPTURE PROBABILITIES

Although survival probability fluctuated among years, on average, fish survival during the study period was above 50% at all sites but Comeya ($0,181 \pm 0,024$, Table 5). Survival at Orandi and Comeya streams was also size-dependent and, for all size classes, estimates were always higher at Orandi (see Table 5). At Orandi stream, average annual survival probabilities ranged from 0.16 (95% CI: 0.05 – 0.40) to 0.78 (95% CI: 0.51 – 0.93) and fluctuated from year to year on similar magnitude across all size classes, with the smallest individuals usually showing the highest survival rates (Fig. 2). At Comeya stream, average annual survival rates ranged from 0.11 (95% CI: 0.02 – 0.36) to 0.67 (95% CI: 0.66 – 0.67) and each size class exhibited different survival rates over the years, with no clear pattern (Fig. 2). At Orbiandi stream, annual survival ranged from 0.41 (95% CI: 0.33 – 0.49) to 0.73 (95% CI: 0.45 – 0.89) (Fig. 3). The proportion of optimal winter days had a positive effect on trout survival at Orbiandi, but this relationship was not statistically significant (Pearson correlation coefficient (95% CI) = 0.53 (-0.51 – 0.99), $P = 0.12$).

Recapture probabilities also fluctuated over the years at each study site but were on average lower at Orandi than at the other streams (Table 5). Estimates of growth and maturation transitions showed opposite dynamics at Orbiandi with respect to Orandi and Comeya (Fig. 4). The probability of moving from an immature to a mature state was significantly lower at Orbiandi than at the remaining streams, as there was no overlapping between both 95% C.I. (Fig. 4).

Table 5. Size-dependent survival (S_1 , S_2 , S_3) and time-constant recapture probabilities (p), with corresponding standard errors (in parenthesis) for each study site. Survival estimates were extracted from model 2, whereas recapture probabilities come from an extra model considering no time effects on this parameter (not shown). Average survival probabilities (\hat{S}) for Orandi and Comeya are drawn from the model without time and size-dependence in survival.

Site	S_1	S_2	S_3	\hat{S}	p
Orandi (A)	0.835 (0.107)	0.587 (0.075)	0.388 (0.045)	0.508 (0.046)	0.311 (0.029)
Orbiandi (B)		0.528 (0.026)			0.697 (0.041)
Comeya (C)	0.097 (0.023)	0.204 (0.031)	0.193 (0.026)	0.181 (0.024)	0.616 (0.086)

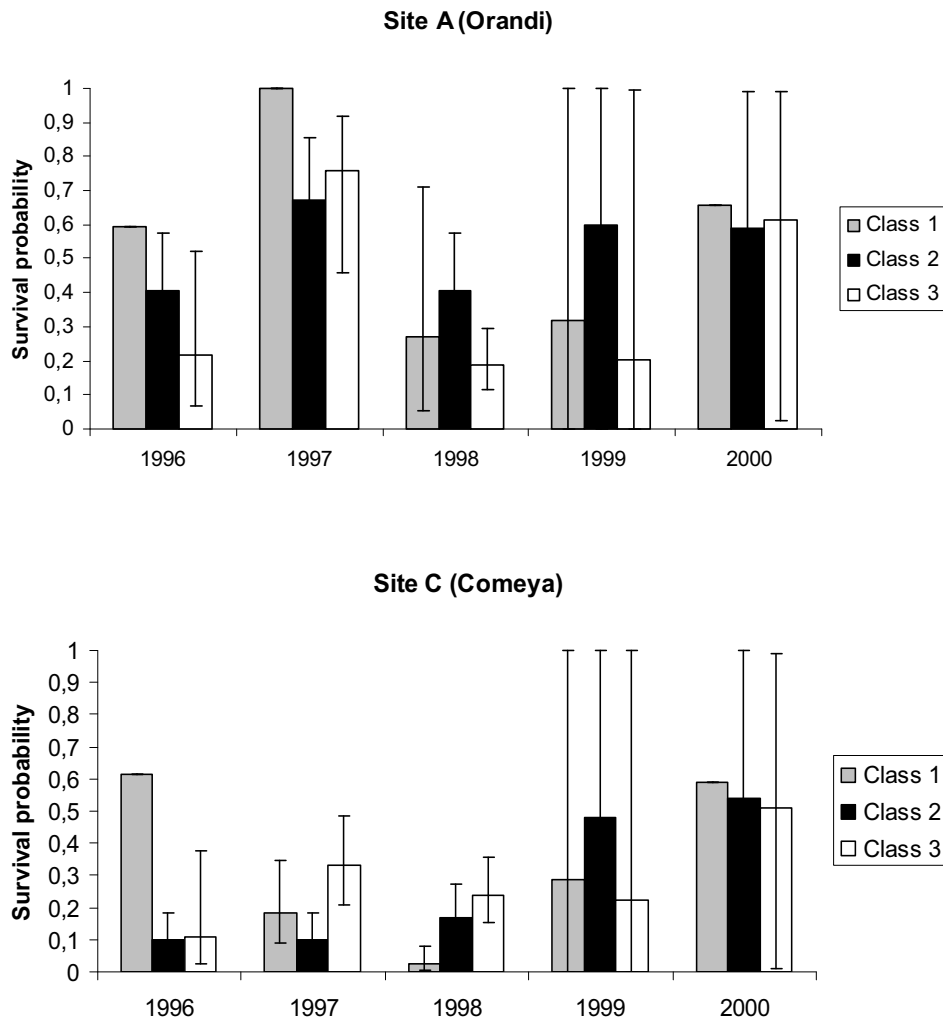


Fig. 2. Annual survival rates (with 95% Confidence intervals) for each size-class at Orandi (site A) and Comeya (site C) streams. Results are from the time-constant consensus model 21.

Discussion

We were able to separate the individual processes of survival and growth, and to assess different biological hypotheses for each life history parameter by conducting model selection under a multistate analytical framework that permitted the treatment of discrete size classes as states and the incorporation of recapture probability, yielding more reliable parameter estimates. This study, by analysing multiple populations and life stages, fits the demands for more comparative quantitative analysis using individual fish observations from different stream

environments monitored over several years (Heggenes *et al.* 1999; Hurst 2007; Xu *et al.* 2010).

PATTERNS OF SURVIVAL ACROSS SIZE-CLASSES AND POPULATIONS

Fish survival fluctuated over time and across size classes at all sites with the exception of Orbiandi (i.e. the smallest and most ecologically distinctive stream), where fish survival was not influenced by the size state of the individual. Winter severity explained a high percentage of the variation in survival at Orbiandi but the time-dependent model was equally well supported and was the best structure for the modelling of survival at the remaining sites. Contrary to our expectation, survival rates at Comeya and Orandi streams were not always higher for the largest (mature) individuals; instead, some years the highest survival rates corresponded to age 0+ or immature individuals, a pattern that could be more frequently observed at Orandi, but because of the variable estimates obtained during the study period, we cannot confirm any consistent pattern of size-dependent survival at Orandi, nor at Comeya.

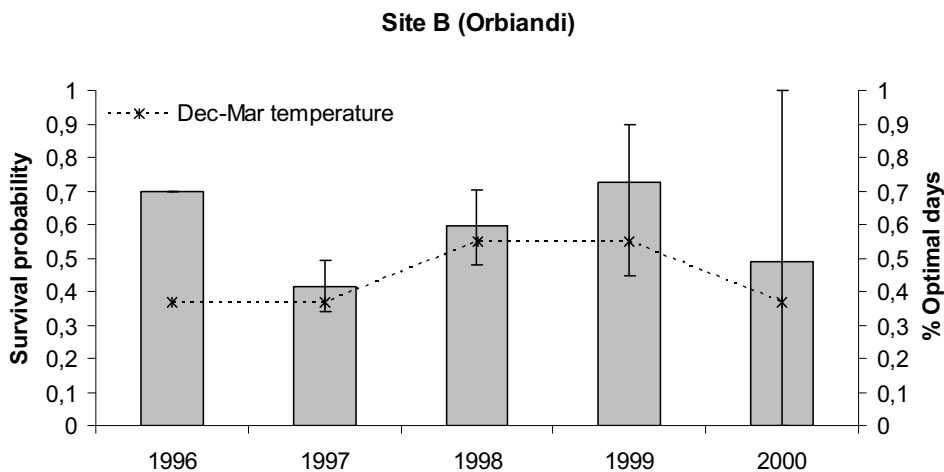


Fig. 3. Annual survival rates (with 95% Confidence intervals) obtained for Orbiandi stream. Results are from the preferred time-constant model 21, which considered no effects of size class on survival at this site. The December to March percentage of optimal temperature days (see *methods*) is given for comparison.

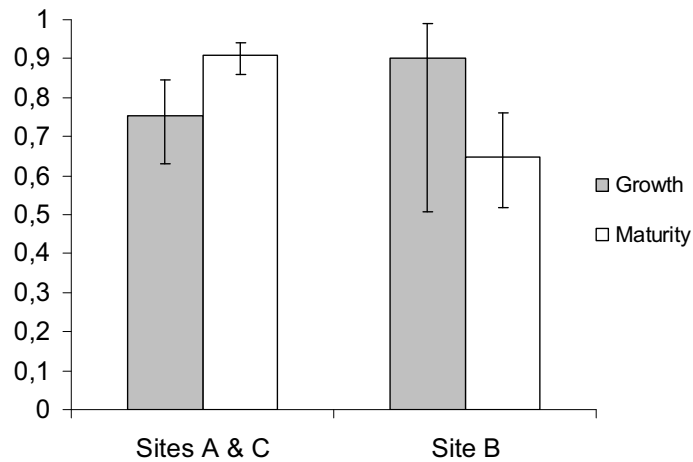


Fig. 4. Contrasting estimates of individual growth and maturation probabilities for Orbiandi (site B) and the remaining streams (sites A and C). Results are from consensus model 21.

Survival rates of trout of any size were always lower at Comeya compared to the equivalent size-dependent estimates for Orandi, possibly reflecting the harsher winter conditions that fish of all sizes experience in high-altitude streams. However, survival rates at the other high-altitude Orbiandi population were on average higher, suggesting that other agents of fish mortality rather than starvation may be also operating at Comeya.

Predation has been found conditioning patterns of size-dependent mortality in many teleosts species (for a review, see Sogard 1997) and influencing overwinter survival of freshwater fish (Garvey *et al.* 2004; Hurst 2007). During winter, smaller fish may deplete their fat reserves more quickly and need to feed to survive, showing a more exposed foraging behaviour that makes them more vulnerable to predation. Therefore, annual differences in size-selective predation may explain the annual differences in size-dependent survival rates recorded in the trout populations of Comeya and Orandi because of predators visiting the sites more or less frequently (Quinn & Peterson 1996). However, despite avian predation was detected at these sites, the local survival of the smallest individuals was the highest most of the years. This could confirm previous studies indicating that herons preferentially select larger classes of individuals (Trexler, Tempe, & Travis 1994) or that local stream habitat provided more suitable refuges for small fish (Heggenes *et al.* 1999), making large individuals less able to avoid predation. Interspecific competition between the eurasian minnow and brown trout during

winter is unlikely to have generated the observed survival patterns in Comeya given the smaller size of minnows and their smaller local densities (this species was rarely captured in the winter surveys). Instead, reproductive costs may have contributed to decrease the survival rates of mature fish in Comeya and Orandi streams some of the years.

Fish in shallower streams may be more exposed to predators and exhibit lower survival rates (Heggenes *et al.* 1999). However, grey herons were not observed at Orbiandi, and neither we recorded beak scrapes at any time, suggesting that heron predation is not a mortality factor in the shallow Orbiandi stream. Indeed, local survival rates were relatively high (above 50% on average) and equal across all size classes, suggesting that small fish were able to feed during winter to survive starvation with no increased predation risks, as expected if predators were around (Garvey *et al.* 2004). Oscillations in winter survival at Orbiandi were consistent with variation in local winter severity, and despite the positive relationship between water temperature and survival was not statistically significant, it explained a large proportion of the variation in the survival parameter. Colder water temperatures resulting from more severe winters delay the start of the period of increased food availability in the environment and this fact, coupled to the absence of crustacean prey in Orbiandi, may increase the nutritional stress of fish, thus lowering local survival rates. Another abiotic factor that could account for unexplained variation in survival in Orbiandi is winter flowrate, because short duration droughts reducing water flow by the end of the winter period and early spring may further increase mortality either directly, by desiccation, or indirectly, by reducing the availability of suitable habitat and increasing the chances for nutritional stress.

INDIVIDUAL GROWTH AND MATURATION PATTERNS BETWEEN POPULATIONS

The probability of moving from an immature to a mature state was significantly lower at Orbiandi, whereas surviving fish were more likely to move to the largest size-state (and thus reach maturity faster) at Comeya and Orandi populations. The lower water temperature of streams located at higher elevations such as Orbiandi may slow down the growth of local fish because of their less productive aquatic environment and this may explain why maturation rates were lower there, but

Comeya, the stream found at similar altitude but with larger length, depth and more associated fauna did not show this pattern. The local trout population in Comeya shared the same maturation rates as the ecologically similar but warmer Orandi stream, so the opposite maturation patterns found in Orbiandi are not a result of differences in environmental temperature only, but probably a consequence of combining lower habitat complexity, reduced stream size and absence of size-selective mortality. Orbiandi offered limited suitable habitat for trout, especially large individuals (i.e. deep stream areas; Heggenes et al. 1999) and carrying capacity could be more easily reached there than at the remaining larger streams, so reduced maturation rates may be a consequence of the local scarcity in resources such as food and space.

In summary, our results confirmed the plasticity of the life history parameters of resident brown trout in mountain streams. Trout living in complex stream environments showed size-dependent survival and faster growth, whereas those inhabiting simpler stream environments did not show size-specific mortality and had significantly lower maturation rates. More complex stream environments probably allow and stimulate faster growth, but such pattern becomes reversed in poorer stream environments with no size-selective mortality. Although a low number of years probably precluded us to find stronger links between temperature and survival, temporal variation in winter mortality seemed to be more linked with winter severity variables in smaller and simpler stream environments than in larger and more complex ones, where interaction among multiple agents of mortality may be masking such environmental links. These results show that comparative studies involving different populations and life-stages in different environmental conditions allow detection and investigation of the causes of spatial variation in life history parameters and should be considered a pre-requisite for a correct management of discrete animal populations.

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Supporting Information

Appendix 1

Specification of the multistate modelling approach in program E-SURGE

Multistate models were built in several stages using program E-SURGE (Choquet & Nogue 2010). Each step represents one of the different parameters to estimate (Φ , ψ , p , see below). This is done by means of row-stochastic matrices, i.e. each row corresponds to a multinomial. Consequently, the total of cell probabilities is 1. Because of this constraint, one and only one cell probability in each row will be calculated as the complement to 1 of the others. This particular cell is denoted with a '*' symbol. Inactive cells, i.e. cells whose associated probability is structurally 0 are denoted with a '-' symbol. An active cell receives an arbitrary letter. Note that the same letter/symbol in two cells does not mean that the two values should be equal.

The individual states (size classes) considered are:

O, Young of the year (size class 1).

I, Immature (size class 2).

M, Mature (size class 3).

†, Dead.

The possible events (field observations) are:

1, seen measuring less than 90mm.

2, seen measuring between 90 and 130mm.

3, seen measuring more than 130mm.

0, not seen.

The symbols for parameters are:

Y, Initial state probability

S, survival probability

ψ , transition probability

p , event probability (=recapture probability)

Initial State probabilities (“Dead” cannot be an initial state)

1x3

O	I	M
Y	Y	*

State transitions, step 1: Survival probability (Note: E-SURGE refers to both survival and transition steps as “transitions” as they are defined using transition matrices)

4x4

From/to	O	I	M	†
O	S	-	-	*
I	-	S	-	*
M	-	-	S	*
†	-	-	-	*

State transitions, step 2: Transition probabilities conditional on survival (Note: because fish do not shrink in length, transitions from a bigger size-state to a smaller size-state are impossible and fixed to zero using symbol “-”. Young-of-the-year fish that have survived a winter may transition either to state I or M, but cannot stay in O. In this case, direct transitions from O to M were considered as the complement of growth transitions from O to I)

5x5

From/to	O	I	M	†
O	-	ψ	*	-
I	-	*	ψ	-
M	-	-	*	-
†	-	-	-	*

Event (= recapture) probabilities

8x5

From/to	(0)	(1)	(2)	(3)
O	*	<i>p</i>	-	-
I	*	-	<i>p</i>	-
M	*	-	-	<i>p</i>
†	*	-	-	-

Chapter 3

When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured seabird population.

Albert Fernández-Chacón, Meritxell Genovart, Roger Pradel, Giacomo Tavecchia, Albert Bertolero, Julia Piccardo, Manuela G. Forero, Isabel Afán, Jordi Muntaner, Daniel Oro (2013). *Ecography* 36, 001–010.

Photo credit: Pierre Beaubrun



When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured seabird population

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Abstract

Dispersal is a key process for the population dynamics of spatially structured populations (at local and metapopulation levels), so the understanding of the mechanisms underlying the movement of individuals in space and time is important for evolutionary and ecological studies. Here we analyzed, for the first time, a long-term (1992–2009) multi-site capture–recapture database collected at four local populations of a long-lived seabird, the Audouin's gull *Larus audouinii*, covering 90% of its total world population. Those local populations show different ecological and demographic features that allow us to assess the influence of several key factors involved in breeding dispersal patterns at large spatio-temporal scales. A recently developed analytical tool in mark–recapture modelling, the multi-event approach, allowed us to obtain separate departure and settlement probabilities and test different biological hypotheses for each step of the dispersal process. Our results revealed that site fidelity was the most common strategy among breeders, and dispersal was only high from the site with the lowest population size and habitat quality. However, departures from the two largest local populations increased over the study period in response to severe ecological perturbations. Dispersers chose different settlement patches depending on their site of origin, with settlement choices determined by the population size of the destination colony rather than by the local reproductive performance, foraging area (a proxy of food availability) or distance to the destination site. Our results indicate that a breeding site is not abandoned by breeders unless a series of cumulative perturbations occur; once dispersing, settlement is directed towards densely populated sites, with dispersers using population size to rapidly assess the quality of the breeding patch.

Introduction

Dispersal is the movement of individuals between patches in space and time and guarantees connectivity of spatially structured populations (Hanski 1999, Clobert et al. 2001). Dispersal, together with birth and mortality, plays a major role in the dynamics of populations at local and metapopulation levels: for instance, dispersal events are responsible for the formation of populations (i.e. colonization) and are also important for their growth (Brown and Kodric-Brown 1977, Gotelli 1991, Oro and Ruxton 2001, Kildaw and Irons 2005). Nevertheless, compared to the factors influencing reproduction and mortality, dispersal and its determinants still remain poorly understood (Greenwood and Harvey 1982, Hanski 1999, Clobert et al. 2001, Liu and Zhang 2008) but this knowledge has much improved in recent years thanks to the advances in the large-scale monitoring of multiple populations and the development of new analytical tools (Nathan 2001).

Dispersal can be seen as a sequential two-step process in which individuals have first to decide whether or not to remain in the current site (fidelity decisions) and secondly, where to go once they have left their previous site (settlement decisions) (Forero et al. 1999, Clobert et al. 2001). The partition of dispersal into fidelity and settlement decisions permits investigation of the key factors involved in each step of the dispersal process (Grosbois and Tavecchia 2003). Fidelity may be preferred because it promotes kinship (Friesen et al. 1996) and it improves foraging efficiency and predator defence thanks to a better knowledge of the environment (Greenwood and Harvey 1982), but it can be negatively affected by factors such as individual or colonial breeding failure by predation or food depletion, mate loss and risk of inbreeding (Danchin et al. 1998, Forero et al. 1999, Serrano et al. 2001, Parejo et al. 2006). On the other hand settlement decisions may be influenced by the presence, larger density or higher breeding success of conspecifics or heterospecifics in a patch (Smith and Peacock 1990, Mönkkönen et al. 1997, Danchin et al. 1998, Cam et al. 2004a, Parejo et al. 2006, Péron et al. 2010) and negatively affected by spatial factors such as distance between patches (Forero et al. 1999, Oro and Pradel 1999, Serrano et al. 2001).

Here we examined the fidelity and settlement components in the dispersal of the Audouin's gull (*Larus audouinii*), a long-lived colonial seabird showing high fidelity but also high dispersal capabilities when the quality of environment

deteriorates (Oro and Muntaner 2000, Oro et al. 2011). An evolutionary history linked to unstable and ephemeral breeding environments has selected for the strong mobility and nomadic behaviour recorded in the species (Martinez-Abraín et al. 2003, Parejo et al. 2006), with both philopatric and dispersing individuals showing similar demographic rates and hence relatively low dispersal costs (Oro et al. 2011). Owing that populations of Audouin's gulls are known to be connected through dispersal of individuals (Oro and Pradel 1999, Tavecchia et al. 2007), we assess here the ecological factors influencing dispersal decisions. We focused on the breeding dispersal (i.e. the dispersal of established breeders) among four local populations monitored simultaneously from 1992 to 2009, covering the 90% of the world population and thus increasing the spatio-temporal scale of previous studies (Cam et al. 2004a). Each of these sites showed particular ecological and demographic features influenced by local environmental stochasticity (see below), providing a useful model to study the determinants of fidelity and settlement in breeding dispersal. Capture-recapture data collected during the study period at each site were analysed using a recently developed analytical tool in mark-recapture modelling, the multi-event approach (Pradel 2005), which permits to split the dispersal process in fidelity and settlement probabilities (Grosbois and Tavecchia 2003) and yields a more robust estimation of the parameters of interest by including extra parameters for latent (i.e. not observable) processes.

Biological hypotheses

The first step in the decision-making dispersal process concerns fidelity to the breeding site. Assuming that decisions regarding where to breed in year $t+1$ are made in year t , conditions experienced in the current breeding patch may influence site fidelity as a first order-Markovian process. Under this assumption, deterioration in habitat quality should trigger dispersal as a response to a poor breeding output (Danchin et al. 1998, Forero et al. 1999, Oro et al. 1999, Serrano et al. 2001, Schaub and von Hirschheydt 2009). However, it is known that experienced breeders of many seabirds, including gulls, show high site tenacity (Greenwood and Harvey 1982), so a low breeding dispersal probability, regardless of the current habitat conditions, could also be expected (Oro et al. 1999, Cam et

al. 2004a). Therefore, we first tested a general null hypothesis of invariant fidelity among years or colonies. We then tested for variability in fidelity among colonies and years as a response to colony-specific habitat quality and/or changing environmental conditions. For instance, fidelity should be higher at sites with denser population sizes and large foraging areas, which should translate into a better protection against predators, higher food supply and good breeding performance (e.g. Oro et al. 2006). Finally, we tested for a temporal negative trend in fidelity at the sites where habitat quality deteriorated during the study (see below).

The second step in the dispersal process concerns settlement decisions, which require a previous assessment of the quality of the available breeding sites. This pace is time demanding and requires an energy investment (Clobert et al. 2001), and individuals may rely on cues such as the density of conspecifics or heterospecifics (Smith and Peacock 1990, Mönkkönen et al. 1997) and their breeding performance (Boulinier and Danchin 1997). We tested the effects of colony size, surface of foraging area and breeding success as indicators of habitat quality for settlement in Audouin's gulls. In our study system, local population size may be a good indicator of habitat quality because of the generally more suitable habitat of the sites containing the largest colonies (see below). Moreover, high immigration rates have been recorded at sites with high population densities (Cam et al. 2004a, Tavecchia et al. 2007) and larger densities have been linked with higher abundance of resources per capita (Ruiz et al. 1998, Oro and Pradel 2000, Tavecchia et al. 2007, Almaraz and Oro 2011). Accordingly, the surface of foraging area or continental shelf around a colony might also be seen as an indicator of habitat quality (via food availability) that may influence settlement decisions. Breeding performance can be also a useful cue for habitat selection if it is temporally auto-correlated, but this information needs to be gathered before settlement by prospecting the different habitat patches during the previous breeding season (Danchin et al. 1998, Clobert et al. 2001) a behaviour documented on pre-breeders or failed breeders (Cadiou et al. 1994, Boulinier et al. 1997, Schjørring et al. 1999). Because breeding activity limits the ability of breeders to prospect potential future breeding sites within the same season (Oro and Ruxton 2001, Hénaux et al. 2007), dispersing individuals may be forced to settle in patches close to their former breeding site due to “information barriers”,

sensu Forbes and Kaiser (1994) (see also Oro and Pradel 1999). Previous studies in Audouin's gull show that breeding adults may forage at distances up to ca. 200km (Arcos and Oro 1996, J.M. Arcos unpub. data), so prospecting other sites while breeding should be rather limited in our study system (see Fig. 1). In addition, breeding success seems not to be temporally auto-correlated in this species (Oro and Ruxton 2001, Cam et al. 2004a), so cueing on reproductive performance may be unreliable. Based on our previous knowledge of the species' population dynamics in the study system, we expected colony size (i.e. the number of breeding pairs) to perform better than the other variables as indicator of local habitat quality and show a positive association with settlement. We also predicted a positive association between settlement and foraging area around each breeding site, but not between breeding success and settlement probability (see above). Finally, we also tested the hypothesis that settlement probabilities would decrease with distance (Oro and Pradel 1999, Péron et al. 2010).

In summary, the aims of the present study are not only to estimate breeding dispersal in Audouin's gulls with reliability, but especially to identify the mechanisms driving breeding dispersal at large spatio-temporal scales by testing meaningful biological hypotheses on fidelity and settlement probabilities in a system with a high heterogeneity in habitat quality.

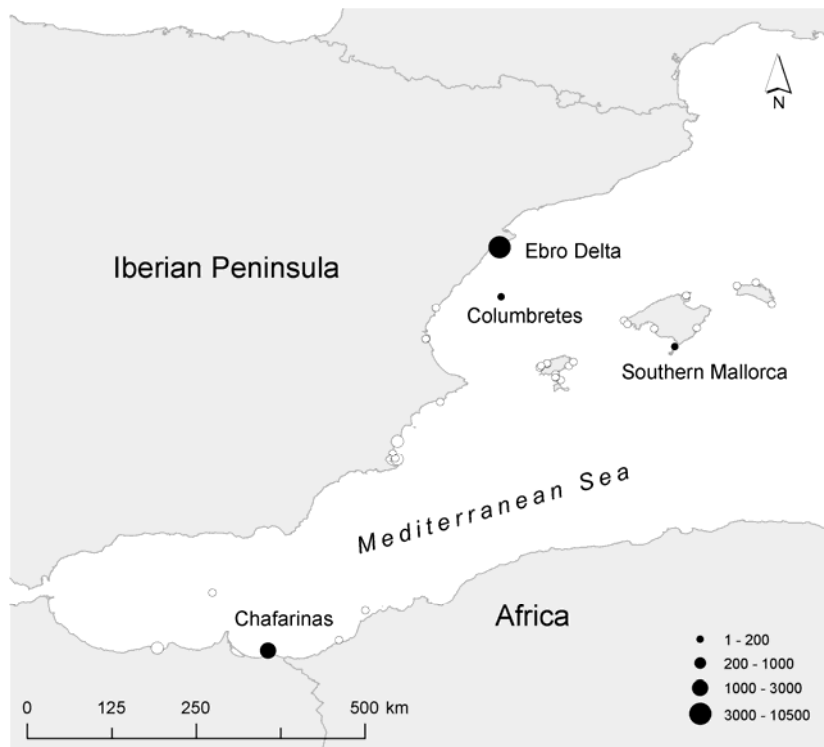


Figure 1. Distribution and size (number of breeding pairs) of the main local populations of Audouin's gull in the western Mediterranean. Black circles indicate the location of the four study sites, with their corresponding names, and white circles represent other colonies known to exist (or have existed at some point in time) out of our study area.

Material and methods

Study populations

We studied four local Audouin's gull populations in the Western Mediterranean (Fig. 1): Punta de la Banya at the Ebro Delta ($40^{\circ}33'N, 0^{\circ}39'E$, 2500 ha), Columbretes islands ($39^{\circ}54'N, 0^{\circ}41'E$, 19 ha), Chafarinas islands, ($35^{\circ}11'N, 2^{\circ}26'W$, 50 ha) and Southern Mallorca islets, in the Balearic islands ($39^{\circ}11'N, 2^{\circ}58'E$, 347 ha). This assemblage holds ca. the 90% of the world's total population of the species, with the remaining 10% found in other localities of the Western Mediterranean (Balearic archipelago, North African coast, South Eastern Iberia) as well as in the Eastern and Central parts of the basin. The Chafarinas islands, off the Moroccan coast, harbour the most distantly located population in

our study area (more than 600 km from the Ebro Delta), whereas the Ebro Delta and Columbretes islands hold the two closest populations, separated by 80 km of sea and partially sharing feeding grounds in the Eastern Iberian continental shelf. Heterogeneity is high in the study system and colonies show very different number of breeding pairs, average breeding success and size of foraging areas (see table 1). All study sites except that in the Ebro Delta are located in offshore small rocky islets and are free of terrestrial predators. Habitat suitability is the highest in the Ebro Delta owing to its larger surface of breeding habitat and larger foraging areas with relative high marine productivity. Here, gulls colonized the site in 1981 and population growth rate followed a logistic shape with extremely high growth rates in the first years (Tavecchia et al. 2007, Almaraz and Oro 2011). However, since 1999, a small number of red foxes (*Vulpes vulpes*) are regularly present in this colony and prey on gulls, so deteriorating their breeding performance over the last years (Tavecchia et al. 2007). Ecological features at Chafarinas are intermediate between those found at mainland and island populations; free of carnivores, relatively small surface but lying within a productive marine area and close to the coast, where secondary prey are available. Here, deterioration of the habitat has also occurred since 2000 caused by several socio-ecological factors: first, an eradication programme aimed at black rats (*Rattus rattus*) has resulted in the weed *Lavatera mauretanica* invading Audouin's gull breeding habitat (own data). Secondly, cessation in the activity of purse-seine fisheries during the spring months, from which gulls easily obtain food (Pedrocchi et al. 2002, González-Solís 2003), may have caused food shortage most of the years; and finally, the recovery of the local population of the predatory and dominant yellow-legged gulls (*Larus michahellis*) after culling during the 90's might have increased the number of competitive interactions between this species and Audouin's gulls (González-Solís 2003).

Table 1. Population sizes, foraging areas and breeding success values for each study site. Population sizes correspond to the mean number (median in parenthesis) of breeding pairs at each colony during the period 1995–2009. Breeding success shows the mean values (variance in parenthesis) calculated for the same period at each colony. Foraging areas are calculated as the surface of continental shelf (in km²) within a 100 km radius from each local population.

Study site	Population size	Foraging area	Breeding success
Ebro Delta	11560 (11328)	10371.51	0.57 (0.10)
Columbretes	157 (75)	9647.13	0.20 (0.08)
Chafarinas	2360 (2124)	3976.74	0.35 (0.06)
Mallorca	291 (303)	5106.71	0.66 (0.30)

Data collection

From 1992 to 2009, a total of 27215 chicks were ringed in the study colonies, and more than 19500 resightings of marked individuals were obtained during the breeding season (from April to June). Details about field protocols can be found elsewhere (Cam et al. 2004a, Tavecchia et al. 2007). Data on marked and resighted individuals at each colony was used to build up a capture-recapture dataset where the first capture occasion in an individual encounter history corresponded to the time it was ringed as a chick, and the first recapture corresponded to the first re-observation in a breeding site. For this study, we analysed the dispersal of breeders and thus we focused in the sequence of encounters after the first resighting of a marked individual in a breeding colony. We omitted the first capture as chick and only one resight per season was retained. Given that in ground-nesting gulls it is not always possible to confirm their breeding status, we assumed all of them to be breeding when observed. However, to reduce the bias caused by resighted non-breeders, we removed from our data eight cases in which an individual was resighted in more than one colony in the same breeding season and their breeding status could not be assessed and all the observations corresponding to immature birds (individuals younger than 3 years old). This makes the earliest possible resighting of a marked bird in a monitored colony to be year 1995, which corresponds to the first possible breeding attempt of an individual belonging to the first cohort (i.e. 1992). Hence, from our 18-year long capture-resighting data collection, we generated a 15-year dataset with 7399 individual histories of adult breeders for the analysis of

breeding dispersal. The number of breeding pairs at each colony was estimated by performing an annual census of nests, and annual breeding success was estimated as the ratio of the number of chicks fledged per breeding pair (see details in Oro and Pradel 2000, Oro and Ruxton 2001). Sizes of foraging areas (as a proxy of food availability) were calculated as the surface of continental shelf within a 100km radius from each local population.

Modelling framework

Our capture-recapture dataset was analyzed using a multi-event modelling approach with program E-SURGE (Pradel 2005, Choquet and Nogue 2010). Multi-event models (Pradel 2005) relate the true state of the individual (i.e. breeding at a given colony - dead) with the observed event (i.e., seen - not seen) through a series of conditional probabilities (see Supplementary material Appendix 1).

We took advantage of the multi-event approach to split the dispersal process in fidelity and settlement probabilities and to incorporate unobservable states in our modelling, such as an unknown location (hereafter “ghost site”) to model dispersal out of our system and obtain more reliable estimates of model parameters (Jenouvrier et al. 2008, Sanz-Aguilar et al. 2011a). Models included the following eight states: four breeding states (one for each breeding site), the state “alive elsewhere” (i.e. the ghost site), a dead state and two additional recapture states (see below). Note that the last three states are also unobservable. Transition probabilities between states were modelled in a three step approach to estimate three underlying parameters: survival, departure (the complement of site-fidelity, conditional on survival) and settlement probabilities (conditional on survival and departure).

We first performed a Goodness-Of-Fit (GOF) test to check if our data followed the assumptions of a departure model, in our case, the Arnason-Schwarz (AS) model which assumes all parameters being time-dependent (Brownie et al. 1993, Pradel et al. 2003). GOF tests were developed using program U-CARE (Choquet et al. 2009), which allowed us to detect the source of heterogeneity (i.e. transience or trap dependence) and incorporate this information into our departure model by increasing its complexity (i.e. number of underlying states). Because we

detected significant trap dependence at the Ebro Delta and Chafarinas sites (see Results), this effect had to be included in our departure model. Following Pradel and Sanz-Aguilar (2012), we introduced two additional recapture states (trap-aware and trap-unaware states) in our modelling by means of a fourth step included after settlement, which allowed us to estimate transitions between the two recapture states for the individuals settling at the Ebro Delta and Chafarinas colonies (see Appendix S1). At these sites, recapture probabilities refer to the transitions between trap-unaware and trap-aware states, whereas for the remaining colonies, recapture and event probabilities are synonyms (Pradel and Sanz-Aguilar 2012). In order to correct for remaining sources of lack of fit, a variance inflation factor (\hat{c}), was used to scale model deviances (Lebreton et al. 1992, Tavecchia et al. 2001). Model selection was based on the Akaike's Information Criterion, corrected for overdispersion (QAIC). We selected our best model as the one with the lowest QAIC value, whereas models that differed in less than 2 points of QAIC ($\Delta\text{QAIC} < 2$) were arbitrarily considered as statistically equivalent.

Model construction followed a step-wise approach to find the most parsimonious structure for the testing of our biological hypotheses. We assessed colony (noted by “c”), and time (“t”) effects in survival (“S”), departure (d), settlement (Ψ) and recapture probabilities (p) by combining constancy (“.”) or interaction (“*”) between these effects. To avoid larger model sets including all the various combinations of potential effects, additive effects of colony with time were not included in the analyses as synchrony among breeding colonies was very unlikely. No age effects were considered, as we focused only on one (adult) age class; however, a permanent effect of time since-marking or relative age of the individual (denoted “a”) was left in survival, distinguishing two classes of individuals (newly-seen vs. resident or previously seen individuals), a common procedure to control for transient effects (Pradel et al. 1997b). We assessed the importance of the identity of the colony of origin on departure probability and the identity of both the departure and destination sites on settlement probabilities. Subsequently, we assessed changes in dispersal probability associated with changing environmental conditions at Chafarinas and the Ebro Delta during the second part of the study by testing two kinds of trends in departure probabilities (d): a “fox” trend in Ebro Delta (starting in 1999) and an “habitat change” trend in Chafarinas (starting in 2000). We also tested the hypothesis of two periods of

distinct d (before and after fox arrival in Ebro Delta and before and after the first socio-ecological changes in Chafarinas). Since we only obtained four estimates of site fidelity, we could not test the effects of covariates on that parameter due to a lack of power. Instead, we addressed the effect of external covariates on settlement due to the larger number of settlement transitions resulting from the various combination of movements from and to the different breeding colonies.

The effect of covariates on settlement probabilities cannot be built in the multi-event modelling because E-SURGE lacks a generalized logit with linear effect of site-covariates. Following Péron et al. (2010) we run a post-hoc analysis retrieving the settlement estimates from the selected model and took into account their variances and covariances with a generalized least square approach using the function *lscov* implemented in MATLAB version 7.0 (see Supplementary material Appendix 2). Following this approach, we assessed the effects and significance of each predictor variable (distance between sites, mean number of breeding pairs, foraging area and mean breeding success at destination) on settlement probability by conducting regression analyses and performing t -tests, using the obtained slopes and their standard errors. The selection of the best predictor(s) of settlement followed a backward approach, departing from the full regression containing all covariates, and removing the least significant ones until all remaining covariates in the model were significant. Transitions from a study site to the ghost site or vice versa were not included in the response variable because this ghost site is not an identifiable location and its local features are unknown. All predictor variables used in the post-hoc analysis were previously standardized.

Results

Gof testing

The AS model did not fit our data adequately ($\chi^2_{261} = 939.4$, $P < 0.005$) and we detected significant transience (3Sr test), trap-dependence (2MITEC test) and memory effects (WBWA test). A closer inspection revealed that the Ebro Delta and Chafarinas colonies were mostly responsible for this lack of fit; in particular,

trap-dependence at the Ebro Delta was large (Test 2CT; $\chi_{12}^2 = 225.34$, $P < 0.005$). Following Pradel and Sanz-Aguilar (2012), transience and trap-dependence effects were integrated into our departure model. Incorporating these effects reduced the structural failure of the model ($\chi_{199}^2 = 422.9$, $P < 0.005$, $\hat{c} = 2.125$) and yielded a lower overdispersion coefficient that was implemented to scale model deviances.

Multi-event modelling

Model selection began by fitting the departure model (model 7, Table 2). This model considered state (site, hereafter) and time interactions in survival, departure, settlement and recapture probabilities and distinguished survival of newly and previously seen birds. Model parsimony increased (i.e. the AIC value decreased) when time effects were removed from settlement probability (model 7 vs. model 6), survival (model 6 vs. model 4) and departure probabilities from Columbretes and Mallorca (model 4 vs. model 2), keeping full site and time interactions only in recapture probability. At this point, we kept the structure of model 2 to assess our hypothesis concerning departure probabilities from the Ebro Delta and Chafarinas. Model selection revealed that models including temporal trends in departures from Chafarinas and the Ebro Delta (“habitat change” and “fox” respectively) were more parsimonious than those considering two periods of constant departure probabilities at these sites (model 3 vs. model 1).

Survival, transience and recapture probabilities, and population sizes

All survival estimates were high, ranging from 0.860 (SE: 0.040) to 0.906 (SE: 0.037, Table 3). In contrast to survival, the proportion of transients (individuals never seen again after first recapture) was very different among patches (Table 3) and increased with decreasing population size (log model, $R^2 = 0.9232$, $F_{1,2} = 37.08$, $P < 0.01$). In the retained model (model 1, Table 2), recapture probabilities were time and site dependent, with the highest mean values corresponding to individuals from the Ebro Delta colony (0.632 ± 0.017). Compared to the Ebro

Delta, Chafarinas showed lower mean recapture rates (0.339 ± 0.021), but still higher than that of the smaller colonies of Southern Mallorca (0.282 ± 0.023) and Columbretes (0.264 ± 0.027). Mean population sizes in the study system ranged from 157 to 11560 breeding pairs (Table 1) and fluctuated across the study period (Fig. 2).

Departure and settlement probabilities

Departure probabilities were very low at all sites indicating high site fidelity of resident breeders except at Columbretes (0.656, SE: 0.115, Table 3), the site with the lowest population size. Estimates from the time-varying models showed that, as expected, departure probability increased during the last years of the study at Chafarinas (with up to 35% of breeders dispersing in 2008) and the Ebro delta (Fig. 3). Settlement estimates from the retained model revealed different behaviours among dispersers depending on where they bred the year before (Table 4). Most birds (82%) leaving the Chafarinas islands chose areas out of the study system to settle (ghost site), whereas those leaving Southern Mallorca and Columbretes dispersed to the Ebro Delta (100% and 96%, respectively). Around 87% of birds leaving the Ebro Delta chose the Columbretes islands as their next breeding location.

Table 2. Ranking of multi-event models of multisite capture-recapture data on Audouin's gull (most parsimonious model in bold), showing the model structure for survival (S), departure (d), settlement (Ψ) and recapture probabilities (p), the number of parameters (np), deviance (DEV) and QAIC values for each one. Δ QAIC is the difference in QAIC value when comparing the current model with the selected best model. Akaike weight (ω_i) is calculated using the relative likelihoods of the models and represents the probability that a model is the best one of the set.

Model	S	d	Ψ	p	np	Deviance	QAIC	Δ QAIC	ω_i
1	a*c	c(EFox,XHab)	c	c*t	155	49571.548	23637.787	0.000	0.999
2	a*c	c(Et,Xt)	c	c*t	179	49529.566	23666.031	28.244	0.000
3	a*c	c(E2T,X2T)	c	c*t	155	49659.424	23681.141	43.354	0.000
4	a*c	c*t	c	c*t	216	49453.317	23704.149	66.362	0.000
5	a*c	c	c	c*t	153	49756.973	23721.046	83.259	0.000
6	a*c*t	c*t	c	c*t	310	49275.968	23808.691	170.904	0.000
7	a*c*t	c*t	c*t	c*t	426	49072.557	23944.968	307.181	0.000
8	a*c	c	c	c	79	51284.051	24291.671	653.884	0.000
9	a	.	.	.	51	53244.909	25158.428	1520.640	0.000

Model notation: E = Ebro Delta. X = Chafarinas. $2T$ = two periods of constant values; before and after the start of habitat deterioration in 1999 (Ebro Delta) and 2000 (Chafarinas). Fox = linear trend in departure probability since year 1999. Hab = linear trend in departure probability since year 2000 ("Habitat change" trend). Age, time, colony effects and constancy on model parameters were denoted as "a", "t", "c" and "." respectively (see *Methods*).

Table 3. Survival estimates and their standard errors obtained from Model 1 for newly seen (S_1) and resident individuals (S_2). The percentage of transients (individuals never seen again after 1st resighting) was calculated from the ratio $1-(S_1/S_2)$. Departure probabilities conditional on survival (d) obtained from the model without trend forcing (Model 2) are also shown, with their standard errors, for each study site.

Study site	S_1	S_2	Transients (%)	d
Ebro Delta	0.839 ± 0.011	0.898 ± 0.008	6.611	$0.029 \pm 0.018^*$
Columbretes	0.656 ± 0.109	0.906 ± 0.037	27.527	0.656 ± 0.115
Chafarinas	0.793 ± 0.043	0.863 ± 0.015	8.089	$0.064 \pm 0.047^*$
Mallorca	0.656 ± 0.078	0.860 ± 0.040	23.799	0.027 ± 0.014

* Average estimates because the retained model included time effects in departure probability at these sites.

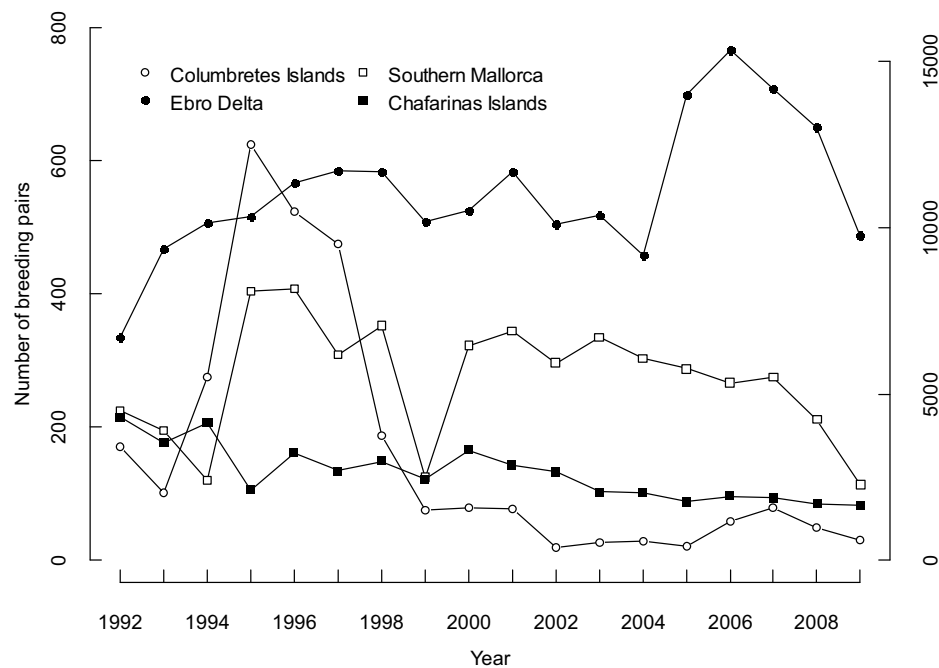


Figure 2. Number of breeding pairs of Audouin's gull at each local population during the study period. The principal Y-axis depicts the numbers for Columbretes and Southern Mallorca colonies whereas the Ebro Delta and Chafarinas islands numbers are depicted in the secondary Y-axis.

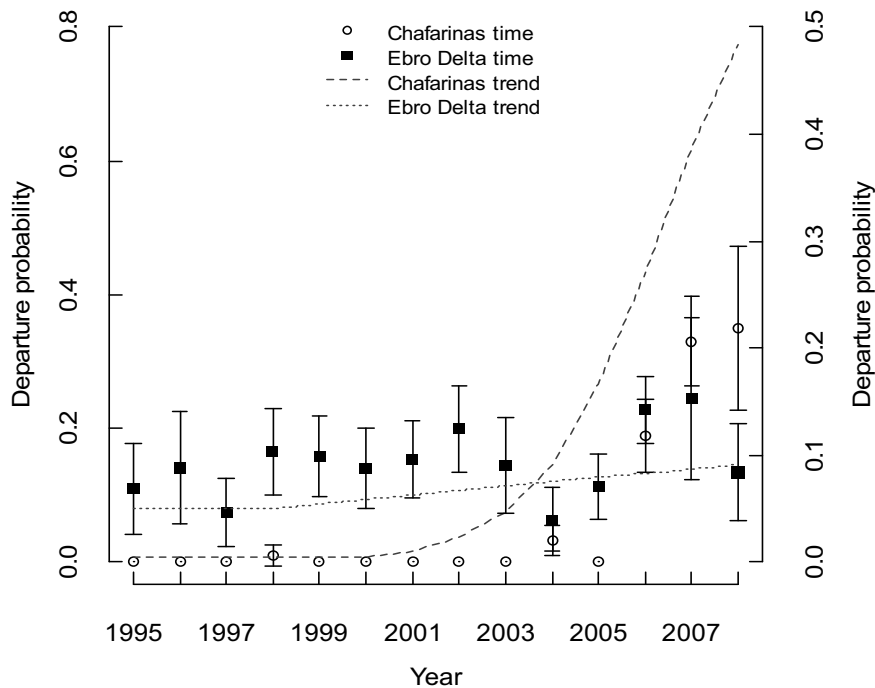


Figure 3. Temporal representation of departure probability estimates for Chafarinas and the Ebro Delta sites obtained from the most parsimonious model and the preferred time dependent model in our set (models 1 and 2, or “trend” and “time” models respectively). Model 2 estimates are given as dots with errors bars whereas estimates of model 1 (which are forced by the fox and habitat trends, see methods) are given as dashed and dotted lines, without error bars. The principal Y-axis depicts departure probabilities at Chafarinas islands whereas the secondary Y-axis depicts the corresponding probabilities for the Ebro Delta colony.

We detected a positive and statistically significant relationship between settlement probabilities and size of the destination colony ($t_{10} = 3.797$; $P = 0.0035$), with settlement probabilities increasing with the number of conspecifics (β slope = 11.613 ;SE = 3.058, Fig. 4). The size of the destination colony was the last remaining predictor of settlement after removing the least significant covariates in a backward approach departing from the full regression model. Foraging area was removed in the first step, followed by breeding success and distance between sites in the second and third steps respectively (see Supplementary material Appendix 3). By conducting separate regression analyses, we also assessed the significance of the relationship between each predictor variable and settlement. Distance alone did not explain the observed settlement

patterns ($t_{10} = -1.549$; $P = 0.152$), although this relationship was negative, with reduced probability of settlement the greater the distance to the destination site (β slope = -7.717 ; SE = 4.981, Fig. 4). Neither foraging area nor breeding success at the destination site influenced settlement decisions ($t_{10} = 1.759$; $P = 0.109$ and $t_{10} = 1.707$; $P = 0.119$ respectively) although the two factors showed a positive relationship with settlement (β slope = 8.762; SE = 4.632; β slope = 8.5006; SE = 3.7942 respectively, see Fig. 4).

Discussion

Our study addresses questions on the factors shaping animal dispersal at large spatio-temporal scales (Paradis et al. 1998, Clobert et al. 2001). We were able to decompose the dispersal process into leaving and settlement decisions, which we have shown can be influenced by different ecological factors. Moreover, the multi-event modelling approach allowed us to account for settlement out of our study area by considering an unobservable state and helped us to solve problems with recapture heterogeneity by including additional recapture states in the model structure. Those methodological improvements resulted in more reliable estimates of survival, recapture, fidelity to the colony and dispersal.

Table 4. Mean settlement probabilities (SE) for Audouin's gulls in our population network, including the ghost site, (Methods). Estimates were obtained from the most parsimonious model (i.e. with the lowest AIC value) in the multi-event modelling.

From/to	Ebro Delta	Columbretes	Chafarinas	S. Mallorca	Ghost site
Ebro Delta		0.870	0.120	0.012	0.000*
Columbrete	0.960		0.000	0.035	0.007*
Chafarinas	0.150	0.02 (0.029)		0 (0.000)	0.832*
Mallorca	1 (0.000)	0 (0.000)	0 (0.000)		0.000*
Ghost site	0 (0.000)	0.026	0.970	0.000*	

*Probabilities that were computed as complement to 1 of the other estimates (complementary transitions; see Supplementary material Appendix 1).

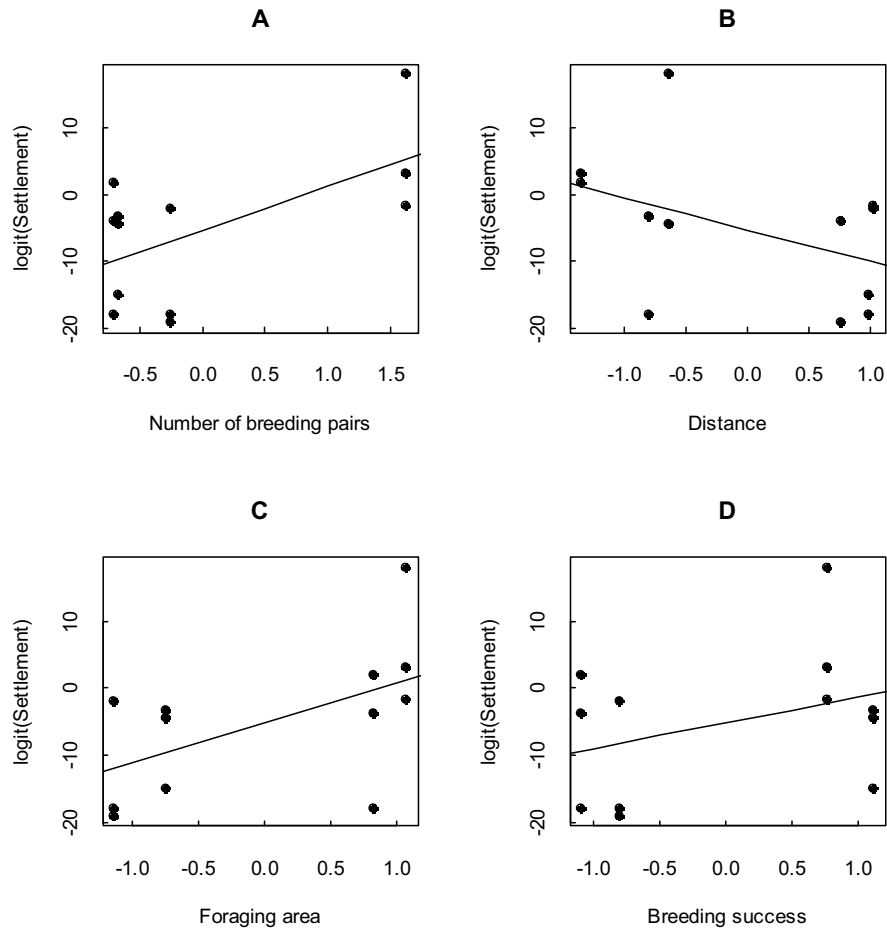


Figure 4. Relationship between settlement probabilities and the corresponding (standardized) predictor variables used in the post-hoc analyses: (A) Number of breeding pairs at destination (averaged over years), (B) Distance between sites, (C) Foraging area at destination and (D) Breeding success at destination (averaged over years). Each point represents an independent logit-transformed estimate of Ψ from the most parsimonious model obtained in the multi-event modelling (model 1, Table 2).

Spatial differences in survival, transience and trends in fidelity

Because Audouin's gull is a long-lived species, it was expected that adult survival should be the less variable demographic trait (Stearns 1992). Indeed, survival was high and very similar among all local populations despite the ecological perturbations (terrestrial predation and deterioration in resource availability) occurred in the last decade at the two patches with highest population densities (Tavecchia et al. 2007, Almaraz and Oro 2011). In contrast, transience, a

demographic parameter that in Audouin's gull has been identified with permanent dispersal (Oro et al. 1999, 2011, Tavecchia et al. 2007), was much higher at the two patches with lower population densities, arguably because of the both their relative low habitat quality and the higher attractiveness of larger colonies (Hanski 1999, Oro and Pradel 2000, Cam et al. 2004a, Serrano et al. 2005). At Columbretes, the site with the lowest area of breeding habitat and the lowest mean breeding success and population densities, fidelity of resident breeders was much lower than in the other sites, confirming previous studies showing that habitat quality influences transience and fidelity to the patch (Serrano et al. 2001, Hoover 2003, Cam et al. 2004a). At the remaining study sites, fidelity was much higher or remained high for most of the study years, probably because individuals with breeding experience in a given site are generally reluctant to disperse due to the benefits of a better knowledge of the local environment (Friesen et al. 1996, Forero et al. 1999). The association between fidelity to the breeding patch and habitat quality was confirmed also when departure probabilities increased at the two largest colonies (Ebro Delta and Chafarinas) following increasing local ecological perturbations, suggesting that the dynamics of source-sink metapopulations or any other spatially structured population depend on particular temporal stochastic environments at each patch of those systems (Doncaster et al. 1997, Oro et al. 2004a). Strikingly, departure probabilities increased several years after habitat quality began to deteriorate, showing a delayed response. This suggests that only when cumulative perturbations go beyond a threshold value above which buffering is not possible for longer, site-fidelity starts to decrease (Kildaw and Irons 2005). A series of bad years in terms of breeding performance (Oro et al. 2006) may have triggered the high departure probabilities recorded from Chafarinas colony, owing to a large decrease in both individual and conspecific success (Danchin et al. 1998, Serrano et al. 2001, Kildaw and Irons 2005, Parejo et al. 2006).

Settlement choices and habitat selection processes

We found a significant positive relationship between settlement probability and population density that confirms the hypothesis of attraction towards patches with more density of conspecifics (Forbes and Kaiser 1994, Oro and Ruxton 2001,

Serrano et al. 2005). Settlement probabilities appeared to decrease with distance to the recipient site, but this relationship was not statistically significant due to some distant sites being settled more frequently than others located at shorter distances, a finding consistent with the low dispersal costs and nomadic behaviour displayed by the species (Oro and Muntaner 2000, Martinez-Abraín et al. 2003, Parejo et al. 2006, Oro et al. 2011). Inter-colony distance also performed poorly as predictor of settlement in a multisite study on roseate terns (Spendelov et al. 1995), another seabird breeding in unstable environments. In other colonial seabirds studied using the same methodology, such as cormorants (Hénaux et al. 2007) and black-headed gulls (Péron et al. 2010), both inter-colony distance and size of the destination colony appeared to influence settlement of breeders, but in all of them, including terns, there was a preference to settle in large colonies. Our results suggest that dispersers used the density of conspecifics as an informative cue that integrates the local availability of resources (e.g. abundance of food, suitable breeding habitat, potential mates; Doligez et al. 2004). This is why neighbouring sites such as Columbretes and Mallorca are not well connected, with dispersers from these sites settling rather at the Ebro Delta. Individuals from Chafarinas, the most distant study site, remained less connected to the other patches in the system and dispersed out of the study area. This, together with the increase in dispersal from the large Ebro Delta colony, may explain the increasing colonization rates (more than 90% relative to the existing and extinct patches, unpublished results) of new patches in recent years (Oro et al. 2011). In our study system, the mean breeding success of the recipient patch was not a significant driver of habitat choice and settlement for dispersing breeders and this may confirm the unreliability of breeding success as indicator of habitat quality in systems where local productivity is unpredictable (Doligez et al. 2003, Parejo et al. 2006).

In summary, our results have showed that breeding dispersal is a relatively uncommon process in our study system, with the movement of breeders increasing when cumulative perturbations (such as predation and lower availability of resources) occurred. Whereas deterioration in habitat quality decreases site fidelity and enhances dispersal, settlement decisions are primarily ruled by the density of conspecifics. Despite the low breeding dispersal probability in this species, the relative large numbers of breeders dispersing from

densely populated patches may have important implications for the persistence and growth of other smaller populations both in and out of our study area.

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Supporting Information

Fernández-Chacón, A. et al. 2012. When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured seabird population. – *Ecography* 36: 001–010. Appendices 1-3.

Appendix 1: specification of the multi-event modeling approach in program E-SURGE

Multi-event models were built in several stages using program E-SURGE (Choquet and Nogue 2010). Each step represents one of the different parameters to estimate (Φ , d , ψ , p' , p , see below). This is done by means of row-stochastic matrices, i.e. each row corresponds to a multinomial. Consequently, the total of cell probabilities is 1. Because of this constraint, one and only one cell probability in each row will be calculated as the complement to 1 of the others. This particular cell is denoted with a ‘*’ symbol. Inactive cells, i.e. cells whose associated probability is structurally 0 are denoted with a ‘-’ symbol. An active cell receives an arbitrary letter. Note that the same Greek letter in two cells does not mean that the two values should be equal.

The individual states considered are:

E, Individual breeding at the Ebro Delta that was not resighted the previous year (unaware state).

C, Individual breeding at the Columbretes archipelago (regardless of having been resighted or not the previous year at the same site).

X, Individual breeding at the Chafarinas islands that was not resighted the previous year (unaware state).

M, Individual breeding at Southern Mallorca (regardless of having been resighted or not the previous year at the same site).

G, Individual alive but out of the study area (*Ghost* site)

E', Individual breeding at the Ebro Delta that was resighted the previous year (aware state).

X', Individual breeding at the Chafarinas islands that was resighted the previous year (aware state).

†, Dead.

The possible events are:

- 1, seen at the Ebro Delta.
- 2, seen at the Columbretes archipelago.
- 3, seen at the Chafarinas islands.
- 4, seen at Southern Mallorca.
- 0, not seen.

The symbols for parameters are:

Y, Initial state probability

Φ, survival probability

d, departure probability (1-fidelity probability)

ψ, settlement probability

p', Unaware-aware transition probability (=recapture probability for the Ebro Delta and Chafarinas sites)

p, event probability (=recapture probability for Columbretes and Southern Mallorca sites)

Initial State probabilities ("Dead" cannot be an initial state)

1x7

E	C	X	M	G	E'	X'
-	Y	-	Y	-	Y	*

Transition probabilities, step 1: Survival

8x8

From/to	E	C	X	M	G	E'	X'	†
E	Φ	-	-	-	-	-	-	*
C	-	Φ	-	-	-	-	-	*
X	-	-	Φ	-	-	-	-	*
M	-	-	-	Φ	-	-	-	*
G	-	-	-	-	Φ	-	-	*
E'	-	-	-	-	-	Φ	-	*
X'	-	-	-	-	-	-	Φ	*
†	-	-	-	-	-	-	-	*

Transition probabilities, step 2: Departure (Note: Departure = "o" and Fidelity = "i"; here we estimate only departure and leave fidelity as the complement "**").

8x15

From/to	Ei	Eo	Ci	Co	Xi	Xo	Mi	Mo	Gi	Go	E'i	E'o	X'i	X'o	†
D	*	d	-	-	-	-	-	-	-	-	-	-	-	-	-
C	-	-	*	d	-	-	-	-	-	-	-	-	-	-	-
X	-	-	-	-	*	d	-	-	-	-	-	-	-	-	-
M	-	-	-	-	-	-	*	d	-	-	-	-	-	-	-
G	-	-	-	-	-	-	-	-	*	d	-	-	-	-	-
D'	-	-	-	-	-	-	-	-	-	-	*	d	-	-	-
X'	-	-	-	-	-	-	-	-	-	-	-	-	*	d	-
†	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*

Transition probabilities, step 3: Settlement

15x8

From/to	E	C	X	M	G	E'	X'	†
Ei	*	-	-	-	-	-	-	-
Eo	-	Ψ	Ψ	Ψ	*	-	-	-
Ci	-	*	-	-	-	-	-	-
Co	Ψ	-	Ψ	Ψ	*	-	-	-
Xi	-	-	*	-	-	-	-	-
Xo	Ψ	Ψ	-	Ψ	*	-	-	-
Mi	-	-	-	*	-	-	-	-
Mo	Ψ	Ψ	Ψ	-	-	-	-	-
Gi	-	-	-	-	*	-	-	-
Go	Ψ	Ψ	Ψ	*	-	-	-	-
E'i	*	-	-	-	-	-	-	-
E'o	-	Ψ	Ψ	Ψ	*	-	-	-
X'i	-	-	*	-	-	-	-	-
X'o	Ψ	Ψ	-	Ψ	*	-	-	-
†	-	-	-	-	-	-	-	*

Transition probabilities, step 4: recapture (Unaware-Aware transitions)

8x8

From/to	E	C	X	M	G	E'	X'	†
E	*	-	-	-	-	p'	-	-
C	-	*	-	-	-	-	-	-
X	-	-	*	-	-	-	p'	-
M	-	-	-	*	-	-	-	-
G	-	-	-	-	*	-	-	-
E'	*	-	-	-	-	p'	-	-
X'	-	-	*	-	-	-	p'	-
†	-	-	-	-	-	-	-	*

Event probabilities, step 1: recapture
8x5

From/to	event (0)	event (1)	event (2)	event (3)	event (4)
E	*	-	-	-	-
C	*	-	<i>p</i>	-	-
X	*	-	-	-	-
M	*	-	-	-	<i>p</i>
G	*	-	-	-	-
E'	-	*	-	-	-
X'	-	-	-	*	-
†	*	-	-	-	-

References

Choquet, R. and Nogue, E. 2010. E-SURGE 1.7 user's manual. - CEFE, Montpellier.

Appendix 2: post hoc linear models for settlement estimates

Problem: the effect of covariates on settlement probabilities cannot be built in the CR model because the desirable link function (logit) is not available. An alternative is to retrieve the estimates of a model without constraint and run a post hoc analysis. However, because the estimates come with a variance matrix, a GLM is not appropriate. A generalized least square is the solution. There are two main difficulties:

1. Obtaining the variance matrix of the right quantities
2. Finding a statistical program that does the GLS model

1. Deriving the Variance matrix

We used E-SURGE to estimate the settlement probabilities. E-SURGE provides the variance matrix of the mathematical parameters (but only the individual standard errors of the reconstituted biological parameters). We can use the delta method to obtain the variance matrix of the reconstituted settlement probabilities. However, because we want to fit a logit linear model, we will have to apply the delta method a second time after that.

Settlement probabilities are estimated for migrants. Thus, there is a settlement probability μ_{ij} for each pair of site (departure= i , arrival= j) with $i \neq j$. In our study, there are 4 sites (1=D=Ebro Delta, 2=C=Columbretes Islands, 3=X=Chafarinas Islands, 4=M= Mallorca) plus a catchall fifth site that we call the ghost location (G) and which serves for all individuals that go to unmonitored sites or skip breeding altogether. Settlement probabilities from a given site of departure i sum to 1. One of them is thus computed as the complement of the others. For our study, it is convenient to choose the ‘settlement on the Ghost Location’ as the complement.

The settlement probabilities from a given site of departure i are estimated in E-SURGE through a generalized logit link function. This is a multivariate function, the exact form of which depends on which settlement probability is computed as the complement of the others. With the ‘settlement on the Ghost Location’ taken

as the complement, the generalized logit for settlement probabilities of individuals departing from the Ebro Delta takes the form:

$$(\mu_{DC} \mu_{DX} \mu_{DM}) \rightarrow (\beta_{D1} \beta_{D2} \beta_{D3})$$

where

$$\beta_{D1} = \ln\left(\frac{\mu_{DC}}{1 - \mu_{DC} - \mu_{DX} - \mu_{DM}}\right),$$

$$\beta_{D2} = \ln\left(\frac{\mu_{DX}}{1 - \mu_{DC} - \mu_{DX} - \mu_{DM}}\right),$$

$$\beta_{D3} = \ln\left(\frac{\mu_{DM}}{1 - \mu_{DC} - \mu_{DX} - \mu_{DM}}\right).$$

There is no simple correspondence between the individual μ s and β s. In particular, the first β , β_{D1} , does not reflect the sole probability of settlement at the Columbretes, reason why its second index is a 1 and not a C.

The generalized logit can be inverted:

$$\mu_{DC} = \frac{e^{\beta_{D1}}}{1 + e^{\beta_{D1}} + e^{\beta_{D2}} + e^{\beta_{D3}}}$$

$$\mu_{DX} = \frac{e^{\beta_{D2}}}{1 + e^{\beta_{D1}} + e^{\beta_{D2}} + e^{\beta_{D3}}}$$

$$\mu_{DM} = \frac{e^{\beta_{D3}}}{1 + e^{\beta_{D1}} + e^{\beta_{D2}} + e^{\beta_{D3}}}$$

Although the β on the numerator does not correspond strictly to the μ on the other side of the equality, it may be simpler to use the same indexes and this is what E-SURGE does. This abuse of notation simplifies the writing of formulas. If we take the ‘settlement on the Ghost Location’ as the complement whatever the site of departure, and replace D, C, X and M respectively with 1, 2, 3 and 4, then we have

$$\mu_{ij} = \frac{e^{\beta_{ij}}}{1 + \sum_{k \neq i} e^{\beta_{ik}}} \text{ for } i=1 \text{ to } 4; j=1 \text{ to } 4; k=1 \text{ to } 4 \text{ and } i \neq j$$

To apply the delta method, we need the partial derivatives of the μ s with respect to the β s. After some algebra, we get

$$\frac{\partial \mu_{ij}}{\partial \beta_{ik}} = -\mu_{ij} \mu_{ik}, k \neq j$$

$$\frac{\partial \mu_{ij}}{\partial \beta_{ik}} = \mu_{ij} (1 - \mu_{ij}), k = j$$

$$\frac{\partial \mu_{ij}}{\partial \beta_{lk}} = 0, l \neq i$$

The matrix D_μ of the first derivatives of the μ s (in rows) with respect to the β s (in columns) is thus

	β_{12}	β_{13}	β_{14}	β_{21}	β_{23}	β_{24}	β_{31}	β_{32}	β_{34}	β_{41}	β_{42}	β_{43}
μ_{12}	$\mu_{12}(1-\mu_{12})-\mu_{12}\mu_{13}$	$-\mu_{12}\mu_{14}$	0	0	0	0	0	0	0	0	0	0
μ_{13}	$\mu_{13}\mu_{12}$	$\mu_{13}(1-\mu_{13})-\mu_{13}\mu_{14}$	0	0	0	0	0	0	0	0	0	0
μ_{14}	$-\mu_{14}\mu_{12}$	$-\mu_{14}\mu_{13}$	$\mu_{14}(1-\mu_{14})$	0	0	0	0	0	0	0	0	0
μ_{21}	0	0	0	$\mu_{21}(1-\mu_{21})-\mu_{21}\mu_{23}$	$-\mu_{21}\mu_{24}$	0	0	0	0	0	0	0
μ_{23}	0	0	0	$-\mu_{23}\mu_{21}$	$\mu_{23}(1-\mu_{23})-\mu_{23}\mu_{24}$	0	0	0	0	0	0	0
μ_{24}	0	0	0	$-\mu_{24}\mu_{21}$	$-\mu_{24}\mu_{23}$	$\mu_{24}(1-\mu_{24})$	0	0	0	0	0	0
μ_{31}	0	0	0	0	0	0	$\mu_{31}(1-\mu_{31})-\mu_{31}\mu_{32}$	$-\mu_{31}\mu_{34}$	0	0	0	0
μ_{32}	0	0	0	0	0	0	$-\mu_{32}\mu_{31}$	$\mu_{32}(1-\mu_{32})-\mu_{32}\mu_{34}$	0	0	0	0
μ_{34}	0	0	0	0	0	0	$-\mu_{34}\mu_{31}$	$-\mu_{34}\mu_{32}$	$\mu_{34}(1-\mu_{34})$	0	0	0
μ_{41}	0	0	0	0	0	0	0	0	0	$\mu_{41}(1-\mu_{41})-\mu_{41}\mu_{42}$	$-\mu_{41}\mu_{43}$	0
μ_{42}	0	0	0	0	0	0	0	0	0	$-\mu_{42}\mu_{41}$	$\mu_{42}(1-\mu_{42})-\mu_{42}\mu_{43}$	0
μ_{43}	0	0	0	0	0	0	0	0	0	$-\mu_{43}\mu_{41}$	$-\mu_{43}\mu_{42}$	$\mu_{43}(1-\mu_{43})$

As per the Delta method, the variance matrix $V(\mu)$ of the μ s is approximated by

$$D_\mu V(\beta) D_\mu^T$$

Where $V(\beta)$ is the variance matrix of the β s and D_μ^T is the transpose of D_μ .

2. Retrieving the Variance matrix of the β s in the E-SURGE output

The difficult point is to identify the β s corresponding to the settlement probabilities among all the mathematical parameters. I proceeded in the following way. In E-SURGE, select the option ‘from last model’, retrieve the model of interest, and open IVFV. Find the settlement probabilities in IVFV (actually their β transforms) and look at the numerical values. In the sheet ‘Beta’ of the Excel output of the same model, find the same values. I did this with model46. The settlement probabilities were the parameters 62 to 76 and with IVFV, I can see that the first one is β_{21} , the next one β_{31} etc... Then going to sheet ‘Var-Cov’, I can extract the submatrix corresponding to these β s.

I could then calculate D_{μ} and $V(\mu)$. This last calculation involving matrix products was done in R.

```
#R-script Delta method for settlement
D<-matrix(0,12,12)
D[1,]<-c(0.117146837,-0.106032943,-0.011113894,0,0,0,0,0,0,0,0,0)
D[2,]<-c(-0.106032943,0.10760978,-0.001576837,0,0,0,0,0,0,0,0,0)
D[3,]<-c(-0.011113894,-0.001576837,0.012690731,0,0,0,0,0,0,0,0,0)
D[4,]<-c(0,0,0,0.046502306,-2.85332E-09,-0.033254435,0,0,0,0,0,0)
D[5,]<-c(0,0,0,-2.85332E-09,3E-09,-1.04892E-10,0,0,0,0,0,0)
D[6,]<-c(0,0,0,-0.033254435,-1.04892E-10,0.033741443,0,0,0,0,0,0)
D[7,]<-c(0,0,0,0,0,0,0.129466761,-0.004614051,-4.91625E-07,0,0,0)
D[8,]<-c(0,0,0,0,0,0,-0.004614051,0.029280926,-9.71293E-08,0,0,0)
D[9,]<-c(0,0,0,0,0,0,-4.91625E-07,-9.71293E-08,3.21699E-06,0,0,0)
D[10,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)
D[11,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)
D[12,]<-c(0,0,0,0,0,0,0,0,0,0,0,0)
M<-
c(0.864490279,0.122653714,0.012856008,0.951107187,0.000000003,0.03496391
9,0.152821028,0.030192514,0.000003217,1,0,0)
VCV<-matrix(0,12,12)
VCV[1,]<-c(0.20614054,0.15905685,0.03321758,1.04026856,-
0.05664936,1.14629378,-0.01732456,-0.01418431,-0.03188666,0,0,0)
VCV[2,]<-c(0.15905685,0.17940281,0.05448564,1.01921411,-
0.05570602,1.15025645,-0.01077763,-0.02180492,-0.03172129,0,0,0)
VCV[3,]<-c(0.03321758,0.05448564,0.15419649,0.67031994,-
0.03361497,0.69258843,-0.00492457,-0.01481698,-0.01980359,0,0,0)
VCV[4,]<-c(1.04026856,1.01921411,0.67031994,7.30974251,-
0.38204743,7.87568008,-0.08578104,-0.12440104,-0.22089041,0,0,0)
VCV[5,]<-c(-0.05664936,-0.05570602,-0.03361497,-0.38204743,0.02101213,-
0.41914279,0.00456552,0.00640252,0.01176308,0,0,0)
```

```

VCV[6,]<-c(1.14629378,1.15025645,0.69258843,7.87568008,-
0.41914279,8.72916172,-0.09225856,-0.14225517,-0.24183528,0,0,0)
VCV[7,]<-c(-0.01732456,-0.01077763,-0.00492457,-0.08578104,0.00456552,-
0.09225856,0.03589406,0.02909819,0.0022974,0,0,0)
VCV[8,]<-c(-0.01418431,-0.02180492,-0.01481698,-0.12440104,0.00640252,-
0.14225517,0.02909819,0.42137069,0.00252894,0,0,0)
VCV[9,]<-c(-0.03188666,-0.03172129,-0.01980359,-0.22089041,0.01176308,-
0.24183528,0.0022974,0.00252894,0.00677493,0,0,0)
VCV[10,]<-c(0,0,0,0,0,0,0,0,0,0,0)
VCV[11,]<-c(0,0,0,0,0,0,0,0,0,0,0)
VCV[12,]<-c(0,0,0,0,0,0,0,0,0,0,0)
#delta method
D%*%VCV%*%t(D)

```

3. Calculating the Variance matrix for the logit of the μ s

Using again the delta method, we get

$$\text{cov}(\text{logit}(u), \text{logit}(v)) = \frac{\text{cov}(u, v)}{u(1-u)v(1-v)}$$

$$\text{var}(\text{logit}(u), \text{logit}(v)) = \frac{\text{var}(u, v)}{u^2(1-u)^2}$$

The variance matrix of the logits can thus be derived from that of the μ s.

4. Post-hoc analysis of the effect of the distance (Standardized distance or distN)

Because we work with *estimates* of the $\text{logit}(\mu)=\text{LTMU}$, not the $\text{logit}(\mu)$ themselves, we must account for their variances and covariances with a generalized least square approach. This procedure is implemented in MATLAB with the function [lscov](#) and in R with the function `lm.gls` of the library MASS.

MATLAB code:

```
A=[ones(12,1) distN]
```

```
A =
```

```

1.0000 -1.3491
1.0000  1.0343
1.0000 -0.6367
1.0000 -1.3491

```

1.0000 0.7592
 1.0000 -0.8010
 1.0000 1.0343
 1.0000 0.7592
 1.0000 0.9933
 1.0000 -0.6367
 1.0000 -0.8010
 1.0000 0.9933

LTMU

LTMU =

1.902573483
 -2.015301302
 -4.393265995
 3.136467656
 -19.11382792
 -3.325105816
 -1.747501714
 -3.897856223
 -14.92720776
 18
 -18
 -18

VLTMU

VLTMU =

0.070 -0.067 -0.080 0.019 -0.015 -0.019 -0.007 0.012 0.001 0.000 0.000 0.000
 -0.067 0.066 0.057 -0.024 0.013 0.026 0.007 -0.013 -0.001 0.000 0.000 0.000
 -0.080 0.057 0.264 0.036 0.027 -0.049 0.007 -0.007 -0.001 0.000 0.000 0.000
 0.019 -0.024 0.036 0.245 -0.449 -0.198 -0.003 0.002 -0.002 0.000 0.000 0.000
 -0.015 0.013 0.027 -0.449 2.053 0.103 -0.001 0.079 0.012 0.000 0.000 0.000
 -0.019 0.026 -0.049 -0.198 0.103 0.215 0.003 -0.019 0.000 0.000 0.000 0.000
 -0.007 0.007 0.007 -0.003 -0.001 0.003 0.030 0.006 -0.004 0.000 0.000 0.000
 0.012 -0.013 -0.007 0.002 0.079 -0.019 0.006 1.018 -0.021 0.000 0.000 0.000
 0.001 -0.001 -0.001 -0.002 0.012 0.000 -0.004 -0.021 0.001 0.000 0.000 0.000
 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000

$V = \text{VLTMU} + \text{eye}(12) * 0.00001$

V =

0.070 -0.067 -0.080 0.019 -0.015 -0.019 -0.007 0.012 0.001 0.000 0.000 0.000
 -0.067 0.066 0.057 -0.024 0.013 0.026 0.007 -0.013 -0.001 0.000 0.000 0.000

```
-0.080 0.057 0.264 0.036 0.027 -0.049 0.007 -0.007 -0.001 0.000 0.000 0.000
0.019 -0.024 0.036 0.245 -0.449 -0.198 -0.003 0.002 -0.002 0.000 0.000 0.000
-0.015 0.013 0.027 -0.449 2.053 0.103 -0.001 0.079 0.012 0.000 0.000 0.000
-0.019 0.026 -0.049 -0.198 0.103 0.215 0.003 -0.019 0.000 0.000 0.000 0.000
-0.007 0.007 0.007 -0.003 -0.001 0.003 0.030 0.006 -0.004 0.000 0.000 0.000
0.012 -0.013 -0.007 0.002 0.079 -0.019 0.006 1.018 -0.021 0.000 0.000 0.000
0.001 -0.001 -0.001 -0.002 0.012 0.000 -0.004 -0.021 0.001 0.000 0.000 0.000
0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000 0.000
```

```
[x,stdx,mse,S]=lscov(A,LTMU,V)
```

```
% x(1) is the intercept; x(2) the slope of the distance
```

```
x =
```

```
 -5.5960
```

```
 -7.7173
```

```
% stdx gives the standard errors
```

```
stdx =
```

```
 3.6554
```

```
 4.9807
```

```
mse =
```

```
 7.5699e+006
```

```
% S is the variance covariance matrix of the intercept and slope
```

```
S =
```

```
 13.3621  6.6140
```

```
 6.6140  24.8077
```

5. problems with boundary parameters

Two settlement probabilities were estimated at 0 and one was estimated at 1. Their asymptotic variances could not be computed by E-SURGE. This led to a non-invertible variance matrix. To solve this problem a solution is to add a small quantity on the diagonal. We added 0.00001 on the diagonal of $V(\text{logit } \mu)$.

```
[V=VLTMU+eye(12)*0.00001]
```


Appendix 3: backward approach for the selection of the best predictor of settlement

In this backward approach, we are proceeding from the full regression model (with all covariates) and removing the least significant until all remaining covariates are significant (see table A). Significance is determined by performing t-tests using the slope estimates and their standard errors (see Table B).

Table A. p-values for each element in the regression function and the effects removed (in bold) at each step of the backward approach, departing from the full regression model.

	Step 1	Step 2	Step 3	Step 4
	t-test df =	t-test	t-test	t-test
	7	df=8	df=9	df=10
Intercept	0.1863	0.1340	0.1145	0.1690
Distance	0.5644	0.3667	0.3468	-
Num. breeding pairs	0.0974	0.0573	0.0098	0.0035
Foraging area	0.9236	-	-	-
Breeding success	0.6753	0.6613	-	-

The removed least significant effects are (in chronological order): Foraging area, Breeding success and Distance.

Table B: Slope estimates and Standard errors (in parenthesis) for each step of the backward approach.

	Step 1	Step 2	Step 3	Step 4
Intercept	-5.4796 (3.7400)	-5.3278 (3.1953)	-4.5868 (2.6250)	-3.5981 (2.4269)
Distance	-4.3425 (7.1805)	-3.7640 (3.9341)	-3.7283 (3.7560)	11.6134 (3.0581)
Num. breeding pairs	12.9490 (6.7718)	12.6553 (5.7031)	10.5686 (3.2363)	-
Foraging area	-0.7569 (7.6182)	-	-	-
Breeding success	-2.6419 (6.0456)	-2.4849 (5.4624)	-	-

Chapter 4

Determinants of extinction-colonization dynamics in Mediterranean butterflies: the role of landscape, climate and local habitat features.

Albert Fernández-Chacón, Constantí Stefanescu, Meritxell Genovart, James D. Nichols, James E. Hines, Ferran Pàramo, Marco Turco, Daniel Oro. *Journal of Animal Ecology* (*under review*).

Photo credit: Constantí Stefanescu



Determinants of extinction-colonization dynamics in Mediterranean butterflies: the role of landscape, climate and local habitat features

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Summary

1. Many species are found today in the form of fragmented populations occupying patches of remnant habitat in human-altered landscapes. The persistence of these population networks requires a balance between extinction and colonization events assumed to be primarily related to patch area and isolation, but the contribution of factors such as the characteristics of patch and matrix habitats, the species' traits (habitat specialization and dispersal capabilities) and the variation in climatic conditions have seldom been evaluated simultaneously.
2. The identification of environmental variables associated with patch occupancy and turnover may be especially useful to enhance the persistence of multiple species under current global change. However, for robust inference on occupancy and related parameters, we must account for detection errors, a commonly overlooked problem that leads to biased estimates and misleading conclusions about population dynamics.
3. Here we provide direct empirical evidence of the effects of different environmental variables on the extinction and colonization rates of a rich butterfly community in the western Mediterranean. The analysis was based on a 17-year dataset containing detection/non-detection data on 73 butterfly species for 26 sites in North-eastern Spain. Using multi-season occupancy models, which take into account species' detectability, we were able to obtain robust estimates of local extinction and colonization probabilities for each species and test the potential effects of site covariates such as the area of suitable habitat, topographic variability, landscape permeability around the site and climatic variability in aridity conditions.
4. Results revealed a general pattern across species with local habitat composition and landscape features as stronger predictors of occupancy dynamics compared to topography and local aridity. Increasing area of suitable habitat in a site strongly decreased local extinction risks and, for a

number of species, both higher amounts of suitable habitat and more permeable landscapes increased colonization rates. Nevertheless, increased topographic variability decreased the extinction risk of bad dispersers, a group of species with significantly lower colonization rates.

5. Our models predicted higher sensitivity of the butterfly assemblages to deterministic changes in habitat features rather than to stochastic weather patterns, with some relationships being clearly dependent on the species' traits.

Key words: Biodiversity Hotspot, Effective precipitation, Lepidoptera, Monitoring scheme, Occupancy dynamics, PRESENCE, Spatial heterogeneity, Species' guild.

Introduction

As a result of human pressure, many animal populations are today restricted to remnant natural and semi-natural habitat patches embedded in landscape matrices mostly unsuitable for their survival. Such populations, occupying a collection of habitat patches, may thus form metapopulations, the persistence of which requires a dynamic equilibrium of colonization and extinction events (Hanski 1999). These dynamic processes are of vital importance for the long-term survival of a species, and investigating the factors governing them is an important subject in ecology and a significant goal in the conservation of biodiversity.

Many butterfly species are known to occur in spatially structured populations that usually follow the classical metapopulation concept, making them good biological models to study extinction and colonization processes (Thomas and Hanski 2004). These dynamic processes are assumed to be primarily related to patch geometry (area and isolation), although in some metapopulation studies –including several on butterflies- area and isolation have performed poorly as predictors of site occupancy (Prugh *et al.* 2008). These and other studies have shown that the characteristics of the patches themselves should not be ignored, as they may have strong effects on occupancy patterns by modifying local survival and colonization rates (Thomas *et al.* 2001, Fleishman *et al.* 2002, Prugh *et al.* 2008, Oliver *et al.* 2010). Thus, environmental variables such as adult food resources, type of land cover and topography can significantly affect the dynamics of spatially structured butterfly populations. Topography, in particular, has often been ignored in most studies assessing occupancy dynamics, despite the

importance of this variable for explaining local survival in butterfly populations (Weiss et al. 1988), its good performance at predicting species richness (Illán et al. 2010, Stefanescu et al. 2011) and forecasting future species' distributions under climate change scenarios (Luoto and Heikkinen 2008).

Likewise, due to the rapid response of butterfly populations and communities to the changing climate (Roy et al. 2001, Devictor et al. 2012), stochastic fluctuations in weather patterns (temperature and precipitation) may affect extinction and colonization patterns as well, either indirectly, through changes in local resource availability, or directly, by conditioning butterfly physiology or behaviour (Ehrlich et al. 1980, Piessens et al. 2009, Cormont et al. 2010).

Moreover, unlike oceanic islands, habitat patches within terrestrial ecosystems are not embedded within a homogeneous hostile matrix. It has been shown that factors such as the type of landscape surrounding a patch, together with the species' traits, may determine the permeability of the matrix for a given species and thus affect the colonization of unoccupied sites (e.g. Ricketts 2001; Opdam & Wascher 2004; Dover & Settele 2008; Lizée *et al.* 2011). In fact, it may even be difficult to differentiate between patch and matrix when both contain resources that directly affect survival, maintenance and reproduction within metapopulations (Vanreusel and Van Dyck 2007, Dennis 2010). Therefore, as pointed out by Dennis (2010), it has become increasingly obvious in butterfly metapopulation studies that there is a need to consider other information about the matrix than the simple presence or absence of a species' larval host plant.

Given all the above considerations, identifying the most relevant environmental variables that are associated with patch occupancy and turnover is not an easy task, but it is still a priority to enhance the persistence of multiple species under current global change (Fleishman et al. 2002, Opdam and Wascher 2004). However, although different species may respond differently to changes in the same environmental variables, depending on their degree of habitat specialization or dispersal abilities, very few studies have focused on the extinction-colonization dynamics of whole communities (Krauss et al. 2003) and, to our knowledge, this has never been attempted for a large number of coexisting butterfly species monitored over an extended time frame.

Most studies on patch-occupancy dynamics assume perfect detection of the species, overlooking the fact that a species may be present at a site and yet go undetected (false absences). Given the ambiguity of non-detections, it is important to account for detection errors in any study aimed at estimating the true state of occupancy and related parameters, as ignoring them may result in misleading model predictions and incorrect conclusions about a population (Moilanen 2002, MacKenzie et al. 2006). Thus, robust inference on occupancy dynamics can only be achieved by explicitly accounting for detection probability, such as in multi-season occupancy models which enable direct estimates of these parameters when detection is imperfect (MacKenzie et al. 2003).

Here we analyzed species' records from the Catalan Butterfly Monitoring Scheme, a network of butterfly recording sites in north-eastern Spain that has provided occupancy data uninterruptedly since 1994. This region of the Western Mediterranean is an important centre of biodiversity (Medail and Quezel 1999) with high levels of butterfly species richness (Hawkins and Porter 2003), but over the last several decades, this and other parts of the Mediterranean basin have been subjected to major changes in land use or cover and most natural habitats have been lost to, for example, intensive agriculture, tree plantations, reservoirs and urbanization (Symeonakis et al. 2007). Species' detection/non-detection data from multiple years were analyzed using multi-season occupancy models to obtain local extinction and colonization rates and to assess the effects of several environmental variables (local topography, suitable habitat area, landscape permeability, weather patterns) and the species traits (e.g. habitat specialization and dispersal capabilities) on these parameters. For instance, we assumed that an increasing aridity may induce higher larval mortality and higher dispersal of adults (because of lack of nectar and oviposition resources; e.g. Piessens *et al.* 2009), increasing both extinction and colonization rates. Model construction followed this and other biological hypotheses, and results were examined across species and compared between species' groups (defined by degree of habitat specialization and dispersal capabilities) to assess the influence of the species' traits on the performance of the predictors of occupancy dynamics. Our modelling approach, by explicitly including species' detection probability, allowed us to control for false absences and make robust inferences about occupancy changes over time. Unlike previous work where the processes governing species'

composition are inferred from observed patterns of species richness, here we focus on the underlying dynamic processes that generate occupancy patterns.

Material and methods

STUDY AREA, DATASET AND VARIABLES MEASURED

We used species' detection/non-detection data obtained from transect counts between 1994 and 2010 in Catalonia and the Balearic Islands (north-eastern Spain), as part of the Catalan Butterfly Monitoring Scheme or CBMS (www.catalanbms.org). This monitoring program is based on standardized weekly surveys of adult butterflies conducted along fixed routes during the flight season (30 weeks, from March 1 to September 26), when all species are available for record. During each visit to a site, observers walk a fixed transect route of about 2 km in length, recording all butterflies seen within a 5-m corridor. Transects are divided into a number of different sections, each corresponding to a particular habitat type (see van Swaay *et al.* 2008 for a summary of the standard methodology) Temporal and spatial heterogeneities in local abundances that affected the recordability of the species were corrected to some degree in the statistical analysis of our data (i.e. via the modelling of detection probabilities, see below).

Given that not all transects in the network had been monitored each year of our study period, we selected those transects with ≥ 10 years of data (24 in the mainland and 2 in the island of Minorca, see Fig. S1). These sites were located at elevations ranging from 0 to 1650 m above sea level and encompassed a wide range of environmental conditions and natural habitats (e.g. from dry Mediterranean habitats to subalpine habitats). Vegetation composition, geographic features and meteorological conditions were measured in and around the monitoring sites to quantify: suitable habitat area, landscape permeability, elevation and topographic variability, and effective precipitation (see below). Species appearing in fewer than 10 sites were excluded from our data, to ensure inferential strength in our analysis (Oliver *et al.* 2010), keeping a total number of 73 species. Also, to simplify data processing, weekly surveys were pooled into

monthly surveys, leaving 7 sampling occasions per season instead of 30. For each species, we finally created a detection/non-detection dataset containing 26 rows (number of monitoring sites) and 119 columns (product of the number of surveys x number of seasons) for statistical analysis.

SUITABLE HABITAT AREA

Botanic surveys conducted during the years 2000-2003 were used to quantify the vegetation composition at each monitoring site. The habitat composition of each section within a transect was characterized by classifying all vegetation types along the recording route into 17 broad habitat categories, following the CORINE Biotopes Manual (Moss and Wyatt 1994). Habitat preferences for each species had been previously determined following the approach of Oliver *et al.* (2010), using count data from all the CBMS network to calculate population densities (i.e. individuals/100 m transect) across the 17 habitat classes (see Stefanescu *et al.* 2011). Note that suitable habitats may include not only breeding habitat but also those habitats used for other purposes such as shelter, nectaring, etc. (i.e. a resource-based habitat view *sensu* Dennis 2010). Then, for any given species and site, we measured the area of suitable habitat in the 5-m corridor along the sampling route.

LANDSCAPE PERMEABILITY

In order to describe the landscape surrounding each of the monitoring sites, we examined the land cover composition in a 2 km buffer centered on each transect using the information contained in the Land Cover Map of Catalonia (MCSC), a high resolution (0.5m) and detailed (61 legend categories) thematic map compiled through photointerpretation of digitalised 1:5000 colour orthophotographs and developed by the Centre for Ecological Research and Forestry Applications (CREAF) in year 2007. Land cover categories were grouped into three major landscape components, following a similar approach as Lizée *et al.* (2012): a first class consisting of green surfaces containing natural vegetation and non-intensive cropland, a second class containing surfaces corresponding to bare soils and intensive cropland, and a third class containing water and impervious surfaces

(buildings, roads, parking areas). Then, we assigned a coefficient of permeability for butterfly dispersal to each class. We assumed that most butterfly species would disperse more easily through more vegetated and natural landscape matrices rather than those with more unvegetated or artificial components. Therefore, we assigned a coefficient of 1 (surfaces with the highest permeability to dispersal) to the 1st class of components in the landscape, a coefficient of 0.5 (surfaces with intermediate permeability) to the 2nd class, and a coefficient of 0 (impermeable surfaces) to the 3rd class. We then calculated the percentage of surface covered by these three major components in the landscape surrounding each transect and multiplied them by their corresponding coefficient. By summing these quantities, we were able to compute a site-specific index of landscape permeability, thus obtaining a measure of the functional connectivity of the landscape for multiple butterfly species.

TOPOGRAPHY

We used the Catalan Digital Elevation Model (MDEC), an altitudinal matrix of 30 m resolution (available at www.icc.cat), to obtain information on elevation and topographic metrics for each sampling site. Topographic slope values were calculated using the Spatial Analyst extension of software ArcGis v. 9.3 ESRI. Local topographic variability was obtained by computing the standard deviation of slopes in a 1 km buffer around each transect.

ARIDITY

Meteorological data was obtained from EOBS v. 5.0 (Haylock *et al.* 2008), a high-resolution (0.25° x 0.25°, approximately 25 km x 25 km) gridded dataset produced using hundreds of stations in Spain over the period 1950-2011. This dataset has been widely used for impact studies of regional climate change (e.g. Gottfried *et al.* 2012). For this study, monthly mean temperature and precipitation values for the EOBS grids containing the sampling stations were used to compute an index of local effective precipitation (EP; Thornthwaite 1948) as the difference between precipitation and potential evapotranspiration ($EP = P - PET$), which is

equivalent to an aridity index, with negative values indicating stronger aridity and positive values indicating wetter conditions.

To analyze the relationship between butterfly dynamics and climate, we defined the periods of the year when aridity could mostly affect extinction and colonization dynamics by examining each species' life cycle (see Appendix S1 for supporting information). Thus, for each butterfly species and year, we computed the mean EP of the months assumed to be most critical for larval survivorship and the mean EP of the months corresponding to the adult flight period.

OCCUPANCY MODELS

Detection/non-detection data for each species were analyzed building multi-season occupancy models in program PRESENCE 4.1 (Hines 2006). Multi-season occupancy models deal with data collected during repeated surveys conducted at multiple sites over an extended time frame (e.g. consecutive sampling periods or seasons), and allow the assessment of seasonal changes in species' occupancy with emphasis on the underlying dynamic processes of extinction and colonization. In our case, these dynamics were modelled as functions of covariates, and we built multi-season models that included parameters for initial occupancy (Ψ_1), colonization (γ), and extinction (ϵ), in addition to probabilities of detection (p) (MacKenzie *et al.* 2003).

MODELLING OCCUPANCY DYNAMICS

We limited our model set to plausible *a priori* hypotheses about the processes underlying detection, colonization and local extinction, and predefined a set of 60 candidate models to investigate these dynamic processes rather than conducting exploratory analyses including all the various combinations of potential covariates (see Appendix S2 for a detailed description of the candidate model set and our expected hypothesis). Because initial occupancy was not of primary interest in our study and because it is only a starting point for the analysis of extinction and colonization dynamics, initial occupancy was never related to a covariate and treated as a free parameter, following Ferraz *et al.* (2007). Species' specific detection probabilities (p) were always expressed as a combination of site and two

survey-specific covariates that may affect the detectability of individuals, i.e. the phenology of the species at the site and the observer conducting the survey. Phenology was introduced as a multiplicative function of month and elevation, given that factors such as the timing of the survey and the elevation of a site (a proxy of temperature) determine the peak of adult emergence (i.e. the peak of abundance of adult butterflies) and hence the species' detection at a given site. In addition, detection probability obviously depends on the skills of the observer. To account for this effect, recorders were classified into three categories of increasing experience (from beginners with no previous experience to recorders with more than 3 years of experience in the network), and this categorical variable was included as an additive effect on the detectability function.

Colonization and extinction probabilities were modelled either as constant parameters or as functions of different combinations of up to four continuous environmental variables: suitable habitat area (hereafter "habitat area"), landscape permeability, topographic variability (hereafter "topography") and seasonal aridity or effective precipitation (hereafter "EP"). For the modelling of colonization probabilities we used the mean EP of the months corresponding to the adult flight period, whereas for the modelling of extinction probability we used the mean EP of the months corresponding to the larval period (see also appendix S2). All these site covariates were normalized prior to the analysis. Topography was never used in the modelling of colonization probability because in our *a priori* hypotheses we considered that topography could only affect the extinction parameter by buffering local butterfly populations against climatic extremes (see appendix S2 for supporting information).

MODEL SELECTION AND ASSESSMENT OF PREDICTOR VARIABLES

Once we ran our candidate model set for each butterfly species, we based model selection on the Akaike's Information Criterion (AIC) and selected our best model as the one with the lowest AIC value. Models that differed in less than 2 points of AIC ($\Delta AIC < 2$) were considered statistically equivalent.

For each covariate, we calculated the summed Akaike weight of all models that contained the respective variable as a measure of the support it received. The sum of model weights cannot exceed 1, and top ranked models always show the

highest values. Therefore, we considered that a covariate was well supported in our modelling when the obtained sum was >0.6 , an indicator that it was included in higher ranked models more often.

The beta coefficients describing the relationship between each predictor and the response variable (extinction or colonization) were extracted from the top ranked models containing the covariate (those showing the most important effects of a predictor). We selected 1 model per species to obtain unique beta coefficients and corresponding Standard Errors (SE) for each type of predictor-response relationship. Species for which these coefficients and their SE were not estimable were removed for further analyses (see below). Standard errors were used to compute a 95% confidence interval of the slope, to facilitate inferences about the modelled relationship.

We examined the proportion of species showing good/bad support of a specific covariate in their models and tested for differences between proportions by performing Chi-square and Fisher-exact tests. We also drew inferences based on results of higher ranked models for all species and for species within ecological groups (see below) by asking whether slope parameter estimates were of the predicted sign more frequently than expected by chance alone using one-tailed z tests. For example, we checked whether the estimated relationship between landscape permeability and colonization probability was more often positive than negative.

ECOLOGICAL GROUPS

Following Stefanescu *et al.* (2011), we assigned each butterfly species to one of four categories of increasing mobility, from 1 (species with very low dispersal ability) to 4 (species showing long-range seasonal migration). In the same way, each species was classified into a category of habitat specialization, from 1 (extreme habitat specialists) to 4 (extreme generalists), based on the Species' Specialization Index (SSI) by Julliard *et al.* (2006) (for its implementation using CBMS data see also Stefanescu *et al.* 2011). To ease comparisons between groups, all species were eventually pooled into 2 categories of dispersal and specialization, respectively: bad dispersers (the above defined dispersal categories 1 and 2, $n=45$) and good dispersers (dispersal categories 3 and 4, $n=28$), and

habitat specialists (the above defined specialization categories 1 and 2, n=32) and habitat generalists (specialization categories 3 and 4, n=41).

Given their high dispersal capabilities, long-range migratory species should show the highest mean colonization rates, whereas the extinction risk of extreme habitat specialists should be highest due to their narrow habitat requirements. Species traits should also affect the performance of the different predictors of extinction and colonization dynamics. We expected topography and habitat area to be more important for bad than for good dispersers at reducing extinction risks, as rescue effects (*sensu* Brown & Kodric-Brown (1977)) may help out local populations of good dispersers more often. Variables such as EP, by inducing changes in dispersal behaviour, and landscape permeability, by influencing individual dispersal through the matrix, could be more important for modelling the colonization of bad dispersers. Finally, we also expected local habitat area to be a stronger predictor of both extinction and colonization rates in specialists than in generalist species.

Results

TOP RANKED MODELS

The most parsimonious model for colonization (being among the top ranked in 77% of species) was the one considering an additive effect of landscape permeability, habitat area and EP, closely followed by the model considering only additive effects of landscape permeability and habitat area (74% of species, see candidate model set in Appendix S2). The associations that appeared more often among the most parsimonious models for extinction were an interaction effect of both habitat area and landscape permeability (52%), and an additive effect of habitat area, landscape permeability and topography (48%).

EFFECTS OF COVARIATES ON EXTINCTION AND COLONIZATION PARAMETERS ACROSS SPECIES

Prior to the examination of the best predictors of extinction and colonization processes among species, we removed from our results those species where the

time-constant model (a model with constancy in extinction and colonization parameters, but time, observer and elevation effects in detectability) was among the most parsimonious models ($\Delta AIC < 2$), to make sure that we were always selecting species for which the inclusion of covariates significantly improved the description of occupancy dynamics.

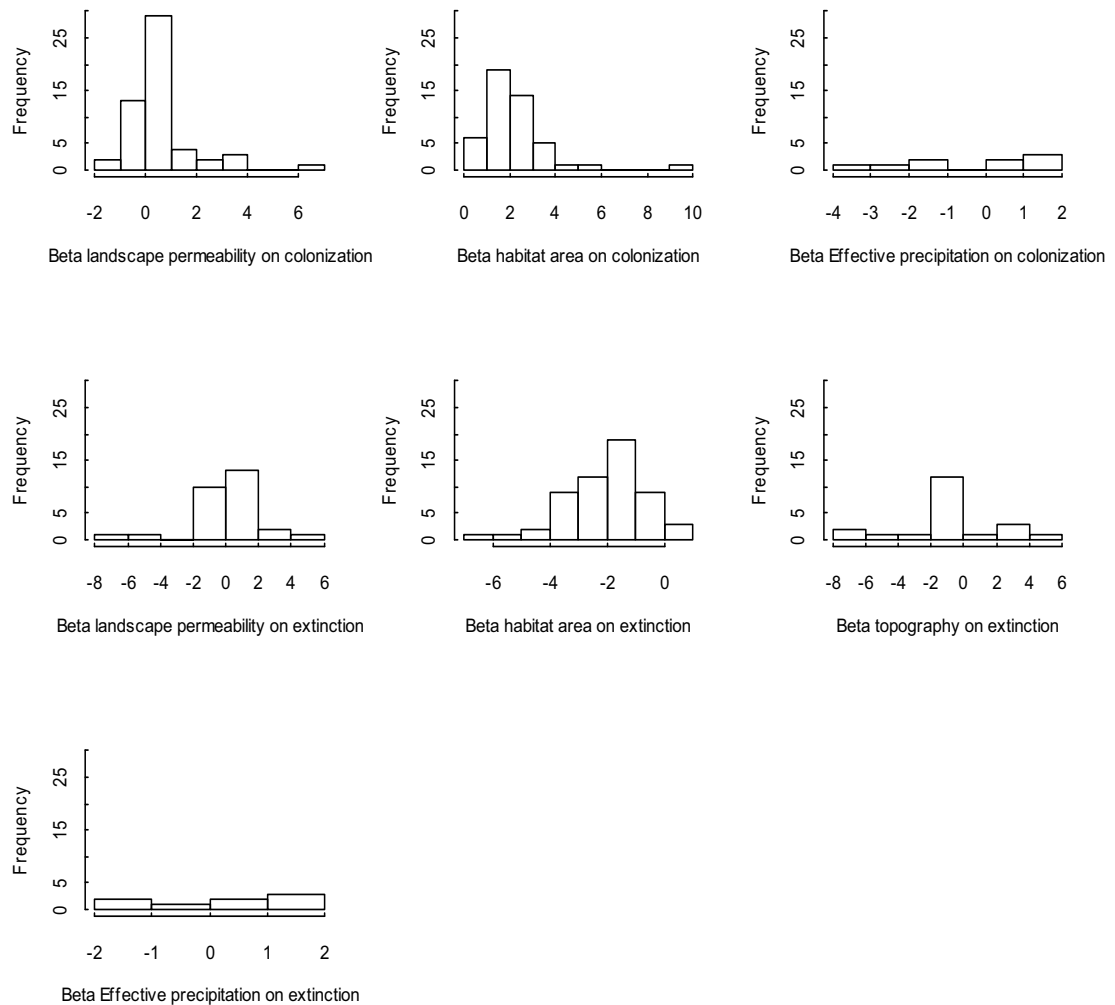


Fig. 1. Relationships between each predictor (environmental or site covariate) and the response variable (extinction or colonization). Beta coefficients defining the predictor/response relationships were extracted from the top ranked models of species where the covariate received good support (summed Akaike weight > 0.6). Large beta coefficients with no estimable standard errors were not included in the histograms.

Twelve species showed no evidence of any effect of environmental covariates on colonization probability (i.e. the time-constant model was the best structure describing colonization dynamics). For the remaining 61 species, landscape permeability was the best supported covariate, occurring in the top ranked models of all of them, and most of the time co-occurring with habitat area, which also received good support in 52 species. EP was only well supported in 15 species (see Appendix S3 for detailed results on summed AIC weights and slope parameter estimates for all species). Permeable landscapes increased colonization probability more often (38 out of 53 species with estimable slope parameters; $z = 3.506$, $P = 0.001$), and habitat area had always a positive effect when selected as a good predictor of colonization (Fig. 1). Thus, transects containing larger surfaces of suitable habitat and surrounded by more permeable landscapes are more likely to be colonized by a large number of species. Of the subset of species for which it was selected as a good predictor, EP showed no evidence of more negative than positive effects on the colonization parameter (Fig. 1).

Seven species showed no evidence of any environmental variable affecting extinction probability, but in the remaining 66 species extinction was always best described as a function of an external covariate: habitat area was well supported in 63 species, followed by landscape permeability (34 species), local topography (25 species) and EP (10 species). Larger habitat area decreased the extinction risk of 55 out of 63 species; of the remaining species, five had no estimable slope parameters and three species showed positive but not statistically significant slopes (Fig. 1). Increasing topographic variability decreased the extinction risk of 16 out of 21 species with well supported results and estimable slope parameters, and this proportion was significantly higher than that of landscape permeability (12 out of 28 species; Fisher exact test, $P = 0.023$). Increasing EP (lower aridity levels) decreased the extinction risk of only 3 out of 10 species, but these relationships were not statistically significant. Thus, for many species, extinction risks will be lower in transects containing larger areas of suitable habitat, and for a subset of species increased topographic complexity may further decrease their probability to become locally extinct.

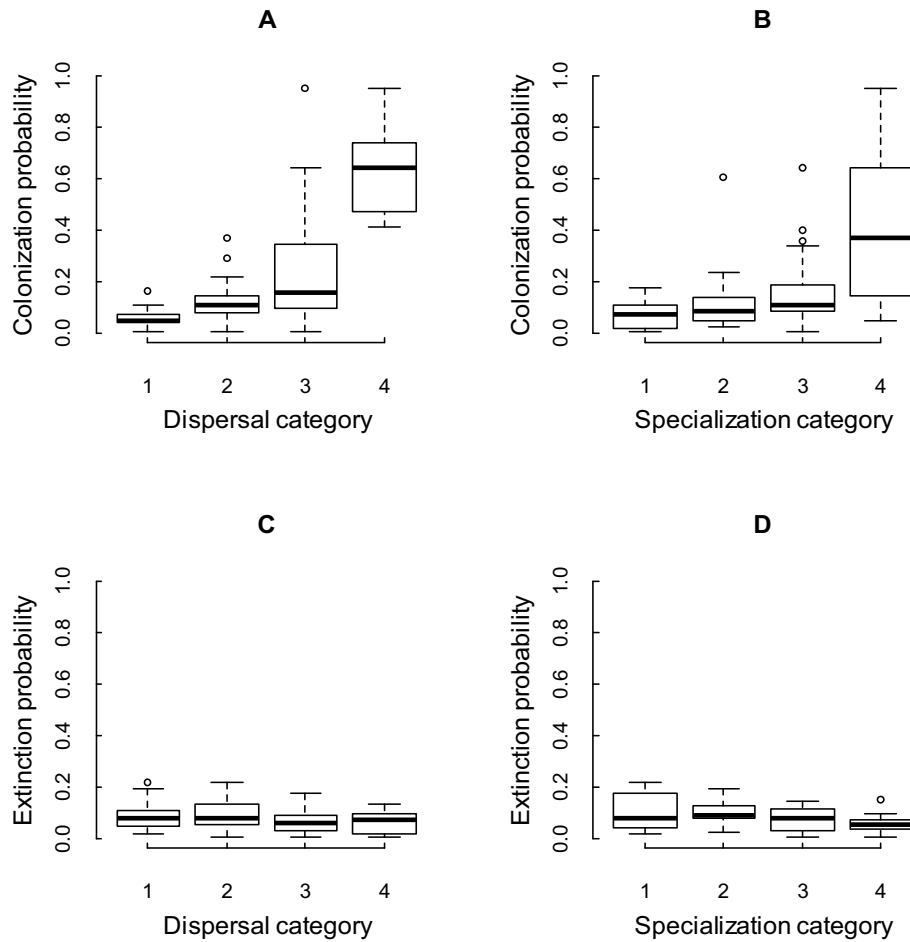


Fig. 2. Range of extinction and colonization estimates obtained for each dispersal and specialization category. Boxes and whiskers depict, in this order, the minimum value, lower quartile, median, upper quartile and maximum values of the observed distribution. Outliers are shown as white circles.

COMPARISON OF EXTINCTION/COLONIZATION RATES BETWEEN ECOLOGICAL GROUPS

Species specific extinction and colonization estimates (Table S1) obtained from the time-constant model allowed us to calculate summary statistics (Fig. 2) and to examine the existent patterns across the different categories of dispersal and specialization. Results revealed similar extinction rates among dispersal and specialization categories but significantly higher colonization probabilities of good dispersers compared to bad dispersers (one-tailed z test: $z = 1.965$, $P = 0.025$).

CONTRASTING MODEL RESULTS BETWEEN GOOD AND BAD DISPERSERS

As predictors of colonization, landscape permeability received identical high support in both dispersal groups and EP received better support in good than in bad dispersers (Fig. 3A), but this difference was not statistically significant ($\chi_1^2 = 0.699$, $P = 0.403$). Both groups showed similar proportions of positive relationships between colonization and the landscape variable (Fisher exact test, $P = 0.751$) and similar proportions of negative slopes for the EP variable (Fisher exact test, $P = 0.619$).

As predictor of extinction, topography performed significantly better in bad than in good dispersers (Fig. 3B; $\chi_1^2 = 4.257$, $P = 0.039$), with more negative than positive effects on extinction rates within the bad dispersers' group ($z = 3.499$, $P = 0.001$). The habitat variable received similar support as predictor of extinction in both groups (Fig 3B), and there were no differences in the proportion of negative slopes between good and bad dispersers (Fisher exact test, $P = 0.284$).

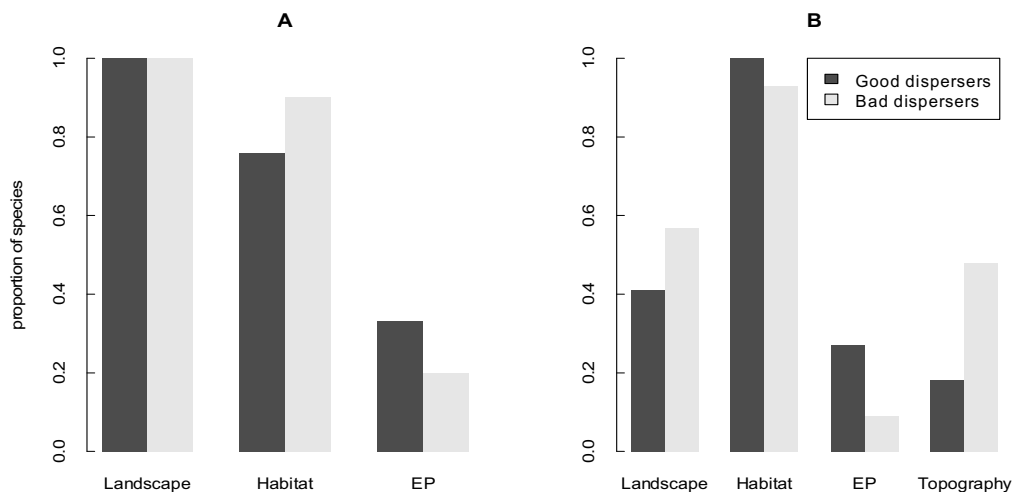


Fig. 3. Performance of the predictors of occupancy dynamics between dispersal categories (good versus bad disperser species). A covariate is identified as a good predictor when its summed AIC weight is above 0.6. Panel **A** shows the proportion of species within each category where the covariate performs well as a predictor of colonization, and panel **B** shows the proportion of species where the covariate is a good predictor of extinction.

CONTRASTING RESULTS BETWEEN HABITAT SPECIALISTS AND GENERALIST SPECIES

Colonization probabilities increased with habitat area more often in specialist than in generalist species (Fig. 4A), and this difference was statistically significant (Fisher exact test: $P = 0.027$). All predictors of extinction performed similarly between groups of specialization (Fig. 4B). Increasing habitat area did not reduce extinction risk of specialists more often, as we found no evidence of a higher proportion of negative slopes in specialists than in generalists (Fisher exact test: $P = 0.238$).

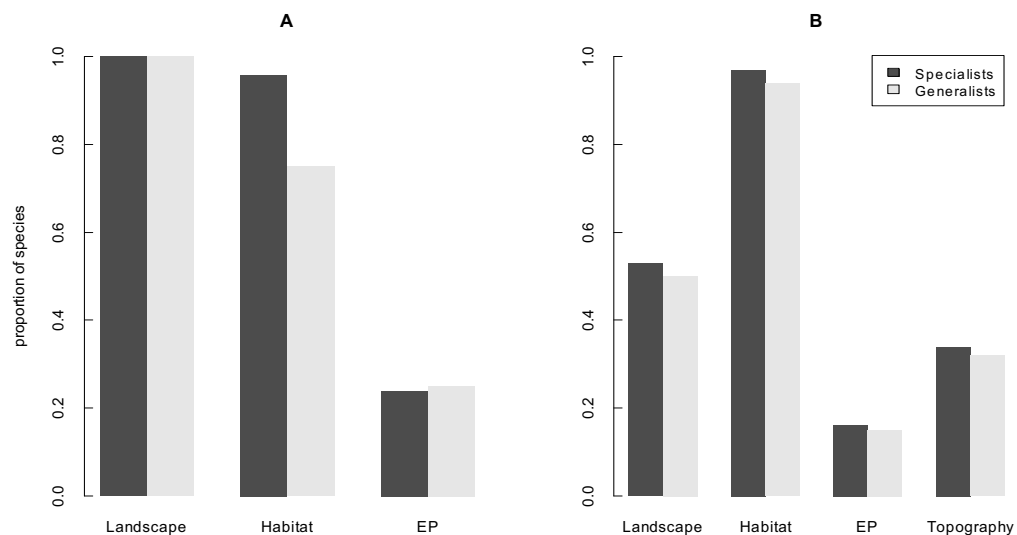


Fig. 4. Performance of the predictors of occupancy dynamics between specialization categories (specialist versus generalist species). A covariate is identified as a good predictor when its summed AIC weight is above 0.6. **A** shows the proportion of species within each category where the covariate performs well as predictor of colonization, whereas **B** shows the proportion of species where the covariate is a good predictor of extinction.

Discussion

By using an analytical framework that incorporated a diverse array of environmental variables and species' characteristic traits, we explored the underlying processes determining occupancy in highly diversified Mediterranean

butterfly assemblages. This approach provided, for the first time, reliable extinction and colonization rates for a large number of coexisting species of butterflies, and shed light upon the factors influencing occupancy dynamics in a region with high environmental diversity and under strong human pressure.

Habitat area was the best predictor of extinction rates across species, with an expected decrease in local extinction risk for increasing areas. According to metapopulation theory, area is a proxy of population size: the larger the area, the larger the population and the lesser the probability to become extinct (Hanski 1999). However, because a too simplistic definition of habitat patch based solely on the presence/absence of the larval resources may overlook other characteristics of the habitat that are equally important (e.g. Thomas *et al.* 2001, Fleishman *et al.* 2002), here we used a much broader –but still species specific– resource-based definition (Dennis 2010); in this way, we are confident that our measure of local habitat area reasonably estimates those portions of the recording transect that may sustain the highest population densities or at least those that provide the diversity and abundance of resources required for the survival of the species.

The local area of suitable habitat strongly affected colonization probability as well, and colonization rates always increased with habitat area. As pointed out by Jaquiéry *et al.* (2008), this positive effect might result from an active choice by dispersing individuals (implying the ability to target the sites containing more suitable habitat) or by a higher probability of successful settlement in larger recipient sites. In our study, habitat area did not perform better as a predictor of local colonization in good dispersers, despite their higher dispersal capabilities and hence increasing ability to detect tracks of suitable habitat in the landscape. Instead, significant differences were found between specialization categories, and colonization probabilities in specialists seemed to be more mediated by the local area of suitable habitat, suggesting that increasing area may be facilitating settlement of dispersing individuals.

Although the area of suitable habitat strongly affected colonization probability, the principal predictor of colonization across species was landscape permeability. Again, as expected, colonization probability increased with increasing permeability of the matrix surrounding the transect. Interestingly, however, the performance of the landscape variable was not affected by the species' traits (note that this similar performance between ecological groups does

not imply similar colonization probabilities, as good dispersers always showed significantly higher colonization rates). Our data thus corroborate the predictions of metapopulation theory that increasing patch isolation will reduce local colonization probabilities; more impermeable landscapes increase the isolation of a site by reducing immigration to it, and thus (re)colonization of empty patches becomes less likely if they are embedded in mostly impermeable matrices. We believe that for community studies such as ours, landscape permeability is a good approximation of patch isolation that permits the modelling of the dynamics of multiple species without the need to account for finer species-specific habitat preferences (such as we did to quantify suitable habitat area). Also, landscape permeability might provide an alternative way to define isolation when distance to the nearest source population (a measure of isolation more relevant to colonization dynamics; Prugh *et al.* 2008) is unknown, because not all habitat patches in the landscape that can potentially sustain a population are sampled.

Landscape permeability was not as good at predicting local extinction as it was at predicting colonization probability, despite the fact that the most often selected model structure for extinction probability included an interaction between habitat area and landscape permeability. Compared to habitat area, the landscape variable scored higher weights less frequently, and in addition to its poorer performance, landscape permeability did not have more negative effects on the extinction of species. This may suggest that extinction dynamics in our studied butterfly assemblages are more affected by within-patch habitat features and that permeability of the landscape may be influencing the extinction parameter in two ways simultaneously: both reducing and increasing local extinction risks by respectively promoting the arrival of immigrants from surrounding populations (rescue effect) and facilitating emigration when the local habitat deteriorates (Hill *et al.* 1996, Kuussaari *et al.* 1996, Mousson *et al.* 1999).

Compared to the previous factors, topography was not a powerful predictor of extinction dynamics across species, but this covariate reduced extinction risk more often than landscape permeability and performed better at predicting the extinction probabilities of the less mobile species. Indeed, we believe that topography might be buffering extinction in a large number of butterfly species in our study area. However, the importance of this variable becomes strongly apparent only for those species that, because of their low dispersal capacity, are

less able to avoid system-wide extinction by colonizing adjacent patches, and hence are more sensitive to the local availability of microclimatic refuges. Note that, by virtue of their patchy distribution, such species were underrepresented in our dataset compared to the most common and evenly distributed ones. This topographic effect is likely to be more important in cases where a species is close to its southern climatic range boundary (i.e. for the so-called “rear-edge” populations; Hampe & Petit 2005). The mountainous landscape of our study area could partly account for the seemingly weaker response of butterfly species to climate warming compared to northern regions. This was already suggested by Parmesan *et al.* (1999) for non-migratory European butterflies to explain the observed smaller changes in distribution in the southern range. Similarly, in a recent analysis, Oliver *et al.* (in prep.) found a marginal effect of topographic heterogeneity in lowering population variability (and hence extinction risk) in Catalan butterflies, but not in British butterflies, where the landscape is much more homogeneous.

Quite surprisingly, our study indicated a poor predictive power of EP for species extinction and colonization rates, with mostly non significant effects. Local variability in effective precipitation thus seemed to contribute very little to the seasonal occupancy dynamics of the butterflies in our study area, despite aridity having been identified as the main predictor of species richness in the Mediterranean basin (Hawkins and Porter 2003, Stefanescu *et al.* 2011). There are several reasons that may explain this apparent paradox: coarse grain data (regional climatic data from a 25 km grid matrix may not adequately reflect smaller-scale local climatic conditions), wrong hypothesis (we may have wrongly assumed a central role of EP on larval mortality and adult dispersal or failed to select the most critical periods for some species) and type of state variable (it may be more likely to see effects of climatic variability on abundance than on occupancy parameters). Moreover, in the studies by Hawkins & Porter (2003) and Stefanescu *et al.* (2011), mean local aridity condition, rather than interannual variability, was measured. The fact that we could not detect a general effect of our aridity measure on extinction-colonization dynamics may also indicate that deterministic processes (e.g. landscape and habitat change) might have played during our study period a more important role in the persistence of the butterfly species than stochastic processes such as more or less dry years. Local variations in

precipitation are one of multiple factors shaping plant assemblages in a site; other factors such as the type of soil, fire regime, grazing and past anthropogenic impacts may influence vegetation composition and structure in a patch. Indeed, all the features that make a patch suitable for a given species are already integrated in our measure of local suitable habitat area, which we have found to be a strong predictor of occupancy dynamics in our butterfly assemblages.

We conclude that increasing environmental quality in the form of increasing suitable habitat area and increasing permeability of the surrounding landscape, together with a more complex topography, all favour species' occupancy in human-altered landscapes and guarantee the coexistence of a large number of species in the studied butterfly assemblages. Conservation planning aimed at maintaining high butterfly diversity should therefore take into account these environmental variables, i.e. to manage habitats in and around occupied sites, and to protect sites with high topographic complexity such as mountain ranges. Moreover, conservation efforts aimed at populations of specialist and less mobile species are also likely to benefit other species in the community.

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Supporting Information

Figure S1. Map of the study region showing the location of the 26 sampling sites of the CBMS network where detection-non detection data for the present study were collected.



Appendix S1**Life cycle for each butterfly species in our study area.***Legend*

	1 st adult breeders of the current year
	1 st adult generation of the current year
	Larval stage
	Pupal stage
	egg stage (only for overwintering species)
	wintering period for migratory species (absence period from the study area)
	wintering period for species without diapause

Phenological periods

esp	early spring	March-April
lsp	late spring	April-May
esu	early summer	June-July
lsu	late summer	July-August
eau	early autumn	September-October
lau	late autumn	October-November
ewi	early winter	December-January
lwi	late winter	January-February

Univoltine species: species with one generation per year

Polivoltine species: species with more than one generation per year

Univoltine species	Prev. year						Current year						Critical period for larval survival				
	esp	lsp	esu	lsu	eau	lau	ewi	lwi	Sampling period					Previous year	Current year		
									esp	lsp	esu	lsu	eau				
<i>Hesperia comma</i>																lsp, esu	
<i>Thymelicus acteon</i>																esp	
<i>Thymelicus sylvestris</i>																esp	
<i>Libythea celtis</i>																lsp	
<i>Callophrys rubi</i>																lsp, esu	
<i>Glaucopsyche alexis</i>																lsp, esu	
<i>Glaucopsyche melanops</i>																lsp, esu	
<i>Lycaena alciphron</i>																esu	esp
<i>Maculinea arion</i>																esu	lsp
<i>Neozephyrus quercus</i>																	esp, lsp
<i>Plebejus argus</i>																	esp, lsp
<i>Polyommatus coridon</i>																	lsp, esu
<i>Polyommatus escheri</i>																	esp
<i>Pseudophilotes panoptes</i>																	lsp, esu
<i>Satyrrium esculi</i>																	esp, lsp
<i>Scolitantides orion</i>																	esu
<i>Tomares ballus</i>																	lsp
<i>Argynnis adippe</i>																	esp, lsp
<i>Argynnis aglaja</i>																	esp, lsp
<i>Argynnis paphia</i>																	esp, lsp

Polyvoltine species	Prev. year						Current year					Critical period for larval survival				
	esp	lsp	esu	lsu	eau	lau	ewi	lwi	Sampling period					Previous year	Current year	
									esp	lsp	esu	lsu	eau			
<i>Carcharodus alceae</i>									1-3-(4)						eau, lau	lsp, esu, lsu
<i>Erynnis tages</i>									1		2				eau, lau	lsp
<i>Ochlodes venatus</i>										1		2				esp, lsp, esu
<i>Pyrgus malvoides</i>									1			2				lsp, esu
<i>Spialia sertorius</i>									1			2		eau	lwi, esp, esu	
<i>Aricia cramera</i>									1-3-(4)					eau	lsp, esu, lsu	
<i>Cupido alcetas</i>										01-mar				eau	esp, lsp, esu	
<i>Celastrina argiolus</i>									1		2-3-(4)			eau, lau	lsp, esu	
<i>Cacyreus marshalli</i>										01-apr					lwi, esp, lsp, esu, lsu	
<i>Cupido argiades</i>										01-mar				eau	esp, lsp, esu	
<i>Lampides boeticus</i>										01-apr					lsp, esu, lsu	
<i>Lycaena phlaeas</i>										1-3-(4)				lau	lsp, esu, lsu	
<i>Leptotes pirithous</i>										01-apr					lsp, esu, lsu	
<i>Polyommatus bellargus</i>											1-2-(3)				esp, esu, lsu	
<i>Polyommatus hispana</i>											1		2		esp, esu	
<i>Polyommatus icarus</i>										1-3-(4)				lau	lsp, esu, lsu	
<i>Boloria dia</i>									1			02-mar			lwi, lsp, lsu	
<i>Cynthia cardui</i>										1-2-(3)					lsp, lsu	
<i>Charaxes jasius</i>											1		2	eau, lau	esp, esu	

<i>Inachis io</i>					1-2-(3)						lsp, esu, lsu lwi, esp, lsp, esu, lsu
<i>Issoria lathonia</i>				01-mar							
<i>Limenitis reducta</i>					1			2-(3)			lsu, eau
<i>Melitaea deione</i>						1-2-(3)					lsu, eau
<i>Melitaea didyma</i>					1				2		eau
<i>Melitaea phoebe</i>					1					2	eau
<i>Polygonia c-album</i>								1-2-(3)			
<i>Vanessa atalanta</i>						1-3-(4)					
<i>Iphiclides podalirius</i>							1		2-(3)		eau
<i>Papilio machaon</i>						01-apr					
<i>Colias alfacariensis</i>						01-mar					eau, lau
<i>Colias crocea</i>						1-3-(4)					eau, lau
<i>Euchloe crameri</i>							1			-2	lsp, esu
<i>Gonepteryx cleopatra</i>										1-(2)	
<i>Leptidea sinapis</i>							1		02-mar		eau
<i>Pieris brassicae</i>						01-apr					eau
<i>Pontia daplidice</i>						1-3-(4)					
<i>Pieris napi</i>						1-3-(4)					eau
<i>Pieris rapae</i>						01-apr					eau
<i>Coenonympha pamphilus</i>								1		02-mar	
<i>Lasiommata megera</i>						01-mar					
<i>Pararge aegeria</i>						1-3-(4)					

Appendix S2

Description of the candidate model set and hypotheses underlying the modelling of extinction and colonization parameters.

In this study, we assumed that extinction probability of local populations of any species could be directly affected by three variables: the area of suitable habitat at the monitoring site (hereafter “habitat area”), the local topographic variability (hereafter “topography”) and the effective precipitation (EP) during the species’ critical months for larval development. An increasing value of habitat area was hypothesized to reduce extinction probability, according to general metapopulation theory (Hanski 1999). Likewise, increasing topographic variability has been shown to reduce extinction probability by buffering butterfly populations against climatic extremes (e.g. Weiss *et al.* 1988) so we also predicted a negative effect of topography on the extinction parameter. Finally, an increasing value of EP (lower aridity) was predicted to reduce extinction probability by reducing larval mortality associated to poor condition of the host plants (e.g. Piessens *et al.* 2009).

These covariates were incorporated into the models either as single predictors of extinction probability or via additive combinations of habitat area plus topography and/or EP. Landscape permeability was considered to affect extinction dynamics indirectly via colonization (a “rescue effect” *sensu* Brown & Kodric-Brown 1977) and hence extinction was never modelled as a function of landscape alone; instead, landscape permeability was modelled always together with habitat area, either as a multiplicative function (full interaction model) or as an additive function (together with topography and/or EP).

We predicted that species’ colonization probability would be related to local climate and habitat features in three different ways: a function of landscape permeability alone, an additive function of landscape permeability plus a second covariate (habitat area or EP), and an additive function of landscape, habitat area and EP. In this case, increasing landscape permeability and decreasing values of EP (major aridity) would lead to increasing colonization rates. We also predicted an increase in local colonization rates with increasing habitat area, as sites containing larger tracks of suitable habitat may attract more immigrants or facilitate their settlement (Stamps 1991; Jaquiéry *et al.* 2008).

Model notation in the candidate model set

Ψ_1 = Initial occupancy parameter

γ = colonization parameter

ε = extinction parameter

p = detection probability

(.) = constancy

(month) = month of the year (timing of the survey)

(elev) = elevation of the monitoring site

(obs) = type of observer conducting the survey (experience category)

(habitat) = suitable habitat area along the transect route

(land) = permeability index of the landscape surrounding the transect

(topo) = variation in slopes within the monitoring site (topographic complexity)

(rainext) = effective precipitation values for the modelling of extinction

(raincol) = effective precipitation values for the modelling of colonization

Candidate model set

1. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{month} * \text{elev} + \text{obs})$
2. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{rainext}), p(\text{month} * \text{elev} + \text{obs})$
3. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{topo}), p(\text{month} * \text{elev} + \text{obs})$
4. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat}), p(\text{month} * \text{elev} + \text{obs})$
5. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat} + \text{topo}), p(\text{month} * \text{elev} + \text{obs})$
6. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat} + \text{land}), p(\text{month} * \text{elev} + \text{obs})$
7. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat} * \text{land}), p(\text{month} * \text{elev} + \text{obs})$
8. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat} + \text{land} + \text{topo}), p(\text{month} * \text{elev} + \text{obs})$
9. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat} + \text{land} + \text{rainext}), p(\text{month} * \text{elev} + \text{obs})$
10. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat} + \text{rainext}), p(\text{month} * \text{elev} + \text{obs})$
11. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat} + \text{topo} + \text{rainext}), p(\text{month} * \text{elev} + \text{obs})$
12. $\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\text{habitat} + \text{land} + \text{topo} + \text{rainext}), p(\text{month} * \text{elev} + \text{obs})$
13. $\Psi_1(\cdot), \gamma(\text{land}), \varepsilon(\cdot), p(\text{month} * \text{elev} + \text{obs})$
14. $\Psi_1(\cdot), \gamma(\text{land}), \varepsilon(\text{rainext}), p(\text{month} * \text{elev} + \text{obs})$
15. $\Psi_1(\cdot), \gamma(\text{land}), \varepsilon(\text{topo}), p(\text{month} * \text{elev} + \text{obs})$
16. $\Psi_1(\cdot), \gamma(\text{land}), \varepsilon(\text{habitat}), p(\text{month} * \text{elev} + \text{obs})$
17. $\Psi_1(\cdot), \gamma(\text{land}), \varepsilon(\text{habitat} + \text{topo}), p(\text{month} * \text{elev} + \text{obs})$
18. $\Psi_1(\cdot), \gamma(\text{land}), \varepsilon(\text{habitat} * \text{land}), p(\text{month} * \text{elev} + \text{obs})$
19. $\Psi_1(\cdot), \gamma(\text{land}), \varepsilon(\text{habitat} + \text{land}), p(\text{month} * \text{elev} + \text{obs})$

60. $\Psi_1(\cdot), \gamma(\text{land}+\text{habitat}+\text{raincol}), \varepsilon(\text{habitat}+\text{land}+\text{topo}+\text{rainext}), p(\text{month}*\text{elev}+\text{obs})$

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Appendix S3

Results on summed AIC weights and slope parameter estimates for all species.

For all species for which the inclusion of covariates significantly improved the description of occupancy dynamics, we provide here:

- a) Corresponding dispersal and habitat specialization categories (from 1 to 4)
- b) Species name
- c) Summed AIC weight of the predictor variable in the modelling (Σ AICweight)
- d) The beta coefficient describing the slope of the relationship between the predictor and the response variable (Beta)*
- e) The Standard error of the beta coefficient (SE)*
- f) The upper and lower limits of the 95% Confidence Intervals (C.I.) of the betas*

*Due to estimability problems, a “-“ sign instead of a real value is given for some beta coefficients, standard errors and C.I.

Colonization parameter (γ)							
Landscape permeability							
Specialization	Dispersal	Species	Σ AICweight	Beta	SE	LowCI	UpCI
1	3	<i>Aglais urticae</i>	0.995	0.127	0.462	-0.779	1.033
3	2	<i>Anthocharis cardamines</i>	1	0.614	0.382	-0.135	1.363
4	2	<i>Anthocharis euphenoides</i>	0.946	0.67	0.249	0.182	1.158
1	1	<i>Aphantopus hyperantus</i>	0.999	-	-	-	-
2	2	<i>Aporia crataegi</i>	0.941	2	2	-0.900	5.490
1	2	<i>Argynnis adippe</i>	0.923	-1	0.936	-2.872	0.798
3	2	<i>Argynnis paphia</i>	0.988	0.245	0.356	-0.453	0.943
4	2	<i>Aricia cramera</i>	0.999	-0.534	0.258	-1.040	-0.028
2	2	<i>Boloria dia</i>	1	1	0.596	-0.079	2.257
2	1	<i>Callophrys rubi</i>	0.834	-0.004	0.32	-0.631	0.623
2	3	<i>Carcharodus alceae</i>	0.991	0.049	0.248	-0.437	0.535
1	3	<i>Charaxes jasius</i>	0.999	0.74	0.311	0.130	1.350
2	1	<i>Coenonympha arcania</i>	1	0.625	0.789	-0.921	2.171
2	2	<i>Coenonympha pamphilus</i>	0.998	0.496	0.64	-0.758	1.750
3	2	<i>Colias alfacariensis</i>	0.986	0.111	0.362	-0.599	0.821
4	4	<i>Cynthia cardui</i>	0.803	-	-	-	-
2	1	<i>Erynnis tages</i>	0.999	-0.373	0.294	-0.949	0.203
2	2	<i>Euphydryas aurinia</i>	0.999	0.249	0.312	-0.363	0.861
1	1	<i>Glaucopteryx alexis</i>	1	0.201	0.332	-0.450	0.852
1	1	<i>Glaucopteryx melanops</i>	0.999	0.523	0.352	-0.167	1.213
4	3	<i>Gonepteryx cleopatra</i>	0.999	4	1	0.867	6.229
4	3	<i>Gonepteryx rhamni</i>	0.923	-1	0.574	-2.363	-0.113
3	1	<i>Hesperia comma</i>	0.945	-	-	-	-
4	1	<i>Hipparchia fidia</i>	1	-0.35	0.286	-0.911	0.211
2	2	<i>Hipparchia semele</i>	0.973	0.828	0.718	-0.579	2.235
3	2	<i>Hipparchia statilinus</i>	0.999	0.253	0.275	-0.286	0.792
3	3	<i>Inachis io</i>	1	0.733	0.664	-0.568	2.034
4	3	<i>Iphiclides podalirius</i>	1	0.362	0.451	-0.522	1.246
3	3	<i>Issoria lathonia</i>	1	-0.084	0.354	-0.778	0.610
4	2	<i>Leptidea sinapis</i>	0.92	-0.225	0.334	-0.880	0.430
3	4	<i>Leptotes pirithous</i>	0.872	-0.387	0.706	-1.771	0.997
1	3	<i>Libythea celtis</i>	0.996	0.379	0.302	-0.213	0.971
4	2	<i>Limenitis reducta</i>	0.985	0.094	0.313	-0.519	0.707
4	2	<i>Maniola jurtina</i>	0.911	0.249	0.28	-0.300	0.798
3	2	<i>Melanargia lachesis</i>	1	7	2	3.042	10.526
2	1	<i>Melitaea cinxia</i>	0.999	0.701	0.587	-0.450	1.852
1	2	<i>Melitaea deione</i>	1	0.061	0.323	-0.572	0.694
2	2	<i>Melitaea didyma</i>	0.999	-0.087	0.352	-0.777	0.603
3	2	<i>Melitaea phoebe</i>	1	0.138	0.267	-0.385	0.661
2	3	<i>Neozephyrus quercus</i>	0.999	1	0.503	0.133	2.105

3	3	<i>Nymphalis antiopa</i>	0.999	3	0.94	0.852	4.536
3	3	<i>Nymphalis polychloros</i>	0.998	0.04	0.447	-0.836	0.916
1	2	<i>Ochlodes venatus</i>	0.999	4	2	0.427	6.809
3	3	<i>Pararge aegeria</i>	0.979	-	-	-	-
4	4	<i>Pieris brassicae</i>	0.91	-	-	-	-
3	3	<i>Pieris napi</i>	0.994	0.431	0.375	-0.304	1.166
4	4	<i>Pieris rapae</i>	0.875	-	-	-	-
1	1	<i>Plebejus argus</i>	1	0.872	0.647	-0.396	2.140
2	3	<i>Polygona c-album</i>	0.998	-0.027	0.278	-0.572	0.518
3	1	<i>Polyommatus bellargus</i>	1	0.891	0.918	-0.908	2.690
2	1	<i>Polyommatus escheri</i>	1	0.426	0.678	-0.903	1.755
3	3	<i>Polyommatus icarus</i>	0.985	-0.447	0.65	-1.721	0.827
2	1	<i>Pseudophilotes panoptes</i>	1	-0.139	0.247	-0.623	0.345
2	2	<i>Pyrgus malvoides</i>	1	0.897	0.812	-0.695	2.489
3	2	<i>Pyronia cecilia</i>	0.986	-0.38	0.289	-0.946	0.186
3	2	<i>Satyrrium esculi</i>	0.933	-	-	-	-
1	1	<i>Spialia sertorius</i>	1	2	0.623	0.567	3.009
4	2	<i>Thymelicus acteon</i>	0.999	0.15	0.287	-0.413	0.713
2	1	<i>Thymelicus sylvestris</i>	0.999	2	1	-0.365	3.919
1	1	<i>Tomares ballus</i>	0.999	-0.555	0.637	-1.804	0.694
4	4	<i>Vanessa atalanta</i>	0.986	-	-	-	-

Colonization parameter (γ)

Habitat area							
Specialization	Dispersal	Species	Σ AICweight	Beta	SE	LowCI	UpCI
1	3	<i>Aglais urticae</i>	0.923	2	0.688	0.914	3.610
3	2	<i>Anthocharis cardamines</i>	1	2	0.455	1.046	2.830
4	2	<i>Anthocharis euphenoides</i>	0	-	-	-	-
1	1	<i>Aphantopus hyperantus</i>	0.997	-	-	-	-
2	2	<i>Aporia crataegi</i>	0.648	2	1	-0.455	3.791
1	2	<i>Argynnis adippe</i>	0.875	2	0.89	0.428	3.916
3	2	<i>Argynnis paphia</i>	0.893	1	0.402	0.212	1.788
4	2	<i>Aricia cramera</i>	0.972	0.769	0.253	0.273	1.265
2	2	<i>Boloria dia</i>	1	3	0.567	1.391	3.613
2	1	<i>Callophrys rubi</i>	0.743	1	0.53	0.192	2.270
2	3	<i>Carcharodus alceae</i>	0.985	3	1	1.199	5.323
1	3	<i>Charaxes jasius</i>	0.999	3	0.611	1.534	3.930
2	1	<i>Coenonympha arcania</i>	1	3	0.697	1.345	4.077
2	2	<i>Coenonympha pamphilus</i>	0.997	2	0.643	0.933	3.453
3	2	<i>Colias alfacariensis</i>	0.723	0.807	0.423	-0.022	1.636
4	4	<i>Cynthia cardui</i>	0.646	-	-	-	-
2	1	<i>Erynnis tages</i>	0.998	2	0.571	1.007	3.245
2	2	<i>Euphydryas aurinia</i>	0.999	2	0.483	1.014	2.908

1	1	<i>Glaucopsyche alexis</i>	1	2	0.434	0.702	2.404
1	1	<i>Glaucopsyche melanops</i>	0.997	1	0.432	0.589	2.283
4	3	<i>Gonepteryx cleopatra</i>	0.984	1	0.509	0.400	2.396
4	3	<i>Gonepteryx rhamni</i>	0.31	-0.403	0.489	-1.361	0.555
3	1	<i>Hesperia comma</i>	0.427	2	0.923	-0.114	3.504
4	1	<i>Hipparchia fidia</i>	1	2	0.473	1.200	3.054
2	2	<i>Hipparchia semele</i>	0.86	3	1	0.401	5.407
3	2	<i>Hipparchia statilinus</i>	0.998	-	-	-	-
3	3	<i>Inachis io</i>	0.945	3	0.755	1.835	4.795
4	3	<i>Iphiclides podalirius</i>	0.999	3	0.75	1.040	3.980
3	3	<i>Issoria lathonia</i>	1	2	0.72	1.010	3.832
4	2	<i>Leptidea sinapis</i>	0.787	0.587	0.261	0.075	1.099
3	4	<i>Leptotes pirithous</i>	0.744	3	1	0.089	4.985
1	3	<i>Libythea celtis</i>	0.83	3	0.658	1.226	3.806
4	2	<i>Limenitis reducta</i>	0.97	1	0.425	0.436	2.102
4	2	<i>Maniola jurtina</i>	0.85	0.706	0.288	0.142	1.270
3	2	<i>Melanargia lachesis</i>	0.272	-0.171	0.777	-1.694	1.352
2	1	<i>Melitaea cinxia</i>	0.953	1	0.43	0.502	2.188
1	2	<i>Melitaea deione</i>	0.964	1	0.406	0.310	1.902
2	2	<i>Melitaea didyma</i>	0.974	2	0.534	0.585	2.679
3	2	<i>Melitaea phoebe</i>	1	0.958	0.235	0.497	1.419
2	3	<i>Neozephyrus quercus</i>	0.999	1	0.394	0.723	2.267
3	3	<i>Nymphalis antiopa</i>	0.996	-	-	-	-
3	3	<i>Nymphalis polychloros</i>	0.997	5	2	1.686	8.872
1	2	<i>Ochlodes venatus</i>	0.996	3	0.858	0.920	4.284
3	3	<i>Pararge aegeria</i>	0.335	-	-	-	-
4	4	<i>Pieris brassicae</i>	0.104	-	-	-	-
3	3	<i>Pieris napi</i>	0.974	2	0.654	0.533	3.097
4	4	<i>Pieris rapae</i>	0.245	-	-	-	-
1	1	<i>Plebejus argus</i>	1	4	1	1.713	5.813
2	3	<i>Polygonia c-album</i>	0.997	2	0.514	0.903	2.917
3	1	<i>Polyommatus bellargus</i>	1	4	1	1.997	6.297
2	1	<i>Polyommatus escheri</i>	1	3	0.885	1.474	4.944
3	3	<i>Polyommatus icarus</i>	0.889	4	3	-2.128	9.404
2	1	<i>Pseudophilotes panoptes</i>	1	2	0.3	0.932	2.108
2	2	<i>Pyrgus malvoides</i>	0.997	2	0.471	0.769	2.615
3	2	<i>Pyronia cecilia</i>	0.821	2	0.669	0.221	2.843
3	2	<i>Satyrium esculi</i>	0.718	-	-	-	-
1	1	<i>Spialia sertorius</i>	0.289	-0.003	0.308	-0.607	0.601
4	2	<i>Thymelicus acteon</i>	0.995	1	0.347	0.612	1.972
2	1	<i>Thymelicus sylvestris</i>	0.918	1	0.515	0.271	2.289
1	1	<i>Tomares ballus</i>	0.992	10	4	1.182	18.614
4	4	<i>Vanessa atalanta</i>	0.593	-	-	-	-

Colonization parameter (γ)							
Effective precipitation							
Specialization	Dispersal	Species	Σ AICweight	Beta	SE	LowCI	UpCI
1	3	<i>Aglais urticae</i>	0.364	1	0.91	-0.287	3.261
3	2	<i>Anthocharis cardamines</i>	0.568	0.924	0.61	-0.270	2.118
4	2	<i>Anthocharis euphenoides</i>	0.326	0.615	0.7	-0.757	1.987
1	1	<i>Aphantopus hyperantus</i>	0.902	-	-	-	-
2	2	<i>Aporia crataegi</i>	0.261	0.949	1	-1.293	3.191
1	2	<i>Argynnis adippe</i>	0.556	-	-	-	-
3	2	<i>Argynnis paphia</i>	0.554	-1	0.87	-3.019	0.383
4	2	<i>Aricia cramera</i>	0.49	-0.8	0.65	-2.064	0.464
2	2	<i>Boloria dia</i>	0.273	0.096	0.47	-0.833	1.025
2	1	<i>Callophrys rubi</i>	0.277	-0.63	0.83	-2.252	0.990
2	3	<i>Carcharodus alceae</i>	0.289	0.164	0.36	-0.547	0.875
1	3	<i>Charaxes jasius</i>	0.353	-0.53	0.61	-1.722	0.666
2	1	<i>Coenonympha arcania</i>	0.711	-2	1	-4.267	0.167
2	2	<i>Coenonympha pamphilus</i>	0.697	-1	0.84	-3.058	0.216
3	2	<i>Colias alfacariensis</i>	0.517	0.834	0.46	-0.070	1.738
4	4	<i>Cynthia cardui</i>	0.701	-	-	-	-
2	1	<i>Erynnis tages</i>	0.314	0.275	0.41	-0.521	1.071
2	2	<i>Euphydryas aurinia</i>	0.28	-0.19	0.59	-1.339	0.959
1	1	<i>Glaucopsyche alexis</i>	0.347	0.389	0.48	-0.548	1.326
1	1	<i>Glaucopsyche melanops</i>	0.279	-0.15	0.45	-1.037	0.731
4	3	<i>Gonepteryx cleopatra</i>	0.292	-0.51	1	-2.721	1.693
4	3	<i>Gonepteryx rhamni</i>	0.443	-2	2	-5.050	1.246
3	1	<i>Hesperia comma</i>	0.337	-2	1	-4.749	0.915
4	1	<i>Hipparchia fidia</i>	0.364	-0.69	0.77	-2.195	0.819
2	2	<i>Hipparchia semele</i>	0.529	-1	1	-3.523	0.531
3	2	<i>Hipparchia statilinus</i>	0.609	0.998	0.62	-0.211	2.207
3	3	<i>Inachis io</i>	0.43	0.648	0.55	-0.432	1.728
4	3	<i>Iphiclides podalirius</i>	0.475	-1	0.78	-2.526	0.528
3	3	<i>Issoria lathonia</i>	0.724	0.863	0.44	0.003	1.723
4	2	<i>Leptidea sinapis</i>	0.546	0.786	0.49	-0.165	1.737
3	4	<i>Leptotes pirithous</i>	0.32	-0.53	0.52	-1.557	0.497
1	3	<i>Libythea celtis</i>	0.82	-1	0.64	-2.731	-0.231
4	2	<i>Limenitis reducta</i>	0.639	1	0.57	-0.068	2.166
4	2	<i>Maniola jurtina</i>	0.351	1	1	-1.073	4.031
3	2	<i>Melanargia lachesis</i>	0.391	2	2	-1.418	4.764
2	1	<i>Melitaea cinxia</i>	0.276	-0.15	0.73	-1.587	1.291
1	2	<i>Melitaea deione</i>	0.99	1	0.43	0.497	2.199
2	2	<i>Melitaea didyma</i>	0.27	0.025	0.66	-1.271	1.321
3	2	<i>Melitaea phoebe</i>	0.278	-0.14	0.45	-1.008	0.736
2	3	<i>Neozephyrus quercus</i>	0.3	0.332	0.62	-0.879	1.543
3	3	<i>Nymphalis antiopa</i>	0.25	0.075	1	-2.802	2.952

3	3	<i>Nymphalis polychloros</i>	0.27	-0.11	0.85	-1.775	1.557
1	2	<i>Ochlodes venatus</i>	0.296	0.242	0.46	-0.660	1.144
3	3	<i>Pararge aegeria</i>	0.959	-	-	-	-
4	4	<i>Pieris brassicae</i>	0.848	-	-	-	-
3	3	<i>Pieris napi</i>	0.396	-1	1	-3.290	1.092
4	4	<i>Pieris rapae</i>	0.668	-	-	-	-
1	1	<i>Plebejus argus</i>	0.293	-0.31	0.7	-1.685	1.067
2	3	<i>Polygonia c-album</i>	0.303	-0.24	0.46	-1.131	0.657
3	1	<i>Polyommatus bellargus</i>	0.544	-1	0.84	-2.853	0.443
2	1	<i>Polyommatus escheri</i>	0.281	0.313	0.94	-1.527	2.153
3	3	<i>Polyommatus icarus</i>	0.309	0.767	1	-1.571	3.105
2	1	<i>Pseudophilotes panoptes</i>	0.304	-0.35	0.61	-1.542	0.834
2	2	<i>Pyrgus malvoides</i>	0.291	-0.21	0.41	-1.016	0.600
3	2	<i>Pyronia cecilia</i>	0.372	0.718	0.77	-0.789	2.225
3	2	<i>Satyrrium esculi</i>	0.352	-	-	-	-
1	1	<i>Spialia sertorius</i>	0.911	1	0.41	0.321	1.925
4	2	<i>Thymelicus acteon</i>	0.371	0.645	0.61	-0.545	1.835
2	1	<i>Thymelicus sylvestris</i>	0.345	-0.74	0.9	-2.499	1.029
1	1	<i>Tomares ballus</i>	0.843	-4	2	-7.631	-0.281
4	4	<i>Vanessa atalanta</i>	0.939	-	-	-	-

Extinction parameter (ϵ)**Landscape permeability**

Specialization	Dispersal	Species	Σ AICweight	Beta	SE	LowCI	UpCI
1	3	<i>Aglais urticae</i>	0.545	1	0.384	0.339	1.845
3	2	<i>Anthocharis cardamines</i>	0.807	1	0.575	0.119	2.373
4	2	<i>Anthocharis euphenoides</i>	0	-	-	-	-
1	1	<i>Aphantopus hyperantus</i>	0.306	-	-	-	-
2	2	<i>Aporia crataegi</i>	0.715	-	-	-	-
1	2	<i>Argynnis adippe</i>	0.2	-	-	-	-
3	2	<i>Argynnis paphia</i>	0.363	0.391	0.755	-1.089	1.871
4	2	<i>Aricia cramera</i>	0.882	-1	0.602	-2.659	-0.299
2	2	<i>Boloria dia</i>	0.449	0.539	0.55	-0.539	1.617
3	2	<i>Brintesia circe</i>	0.349	-0.12	0.786	-1.661	1.421
1	2	<i>Cacyreus marshalli</i>	0.658	1	0.552	0.034	2.198
2	1	<i>Callophrys rubi</i>	0.271	-0.082	0.441	-0.946	0.782
2	3	<i>Carcharodus alceae</i>	0.323	0.001	0.243	-0.475	0.477
4	3	<i>Celastrina argiolus</i>	0.475	-0.257	0.262	-0.771	0.257
1	3	<i>Charaxes jasius</i>	0.998	0.175	0.615	-1.030	1.380
2	1	<i>Coenonympha arcania</i>	0.328	0.898	1	-1.084	2.880
2	2	<i>Coenonympha pamphilus</i>	0.557	0.918	0.62	-0.297	2.133
3	2	<i>Colias alfacariensis</i>	0.457	1	0.709	-0.328	2.452
4	4	<i>Cynthia cardui</i>	0.273	0.249	0.27	-0.280	0.778

2	1	<i>Erynnis tages</i>	0.468	0.412	0.933	-1.417	2.241
4	2	<i>Euchloe crameri</i>	0.475	-0.031	0.556	-1.121	1.059
2	2	<i>Euphydryas aurinia</i>	0.938	2	0.638	0.335	2.835
1	1	<i>Glaucopsyche alexis</i>	0.784	1	0.401	0.284	1.856
1	1	<i>Glaucopsyche melanops</i>	0.961	2	0.911	0.433	4.005
3	1	<i>Hesperia comma</i>	0.767	5	3	-1.491	11.331
4	1	<i>Hipparchia fidia</i>	0.339	0.793	0.952	-1.073	2.659
2	2	<i>Hipparchia semele</i>	0.975	-5	2	-8.592	-1.434
3	2	<i>Hipparchia statilinus</i>	0.461	-0.784	0.494	-1.752	0.184
3	3	<i>Inachis io</i>	0.771	0.734	0.395	-0.040	1.508
4	3	<i>Iphiclides podalirius</i>	0.985	0.847	0.611	-0.351	2.045
3	3	<i>Issoria lathonia</i>	0.476	-1	0.513	-2.148	-0.138
2	4	<i>Lampides boeticus</i>	0.412	-0.363	0.227	-0.808	0.082
4	2	<i>Leptidea sinapis</i>	0.27	0.043	0.327	-0.598	0.684
3	4	<i>Leptotes pirithous</i>	0.958	2	0.627	0.750	3.208
1	3	<i>Libythea celtis</i>	0.432	0.563	0.503	-0.423	1.549
4	2	<i>Limenitis reducta</i>	0.91	2	0.74	0.295	3.195
3	3	<i>Lycaena phlaeas</i>	0.736	-0.898	0.508	-1.894	0.098
4	2	<i>Maniola jurtina</i>	0.744	-1	0.333	-1.865	-0.559
3	2	<i>Melanargia lachesis</i>	1	1	0.474	0.448	2.306
2	1	<i>Melitaea cinxia</i>	0.741	-0.984	0.484	-1.933	-0.035
1	2	<i>Melitaea deione</i>	1	-0.205	0.484	-1.154	0.744
2	2	<i>Melitaea didyma</i>	0.993	-0.135	0.562	-1.237	0.967
3	2	<i>Melitaea phoebe</i>	0.328	0.78	0.667	-0.527	2.087
2	3	<i>Neozephyrus quercus</i>	0.654	-0.479	0.295	-1.057	0.099
3	3	<i>Nymphalis antiopa</i>	0.659	-2	0.94	-3.695	-0.011
3	3	<i>Nymphalis polychloros</i>	0.305	-2	0.72	-3.270	-0.448
1	2	<i>Ochlodes venatus</i>	0.997	1	0.399	0.426	1.990
3	3	<i>Pararge aegeria</i>	0.996	-	-	-	-
4	4	<i>Pieris brassicae</i>	0.329	-	-	-	-
3	3	<i>Pieris napi</i>	0.518	0.533	0.366	-0.184	1.250
1	1	<i>Plebejus argus</i>	0.921	-	-	-	-
2	3	<i>Polygonia c-album</i>	0.553	0.088	0.338	-0.574	0.750
3	1	<i>Polyommatus bellargus</i>	0.645	2	0.963	-0.105	3.669
2	1	<i>Polyommatus escheri</i>	0.934	-1	1	-3.506	0.664
3	3	<i>Polyommatus icarus</i>	0.705	-0.517	0.308	-1.121	0.087
4	4	<i>Pontia daplidice</i>	0.268	0.052	0.292	-0.520	0.624
2	1	<i>Pseudophilotes panoptes</i>	0.996	-7	3	-12.408	-1.746
2	2	<i>Pyrgus malvoides</i>	0.321	-0.098	0.636	-1.345	1.149
4	2	<i>Pyronia bathseba</i>	0.998	-	-	-	-
3	2	<i>Pyronia cecilia</i>	0.989	0.125	0.528	-0.910	1.160
1	2	<i>Pyronia tithonus</i>	0.852	-	-	-	-
1	1	<i>Spialia sertorius</i>	0.423	-2	1	-4.809	0.139
4	2	<i>Thymelicus acteon</i>	0.969	2	0.749	0.647	3.583

2	1	<i>Thymelicus sylvestris</i>	0.399	-1	1	-4.067	1.073
1	1	<i>Tomares ballus</i>	0.674	-	-	-	-
4	4	<i>Vanessa atalanta</i>	0.358	0.312	0.396	-0.464	1.088

Extinction parameter (ϵ)

Specialization	Dispersal	Species	Σ AICweight	Habitat area			
				Beta	SE	LowCI	UpCI
1	3	<i>Aglais urticae</i>	1	-2	0.678	-3.518	-0.860
3	2	<i>Anthocharis cardamines</i>	0.999	-2	0.463	-2.510	-0.696
4	2	<i>Anthocharis euphenoides</i>	0	-	-	-	-
1	1	<i>Aphantopus hyperantus</i>	0.999	-	-	-	-
2	2	<i>Aporia crataegi</i>	0.877	-	-	-	-
1	2	<i>Argynnis adippe</i>	0.481	-0.207	0.377	-0.946	0.532
3	2	<i>Argynnis paphia</i>	0.972	-1	0.399	-1.795	-0.231
4	2	<i>Aricia cramera</i>	0.916	0.422	0.5	-0.558	1.402
2	2	<i>Boloria dia</i>	1	-2	0.564	-3.411	-1.201
3	2	<i>Brintesia circe</i>	1	-4	1	-7.247	-1.421
1	2	<i>Cacyreus marshalli</i>	0.874	-0.593	0.322	-1.224	0.038
2	1	<i>Callophrys rubi</i>	0.997	-3	1	-5.216	-0.842
2	3	<i>Carcharodus alceae</i>	1	-2	0.876	-4.139	-0.705
4	3	<i>Celastrina argiolus</i>	0.999	-2	0.65	-3.173	-0.625
1	3	<i>Charaxes jasius</i>	0.999	-0.918	0.545	-1.986	0.150
2	1	<i>Coenonympha arcania</i>	0.999	-2	0.588	-3.033	-0.729
2	2	<i>Coenonympha pamphilus</i>	0.999	-4	1	-6.035	-1.641
3	2	<i>Colias alfacariensis</i>	1	-1	0.446	-2.366	-0.618
4	4	<i>Cynthia cardui</i>	0.736	-0.361	0.249	-0.849	0.127
2	1	<i>Erynnis tages</i>	0.999	-5	2	-9.394	-1.546
4	2	<i>Euchloe crameri</i>	0.917	-0.646	0.307	-1.248	-0.044
2	2	<i>Euphydryas aurinia</i>	0.999	-4	1	-7.086	-1.872
1	1	<i>Glaucopteryx alexis</i>	1	-2	0.516	-3.066	-1.044
1	1	<i>Glaucopteryx melanops</i>	0.999	-2	0.522	-2.806	-0.760
3	1	<i>Hesperia comma</i>	0.998	-3	1	-5.892	-0.396
4	1	<i>Hipparchia fidia</i>	0.943	-1	0.562	-2.369	-0.165
2	2	<i>Hipparchia semele</i>	0.999	-0.73	0.611	-1.928	0.468
3	2	<i>Hipparchia statilinus</i>	0.703	0.265	0.194	-0.115	0.645
3	3	<i>Inachis io</i>	0.978	-2	0.638	-3.536	-1.036
4	3	<i>Iphiclides podalirius</i>	0.999	-2	0.534	-2.548	-0.454
3	3	<i>Issoria lathonia</i>	1	-2	0.576	-3.103	-0.845
2	4	<i>Lampides boeticus</i>	0.998	-1	0.403	-1.938	-0.358
4	2	<i>Leptidea sinapis</i>	0.994	-1	0.403	-2.075	-0.495
3	4	<i>Leptotes pirithous</i>	1	-0.943	0.434	-1.794	-0.092
1	3	<i>Libythea celtis</i>	1	-4	0.966	-5.419	-1.633
4	2	<i>Limenitis reducta</i>	0.999	-3	0.944	-5.017	-1.317
3	3	<i>Lycaena phlaeas</i>	0.999	-2	0.593	-2.799	-0.475

4	2	<i>Maniola jurtina</i>	0.846	0.376	0.313	-0.237	0.989
3	2	<i>Melanargia lachesis</i>	1	-2	0.585	-3.308	-1.014
2	1	<i>Melitaea cinxia</i>	0.994	-1	0.532	-2.374	-0.288
1	2	<i>Melitaea deione</i>	1	-0.595	0.379	-1.338	0.148
2	2	<i>Melitaea didyma</i>	0.998	-0.711	0.449	-1.591	0.169
3	2	<i>Melitaea phoebe</i>	0.561	-0.281	0.384	-1.034	0.472
2	3	<i>Neozephyrus quercus</i>	0.998	-1	0.419	-1.964	-0.322
3	3	<i>Nymphalis antiopa</i>	0.791	-3	4	-9.975	4.015
3	3	<i>Nymphalis polychloros</i>	0.999	-3	1	-5.363	-1.423
1	2	<i>Ochlodes venatus</i>	0.999	-3	0.711	-4.624	-1.836
3	3	<i>Pararge aegeria</i>	0.998	-2	0.649	-3.463	-0.919
4	4	<i>Pieris brassicae</i>	1	-	-	-	-
3	3	<i>Pieris napi</i>	0.999	-1	0.409	-2.104	-0.500
1	1	<i>Plebejus argus</i>	1	-	-	-	-
2	3	<i>Polygonia c-album</i>	0.999	-2	0.469	-2.995	-1.157
3	1	<i>Polyommatus bellargus</i>	0.998	-2	0.79	-3.857	-0.761
2	1	<i>Polyommatus escheri</i>	0.976	-1	0.595	-2.195	0.137
3	3	<i>Polyommatus icarus</i>	1	-3	1	-5.517	-1.057
4	4	<i>Pontia daplidice</i>	0.917	-0.511	0.243	-0.987	-0.035
2	1	<i>Pseudophilotes panoptes</i>	1	-7	3	-12.059	-1.867
2	2	<i>Pyrgus malvoides</i>	1	-2	0.644	-3.543	-1.019
4	2	<i>Pyronia bathseba</i>	1	-	-	-	-
3	2	<i>Pyronia cecilia</i>	0.999	-4	1	-6.360	-1.602
1	2	<i>Pyronia tithonus</i>	1	-	-	-	-
1	1	<i>Spialia sertorius</i>	0.994	-2	0.487	-2.532	-0.622
4	2	<i>Thymelicus acteon</i>	0.995	-1	0.503	-2.147	-0.175
2	1	<i>Thymelicus sylvestris</i>	0.998	-2	0.713	-3.886	-1.092
1	1	<i>Tomares ballus</i>	0.994	-	-	-	-
4	4	<i>Vanessa atalanta</i>	0.999	-2	0.828	-3.551	-0.305

Extinction parameter (ϵ)**Topography**

Specialization	Dispersal	Species	Σ AICweight	Beta	SE	LowCI	UpCI
1	3	<i>Aglais urticae</i>	0.356	0.809	0.555	-0.279	1.897
3	2	<i>Anthocharis cardamines</i>	0.856	-2	0.596	-2.743	-0.407
4	2	<i>Anthocharis euphenoides</i>	0.894	3	1	0.636	4.694
1	1	<i>Aphantopus hyperantus</i>	0.255	-	-	-	-
2	2	<i>Aporia crataegi</i>	1	-	-	-	-
1	2	<i>Argynnis adippe</i>	0.838	-2	0.81	-3.484	-0.308
3	2	<i>Argynnis paphia</i>	0.834	-1	0.539	-2.326	-0.214
4	2	<i>Aricia cramera</i>	0.475	0.887	0.616	-0.320	2.094
2	2	<i>Boloria dia</i>	0.244	0.13	0.514	-0.877	1.137
3	2	<i>Brintesia circe</i>	0.326	-0.764	0.795	-2.322	0.794

1	2	<i>Cacyreus marshalli</i>	0.405	-0.947	0.521	-1.968	0.074
2	1	<i>Callophrys rubi</i>	0.999	-2	0.529	-2.982	-0.908
2	3	<i>Carcharodus alceae</i>	0.343	0.245	0.303	-0.349	0.839
4	3	<i>Celastrina argiolus</i>	0.33	0.662	0.551	-0.418	1.742
1	3	<i>Charaxes jasius</i>	0.001	-1	0.705	-2.714	0.050
2	1	<i>Coenonympha arcania</i>	0.806	-2	0.981	-3.797	0.049
2	2	<i>Coenonympha pamphilus</i>	0.706	-2	0.658	-2.836	-0.256
3	2	<i>Colias alfacariensis</i>	0.618	-1	0.828	-3.102	0.144
4	4	<i>Cynthia cardui</i>	0.223	0.107	0.248	-0.379	0.593
2	1	<i>Erynnis tages</i>	0.651	2	0.941	0.265	3.953
4	2	<i>Euchloe crameri</i>	0.588	-0.813	0.316	-1.432	-0.194
2	2	<i>Euphydryas aurinia</i>	0.285	-1	2	-5.229	2.443
1	1	<i>Glaucopteryx alexis</i>	0.304	0.355	0.732	-1.080	1.790
1	1	<i>Glaucopteryx melanops</i>	0.482	-1	0.931	-3.179	0.471
3	1	<i>Hesperia comma</i>	0.307	-3	3	-9.674	2.822
4	1	<i>Hipparchia fidia</i>	0.979	-7	3	-11.922	-1.404
2	2	<i>Hipparchia semele</i>	0.508	1	0.857	-0.304	3.056
3	2	<i>Hipparchia statilinus</i>	0.839	-2	0.61	-2.834	-0.442
3	3	<i>Inachis io</i>	0.375	-0.707	0.539	-1.763	0.349
4	3	<i>Iphiclides podalirius</i>	0.025	-2	0.688	-3.047	-0.351
3	3	<i>Issoria lathonia</i>	0.68	-1	0.513	-2.239	-0.229
2	4	<i>Lampides boeticus</i>	0.557	-0.395	0.211	-0.809	0.019
4	2	<i>Leptidea sinapis</i>	1	-3	0.593	-4.095	-1.771
3	4	<i>Leptotes pirithous</i>	0.522	-0.597	0.346	-1.275	0.081
1	3	<i>Libythea celtis</i>	0.364	0.64	0.52	-0.379	1.659
4	2	<i>Limenitis reducta</i>	0.999	-6	2	-9.841	-2.545
3	3	<i>Lycaena phlaeas</i>	0.989	2	0.671	0.735	3.365
4	2	<i>Maniola jurtina</i>	0.473	-0.887	0.247	-1.371	-0.403
3	2	<i>Melanargia lachesis</i>	0.019	-0.835	0.836	-2.474	0.804
2	1	<i>Melitaea cinxia</i>	0.427	1	1	-1.000	3.544
1	2	<i>Melitaea deione</i>	0	-0.034	0.453	-0.922	0.854
2	2	<i>Melitaea didyma</i>	0.002	-0.384	0.512	-1.388	0.620
3	2	<i>Melitaea phoebe</i>	0.753	-0.681	0.272	-1.214	-0.148
2	3	<i>Neozephyrus quercus</i>	0.32	0.478	0.484	-0.471	1.427
3	3	<i>Nymphalis antiopa</i>	0.76	4	1	1.271	6.901
3	3	<i>Nymphalis polychloros</i>	0.386	0.638	0.502	-0.346	1.622
1	2	<i>Ochlodes venatus</i>	0.042	-2	2	-5.819	2.319
3	3	<i>Pararge aegeria</i>	0.364	-	-	-	-
4	4	<i>Pieris brassicae</i>	0.26	-	-	-	-
3	3	<i>Pieris napi</i>	0.395	0.573	0.392	-0.195	1.341
1	1	<i>Plebejus argus</i>	0.634	-	-	-	-
2	3	<i>Polygonia c-album</i>	0.245	-0.219	0.317	-0.840	0.402
3	1	<i>Polyommatus bellargus</i>	0.415	2	1	-0.746	4.244
2	1	<i>Polyommatus escheri</i>	0.046	1	0.832	-0.144	3.118

3	3	<i>Polyommatus icarus</i>	0.238	0.418	0.793	-1.136	1.972
4	4	<i>Pontia daplidice</i>	0.957	-0.897	0.288	-1.461	-0.333
2	1	<i>Pseudophilotes panoptes</i>	0.955	-6	2	-9.677	-1.433
2	2	<i>Pyrgus malvoides</i>	0.9	1	0.505	0.192	2.172
4	2	<i>Pyronia bathseba</i>	0.005	-	-	-	-
3	2	<i>Pyronia cecilia</i>	0.014	-2	0.65	-2.841	-0.293
1	2	<i>Pyronia tithonus</i>	0.75	-	-	-	-
1	1	<i>Spialia sertorius</i>	0.235	0.06	0.395	-0.714	0.834
4	2	<i>Thymelicus acteon</i>	0.801	-2	0.823	-3.322	-0.096
2	1	<i>Thymelicus sylvestris</i>	0.32	-0.981	1	-2.986	1.024
1	1	<i>Tomares ballus</i>	0.768	-	-	-	-
4	4	<i>Vanessa atalanta</i>	0.28	0.078	0.413	-0.731	0.887

Extinction parameter (ϵ)**Effective precipitation**

Specialization	Dispersal	Species	Σ AICweight	Beta	SE	LowCI	UpCI
1	3	<i>Aglais urticae</i>	0.4	-1	0.786	-2.643	0.439
3	2	<i>Anthocharis cardamines</i>	0.364	-0.583	0.691	-1.937	0.771
4	2	<i>Anthocharis euphenoides</i>	0.029	0.182	0.805	-1.396	1.760
1	1	<i>Aphantopus hyperantus</i>	0.255	-	-	-	-
2	2	<i>Aporia crataegi</i>	0.558	-	-	-	-
1	2	<i>Argynnis adippe</i>	0.204	0.439	0.978	-1.478	2.356
3	2	<i>Argynnis paphia</i>	0.389	0.729	0.577	-0.402	1.860
4	2	<i>Aricia cramera</i>	0.243	-0.156	0.582	-1.297	0.985
2	2	<i>Boloria dia</i>	0.259	0.227	0.405	-0.567	1.021
3	2	<i>Brintesia circe</i>	0.308	-2	2	-4.581	1.565
1	2	<i>Cacyreus marshalli</i>	0.24	0.245	0.509	-0.753	1.243
2	1	<i>Callophrys rubi</i>	0.705	2	0.956	-0.140	3.608
2	3	<i>Carcharodus alceae</i>	0.258	-0.052	0.374	-0.785	0.681
4	3	<i>Celastrina argiolus</i>	0.254	0.009	0.397	-0.769	0.787
1	3	<i>Charaxes jasius</i>	0	0.4	0.511	-0.602	1.402
2	1	<i>Coenonympha arcania</i>	0.541	0.784	0.52	-0.235	1.803
2	2	<i>Coenonympha pamphilus</i>	0.364	0.566	0.489	-0.392	1.524
3	2	<i>Colias alfacariensis</i>	0.339	-0.747	0.573	-1.870	0.376
4	4	<i>Cynthia cardui</i>	0.839	-0.89	0.4	-1.674	-0.106
2	1	<i>Erynnis tages</i>	0.507	2	0.966	-0.342	3.444
4	2	<i>Euchloe crameri</i>	0.195	0.081	0.363	-0.630	0.792
2	2	<i>Euphydryas aurinia</i>	0.254	0.3	0.544	-0.766	1.366
1	1	<i>Glaucopsyche alexis</i>	0.217	0.413	0.949	-1.447	2.273
1	1	<i>Glaucopsyche melanops</i>	0.321	0.907	0.856	-0.771	2.585
3	1	<i>Hesperia comma</i>	0.429	4	2	-0.017	8.967
4	1	<i>Hipparchia fidia</i>	0.262	-0.23	0.821	-1.839	1.379
2	2	<i>Hipparchia semele</i>	0.214	-0.279	0.86	-1.965	1.407
3	2	<i>Hipparchia statilinus</i>	0.193	-0.15	0.476	-1.083	0.783

3	3	<i>Inachis io</i>	0.267	-0.219	0.469	-1.138	0.700
4	3	<i>Iphiclides podalirius</i>	0.009	0.392	0.489	-0.566	1.350
3	3	<i>Issoria lathonia</i>	0.836	-1	0.568	-2.414	-0.188
2	4	<i>Lampides boeticus</i>	0.996	1	0.296	0.506	1.666
4	2	<i>Leptidea sinapis</i>	0.287	0.261	0.532	-0.782	1.304
3	4	<i>Leptotes pirithous</i>	0.726	0.79	0.334	0.135	1.445
1	3	<i>Libythea celtis</i>	0.244	-0.002	0.498	-0.978	0.974
4	2	<i>Limenitis reducta</i>	0.628	0.905	0.537	-0.148	1.958
3	3	<i>Lycaena phlaeas</i>	0.271	0.087	0.485	-0.864	1.038
4	2	<i>Maniola jurtina</i>	0.171	0.234	0.597	-0.936	1.404
3	2	<i>Melanargia lachesis</i>	0.016	0.386	0.569	-0.729	1.501
2	1	<i>Melitaea cinxia</i>	0.404	0.707	0.578	-0.426	1.840
1	2	<i>Melitaea deione</i>	0	-0.028	0.39	-0.792	0.736
2	2	<i>Melitaea didyma</i>	0.005	-0.804	0.531	-1.845	0.237
3	2	<i>Melitaea phoebe</i>	0.133	0.043	0.372	-0.686	0.772
2	3	<i>Neozephyrus quercus</i>	0.751	-1	0.498	-2.009	-0.057
3	3	<i>Nymphalis antiopa</i>	0.179	-0.541	1	-2.672	1.590
3	3	<i>Nymphalis polychloros</i>	0.346	0.848	0.731	-0.585	2.281
1	2	<i>Ochlodes venatus</i>	0.055	-0.933	0.53	-1.972	0.106
3	3	<i>Pararge aegeria</i>	0.117	-0.586	0.952	-2.452	1.280
4	4	<i>Pieris brassicae</i>	0.768	-	-	-	-
3	3	<i>Pieris napi</i>	0.255	0.222	0.406	-0.574	1.018
1	1	<i>Plebejus argus</i>	0.212	0.435	1	-1.670	2.540
2	3	<i>Polygonia c-album</i>	0.183	-0.116	0.431	-0.961	0.729
3	1	<i>Polyommatus bellargus</i>	0.235	0.02	0.669	-1.291	1.331
2	1	<i>Polyommatus escheri</i>	0.056	0.859	0.499	-0.119	1.837
3	3	<i>Polyommatus icarus</i>	0.273	0.685	0.647	-0.583	1.953
4	4	<i>Pontia daplidice</i>	0.521	0.544	0.341	-0.124	1.212
2	1	<i>Pseudophilotes panoptes</i>	0.261	0.036	1	-1.934	2.006
2	2	<i>Pyrgus malvoides</i>	0.475	0.652	0.485	-0.299	1.603
4	2	<i>Pyronia bathseba</i>	0.001	-0.004	1	-2.180	2.172
3	2	<i>Pyronia cecilia</i>	0.005	0.506	0.718	-0.901	1.913
1	2	<i>Pyronia tithonus</i>	0.363	-0.299	1	-2.692	2.094
1	1	<i>Spialia sertorius</i>	0.544	0.737	0.49	-0.223	1.697
4	2	<i>Thymelicus acteon</i>	0.537	-0.906	0.655	-2.190	0.378
2	1	<i>Thymelicus sylvestris</i>	0.634	1	0.782	-0.268	2.798
1	1	<i>Tomares ballus</i>	0.728	-	-	-	-
4	4	<i>Vanessa atalanta</i>	0.285	0.126	0.468	-0.791	1.043

Appendix S4

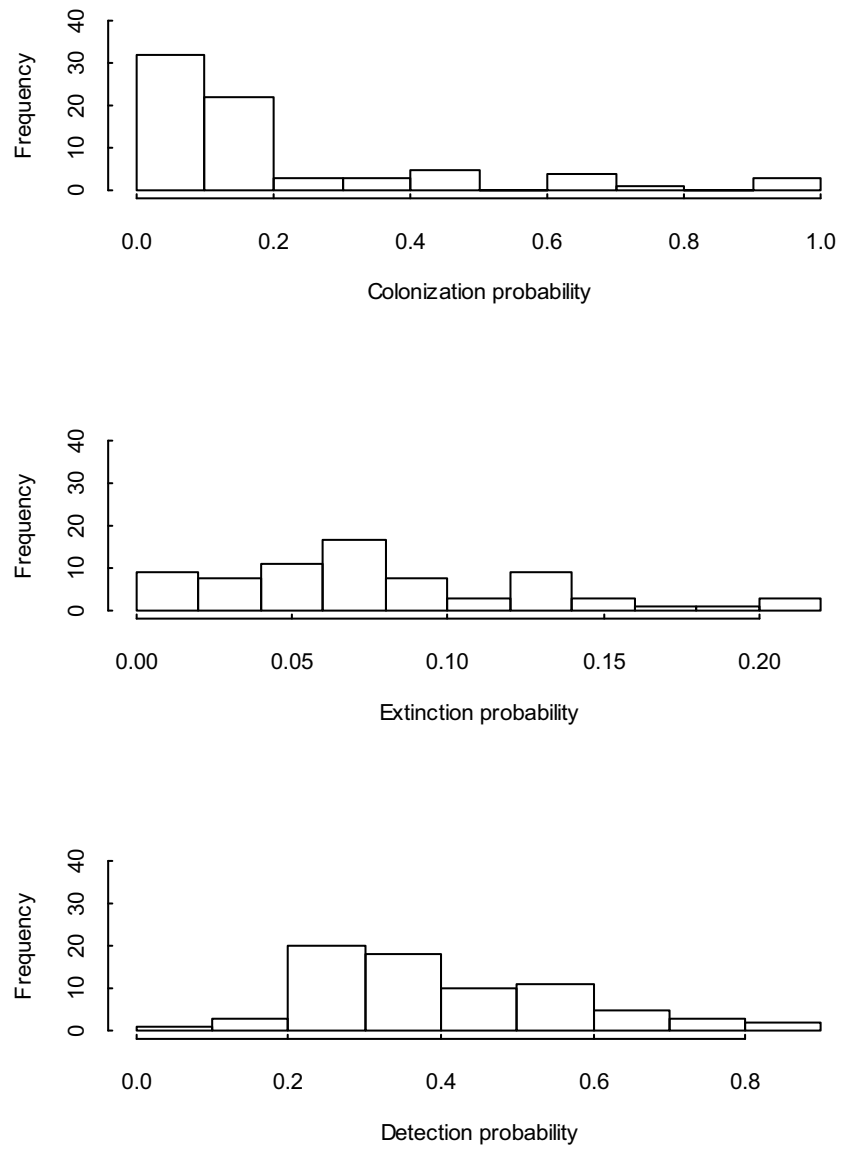
Tables and figures showing species-specific estimates of extinction, colonization and detection probabilities.

Table S4: Species-specific estimates of colonization (γ), extinction (ε) and detection probabilities (p), with corresponding standard errors (SE). Extinction and colonization rates were obtained from the time-constant model (see *results* section) whereas species' specific detection probabilities were obtained from an extra model without external covariates and constancy in all parameters [$\Psi_1(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$]. Note that the p estimates reflect the average detectability of the species, overlooking time, elevation and observer effects. Dispersal and specialization categories for each species are also given.

Specialization	Dispersal	Species name	γ	SE	ε	SE	p	SE
1	3	<i>Aglais urticae</i>	0.004	0.004	0.056	0.018	0.224	0.019
3	2	<i>Anthocharis cardamines</i>	0.104	0.031	0.077	0.025	0.236	0.011
4	2	<i>Anthocharis euphenoides</i>	0.046	0.017	0.041	0.020	0.273	0.015
1	1	<i>Aphantopus hyperantus</i>	0.004	0.004	0.018	0.017	0.259	0.022
2	2	<i>Aporia crataegi</i>	0.021	0.016	0.020	0.020	0.236	0.014
1	2	<i>Argynnis adippe</i>	0.017	0.014	0.078	0.032	0.240	0.020
3	2	<i>Argynnis paphia</i>	0.109	0.029	0.065	0.018	0.405	0.013
4	2	<i>Aricia cramera</i>	0.143	0.038	0.072	0.019	0.415	0.013
2	2	<i>Boloria dia</i>	0.107	0.024	0.128	0.028	0.536	0.016
3	2	<i>Brintesia circe</i>	0.109	0.043	0.023	0.014	0.356	0.011
1	2	<i>Cacyreus marshalli</i>	0.117	0.026	0.218	0.052	0.218	0.018
2	1	<i>Callophrys rubi</i>	0.165	0.052	0.042	0.013	0.328	0.011
2	3	<i>Carcharodus alceae</i>	0.234	0.043	0.126	0.026	0.501	0.014
4	3	<i>Celastrina argiolus</i>	0.642	0.104	0.053	0.014	0.557	0.011
1	3	<i>Charaxes jasius</i>	0.089	0.026	0.077	0.023	0.382	0.014
2	1	<i>Coenonympha arcania</i>	0.044	0.019	0.076	0.025	0.322	0.014
2	2	<i>Coenonympha pamphilus</i>	0.079	0.025	0.076	0.020	0.666	0.012
3	2	<i>Colias alfacariensis</i>	0.083	0.020	0.131	0.031	0.551	0.017
4	4	<i>Colias crocea</i>	0.956	0.046	0.012	0.006	0.756	0.009
4	4	<i>Cynthia cardui</i>	0.956	0.046	0.071	0.015	0.592	0.011
2	1	<i>Erynnis tages</i>	0.052	0.017	0.193	0.049	0.424	0.025
4	2	<i>Euchloe crameri</i>	0.215	0.040	0.147	0.030	0.287	0.014
2	2	<i>Euphydryas aurinia</i>	0.120	0.030	0.140	0.039	0.184	0.012
1	1	<i>Glaucopsyche alexis</i>	0.052	0.020	0.041	0.025	0.150	0.014
1	1	<i>Glaucopsyche melanops</i>	0.092	0.026	0.094	0.036	0.221	0.016
4	3	<i>Gonepteryx cleopatra</i>	0.478	0.095	0.035	0.011	0.550	0.011
4	3	<i>Gonepteryx rhamni</i>	0.082	0.035	0.013	0.009	0.546	0.012
3	1	<i>Hesperia comma</i>	0.042	0.018	0.121	0.044	0.214	0.019

4	1	<i>Hipparchia fidia</i>	0.059	0.021	0.067	0.030	0.297	0.019
2	2	<i>Hipparchia semele</i>	0.046	0.019	0.075	0.033	0.319	0.018
3	2	<i>Hipparchia statilinus</i>	0.173	0.032	0.142	0.029	0.264	0.013
3	3	<i>Inachis io</i>	0.079	0.033	0.091	0.029	0.396	0.014
4	3	<i>Iphiclides podalirius</i>	0.125	0.039	0.041	0.014	0.564	0.012
3	3	<i>Issoria lathonia</i>	0.110	0.027	0.104	0.024	0.533	0.015
2	4	<i>Lampides boeticus</i>	0.604	0.084	0.104	0.020	0.358	0.012
4	3	<i>Lasiommata megera</i>	0.956	0.046	0.006	0.004	0.877	0.007
4	2	<i>Leptidea sinapis</i>	0.289	0.061	0.069	0.015	0.650	0.011
3	4	<i>Leptotes pirithous</i>	0.641	0.108	0.133	0.028	0.309	0.013
1	3	<i>Libythea celtis</i>	0.173	0.032	0.174	0.037	0.328	0.015
4	2	<i>Limenitis reducta</i>	0.191	0.047	0.077	0.022	0.369	0.013
3	3	<i>Lycaena phlaeas</i>	0.402	0.100	0.037	0.011	0.697	0.010
4	2	<i>Maniola jurtina</i>	0.368	0.084	0.044	0.012	0.595	0.011
3	2	<i>Melanargia lachesis</i>	0.116	0.049	0.040	0.013	0.338	0.011
2	1	<i>Melitaea cinxia</i>	0.042	0.015	0.081	0.028	0.296	0.016
1	2	<i>Melitaea deione</i>	0.099	0.022	0.211	0.040	0.365	0.018
2	2	<i>Melitaea didyma</i>	0.075	0.022	0.083	0.025	0.417	0.015
3	2	<i>Melitaea phoebe</i>	0.194	0.036	0.130	0.030	0.346	0.015
2	3	<i>Neozephyrus quercus</i>	0.137	0.031	0.146	0.037	0.272	0.015
3	3	<i>Nymphalis antiopa</i>	0.014	0.009	0.024	0.022	0.253	0.016
3	3	<i>Nymphalis polychloros</i>	0.157	0.043	0.091	0.042	0.166	0.013
1	2	<i>Ochlodes venatus</i>	0.108	0.026	0.104	0.024	0.425	0.015
4	4	<i>Papilio machaon</i>	0.740	0.087	0.077	0.017	0.462	0.011
3	3	<i>Pararge aegeria</i>	0.359	0.140	0.016	0.007	0.838	0.008
4	4	<i>Pieris brassicae</i>	0.471	0.173	0.015	0.007	0.658	0.010
3	3	<i>Pieris napi</i>	0.097	0.034	0.072	0.017	0.630	0.012
4	4	<i>Pieris rapae</i>	0.423	0.220	0.006	0.004	0.795	0.008
1	1	<i>Plebejus argus</i>	0.014	0.009	0.048	0.023	0.397	0.021
2	3	<i>Polygonia c-album</i>	0.191	0.043	0.091	0.022	0.480	0.013
3	1	<i>Polyommatus bellargus</i>	0.043	0.015	0.076	0.027	0.421	0.020
2	1	<i>Polyommatus escheri</i>	0.053	0.021	0.078	0.037	0.263	0.016
3	3	<i>Polyommatus icarus</i>	0.336	0.105	0.022	0.008	0.712	0.010
4	4	<i>Pontia daplidice</i>	0.663	0.083	0.098	0.020	0.422	0.012
2	1	<i>Pseudophilotes panoptes</i>	0.089	0.021	0.128	0.031	0.241	0.016
2	2	<i>Pyrgus malvoides</i>	0.094	0.024	0.129	0.032	0.446	0.017
4	2	<i>Pyronia bathseba</i>	0.153	0.039	0.066	0.019	0.321	0.012
3	2	<i>Pyronia cecilia</i>	0.096	0.030	0.052	0.019	0.333	0.013
1	2	<i>Pyronia tithonus</i>	0.023	0.016	0.027	0.012	0.372	0.012
3	2	<i>Satyrrium esculi</i>	0.004	0.004	0.006	0.004	0.310	0.011
1	1	<i>Spialia sertorius</i>	0.106	0.024	0.216	0.054	0.291	0.020
4	2	<i>Thymelicus acteon</i>	0.120	0.031	0.084	0.023	0.288	0.013
2	1	<i>Thymelicus sylvestris</i>	0.043	0.015	0.056	0.025	0.239	0.016
1	1	<i>Tomares ballus</i>	0.026	0.012	0.041	0.027	0.096	0.015
4	4	<i>Vanessa atalanta</i>	0.411	0.126	0.033	0.010	0.547	0.011

Figure S4: Histograms showing the frequencies of the parameter estimates shown in table S4.



General discussion

Population analysis across different taxa and scales of ecological complexity, following a transversal approach, increase the quality of research in the population ecology field by increasing the range of possible questions that can be addressed using rather simple observational data. This thesis demonstrates, through 4 case studies based on longitudinal data collected in the field, the flexibility and robustness of a set of analytical tools (PVA, capture-recapture and occupancy models) for the study of populations, and their usefulness to address a diversity of topics ranging from the evolution of life histories to the conservation of biological entities.

From single populations to metapopulations

Each case study in this thesis exemplifies a real-world situation in the study of population dynamics at varying scales of complexity, asking different ecological questions (table 1) and dealing with different methodological challenges (table 2). In chapters 1 and 2, I studied discrete population units, with no individual exchanges with other populations and with their dynamics exclusively driven by birth and mortality processes (i.e. without dispersal processes). Chapters 1 and 2 are also examples of populations sampled via capture-recapture techniques; the fact that the local sampled populations occupy a reduced area and that individuals are unlikely to be lost by permanent emigration reduces the costs of monitoring individually marked animals over time, making these populations ideal to conduct such studies. Isolated populations in small areas free from human disturbances are also excellent biological models to study the effects of local environmental variables, such as precipitation (chapter 1) or temperature (chapter 2), on population dynamics; these effects were examined under both the unistate (chapter 1) and multistate (chapter 2) capture-recapture approaches by means of covariate modelling. In addition, both chapters 1 and 2 focused on stage-structured populations, which allowed to address questions regarding individual growth and maturity rates (chapter 2) and age or size-dependence effects in survival (chapters 1 and 2), thanks to the stratification of the capture-recapture

data in permanent groups and/or dynamic individual states. In the case of chapter 2, the multistate approach allowed estimating growth and maturity rates setting to zero impossible degrowth transitions, and at the same time, the use of data from three different populations also allowed examining the existence of interpopulation differences with respect to their life history parameters. Because the Mediterranean tortoise is a species of conservation concern in Spain and potentially vulnerable to rapid environmental change, in chapter 1 I also performed a demographic PVA using known vital rate estimates and their association to environmental variables to evaluate the global extinction risk of the species under different precipitation scenarios. In this case, the use of vital rate estimates and covariate effects obtained by means of capture-recapture modelling and the incorporation of environmental stochasticity in the population projections increased the realism of the simulations and the robustness of the results shown.

In chapters 3 and 4, I studied population networks of seabirds and butterflies respectively (two taxa showing high dispersal capabilities), increasing the spatial scale and complexity of previous analysis. By focusing on connected populations in space and time, I could evaluate the effect of both local and surrounding environmental conditions on population dynamics that couldn't be addressed by focusing on single populations alone. The studies presented in chapters 3 and 4 relied on large-scale monitoring programs that generated large amounts of data, requiring the use of both efficient and robust analytical tools for the analyses. In chapter 3, I analysed a unique multisite dataset on Audouin's gull collected by means of capture-recapture techniques and I focused on the adult fraction of the population to study their survival and breeding dispersal dynamics. To deal with the complexity of the dataset and the biological hypotheses to be tested, several analytical innovations and modelling advances were applied in this chapter. Firstly, following the approach of Grosbois and Tavecchia (2003), I examined the fidelity and settlement components of dispersal and addressed different biological hypotheses for each component separately, getting a clearer picture of the dispersal process; at the same time, I took advantage of the multievent approach to control temporal emigration from the study area and to correct heterogeneities in recapture probabilities, thus yielding more robust and reliable outputs, and finally, I performed a novel post-hoc analysis to determine

the drivers of settlement by taking into account the covariance of the model estimates. In chapter 4, I analysed a multi-species dataset collected by means of detection-non detection surveys aimed at butterflies over a large geographic area in North-Eastern Spain; under this sampling scheme, each site containing a given species was regarded as a population unit of the species, providing a useful baseline for the study of metapopulation dynamics. The use of multi-season occupancy models in chapter 4 permitted to address biological hypothesis on the causes of population turnover over time by applying a candidate model set repeatedly on each species' dataset. By performing a comparison of results across species and between species' groups, I could derive both general and group-specific patterns of extinction and colonization, in order to assess the influence of the species' traits on population turnover and to identify the major drivers of occupancy dynamics in the study area.

Dealing with heterogeneity

The analysis of capture-recapture data always requires performing a Goodness of Fit (GOF) test of the data to a specified departure model. All departure models have assumptions and what the GOF does is to test whether these assumptions are met in the dataset, in order to correct or incorporate the sources of lack of fit into the modelling, as ignoring individual heterogeneities may result in biased vital rate estimates and wrong conclusions about population dynamics.

Table 1. Description of the different case studies and the main biological questions addressed in this thesis.

Chapter	Taxon	Population units	Characteristics	Biological questions addressed
I	<i>Testudo hermanni</i>	1	Long-lived species with low dispersal capabilities. Hibernates underground.	Climate-survival relationships and population response under different climatic scenarios
II	<i>Salmo trutta</i>	3	Non-migratory and iteroparous freshwater trout populations not connected by dispersal and experiencing different environmental conditions	Differences in survival and growth dynamics among streams. Effects of fish size and water temperature on survival.
III	<i>Larus audouinii</i>	4	Long-lived colonial seabird with high dispersal capabilities that overwinters in Western Africa and breeds in the Mediterranean.	Differences in survival and dispersal dynamics among local populations. Trends in site-fidelity and determinants of settlement.
IV	Ropalocera	26	Short-lived, strong variability in life cycles (univoltine, polivoltine) and species' traits (dispersal capabilities and degree of habitat specialization)	Role of species' traits, local environment and landscape features on extinction-colonization dynamics.

Transient effects are common in many capture-recapture studies because most of the time, many individuals that do not belong to the resident fraction of the population are marked, but never recaptured again. This is the case of species showing high dispersal capabilities, such as seabirds (chapter 3), in which transient effects are usually detected and modelled as an “age” effect, distinguishing newly marked from previously marked animals (Pradel et al. 1997). This solution also permits to calculate a proportion of transients in the population which can be used as an indicator of permanent emigration and compared among populations (chapter 3). Transient effects are less pronounced in isolated populations occupying reduced areas from which individuals are less likely or unable to disperse, such as the tortoise and trout populations in chapters 1 and 2; the absence of permanent emigration coupled to a high recapture probability make the apparent survival estimates obtained for these populations really close to true survival rates.

The stratification of the data in states or groups may also reduce heterogeneities because individuals are already placed in different states or categories that account for observed differences in survival and recapture. In chapter 2, capture-recapture data on brown trout was split in 3 groups, indicating the population (stream) where the individuals were sampled, and within each category, data was stratified according to the length of the individual at each capture occasion, by means of size states or dynamic size classes. This stratification of the field data, coupled to the absence of permanent emigration in the system, allowed a good fit of the departure Arnason-Schwarz model to the data (see chapter 2).

Individual heterogeneities are typical of wild populations and may be more easily detected when the amount of sampled individuals increases (Crespin et al. 2008, Nussey et al. 2008). This is the case of the Audouin's gull populations studied in chapter 3, where, despite stratification in multiple states, both transience and trap-dependence effects were detected in the GOF test and had to be modelled. In chapter 3, I found that multievent models are a useful tool to handle trap-dependence via the addition of extra states in the transition matrices, applying the "aware-unaware" method recently proposed by Pradel and Sanz-Aguilar (2012). In this case, these type of transitions were only modelled at the two sites where recapture heterogeneities were detected (the two largest colonies in the system, see chapter 3). Transitions from the naïve "unaware" state to the recently captured or "aware" state are equivalent to recapture probabilities and show the actual probability that an animal with no previous knowledge of the "trap" is captured.

Table 2. Analytical tools, main goals and methodological challenges faced in each case study.

Chapter	Analytical tools	Reported quantities	Goals	Limitations
I	CJS models and matrix population models (Demographic PVA)	<ul style="list-style-type: none"> – Survival and recapture probabilities. – Population growth rates. – Time to quasi-extinction. 	<p>Age effects, time dependence and covariate modelling in survival.</p> <p>Population projections with environmental stochasticity.</p>	<p>Unknown density-dependence effects.</p> <p>Demographic stochasticity not incorporated in the population projections.</p>
II	Multistate models	<ul style="list-style-type: none"> – Survival and recapture probabilities. – State transition probabilities of growth and maturation. 	<p>Group effects in transition probabilities.</p> <p>Group effects size dependence and covariate modelling in survival.</p>	<p>Large confidence intervals in some estimates. Not significant covariate effects.</p>
III	Multievent models	<ul style="list-style-type: none"> – Survival and recapture probabilities. – State transition probabilities of departure and settlement. – Proportion of transients. 	<p>Decomposition of dispersal in fidelity and settlement parameters.</p> <p>Correction of recapture heterogeneities.</p> <p>Model structure accounting for temporal emigration.</p> <p>Trends in departure probabilities.</p> <p>Covariate modelling of settlement.</p>	<p>Large number of model parameters and increased computational efforts.</p> <p>Need to retrieve settlement estimates, obtain the variance matrix of the right quantities and perform a post-hoc analysis by means of a least square approach.</p>
IV	Multiseason occupancy models	<ul style="list-style-type: none"> – Extinction, colonization and detection probabilities. – Covariate weights and beta coefficients. 	<p>Application of a common candidate model set to 73 datasets.</p> <p>Covariate modelling of extinction, colonization and detection probabilities.</p> <p>Effects of species' traits on predictor-response relationships.</p>	<p>Considerable computational efforts.</p> <p>No Goodness of fit test.</p> <p>Need to perform multiple summary statistics for the presentation of results.</p> <p>Some beta coefficients not estimable.</p>

Occupancy models make the assumption that site occupancy remains constant and closed to changes during the entire sampling season. Such assumption is usually met by conducting surveys at times when the availability of the species is uninterrupted, but sometimes, individuals may be using a territory early in the season and permanently emigrate from it or establish in the site at the end of our study period, leading to processes of extinction and colonization within the sampling season. Currently, no GOF test is available for multi-season occupancy models (James D. Nichols pers. comm.), so a first step to avoid bias in occupancy should be to study the species' phenology and design our sampling scheme in accordance with the closure assumption. Pooling of field data and the use of both site and survey-specific covariates when modelling detection probabilities are methods to control for further heterogeneities and reduce bias in occupancy and related parameters (MacKenzie et al. 2006). In chapter 4, I applied all the above recommendations to reduce bias in extinction and colonization parameters as much as possible: first, surveys were conducted during the period of the year when butterflies were available for sampling; then, weekly surveys were pooled into single monthly values, and finally several covariates were collected to model variation in detection probabilities caused by differences in the local abundance and recordability of the species.

Studying demography with an eye on the species traits and the environment

Survival, growth and maturity patterns

Demographic studies measuring stage-specific mortality and reproduction are the key to life history theory, establishing a direct link between population ecology and evolution by focusing on individual variation in fitness components. Mortality and fecundity vary with age and size and changes in these basic life history traits translate into changes in population growth; for instance, delaying age at maturity may reduce population growth rates (Stearns 1992). According to life history theory, adult survival is the key to the well-being of populations of long-lived vertebrates so knowledge on this parameter and its dynamics is an important goal in the conservation of these species as population status may be directly measured

by looking at this vital rate (Eberhardt 2002). In this thesis, survival has been a recurrent parameter examined across different life stages (chapters 1 and 2) and populations (chapters 2 and 3), using several capture-recapture modelling approaches to address several hypotheses about their dynamics in time and/or space. In addition to survival, growth and maturity rates have been closely examined in chapter 2 by means of multistate capture-recapture models, providing a more detailed description of the life history strategies of the studied populations.

As expected for populations of a long-lived organism in a natural area free from anthropogenic causes of mortality, adult survival in the tortoise population at the Ebro Delta was high and constant (chapter 1), whereas survival of the younger age classes were generally lower and varied from year to year. In this chapter, the modelling using external covariates (temperature and precipitation) allowed finding a positive correlation between juvenile survival and winter precipitation that explained most of the temporal variation detected in this parameter and highlighted the higher sensitivity of the younger life stages to climatic variability. Deterministic projections for this population corroborated the importance of high adult survival rates for population growth, but simulations under dry winter scenarios that permanently decreased juvenile survival predicted the local extinction of this population in the long-term, suggesting that the contribution of recruitment in the population persistence of long-lived species should not be underestimated. Adult survival rates of the long-lived Audouin's gull (chapter 3) also remained high and constant over the years and were very similar among populations under different ecological conditions, indicating a clear energetic investment towards a maximization of adult survival rates. However, in chapter 2, I found clear differences in survival between populations of brown trout inhabiting different streams environments. In this case, I found substantial variation in survival in all life stages and no evidence that the largest (mature) individuals consistently survived better than the smaller (immature) ones; however, at the smallest stream, I found evidence of a positive, yet not significant, correlation between water temperature and winter survival of trout that explained a large proportion of the variation recorded in this parameter. Patterns of maturity also differed between stream environments, with slower growth and delayed

maturity in simpler (poorer) stream environments, results consistent with the adaptativeness and plasticity in life history traits displayed by brown trout.

Dispersal

The transfer of individuals in space and time is a fundamental biological process with implications for survival, growth and reproduction and ultimately population size and stability (Clobert et al. 2001). Dispersal is also a multiple-step process in which individuals first decide to leave a site (emigration), move (transfer) and then settle in a new habitat patch, that can be either empty (colonization) or contain a previously established population (immigration). Intrinsic factors such as age or lifetime experience of the individuals may strongly influence their dispersal behaviour as well as changes in local conditions that affect individual fitness (Oro et al. 2004, Hénaux et al. 2007, Becker and Bradley 2007). In many species, most dispersal events occur prior to recruitment and become rare once breeding has started, with site fidelity increasing as more breeding experience is accumulated (Serrano et al. 2001, Hénaux et al. 2007). Nevertheless, breeding dispersal events may also occur if increasing fidelity translates into a decrease in fitness (Cam et al. 2004).

In this thesis, specific questions about dispersal were addressed in chapter 3 using novel multievent models that provided the statistical framework for a robust assessment of the factors involved in the mechanisms of dispersal. This chapter focused on the movement of adult individuals within a network of breeding colonies of Audouin's gull monitored by means of capture-recapture techniques, and I examined the breeding dispersal of gulls within the system by addressing finer questions regarding individual fidelity and settlement decisions. This approach corroborated the strong fidelity displayed by established breeders, with emigration been higher only for adults breeding in lower quality sites, a result also confirmed by the larger proportion of transient individuals found at these locations. This first result suggested a dispersal response to spatial variation in fitness within the system, which was further confirmed when analysing temporal variation in fidelity, observing an increase in dispersal over the years (decreasing trend in fidelity) at the largest populations where agents decreasing

fitness (predator disturbances and habitat deterioration) were increasing in later years. The examination of settlement revealed that dispersal was directed towards sites harbouring large populations, confirming the use of population size as a proxy or cue of habitat quality. Long-distance dispersal events were not rare and may have implications for populations either in and out of our study system; nevertheless, given the stochasticity and low frequency of breeding dispersal, other individuals transfers such as natal dispersal should be operating and probably better explain recorded colonization events and recent population expansion of the species in the Mediterranean. Natal dispersal was not examined in this chapter, but preliminary analyses using the same methodology indicated higher dispersal probabilities for juveniles than adults within the study area and low fidelity to the natal site, especially in the smaller colonies, with strong implications in local recruitment and gene flow (manuscript in preparation).

Population turnover

The study of population networks may be either based on individuals or populations as fundamental units. However, when the main research objective are the factors influencing the persistence of entire metapopulations, parameters describing site occupancy dynamics may be more reasonable and less costly to measure than descriptors of local changes in abundance (i.e. survival and dispersal rates)(MacKenzie et al. 2006). Consequently, species' traits become increasingly important in such large-scale studies involving multiple interacting populations because the population turnover observed in the spatial network is always a result of the interplay between the external environment and the intrinsic life histories, dispersal capacities and degrees of habitat specialization shown by the organisms under study.

Metapopulations go extinct when the rate of extinction of individual patches is greater than the rate of colonization of empty patches, so, from a conservation point of view, conditions favouring colonization and decreasing local extinction risks must be identified. Theory predicts that larger habitat patches reduce local extinction risks because they may sustain larger populations, whereas patch isolation caused by habitat fragmentation decreases colonization

rates and indirectly increases extinction risks (Hanski 1999). However, as a result of the species' traits, the observed population turnover may not always follow theoretical predictions (Davies et al. 2000). For instance, regardless of patch and matrix characteristics, species with low dispersal capacities will be always more vulnerable to local extinction than good dispersers due to their intrinsic lower colonization rates and rare species' that naturally occur at low abundance may be more extinction-prone than common species' with broader habitat requirements. Similarly, the same environmental variable may trigger different population responses in species' showing different habitat requirements or dispersal capacities.

The extinction-colonization dynamics of species occurring in metapopulations were thoroughly examined in chapter 4 by focusing on diurnal butterflies and their occupancy dynamics in space and time. The analysis performed in chapter 4 is the first of its kind in terms of the number of butterfly species' analysed simultaneously using multi-season occupancy models, and also innovative in the type and number of external covariates used in the modelling of occupancy dynamics, which are usually expressed simply as functions of patch area and isolation. A first result of this analysis were the low mean local extinction rates obtained for the majority of species compared to the corresponding mean colonization rates. As expected, increasing dispersal ability was correlated to increasing colonization rates but contrary to our expectations, mean extinction probabilities were independent of the species' traits. Although population turnover in some species' was not affected by external covariates, for the vast majority of species, habitat and landscape variables were important predictors of extinction and colonization dynamics. When the sign of the predictor-response relationships was examined, I found that increasing habitat area and landscape permeability (which also reflects decreasing patch isolation) both increased colonization probability and that extinction risks decreased as the amount of local suitable habitat increased, confirming predictions of the metapopulation theory regarding isolation effects on colonization and extinction-area relationships. The negative relationship between habitat area and extinction probability was a common feature of all species showing habitat effects on their dynamics, regardless of their ecological traits. When comparing species' groups,

an interesting result was to find significant differences in the performance of topography as a predictor of extinction. In this case, the species showing poorer dispersal capacities were at less risk of extinction if the site had increasing topographic complexity. This result is the first empirical evidence of the buffering capacity of landscape topography in the extinction of species and may explain why some non-migratory butterfly species do not go extinct at the southern margins of their distribution, as predicted by climate warming (Parmesan et al. 1999). Surprisingly for an insect group that shows rapid responses to environmental variability, seasonal changes in precipitation did not successfully explained metapopulation dynamics in this butterfly community. However, despite local variation in precipitation may cause changes in abundance, species' may avoid system-wide extinction thanks to the buffering effects of topography and the quality of the habitats both within and around the local patch, which increase microclimatic refugia and allow rescue-effects from surrounding populations.

Process prediction and implications for conservation

The use of models to predict population responses to future changes requires reliable inferences about vital rates and the factors influencing their dynamics in space and time. The reliability of our results are primarily affected by the data and the methodological approach used in their analysis; analytical problems are typically reduced when data is collected following standardized sampling protocols and the gathering of extra information about the individuals and populations under study increases their potential for more detailed studies on population dynamics, especially if this information is gathered at large spatiotemporal scales. In this sense, the datasets analysed in this thesis can be considered of high quality, as they have been collected following strict protocols, usually as part of long-term monitoring programs, and have been accompanied by the collection of valuable information on both individual and environmental characteristics.

Data collected in the field is the result of both ecological and observation processes that need not to be confounded to avoid spurious inferences about the processes causing the observed responses. In this thesis, I have consistently used a

methodological approach that partitions the observed population response into a component describing the ecological process of interest and a component accounting for their imperfect observation. Imperfect observations or detection errors are managed by the recapture and detection probability parameters incorporated in the capture-recapture and occupancy models used throughout the case studies presented in this thesis. The modelling of these “nuisance” parameters is the key to the estimation and modelling of vital rate parameters for a rigorous scientific approach to conservation (Kéry and Schaub 2011) as inaccuracies and imprecision in key vital rates may compromise decision-making based on reliable scientific evidences (Williams et al. 2002). Methodological advances that reduce the bias caused by individual heterogeneities and state uncertainty (chapter 3) and the use of models that explicitly account for detection errors have increased the reliability of the vital rate estimates reported in this thesis.

Good predictions about the future status and dynamics of biological systems can only be achieved by means of a previous understanding of the ecological factors responsible of the observed dynamics. Confusion about the appropriate descriptors and lack of knowledge about the influences of external factors on fundamental biological processes are important sources of uncertainty that decrease the reliability of model predictions (Williams et al. 2002). In this thesis I have demonstrated that capture-recapture and occupancy modelling tools allow investigation of the responses of complex biological systems to change by asking meaningful questions about the ecological drivers of change in vital rates via the incorporation of external covariates in the models. Covariate modelling has been a significant part of my research aimed at the identification of useful model structures among multiple alternative hypotheses. For each case study, rather than conducting exploratory analyses with all possible combinations of effects, I limited model construction to a set of *a priori* biological hypotheses based on previous knowledge about the species and the environmental covariates that could be more relevant for their dynamics, and based model selection in the Akaike Information Criterion (AIC) seeking a balance between model fit and precision in the estimates in order to select the best model structure.

The modelling with external covariates performed in this thesis has provided empirical evidences of population responses to environmental change in a wide range of animal taxa, allowing the identification of species, populations or life stages vulnerable to changes in environmental conditions. These findings provide useful information for the direction of conservation efforts and the development of management plans; for example, in the case of butterflies (chapter 4) actions such as the protection of mountain ranges would benefit populations of poor dispersers given that increased topographic complexity reduced local extinction risks in these species. Given that a large number of butterfly species showed similar responses to landscape permeability, this result also provides insights for the conduct of management actions that would benefit entire communities, which are essential for the conservation of biodiversity.

The identification of links between vital rates and environmental variables allows increasing realism in population projections and evaluate the consequences of different environmental scenarios in the fate of these populations. Population projections with environmental stochasticity performed for the Mediterranean tortoise (chapter 1) revealed low population growth rates and higher extinction risks at the Eastern and Western margins of the species' distribution, where drought conditions are expected to be more frequent in the future, an alarming result considering that in most of these areas tortoise populations are also suffering from non-climatic sources of mortality. Such demographic PVA was based in reliable vital rate estimates and predictor-response relationships obtained via the capture-recapture modelling of age-structured populations. In this case, a robust conservation diagnosis was possible by combining both analytical tools but results may be considered "optimistic" as demographic stochasticity and density dependence effects were not integrated in the population modelling.

Despite models are always highly simplified representations of true biological populations, such scientific approaches are strongly needed in conservation because often the alternative to quantitative analyses are unsustained opinions and politically-motivated priority settings (Morris and Doak 2002). Overall, in this thesis I could make reliable inferences about different ecological processes and the causal factors affecting their dynamics by means of a

transversal approach, applying a set of modelling tools for the analysis of diverse population data. All the quantities and environmental effects here reported provide useful evidence-based information for conservation practitioners. As new analytical tools remain to be developed and integrated into the population analysis' toolbox, this thesis should be viewed as a work in progress, which I expect to continue contributing in the future.

Conclusions

- 1) Population analysis using rather simple longitudinal data and their transversal application across multiple taxa and scales of ecological complexity allows addressing a wide range of biological questions that permit to integrate ecological, evolutionary and conservation fields in scientific research.
- 2) In this thesis, the high quality of the datasets and the use of capture-recapture and occupancy models that accounted for detection errors, reduced analytical problems and increased the reliability of the parameter estimates. In the case of large capture-recapture datasets, multievent models offered an ideal framework to handle recapture heterogeneities in the data.
- 3) The use of covariates in capture-recapture and occupancy modelling is the key to address questions about the responses of ecological systems to changes in habitat and climate that are relevant conservation problems. Covariate modelling reduced confusion about the external factors influencing the population dynamics of the species analyzed.
- 4) The application of capture-recapture models to the analysis of individual data yielded robust estimates of survival, growth and dispersal and model selection allowed addressing finer questions on these biological processes. The vital rate estimates and predictor-response relationships provided by these models translated into more realistic simulations and robust predictions about population viability.
- 5) Occupancy models applied to the analysis of data from biodiversity monitoring programs allowed the simultaneous investigation of the dynamics of multiple populations at large spatiotemporal scales. Multiseason occupancy models by linking extinction and colonization rates to external variables provided an alternative way to evaluate species' vulnerability to environmental change.

- 6) As expected for long-lived species, adult survival rates in Mediterranean tortoises and Audouin's gulls were found to be high and constant and, in the case of gulls, similar among populations as well. In brown trout, stage-dependent survival patterns varied over time and among populations and the survival of individuals from the smallest stream was mostly explained by winter severity. Juvenile survival rates in tortoises showed a temporal variation influenced by rainfall.
- 7) Population projections with environmental stochasticity conducted under future precipitation scenarios forecasted declining trends and quasi-extinction events at the Eastern and Westernmost populations of Mediterranean tortoise due to the lower juvenile survival rates predicted at these sites. These findings highlight the importance of recruitment for the long-term persistence of the species and the need to implement climate-smart conservation strategies.
- 8) Growth transitions examined in the multistate analysis of the brown trout populations confirmed the plasticity in life history traits of the species and revealed contrasting patterns of maturation between streams, probably as a result of differences in habitat quality.
- 9) The examination of the breeding dispersal process in Audouin's gull confirmed the site-tenacity of adult individuals to their breeding patch, except when the local habitat deteriorated. Dispersing gulls settled preferably at densely populated sites and used population size as a cue for habitat quality. Departures from the largest colonies and the movement of individuals out of the study area may have contributed to the recent population expansion of the species.
- 10) The analysis of CBMS data highlighted the importance of deterministic variables in the population turnover of the species analyzed. Models revealed extinction-area relationships and landscape effects in local colonization that fit the predictions of the metapopulation theory. For sedentary species, greater topographic variability resulted in a lower risk of local extinction. Such results can be used to implement management strategies aimed at maintaining butterfly diversity in human-altered landscapes.

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Resum de la tesi

INTRODUCCIÓ GENERAL

L'estudi de poblacions en ecologia

L'ecologia s'interessa principalment pels processos que fan que l'estat dels sistemes biològics canviï en el temps i en l'espai (Krebs 2001, Kéry and Schaub 2011) i tracta d'entendre els mecanismes responsables de les dinàmiques d'aquests sistemes biològics fent inferències a través de diferents nivells d'organització, des de grups d'individus o poblacions fins a conjunts de comunitats o metacomunitats (Begon et al. 1986).

Una població és un conjunt d'individus de la mateixa espècie que es troba ocupant un espai concret en un temps determinat (Begon et al. 1986). Les poblacions reals estan obertes a pèrdues i guanys d'individus que fan que la seva mida i estructura canviï al llarg del temps. Els naixements i la immigració constitueixen els guanys, mentre que les morts i l'emigració constitueixen pèrdues; si els guanys superen les pèrdues, la població creixerà i en el cas contrari, davallarà o s'extingirà (Lande and Ozarck 1988, Sinclair et al. 2009).

L'ecologia de poblacions és la branca de l'ecologia que s'ocupa de l'estudi de les poblacions com a unitats biològiques fonamentals i analitza canvis en les característiques poblacionals (mida, estructura) en els temps i en l'espai, que són el resultat acumulatiu de processos individuals (naixements, morts, immigració i emigració) (Begon et al. 1996, Sutherland et al. 1996). L'estudi de les dinàmiques poblacionals abasta des de poblacions discretes fins a conjunts de poblacions interconnectades o metapoblacions (Hanski 1998). Els nivells superiors d'organització (comunitats, metacomunitats) són versions més grans d'aquest mateix concepte poblacional i poden ser descrits per variables d'estat anàlogues (variables que quantifiquen l'estat del sistema, com l'abundància o la taxa d'ocupació) i taxes vitals similars (els paràmetres que governen els canvis en les variables d'estat, com la supervivència, la fecunditat, el reclutament o la dispersió). Per tant, l'estudi de sistemes biològics inclosos dins d'escala d'organització superiors i l'ús de descriptors quantitius aplicables a tots els

nivells d'integritat ecològica converteixen a l'ecologia de poblacions en el marc científic ideal per a l'estudi i gestió de poblacions, metapoblacions i comunitats, enllaçant la recerca en ecologia fonamental amb disciplines més aplicades com la biologia de la conservació i la gestió de la fauna (Morris and Doak 2002, Weddell 2002, Mills 2007, Sinclair et al. 2009).

L'ecologia de poblacions i la conservació de la biodiversitat

L'ésser humà afecta els recursos naturals tant de manera directa, per mitjà d'interaccions com la caça i la pesca, com de manera indirecta, per mitjà d'activitats que modifiquen el medi ambient local i global. Des de la segona meitat del segle XX, l'augment generalitzat en la població humana i el consum de recursos naturals ha accelerat la pèrdua de biodiversitat arreu del món degut a l'expansió de problemes ambientals com la sobreexplotació dels recursos, la contaminació, la destrucció dels hàbitats naturals i les introduccions d'espècies exòtiques, fent que la taxa d'extinció d'espècies s'alcí molt per sobre dels nivells de fons i causi el que ja s'ha batejat com el 6è episodi d'extinció massiva en la història de la Terra (Leakey and Lewin 1995, Thomas et al. 2004, Burney and Flannery 2005, Mills 2007).

Fins èpoques recents, els recursos vius eren només apreciats en termes econòmics, seguint una visió utilitària de la biodiversitat, i la conservació es limitava a polítiques de regulació de la caça i la pesca, malgrat que moltes espècies no comercials proporcionen serveis molts valorats pels humans com la descomposició, la pol·linització, el control de plagues i la producció de substàncies d'ús mèdic (Grifo and Rosenthal 1997, Weddell 2002, Mills 2007). Impulsada per la crisi de biodiversitat de finals dels segle XX, la conservació i gestió dels recursos vius va passar d'un enfoc utilitari a un enfoc més "preservacionista" on tots aquests recursos, independentment del seu valor econòmic, havien de ser protegits, donant lloc a la "disciplina de crisi" coneguda com a biologia de la conservació (Soulé 1985, 1991, Weddell 2002).

La biologia de la conservació és una disciplina sintètica que s'interessa per les dinàmiques i problemes de les espècies, comunitats i ecosistemes afectats per l'activitat humana (Soulé 1985). La fita de tots els esforços de conservació és la protecció de la biodiversitat i l'èxit d'aquests esforços requereix d'un

coneixement previ dels components individuals (ex: poblacions) que constitueixen les comunitats i els ecosistemes (Soulé 1985, 1991, Morris and Doak 2002, Weddell 2002, Mills 2007).

El camp de la conservació es fa preguntes sobre el món real (ex: Quants individus hi ha? És la supervivència alta? Quin és el risc d'extinció de la població?) que demanen respostes quantitatives (ex: mides poblacionals, taxes de supervivència i probabilitats d'extinció) i la disciplina de l'ecologia de poblacions ofereix el marc ideal per a respondre aquestes qüestions per mitjà de l'anàlisi i modelització de dades demogràfiques (Williams et al. 2002). L'ús de dades longitudinals obtingudes per mitjà del seguiment d'espècies o individus al llarg del temps permet l'estimació de variables quantitatives importants per a la conservació de poblacions com el percentatge de llocs ocupats o les abundàncies locals, a més de paràmetres com la supervivència, la fecunditat, la dispersió i les taxes d'extinció i colonització responsables dels canvis en l'estat de les poblacions, generant un ampli coneixement de les poblacions aplicable també a les tasques de conservació dirigides a nivells superiors d'integritat ecològica com les metapoblacions i les comunitats (Dorazio et al. 2010, Kéry and Schaub 2011).

L'anàlisi poblacional: de les observacions de camp a la predicció de processos

El seguiment dels sistemes biològics en el temps és necessari per tal de millorar el coneixement científic sobre el qual basar les accions de maneig (Nichols and Williams 2006). Dit això, els programes de monitoratge són una peça clau del llarg procés científic orientat a la conservació i la gestió dels sistemes biològics i representen el primer pas cap a la producció d'estimes sobre l'estat d'aquests sistemes i altres variables (taxes vitals del sistema) que poden ser contrastades amb les prediccions de models matemàtics per tal d'afavorir el nostre aprenentatge sobre el funcionament dels sistemes biològics (Mackenzie et al. 2006, Nichols and Williams 2006). En els estudis poblacionals, les hipòtesis més freqüents es centren en les taxes vitals (ex: supervivència, fecunditat, immigració/emigració) responsables dels canvis en les variables quantitatives que defineixen l'estat del sistema (ex: mida poblacional). L'objectiu principal és entendre com les poblacions o comunitats responen a una varietat de factors (ex: depredació, caça furtiva, canvi climàtic, canvis en l'hàbitat, contaminació,

malalties etc.), i per assolir aquest objectiu, hem de discriminar entre una sèrie d'hipòtesis sobre la possible influència dels factors considerats en les dinàmiques del sistema, amb la intenció última de ser capaços de predir l'estat del sistema en el següent pas de temps donat el seu estat previ i el coneixement adquirit sobre els factors externs operant entre temps t i $t+1$ (Williams et al. 2002).

En general, les anàlisis poblacionals tenen 3 objectius fonamentals: 1) estimar directament les taxes vitals o variables indicadores de l'estat de la població, 2) modelitzar relacions causa-efecte entre paràmetres poblacionals i factors causals i 3) fer prediccions sobre la magnitud de la variable resposta en $t+1$ tenint en compte les condicions en temps t . Per assolir aquests objectius, les anàlisis poblacionals es recolzen en dades recollides durant estudis observacionals, doncs les poblacions silvestres no solen ser sotmeses a manipulació experimental, la qual, en alguns casos (ex: recerca en espècies amenaçades), podria arribar a ser fins hi tot inacceptable. No obstant això, un problema dels estudis observacionals en ecologia de poblacions és que l'estat real del sistema no és directament observable degut a una imperfecta detecció dels individus (Seber 1982, Lebreton et al. 1992, Williams et al. 2002). Per tant, degut a que les dades de camp són una combinació de processos ecològics i observacionals, la inferència sobre l'estat del sistema i les seves dinàmiques s'ha de fer tenint en compte aquesta detecció imperfecta (Mackenzie et al. 2002, 2003, Royle et al. 2005, Kéry and Schaub 2011).

Les anàlisis poblacionals són eines útils per entendre el comportament dels sistemes ecològics sota condicions en que aquests no poden ser directament observables, per mitjà de la modelització de les dades de camp i la incorporació dels errors de detecció (Pradel et al. 1997, Pradel 2005, Mackenzie et al. 2009, Gimenez et al. 2012). Un model és una representació abstracta d'un sistema que pot ser utilitzada per fer prediccions sobre el seu comportament sota unes condicions especificades. Normalment, el tipus de modelització que s'empra en l'anàlisi poblacional implica traduir les nostres idees sobre el funcionament del sistema a una sèrie d'equacions matemàtiques que contenen paràmetres predefinits que simbolitzen els processos clau d'aquest sistema (Nichols 2001, Williams et al. 2002). Tant els processos ecològics com els observacionals s'integren en l'estructura del model per mitjà dels diferents paràmetres i la formulació de les diferents hipòtesis biològiques es realitza per mitjà de la

construcció de diferents models matemàtics (Kendall 2001, Nichols 2001). L'exercici de la selecció de models implica ajustar una sèrie de models candidats al mateix conjunt de dades i determinar formalment quin model (i per tant quina hipòtesi) rep el major suport donades les dades de les que disposem (ex: el model més parsimònic). El model seleccionat serà el més adequat per a fer prediccions sobre el comportament del sistema i el tipus de model emprat en exercicis de simulació. Aquestes simulacions es realitzen donant uns certs valors a les variables del model i realitzant una sèrie de càlculs sota un ampli rang d'escenaris possibles, la qual cosa és de gran valor en investigacions sobre espècies plaga o espècies amenaçades, doncs no requereix cap manipulació arriscada de les poblacions estudiades.

Caixa d'eines per a l'anàlisi poblacional

Moltes eines analítiques diferents es troben a l'abast per assolir els objectius principals de l'anàlisi de dades poblacionals. Aquest ha estat un camp de recerca intensa en els darrers 20 anys, amb avenços significatius en l'anàlisi estadística de dades observacionals recollides per mitjà de la tècnica de captura-recaptura o els mostrejos de presència-absència (veure a continuació). Aquests avenços permeten estimar un ampli rang de paràmetres biològics interessants i, bàsicament, l'elecció de l'eina en qüestió depèn del tipus de pregunta o preguntes que volem respondre. No obstant això, donat que els recursos en conservació són limitats i les dades de camp sovint són registres individuals escassos o incomplets, l'optimització dels esforços de mostreig i el tipus de dades disponibles condicionarà en gran mesura les variables quantitatives d'interès i el tipus d'anàlisi realitzat respectivament.

Models de captura-recaptura

L'interès en els fluxos individuals (guanys i pèrdues) és central en l'ecologia de poblacions i ha condicionat el desenvolupament d'aproximacions empíriques per tal de mesurar-los. Una d'aquestes aproximacions és el mètode de la captura-recaptura que fa servir observacions repetides d'individus marcats per tal de proporcionar informació sobre els mecanismes poblacionals. Sota aquesta aproximació, la informació demogràfica es genera per mitjà del seguiment

d'individus al llarg del temps, de manera que els individus han de ser identificats en cada ocasió de mostreig i, tradicionalment, això s'ha aconseguit per mitjà del marcatge amb marques artificials, com és el cas de les anelles metàl·liques utilitzades en l'estudi de les poblacions d'aus. Tanmateix, la identificació pot venir donada per marques naturals (ex: taques, cicatrius, diferències de color etc...) i el seguiment individual es pot realitzar per mitjà del mostreig (o "trampeig") fotogràfic o la recolecció de pèl o restes fecals per a l'anàlisi genètic (Caniglia et al. 2012), tal com s'aplica en l'estudi de grans carnívors (Karanth 1995, Royle and Nichols 2009) i mamífers marins (Langtimm and Beck 2004, Mackey and Durban 2008). De manera ideal, quan s'utilitzen marques artificials, aquestes no s'han de perdre ni han de tenir efectes negatius en les taxes vitals dels organismes estudiats. La pèrdua de marques es pot evitar per mitjà d'un doble marcatge dels individus i l'ús de transmissors o marques visibles a distància poden contribuir a reduir l'estrès dels animals, doncs aquests només han de ser capturats físicament una vegada i el seu seguiment posterior es pot realitzar per mitjà d'encontres visuals o per teledetecció (Minta and Mangel 1989, Devillard and Bray 2009).

Tal i com es descriu en Lebreton et al. (1992), les dades de captura-recaptura es resumeixen en encontres individuals per a la seva anàlisi posterior. Aquestes històries individuals es tradueixen en una fila de números que contenen informació sobre si l'individu fou capturat o no en cada ocasió de mostreig. Aquesta informació es codifica per mitjà d'un codi binari on "1" significa que l'individu va ser capturat en aquella ocasió i "0" indica que l'individu no va ser capturat. El fet de que un individu sigui trobat o no en cada ocasió de captura depèn de dues probabilitats: la probabilitat de que l'individu sobrevisqui fins a aquella ocasió (Φ_i) i la probabilitat de que a més sigui capturat dins l'àrea d'estudi en aquella mateixa ocasió (p_i). Tenint en compte que qualsevol encontre es el producte d'aquestes dues probabilitats, les històries individuals poden ser traduïdes a una seqüència d'esdeveniments probabilístics que ens permeten obtenir estimes de màxima versemblança dels paràmetres Φ_i i p_i .

Inicialment, els programes de captura-recaptura es varen dissenyar per a estimar la mida poblacional (Seber 1982, Minta and Mangel 1989), amb un interès en els processos responsables dels fluxos individuals més aviat baix, però que amb el temps va anar guanyant importància fins a esdevenir el principal objectiu

d'aquests estudis (Lebreton et al. 1992, Clobert et al. 2001, Morris and Doak 2002). De manera paral·lela, aquest canvi va iniciar el desenvolupament i la diversificació dels models de captura-recaptura per tal d'estimar paràmetres demogràfics tenint en compte la detecció imperfecta dels individus, donant lloc a estimes més fiables dels paràmetres responsables dels fluxos individuals i proporcionant una important font d'informació sobre les poblacions i les seves taxes vitals (Lebreton et al. 2009, Gimenez et al. 2012).

Molts estudis poblacionals que s'interessen pels processos de supervivència en poblacions naturals fan servir el model Cormack-Jolly-Seber (CJS) com a model de partida per a l'anàlisi de dades de captura-recaptura degut a que permet obtenir estimes anuals de supervivència i probabilitats de recaptura (Lebreton et al. 1992). Aquests models donen estimes de supervivència "aparent" o local, doncs el destí dels individus que no són mai capturats és desconegut i els processos de mortalitat es confonen amb l'emigració permanent cap a fora de l'àrea d'estudi. Els models CJS assumeixen un destí independent dels individus però una homogeneïtat en les seves taxes vitals, assumpcions que han de ser testades abans de la construcció dels models matemàtics per mitjà de proves de bondat d'ajust, que evaluen l'existència d'heterogeneïtats individuals en les probabilitats de supervivència i recaptura (Pradel et al. 1997, Choquet et al. 2009). Normalment, els models CJS s'utilitzen per a respondre qüestions sobre variabilitat temporal o constància en la supervivència aparent dels individus, però també permeten comprovar un efecte de l'edat i el grup (ex: mascle, femella) al qual pertanyen els individus en les seves taxes vitals. Un gran nombre d'estudis es recolzen en l'ús de models CJS per testar efectes de factors ambientals (temperatura, precipitació, qualitat de l'hàbitat, disponibilitat d'aliment) i factors intrínsecs (sexe, edat, densitat de població, malalties) en la supervivència local (Cezilly et al. 1996, Barbraud et al. 1999, Hakkarainen et al. 2002, Barbraud and Weimerskirch 2003) i també per estudiar processos més específics com la senescència (Jorgeson and Festa-Bianchet 1997, Toïgo et al. 2007) o anàlisis retrospectives sobre l'efecte de diferents accions de maneig en la supervivència de poblacions amenaçades (Bertolero et al. 2007, Tuberville et al. 2008).

Les històries de captura-recaptura no es limiten a una sèrie d'uns i zeros, doncs, si disposem d'informació adicional sobre els individus marcats recollida durant el procés de mostreig (ex: localitat de captura, activitat reproductora),

aquesta pot ser codificada per mitjà de diferents números o lletres que representen “l’estat” de l’individu en cada ocasió de captura. Aquestes històries “multiestat” formen la base de dades per a l’anàlisi mitjançant models multiestat de captura-recaptura, un pas més enllà en l’estudi de les dinàmiques de les poblacions animals (Lebreton and Pradel 2002, Lebreton et al. 2009). Els models multiestat es varen desenvolupar, inicialment, per a estudiar els moviments individuals entre poblacions estructurades en l’espai (Hestbeck et al. 1991, Spendelov et al. 1995), de manera que els “estats” individuals es corresponien amb les localitats geogràfiques on els individus marcats es podien trobar en cada ocasió de mostreig. No obstant això, el potencial dels models multiestat és molt més gran i, de la mateixa forma que permeten estudiar moviments entre localitats, també permeten estudiar “moviments” o canvis d’estat reproductor o estats dinàmics que en resulten de la seva combinació com “criant en la localitat A” i que permeten estudiar tant processos de dispersió com reproductors, els quals no poden ser investigats per mitjà dels models CJS o “uniestat”. Els models multiestat, a més d’estimar probabilitats de supervivència i recaptura, permeten estimar un tercer paràmetre anomenat probabilitat de transició i que reflexa la taxa de moviment entre estats. Els paràmetres de supervivència, transició i recaptura es solen modelitzar de manera independent, assumint un procés markovià de primer ordre: l’individu primer ha de sobreviure en l’estat s en temps i i després es mou per ocupar un estat r en temps $i+1$.

Encara que els models multiestat demanen un tipus d’informació que exigeix un major esforç en la recolecció de dades de camp, l’aparició del paràmetre de transició és un salt qualitatiu en comparació amb els models CJS, doncs qüestions importants sobre moviment i trets de vida poden ara ser adreçades per mitjà de l’estimació i la modelització de les probabilitats de transició, oferint un marc comú per a l’estudi simultani de diferents processos biològics (Lebreton et al. 2009). La identificació d’estats com a localitats permet estudiar processos de dispersió, que son d’interés fonamental en la teoria metapoblacional (Hanski 1999). L’estudi de la dispersió usant models multiestat permet respondre a preguntes com quan, on i perquè dispersen els individus i els beneficis o costos que això implica per a les poblacions (Clobert et al. 2001). Les probabilitats de transició asimètriques entre dos localitats geogràfiques poden ser indicadores de diferències en les qualitats dels hàbitats respectius (Cam et al. 2004a, Lyet et al.

2009). Els models multiestat permeten testar l'efecte de múltiples factors ambientals i poblacionals en els processos de dispersió i aquesta metodologia ha resultat ideal per a l'estudi d'aus colonials que de manera natural viuen en poblacions estructurades en l'espai, com els xatracos (Spendelov et al. 1995), les oques del canadà (Hestbeck et al. 1991), les gavines (Gosbois and Tavecchia 2003) i els corbs marins (Hénaux et al. 2007).

Per mitjà de la definició d'estats reproductors, els models multiestat permeten estudiar processos demogràfics clau com el reclutament i compromisos evolutius, com el cost de la reproducció. Un problema a l'hora d'estudiar aquests processos és que, en moltes situacions, els individus no reproductors no són observables perquè només es mostreja la població reproductora, dificultant l'estudi de processos on tant individus reproductors com no reproductors hi estan involucrats. Un aspecte interessant dels models multiestat és que permeten estimar les probabilitats de supervivència i transició associades als estats "no observables" fixant a zero les seves probabilitats de recaptura, solucionant el problema de l'estudi de processos amb estats no observables (Kendall and Nichols 2002, Jenouvrier et al. 2008). Abans de la consolidació dels models multiestat, les qüestions sobre el reclutament i els costos de la reproducció s'adreçaven per mitjà de models uniestat, sense un marc analític unificat (Clobert et al. 1994, Pradel 1996, Schwarz and Arnason 2000, Tavecchia et al. 2001). Els models multiestat, utilitzant combinacions d'estats geogràfics i reproductors, permeten estudiar processos de dispersió i reclutament de manera simultània (Lebreton et al. 2003) i examinar els factors que determinen el reclutament al mateix temps que s'evaluen diferències en els patrons de dispersió entre juvenils no reproductors i adults reproductors (Crespin 2006, Hénaux et al. 2007). La modelització en multiestat fent servir únicament estats reproductors ha estat aplicada a l'estudi dels costos de reproducció en un ampli rang d'espècies incloent-hi ovelles (Tavecchia et al. 2005), foques (Hadley et al. 2007), ocells de tempesta (Sanz-Aguilar et al. 2008), i talpons (Nichols et al. 1994), proporcionant un marc ideal per a l'estudi de la evolució de diferents històries de vida.

Els models multiestat assumeixen que l'estat en el que es troben els individus és sempre conegut, malgrat que en moltes situacions desconeixem l'estat real en que es troba un individu, fins hi tot un cop capturat. En termes generals, l'incertesa pot afectar tant a l'estat reproductor o la localitat geogràfica

com altres tipus d'informació com el sexe de l'individu, de manera que a l'hora de parlar de les observacions de camp, en comptes d'estats s'hauria de parlar d'esdeveniments (ex: “no vist”, “vist covant al lloc A”), per descriure millor aquest tipus d'informació. Una extensió dels models multiestat amb incertesa en l'assignació d'estats individuals són els models multievent (Pradel 2005). En l'aproximació multievent, tant els “uns com els zeros” són informatius, permetent l'ús d'encontres d'estat desconegut i registres individuals incomplets. Els esdeveniments observats (*events*, en anglès) són el resultat de diferents processos lligats a diferents estats reals. Per exemple, un zero en una història de captura-recaptura pot ser causat per diferents processos com un error de detecció, l'emigració temporal de l'individu fora de l'àrea d'estudi o la mort de l'animal (Péron et al. 2010, Sanz-Aguilar et al. 2011a). Les observacions de camp es codifiquen com a *events*, mentre que el estats només s'inclouen en la definició del model, condicionant la probabilitat de cadascun dels *events*. La definició d'estats no observables esdevé molt més flexible en l'enfoc multievent, doncs el nombre d'estats no ha de ser idèntic al nombre d'*events* i es poden afegir estats addicionals en el model que poden anar lligats a l'*event* “0”. Aquesta metodologia és especialment útil per investigar processos com l'emigració temporal, que es modelitza per mitjà d'estats no observables o “fantasma” amb les seves pròpies probabilitats de transició associades (capítol 3). Un altre aplicació d'aquests estats “fantasma” és la modelització de les heterogeneïtats individuals. En molts estudis on es mostregen un gran nombre d'individus, és fàcil detectar heterogeneïtats en la probabilitat de recaptura degut a les diferents respostes dels individus al procés de captura i monitoratge. Els models multievent, per mitjà de l'addició d'estats extra que reflecteixen les diferents respostes individuals permeten corregir aquestes heterogeneïtats i proporcionar estimes més robustes de les taxes vitals d'interés (Pradel and Sanz-Aguilar 2012).

Els models Multievent són la més recent incorporació a la caixa d'eines de la captura-recaptura i la més unificadora, doncs ofereixen un marc analític general tant per als models multiestat com els uniestat (CJS), sent també una eina útil per examinar processos ocults (per exemple, la realització de “sabàtics” reproductors o la influència de la “memòria” sobre estats anteriors en les futures probabilitats de transició; Giménez . 2012) aprofitant tot tipus de registres individuals. Malgrat que els models multievent representen un salt considerable en complexitat i la

seva aplicació ha estat relativament baixa en comparació amb altres mètodes de modelització de captura-recaptura, aquests han demostrat ser molt útils a l'hora de distingir entre errors de detecció i processos d'emigració temporal fora de la zona d'estudi (Sanz-Aguilar et al. 2011a) i han permès tractar amb èxit problemes amb l'heterogeneïtat de recaptura en poblacions obertes (Crespin et al. 2008) i la incertesa en l'assignació d'estats (Genovart et al. 2012).

Models d'ocupació

Els estudis ecològics sovint intenten comprendre els patrons de distribució i abundància de les espècies en el paistage (Andrewartha and Birch 1954), però a vegades, aquestes variables són difícils de mesurar o estimar i pot ser més apropiat fer servir variables menys informatives però més fàcils de mesurar com la ocupació (MacKenzie et al. 2006, Kéry and Schaub 2011). L'estudi de la ocupació simplement consisteix en determinar la presència d'una o més espècies en unitats de mostreig i els programes encaminats a obtenir una proporció de llocs ocupats o estima d'ocupació (ψ) parteixen d'una situació en que diverses unitats espacials són visitades pels investigadors per tal de registrar la presència o absència d'una o diverses espècies concretes. La mida de la unitat espacial pot venir definida de manera natural (illa, bassa, fragment de bosc) o artificial (quadrícula o transecte) i mentre dura el mostreig, els investigadors dediquen el seu temps a cercar individus o evidències de la presència de les espècies d'interès dins de la unitat espacial. El resultat d'aquests mostrejos és una llista de llocs que estan "ocupats" (on s'ha detectat l'espècie) i llocs "desocupats" (on l'espècie no s'ha detectat). Al contrari que en la captura-recaptura, aquí les històries de seguiment no s'associen a individus marcats sinó a unitats de mostreig, les quals constitueixen les nostres poblacions d'estudi.

Els principal problema dels mostrejos de presència-absència, o més ben dit, detecció-no detecció, radica en l'existència de llocs que, tot i estar ocupats, es classifiquen erròniament com a desocupats degut a que en el moment de mostreig no s'han detectat evidències de la presència de l'espècie, generant "falses absències" en les nostres dades de camp (MacKenzie et al. 2002). Moltes vegades, la probabilitat de detectar una espècie ve influenciada per les condicions ambientals durant la realització del mostreig o per la naturalesa crítica de la

pròpia espècie. El principal avantatge dels models d'ocupació és que tenen en compte la probabilitat de detecció a l'hora d'estimar les taxes d'ocupació (equivalent a la probabilitat de recaptura en els models de captura-recaptura). De la mateixa manera que en els models de captura-recaptura, cada història de detecció és un enunciat matemàtic que es defineix per mitjà de paràmetres associats a processos ecològics (ocupació) i a processos observacionals (detecció), els quals són estimats fent servir el mètode de la màxima versemblança (MacKenzie et al. 2006).

Els models d'ocupació que analitzen dades recollides durant una única temporada de mostreig s'anomenen models d'ocupació estàtica (MacKenzie et al. 2002, 2006). Aquests models permeten obtenir estimes d'ocupació i detecció gràcies a un tipus de mostreig a dos nivells o disseny robust (Pollock 1982) on dintre d'una mateixa temporada de mostreig o mostreig primari, es van alternant mostrejos secundaris separats entre si per espais de temps curt. Les estimes d'ocupació obtingudes estan associades al període de mostreig primari i no varien en el temps, encara que sí poden fer-ho en l'espai, mentre que les probabilitats de detecció estan associades als mostrejos secundaris i poden variar tant en el temps com en l'espai. Si aquest tipus de mostreig es repeteix durant més d'una temporada o anys consecutius, podem fer inferències sobre els canvis en ocupació al llarg del temps. Aquests canvis vénen determinats per processos locals d'extinció i colonització, que poden ser inclosos explícitament dintre de l'estructura dels models com a nous paràmetres i ser modelitzats tenint en compte hipòtesis amb sentit biològic. Aquests models es coneixen com a models d'ocupació dinàmica (MacKenzie et al. 2003) i resulten especialment útils per a l'estudi de metapoblacions (Hanski 1998). Una extensió recent dels models d'ocupació va més enllà de la simple determinació de la presència o absència d'espècies en unitats de mostreig i es centra en "l'estat" en el qual es troben les espècies en un lloc concret (Nichols et al. 2007, MacKenzie et al. 2009). Els models d'ocupació multiestat són una generalització tant dels models d'ocupació estàtica com dinàmica en els quals l'estat d'ocupació es mou d'una temporada a l'altre entre una sèrie d'estats finits que poden representar diferents abundàncies relatives o informació sobre l'activitat reproductora de les espècies, permetent un major coneixement dels processos dinàmics que governen els sistemes poblacionals (Martin et al. 2009, 2010).

Moltes línies de recerca requereixen d'informació fiable sobre taxes d'ocupació i busquen predir l'ocurrència d'espècies per raons tan d'ecologia fonamental com aplicades a la conservació. Els models d'ocupació estàtica són útils per desentranyar relacions espècie-hàbitat que poden ser interessants per estudis de nínxol ecològic i per fer prediccions sobre la distribució de les espècies en el futur o assenyalar les millors àrees per a projectes de reintroducció (Guisan and Thuiller 2005, Price et al. 2011, Breck et al. 2012, Barber-Meyer et al. 2013). Donat que l'estudi de l'ocupació implica recollir dades a diferents unitats espacials, el disseny de mostreig proporciona un marc natural per a l'estudi de les dinàmiques metapoblacionals. Per mitjà dels models d'ocupació dinàmica, els processos de canvi en les taxes d'ocupació al llarg del temps poden ser descrits per paràmetres com l'extinció o la colonització, les taxes vitals del model metapoblacional primari (Levins 1969). Els models d'ocupació dinàmica permeten obtenir estimes fiables d'extinció i colonització i adreçar de manera robusta qüestions importants sobre dinàmiques metapoblacionals, com les relacions àrea-extinció o l'efecte de l'aïllament en la colonització de fragments d'hàbitat, així com tendències en colonització o extinció al llarg del temps, amb clares implicacions per a l'estudi i conservació d'espècies que viuen en paisatges fragmentats (Ferraz et al. 2007, Van Strien et al. 2011). Els baixos costos comparats amb els mostrejos de captura-recaptura i la flexibilitat de les eines de modelització disponibles fan de l'ocupació una variable quantitativa més apropiada que l'abundància per tal de descriure l'estat i les fluctuacions de les poblacions animals al llarg d'àmplies regions geogràfiques. L'ocupació és un variable important per al monitoratge de la biodiversitat i d'interès primari en programes de monitoratge a gran escala on es recullen dades sobre múltiples espècies, desde papallones (veure capítol 4), a amfibis (Weir et al. 2009), passant per les aus (Mattson and Marshall 2009). En anys recents, el desenvolupament dels models d'ocupació multiestat ha permès respondre a qüestions més fines sobre les relacions hàbitat-ocupació (MacKenzie et al. 2011), amb aplicacions prometedores en el maneig d'espècies bandera (Martin 2009, 2010), la qual cosa representa una millora metodològica en l'ús de dades relativament simples recollides sobre àrees extenses amb un cost mínim i un impacte zero sobre les poblacions mostrejades.

Anàlisi de viabilitat poblacional

Els models de captura-recaptura i ocupació són eines útils per estimar taxes vitals clau i examinar els factors que afecten a les dinàmiques poblacionals en l'espai i en el temps. No obstant això, la manera en que aquestes taxes vitals i la seva variació es tradueixen en la viabilitat de les poblacions és una qüestió important en situacions més aplicades de maneig d'espècies de flora i fauna (Caswell and Fujiwara 2004, Mills 2007). Les poblacions viables són aquelles que tenen una probabilitat baixa d'extingir-se en un horitzó de temps determinat (Morris and Doak 2002) i la quantificació d'aquesta viabilitat s'aconsegueix per mitjà de projeccions poblacionals que permeten estimacions de mides poblacionals futures, taxes de creixement poblacional (λ) i probabilitats de quasi-extinció.

Les anàlisis de viabilitat poblacional (PVA) són eines analítiques que fan servir dades demogràfiques i models per estimar la probabilitat de que una població persisteixi durant un temps definit en el futur, fent èmfasi en la quantificació de la probabilitat de quasi-extinció (Beissinger and Westphal 1998, Mills 2007). La probabilitat de quasi-extinció reflecteix la probabilitat de que la mida poblacional baixi fins a un llindar establert com el nombre mínim d'individus (sovint femelles) per sota del qual la població està funcionalment extinta (Morris and Doak 2002, Mills 2007). Els PVA es poden realitzar per mitjà de l'anàlisi de series temporals d'abundància (PVA basat en censos) o per mitjà de models de matrius poblacionals, fent servir informació sobre taxes vitals clau (PVA demogràfics). Desde el punt de vista de la conservació, els PVA demogràfics resulten molt més útils, doncs permeten avaluar les conseqüències de diferents accions de maneig sobre la recuperació de poblacions petites o en declivi, a més a més de proporcionar informació sobre els efectes a llarg termini de canvis en les taxes vitals sobre el creixement poblacional (Mills 2007).

Els PVA demogràfics es basen en el desenvolupament de models de matrius poblacionals, els quals permeten predir la mida d'una població en temps $t+1$ a través d'informació sobre les taxes vitals dels individus en temps t (Caswell 2001, Beissinger et al. 2008.) Per realitzar una projecció poblacional, primer s'ha de construir una matriu poblacional on tant l'estructura de la població (classes d'individus o estadis vitals) com les corresponents taxes vitals hi estiguin

representades. Els valors de taxes vitals com la supervivència s'obtenen per mitjà dels models de captura-recaptura i un cop la matriu està completa, aquesta pot ser projectada en el temps a través de la seva multiplicació amb un vector d'elements que conté el nombre d'individus present en cada estadi de la població (Caswell 2001, Mills 2007). Les projeccions poblacionals poden ser deterministes, en les quals les taxes vitals sempre tenen el mateix valor, o be estocàstiques, en el cas de que el valor de les taxes vitals pugui canviar al llarg del temps. L'addició d'estocasticitat (demogràfica i ambiental) en els models matricials permet realitzar projeccions poblacionals més realistes i això s'aconsegueix fent que les taxes vitals prenguin un valor diferent a cada pas de temps el qual es pren de distribucions centrades en la mitjana de la taxa vital corresponent (Morris and Doak 2002, Mills 2007). El valor de les taxes vitals també pot ser canviat de manera deliberada per tal de quantificar l'importància de les diferents taxes vitals i els efectes que diferents accions de maneig poden tenir en la població. Aquests exercicis se'ls coneix com a anàlisis de sensibilitat, quan s'evaluen canvis absoluts en les taxes vitals i la taxa de creixement poblacional, o be anàlisis d'elasticitat, quan s'evaluen canvis proporcionals entre les taxes vitals i les de creixement poblacional (Caswell 2001, Naujokaitis-Lewis et al. 2009, Chirakkal and Gerber 2010). Les sensitivitats i elasticitats de la supervivència per edats o la fecunditat, proporcionen als gestors informació sobre la contribució relativa dels diferents estadis d'història de vida al creixement poblacional a llarg termini (Mills 2007).

Els PVA demogràfics s'han aplicat per fer prediccions sobre respostes a canvis ambientals, proporcionant estimes de quasi-extinció sota diferents escenaris, de canvi global o climàtic (Jenouvrier et al. 2009, Hunter et al. 2010, Sanz-Aguilar et al. 2011b), per avaluar l'estat de conservació d'espècies poc conegudes (Fujiwara and Caswell 2001, Oro et al 2004b), o per avaluar el resultat futur d'accions de maneig sobre el destí de les poblacions (Doak et al. 1994, Fernández-Olalla et al. 2012). En tot cas, l'ús de PVA proporciona respostes sobre les conseqüències d'accions de maneig particulars o futurs canvis ambientals que són de gran valor en la presa de decisions en conservació, la qual cosa converteix aquestes simulacions en una eina essencial en la biologia de la conservació. La fita dels PVA és permetre una presa de decisions en conservació més informada, amb

vistes a llarg termini i per mitjà de la comparació dels riscos associats a diferents escenaris futurs.

OBJECTIUS

Al llarg d'aquesta tesi m'he mogut entre la ciència ecològica bàsica i l'aplicada amb l'objectiu d'explorar les aplicacions de diferents eines analítiques, tant de clàssiques com de recentment desenvolupades, per a l'estudi de les dinàmiques poblacionals a diferents escales i en diferents taxons animals (rèptils, peixos, aus i insectes) mostrant una gran varietat d'històries de vida i estats de conservació. Aquesta tesi està dividida en 4 capítols o casos d'estudi, cadascun d'ells representant diferents qüestions biològiques i enfoc analítics (figura 1), i ordenats seguint un nivell creixent de complexitat ecològica, des d'estudis sobre poblacions discretes i aïllades fins a estudis sobre múltiples espècies formant xarxes poblacionals en l'espai.

Les dades de camp necessàries per al desenvolupament de la tesi han estat en la seva gran majoria proporcionades per diferents investigadors a través d'un seguit de col·laboracions establertes al llarg dels 4 anys de doctorat amb diferents institucions i organitzacions. Durant tres anys consecutius (2009-2011), vaig participar personalment en la recollida de dades de captura-recaptura de la tortuga mediterrània (*Testudo hermanni*; Capítol 1) i la gavina corsa (*Larus audouinii*; Capítol 3) al Parc Natural del Delta de l'Ebre (Tarragona); desde fa més de 20 anys, aquestes dues espècies han estat sotmeses a un seguiment continuat en aquest espai natural, la qual cosa m'ha permès basar les meves anàlisis en les dades de seguiment a llarg termini presents tant en el meu grup de recerca (IMEDEA) com les proporcionades pel Dr. Albert Bertolero Badenes (IRTA) i personal responsable del seguiment de la gavina corsa a la resta de colònies espanyoles de l'espècie (Govern Balear, Estació Biològica de Doñana i Associació Picampall), els quals estan presents com a coautors de l'estudi presentat en el capítol 3 d'aquesta tesi. El Dr. Alfredo G. Nicieza, professor a la Universitat d'Oviedo, proporcionà les dades de captura-recaptura necessàries per a l'anàlisi del capítol 2, mentre que la col·laboració amb el Dr. Constantí Stefanescu, coordinador del programa de seguiment de rojalòcers de Catalunya o

Catalan Butterfly Monitoring Scheme (CBMS) proporcionà les dades de detecció-no detecció emprades per a l'anàlisi realitzat en el capítol 4. A continuació faig una descripció general de cadascun dels capítols que conformen aquesta tesi.

En el capítol 1, amb l'objectiu de realitzar un diagnòstic de conservació robust, vaig estudiar els efectes de la variabilitat climàtica en la supervivència, el creixement poblacional i la persistència de diferents poblacions de tortuga mediterrània, una espècie amenaçada a Espanya i potencialment vulnerable al canvi climàtic. Per assolir aquest objectiu, primerament vaig analitzar una base de dades de captura-recaptura de bona qualitat recollida per mitjà del seguiment de la població de tortuga mediterrània del Parc Natural del Delta de l'Ebre. Aplicant models CJS, vaig obtenir estimes de supervivència per cada classe d'edat i vaig poder examinar la relació entre la supervivència per edats i diferents variables meteorològiques. Seguidament, vaig construir una matriu poblacional amb estructura d'edats per tal de realitzar un PVA demogràfic i vaig projectar la població d'estudi sota 3 escenaris climàtics futurs per al segle XXI, repetint aquest exercici per a 10 poblacions addicionals de l'espècie repartides al llarg de la seva distribució mundial. Al meu entendre, aquesta és la primera vegada en que s'han intentat modelitzar respostes poblacionals al canvi climàtic al llarg de tota l'àrea de distribució d'una espècie de rèptil.

En el capítol 2, vaig estendre la modelització de les taxes vitals a més d'una població i grups d'individus dintre de cada població fent servir models multiestat. Vaig analitzar una base de dades de captura-recaptura recollida al llarg de 6 anys en un sistema de rierols de muntanya al Parc Nacional dels Picos de Europa (Astúries) per tal d'investigar si les diferents característiques de cada rierol (hàbitat, temperatura) estaven determinant diferències espacials en les taxes individuals de supervivència i creixement. En aquest cas, els models multiestat van permetre tractar les diferents classes de longitud dels individus com a diferents estats dinàmics i estimar-ne probabilitats tant de supervivència com de creixement i maduració per a cada població, obtenint patrons de creixement contrastats entre rierols, així com evidències d'efecte de la mida de l'individu en la supervivència a totes les poblacions tret de la població present al rierol més petit, on la supervivència local semblava estar més afectada per la temperatura de l'aigua durant els mesos d'hivern. Aquest capítol representa una aplicació de caire

més evolutiu dels models de captura-recaptura i en concret de l'estudi dels trets d'història de vida i les forces selectives implicades en la seva evolució.

En el capítol 3 em vaig centrar en l'estudi del procés de dispersió, aplicant models multievent a una extensa base de dades de captura-recaptura recollida en un sistema de 4 colònies de gavina corsa al mediterrani occidental. Les dificultats pràctiques a l'hora d'obtenir informació sobre immigració i emigració han fet de la dispersió un procés històricament ignorat en molts estudis poblacionals, tot i la seva rellevància en les dinàmiques poblacionals i en la persistència de conjunts de poblacions o sistemes metapoblacionals. En aquest cas, vaig treure profit dels models multievent per tal d'examinar processos no observables com l'emigració temporal i corregir heterogeneïtats en recaptura. Aquesta modelització també em va permetre descomposar el procés de dispersió en els seus components (processos de fidelitat/emigració i processos d'assentament) per tal d'investigar els mecanismes involucrats en les decisions de fidelitat i assentament. Aquest enfoc em va permetre obtenir diferents estimes de fidelitat a la colònia i comparar-les entre localitats, així com testar hipòtesis sobre un descens en la fidelitat (augment de l'emigració) a les colònies més grans al llarg del temps. Les estimes d'assentament també van permetre obtenir informació sobre la destinació dels dispersors, revelant un cert moviment d'individus cap a zones fora de l'àrea d'estudi. Atesa la novetat del software utilitzat per la modelització multievent, l'anàlisi dels diferents factors implicats en el procés d'assentament es va haver de realitzar per mitjà d'una anàlisi estadística *post-hoc*, la qual va permetre identificar la mida poblacional com el principal predictor d'assentament dins de l'àrea d'estudi.

En el capítol 4, vaig ampliar l'estudi de les dinàmiques de poblacions estructurades en l'espai a múltiples espècies de papallones i vaig fer servir models d'ocupació dinàmica per tal d'obtenir estimes fiables d'extinció i colonització d'espècies així com per avaluar els efectes de diferents variables ambientals tant a escala local com de paisatge en les dinàmiques d'extinció i colonització. Més específicament, vaig aplicar un conjunt de 60 models candidats a dades de detecció-no detecció de 73 espècies de papallones mostrejades sota el CBMS, el programa de seguiment de papallones diürnes més antic i extens de tot el sud d'Europa, amb l'objectiu de fer un diagnòstic de l'estat d'aquesta rica comunitat de papallones i determinar els principals factors externs influenciant les seves

dinàmiques en l'espai i en el temps. L'anàlisi dels resultats dels models per a cada espècie va permetre fer inferències sobre els principals factors condicionant el recanvi poblacional tant a nivell general com a nivell de les diferents categories d'espècies definides per la seva capacitat de dispersió i grau d'especialització, proporcionant informació científica útil per al desenvolupament de plans de conservació dirigits tant a espècies concretes com a comunitats senceres.

DISCUSSIÓ GENERAL

Les anàlisis demogràfiques aplicades de manera transversal a diferents tàxons i escales de complexitat ecològica augmenten la qualitat de la recerca en el camp de l'ecologia de poblacions mitjançant l'augment de la gamma de possibles preguntes que poden ser abordades partint de dades observacionals més aviat simples. En aquesta tesi es demostra, a través de 4 casos d'estudi basats en dades longitudinals recollides sobre el terreny, la flexibilitat i la solidesa d'un conjunt d'eines analítiques (models d'ocupació, captura-recaptura i PVA) per a l'estudi de les poblacions i la seva utilitat per fer front a una diversitat de temes que van des de l'evolució dels trets d'història de vida a la conservació de les entitats biològiques.

De poblacions discretes a metapoblacions

Els casos d'estudi presentats en aquesta tesi són tots exemples de situacions reals en l'estudi de les dinàmiques poblacionals centrades en diferents qüestions ecològiques (taula 1) i que s'enfronten a diferents reptes metodològics (taula 2). En els capítols 1 i 2 vaig estudiar poblacions discretes, sense intercanvis individuals amb altres poblacions i amb les seves dinàmiques locals governades exclusivament per processos de naixement i mortalitat (és a dir, sense processos de dispersió). Els capítols 1 i 2 també són exemples de poblacions mostrejades per mitjà de tècniques de captura-recaptura; el fet que les poblacions mostrejades ocupin una àrea reduïda i la poc probable pèrdua d'individus per emigració redueixen els costos de seguiment dels individus marcats, fent aquestes poblacions ideals per dur a terme aquest tipus d'estudis. Les poblacions aïllades en petites àrees lliures de pertorbacions humanes també són excel·lents models

biològics per estudiar els efectes de variables ambientals locals, com la precipitació (capítol 1) o la temperatura (capítol 2), en les seves dinàmiques; aquests efectes varen ser examinats per mitjà de la modelització amb covariables externes, fent servir tant models de captura-recaptura uniestat (capítol 1) com multiestat (capítol 2). Els capítols 1 i 2 també es varen centrar en poblacions estructurades, la qual cosa va permetre abordar qüestions relacionades amb el creixement individual i la maduració (capítol 2) i els efectes de l'edat o la mida corporal en la supervivència (capítols 1 i 2 respectivament), gràcies a l'estratificació de les dades de captura-recaptura en grups permanents i/o estats individuals dinàmics. En el cas del capítol 2, l'enfocament multiestat va permetre una estimació de les transicions de creixement en truites fixant a zero les transicions impossibles de decreixement, i al mateix temps, l'ús de dades de 3 poblacions diferents va permetre també comprovar l'existència de diferències entre poblacions pel que fa als paràmetres de supervivència, creixement i maduració dels individus. Degut a que la tortuga mediterrània és una espècie amenaçada a Espanya i potencialment vulnerable a ràpids canvis ambientals, en el capítol 1 també vaig realitzar un PVA demogràfic utilitzant estimes conegudes de les taxes vitals i la seva relació amb variables ambientals per tal d'avaluar el risc d'extinció global de l'espècie sota diferents escenaris futurs de precipitació. En aquest cas, l'ús d'estimes de supervivència i els efectes de la precipitació obtinguts a través dels models de captura-recaptura en les matrius poblacionals, en conjunt amb la incorporació d'estocasticitat ambiental en les projeccions, augmentà el realisme de les simulacions i la robustesa dels resultats mostrats.

En els capítols 3 i 4, vaig estudiar xarxes poblacionals d'aus i papallones, respectivament (dos tàxons que mostren altes capacitats de dispersió), augmentat l'escala espacial i la complexitat respecte a les anàlisis anteriors. L'estudi de poblacions connectades en l'espai i en el temps em va permetre avaluar l'efecte de variables ambientals en les dinàmiques poblacionals tant a escala local com regional, qüestions que no es poden abordar per mitjà de l'estudi d'una única població. Els estudis presentats en els capítols 3 i 4 es varen basar en programes de monitorització a gran escala que generaren grans quantitats de dades, les quals varen requerir de l'ús d'eines eficients i robustes per a la seva anàlisi estadística. En el capítol 3 vaig analitzar un conjunt de dades de captura-recaptura de gavina corsa recollides en diferents localitats i em vaig centrar en la fracció adulta de la

població per tal d'estudiar la seva supervivència i les dinàmiques de dispersió reproductora. Per fer front a la complexitat del conjunt de dades i les hipòtesis biològiques a testar, en aquest capítol es varen aplicar una sèrie d'innovacions i avenços analítics en el procés de modelització. En primer lloc, seguint l'enfocament de Grosbois i Tavecchia (2003), vaig examinar els components de fidelitat i assentament en el procés de transferència individual i vaig formular diferents hipòtesis biològiques dirigides a cadascun d'aquests components per separat, per tal d'obtenir una imatge més clara del procés de dispersió reproductora; al mateix temps, vaig aprofitar l'enfocament multievent per controlar l'emigració temporal de la zona d'estudi i per corregir heterogeneïtats en les probabilitats de recaptura, produint d'aquesta manera resultats més robustos i fiables, i, finalment, vaig dur a terme una anàlisi estadística *post-hoc* per determinar els predictors d'assentament tenint en compte la covariància de les estimes del millor model. En el capítol 4, vaig analitzar un conjunt de dades de múltiples espècies recollides a través de mostrejos de detecció de no-detecció de papallones realitzats a diferents localitats del nord-est d'Espanya; sota aquest esquema de mostreig, cada lloc amb presència d'una espècie determinada va ser considerat com una unitat de població de l'espècie, proporcionant un marc conceptual útil per a l'estudi posterior de les dinàmiques metapoblacionals. L'ús de models d'ocupació dinàmica al capítol 4 va permetre comprovar hipòtesis biològiques sobre les causes del recanvi poblacional al llarg del temps en diferents espècies per mitjà de l'aplicació d'un mateix conjunt de models candidats als historials de detecció de cada espècie. En realitzar una comparació dels resultats entre les espècies i entre categories d'espècies, es varen poder derivar patrons d'extinció i colonització tant de generals com d'específics, per tal d'avaluar la influència de les característiques ecològiques de les espècies en el seu recanvi poblacional i poder també identificar els principals determinants de les dinàmiques d'ocupació en l'àrea d'estudi.

Tractant l'heterogeneïtat

L'anàlisi de les dades de captura-recaptura sempre requereix de la realització d'un test de bondat d'ajust o "Goodness of fit" (GOF), per tal de comprovar l'ajust d'un model de partida a les nostres dades. Tots els models de partida tenen

assumpcions i el que fa el GOF és veure si aquestes assumpcions es compleixen en les dades recollides per tal de corregir o incorporar en els models les fonts d'heterogeneïtat o manca d'ajust, doncs ignorar-les ens pot portar a estimes esbiaixades de les taxes vitals i a conclusions errònies sobre les dinàmiques poblacionals.

L'efecte transeünt o “transient” és un efecte comú en molts estudis de captura-recaptura degut a que en moltes ocasions hi ha individus que no pertanyen a la població que són marcats dins l'àrea d'estudi i no es tornen a recapturar mai. Aquest és el cas d'espècies amb altes capacitats de dispersió, com les aus marines (capítol 3), en les quals aquest efecte *transient* sol ser detectat i modelitzat com un efecte de l'edat relativa al moment del marcatge, distingint entre individus nous i individus ja capturats amb anterioritat o residents (Pradel et al. 1997). Aquesta solució permet també calcular una proporció de transeünts dins la població que pot ser utilitzada com indicadora d'emigració permanent i ser comparada entre poblacions (capítol 3). L'efecte *transient* és menys pronunciat en poblacions aïllades que ocupen àrees reduïdes des d'on els individus dispersen poc o gens, com és el cas de les poblacions de tortugues i truites analitzades en els capítols 1 i 2 respectivament; l'absència d'emigració permanent afegida a un alta probabilitat de recaptura dels individus fa que la supervivència aparent obtinguda en aquests casos estigui molt propera a la supervivència real dels individus.

L'estratificació de les dades en estats o grups també ajuda a reduir les heterogeneïtats, doncs a cada ocasió de mostreig els individus són classificats en diferents categories o estats, els quals duen associats probabilitats de supervivència i detecció concretes. En el capítol 2, les dades de captura-recaptura de truita comuna es varen separar per grups (3 poblacions o rierols) i dintre de cada població els individus van ser classificats en cada ocasió de mostreig en 3 categories de longitud corporal que van ser identificades amb estats dinàmics. Aquesta estratificació de les dades de camp, en conjunt amb l'absència d'emigració en el sistema, va permetre obtenir un bon grau d'ajust del model Arnason-Schwarz a les nostres dades (veure el capítol 2).

Les heterogeneïtats individuals són típiques de poblacions naturals i són més fàcils de detectar quan el nombre d'individus mostrejats augmenta (Crespin et al. 2008, Nussey et al. 2008). Aquest és el cas de les poblacions de gavina corsa estudiades en el capítol 3 on, tot i l'estratificació de les dades en múltiples estats,

tant heterogeneïtats en supervivència (efecte transient) com en probabilitat de recaptura (resposta de captura o “trap dependence”) van ser detectades en el GOF i van haver de ser modelitzades. En el capítol 3 vaig poder comprovar que els models multievent són una eina molt útil per corregir aquestes heterogeneïtats i en especial l’heterogeneïtat de recaptura per mitjà d’estats addicionals en les matrius de transició, aplicant el mètode proposat recentment per Pradel i Sanz-Aguilar (2012). En aquest cas, les transicions entre estats de recaptura addicionals varen ser modelitzades a les dues poblacions on les heterogeneïtats de recaptura van ser detectades (les colònies amb més densitat de població, veure el capítol 3). Les transicions des de l’estat “capturable” al “capturat” són equivalents a les probabilitats de recaptura individuals.

Els models d’ocupació assumeixen que l’estat d’ocupació de les unitats mostrejades roman sense canvis durant tota la temporada de mostreig. Per tal de complir aquesta assumptió, molts estudis d’ocupació tenen lloc en el moment de l’any en que la disponibilitat de les espècies per al mostreig es manté ininterrompuda, però de vegades, els processos individuals de dispersió poden fer que aquesta disponibilitat es vegi interrompuda durant una mateixa temporada de mostreig. Actualment no existeix cap test de bondat d’ajust per als models d’ocupació dinàmica (James D. Nichols, comunicació personal), de manera que un primer pas per evitar biaixos consisteix a dissenyar el procés de mostreig tenint en compte la biologia i fenologia de les espècies objectiu. L’agrupament de les dades de camp i l’ús de covariables associades als diferents punts i ocasions de mostreig per a modelitzar les probabilitats de detecció ajuda a controlar heterogeneïtats i a reduir encara més els biaixos en les estimes d’ocupació i paràmetres relacionats (MacKenzie et al. 2006). En el capítol 4 vaig aplicar totes aquestes recomanacions per tal de reduir els biaixos en extinció i colonització tot el possible: primerament, els mostrejos varen ser realitzats durant el període de vol de la gran majoria d’espècies de papallones; després, els mostrejos setmanals van ser resumits en mostrejos mensuals i finalment, tota una sèrie de variables ambientals recollides durant els mostrejos van ser utilitzades en la modelització i en particular per corregir variacions en la detecció causades per les diferències locals en els pics d’emergència de les espècies.

Estudiant la demografia tenint en compte els trets de les espècies i l'ambient

Patrons de creixement, maduresa i supervivència

Els estudis demogràfics on es mesuren taxes de mortalitat i fecunditat per als diferents estadis de la població (estadis vitals) ajuden a establir un lligam entre l'ecologia de poblacions i la biologia evolutiva per mitjà del seu interès central en la variació individual dels trets d'història de vida. La mortalitat i la fecunditat varien amb l'edat i la mida dels individus i els canvis en aquests paràmetres vitals es tradueixen en canvis en el creixement poblacional; per exemple, endarrerir l'edat de maduració sexual pot reduir la taxa de creixement poblacional (Stearns 1992). Segons la teoria de les històries de vida, la supervivència adulta és clau per a la persistència de les poblacions d'espècies de vida llarga, de manera que l'obtenció d'informació sobre aquesta taxa vital i les seves dinàmiques representa un pas important en la conservació d'aquestes espècies doncs el seu estat de conservació pot ser mesurat directament per mitjà de l'estimació d'aquest paràmetre (Eberhardt 2002). En aquesta tesi, la supervivència ha sigut un paràmetre recurrent en l'anàlisi i modelització de les dades, i a més s'ha pogut examinar al llarg de diferents estadis vitals (capítols 1 i 2) i poblacions (capítols 2 i 3), fent servir diferents models de captura-recaptura per a respondre hipòtesis concretes sobre les dinàmiques de supervivència en el temps i en l'espai. A més de la supervivència, les taxes de creixement i maduració també han estat examinades detalladament al capítol 2 per mitjà de models multiestat, oferint una descripció més completa de les estratègies d'història de vida de les poblacions estudiades.

Com era d'esperar en poblacions d'espècies de vida llarga habitant espais naturals lliures de la mortalitat causada pels humans, la supervivència adulta en la població de tortuga mediterrània del Delta de l'Ebre va ser alta i constant en el temps (capítol 1), mentre que la supervivència dels juvenils va ser generalment més baixa i variable entre anys. En aquest capítol, la modelització amb variables externes (temperatura i precipitació) va permetre trobar una relació positiva entre la supervivència juvenil i la pluja d'hivern que explicà gran part de la variació temporal detectada en aquest paràmetre i destacà la sensibilitat dels individus més joves als canvis en el règim de precipitacions. Les projeccions poblacionals

deterministes van corroborar la importància de la supervivència adulta en el creixement poblacional, però les simulacions sota escenaris més secs que redueixen de manera permanent la supervivència juvenil varen predir el declivi i en alguns casos, l'extinció d'aquesta i altres poblacions de tortuga mediterrània al llarg de la seva distribució geogràfica, suggerint que la contribució del reclutament al manteniment de les poblacions a llarg termini no ha de ser subestimada. Les taxes de supervivència adulta de gavina corsa (capítol 3) van resultar altes, constants i similars entre poblacions sotmeses a diferents ambients, indicant una inversió energètica clara en l'espècie cap a la maximització de la supervivència adulta. No obstant això, en el capítol 2, vaig trobar diferències clares en supervivència entre poblacions de truita comuna ocupant rierols diferents. En aquest cas, vaig trobar variacions temporals en supervivència per a tots els estadis vitals però cap evidència consistent de que els individus madurs mostressin una supervivència més alta que els immadurs. La supervivència dels individus del riu més petit va ser idèntica entre estadis vitals i la seva variació va ser explicada en gran part per la temperatura de l'aigua a l'hivern. Els patrons de maduració i creixement també van ser diferents entre el rierol més petit, on el creixement i maduració foren més lents, i la resta de rius, on la taxa de maduració fou significativament més alta, destacant la plasticitat de la truita comuna pel que fa als seus trets d'història de vida.

Dispersió

La transferència d'individus en l'espai i en el temps és un procés biològic fonamental amb implicacions per a la supervivència, el creixement, la reproducció i l'estabilitat poblacional (Clobert et al. 2001). La dispersió és també un procés de presa de decisions en que els individus primer decideixen emigrar (decisiones de fidelitat), es mouen (transferència) i finalment decideixen establir-se en un nou hàbitat (assentament). Factors intrínsecs com l'edat o l'experiència acumulada en un hàbitat concret poden afectar aquestes decisions de dispersió, així com factors externs que redueixen l'èxit reproductor o la supervivència local (Oro et al. 2004, Hénaux et al. 2007, Becker and Bradley 2007). En moltes espècies, la dispersió sol ocórrer abans de reclutar i esdevé rara un cop els individus inicien l'etapa reproductora (Serrano et al. 2001, Hénaux et al. 2007), encara que els individus

reproductors també poden dispersar si una major fidelitat a la zona de cria es tradueix en una reducció de les seves aptituds a l'hora de deixar descendència (Cam et al. 2004).

En aquesta tesi, qüestions específiques sobre dispersió foren abordades al capítol 3 fent servir models multievent que proporcionaren el marc estadístic per a l'estudi dels factors involucrats en els mecanismes de dispersió. En concret, en aquest capítol s'analitzen els moviments d'individus adults entre colònies de gavina corsa per tal d'examinar el procés de dispersió reproductora i abordar hipòtesis concretes en relació a les decisions de fidelitat i assentament dels individus. Aquest enfoc confirmà l'elevada fidelitat mostrada pels individus reproductors a pràcticament totes les colònies tret de les més petites i amb hàbitat de pitjor qualitat, on les taxes d'emigració i de transeünts van ser més altes. Aquest primer resultat indicà diferents respostes de dispersió en relació a la variació espacial en la qualitat de l'hàbitat de les zones de cria, la qual cosa pogué ser confirmada novament amb l'anàlisi de la fidelitat, trobant tendències positives en emigració a les colònies més grans on la qualitat de l'hàbitat minvà al llarg del període d'estudi. L'examen de les probabilitats d'assentament revelà processos de dispersió dirigits cap a les colònies més grans, confirmant l'ús de la mida poblacional com a indicador de qualitat de l'hàbitat. Esdeveniments de dispersió a llarga distància o fora de l'àrea d'estudi van ser detectats i aquests fenòmens podrien tenir implicacions per al manteniment de les poblacions tant dins com fora de l'àrea d'estudi; no obstant això, donada l'estocasticitat i baixa freqüència de la dispersió reproductora, altres tipus de transferència individual, com la dispersió pre-reproductora, podrien estar operant i probablement expliquin millor l'expansió poblacional recent de l'espècie a la Mediterrània. La dispersió juvenil o pre-reproductora no va ser examinada en aquest capítol, però anàlisis preliminars fent servir la mateixa metodologia aplicada a dades d'individus de diferents edats varen mostrar taxes de dispersió juvenil més elevades que les de dispersió reproductora i una baixa fidelitat a la colònia de naixement, especialment a les colònies petites, amb implicacions per al reclutament local i els fluxos genètics (manuscrit en preparació).

Recanvi poblacional

L'estudi de les xarxes poblacionals pot tenir com a unitats fonamentals tant l'individu com la població. No obstant això, quan l'objectiu principal es centra en els factors responsables de la persistència de les metapoblacions, els paràmetres de les dinàmiques d'ocupació poden resultar uns descriptors molt més adequats que els descriptors dels canvis locals en abundància (supervivència i dispersió) (MacKenzie et al. 2006). Conseqüentment, els trets ecològics de les espècies esdevenen importants en aquests estudis poblacionals a gran escala, doncs el recanvi poblacional observat és fruit de l'interacció entre l'ambient extern i les característiques pròpies de les espècies pel que fa a la seva capacitat de dispersió i grau d'especialització.

Les metapoblacions córren risc de desaparèixer si les taxes d'extinció local superen les de colonització, de manera que des del punt de vista de la conservació, cal identificar aquelles condicions que afavoreixen la colonització dels hàbitats i en redueixen els riscos d'extinció local. La teoria prediu que els riscos d'extinció disminueixen amb la mida del fragment d'hàbitat i que el seu aïllament redueix les probabilitats de colonització i indirectament augmenta els riscos d'extinció (Hanski 1999). No obstant això, degut als trets característics de les espècies, les dinàmiques observades poden no sempre ajustar-se a les esperades (Davies et al. 2000); per exemple, una espècie amb poca capacitat de dispersió sempre mostrarà taxes de colonització més baixes, independentment del grau d'aïllament dels fragments d'hàbitat. De manera similar, una mateixa variable ambiental pot estimular diferents respostes en les dinàmiques espacials de les espècies a través de diferents respostes fisiològiques o de comportament.

Les dinàmiques d'extinció i colonització d'espècies formant metapoblacions varen ser examinades al capítol 4 aplicant models d'ocupació dinàmica a una extensa i detallada base de dades de seguiment de papallones. Aquest tipus d'anàlisi és pioner en el nombre d'espècies analitzades i en el nombre de variables externes utilitzades en la modelització, que van més enllà del paradigma àrea-aïllament emprat tradicionalment. Un primer resultat d'aquesta anàlisi va ser l'obtenció d'estimes promig d'extinció bastant baixes per a la majoria d'espècies i estimes de colonització que van resultar significativament majors per a les espècies amb majors capacitats de dispersió, però al contrari de l'esperat, no es detectà una major probabilitat d'extinció en les espècies amb un grau d'especialització alt. Malgrat que algunes espècies no mostraren cap efecte

de les variables ambientals en les seves dinàmiques, per a la gran majoria d'espècies, les variables d'hàbitat i paisatge utilitzades van resultar bons predictors de les dinàmiques d'extinció i colonització. En concret, a l'examinar el signe de la relació, es va veure que una major àrea d'hàbitat i permeabilitat del paisatge (que implica un grau d'aïllament menor) afavoria la probabilitat de colonització mentre que el risc d'extinció es reduïa quan la quantitat d'hàbitat favorable augmentava, confirmant les prediccions de la teoria metapoblacional pel que fa al paradigma àrea-aïllament. Independentment de les seves característiques ecològiques, la relació negativa entre àrea i extinció va ser un tret comú de totes es espècies amb efectes de l'àrea d'hàbitat en la probabilitat d'extinció. En comparar grups d'espècies, un resultat interessant va ser trobar diferències significatives en el rendiment de la topografia com a predictor d'extinció, en concret, una major variabilitat topogràfica ajudava a reduir els riscos d'extinció local de les espècies amb menor capacitat dispersora. Aquest és el primer resultat empíric de l'efecte amortiguador de la topografia en l'extinció d'espècies i que pot ajudar a explicar perquè moltes espècies als límits sud de la seva àrea de distribució no s'acaben extingint com a conseqüència de l'escalfament global (Parmesan et al. 1999). Sorprenentment per a un tàxon amb resposta ràpida a la variabilitat ambiental, els canvis estacionals en precipitació no varen explicar be les dinàmiques metapoblacionals observades en la comunitat de papallones. No obstant això, encara que la variació en precipitació local pot causar canvis en abundància, les espècies poden evitar la seva extinció regional gràcies als efectes de la topografia i la qualitat de l'hàbitat a nivell local i de paisatge, la qual cosa augmenta el nombre de refugis microclimàtics i l'efecte rescat desde poblacions circumdants.

La predicció de processos i les implicacions per a la conservació

L'ús de models per predir les respostes poblacionals a canvis futurs requereix fer inferències fiables sobre les taxes vitals i els factors que influencien les seves dinàmiques en l'espai i en el temps. La fiabilitat dels resultats està condicionada per les dades i les eines analítiques utilitzades en la seva anàlisi; els problemes analítics es redueixen si les dades es recullen seguint protocols de mostreig estandaritzants i la recollida d'informació addicional sobre els individus i/o

poblacions estudiades incrementa el seu potencial per fer estudis més detallats, sobretot si aquestes dades es recullen a una escala espacial i temporal alta. En aquest sentit, els conjunts de dades analitzats en aquesta tesi poden ser considerats de gran qualitat.

Les dades de camp són el resultat tant de processos ecològics com d'observacionals, els quals no han de ser confosos per tal d'evitar biaixos i conclusions errònies sobre els processos causants de les respostes poblacionals observades. En aquesta tesi, de manera constant, he fet servir un enfoc metodològic que separa les observacions obtingudes en un component que descriu el procés biològic d'interès i un component que té en compte la seva imperfecta detecció. Les observacions imperfectes o errors de detecció són controlades pels paràmetres de recaptura i detecció dels models de captura-recaptura i ocupació respectivament, i que he utilitzat al llarg de la meua tesi. La modelització d'aquests paràmetres és la clau per a l'estimació i la modelització de les taxes vitals, la qual cosa permet dur a terme un enfoc científic rigorós per a la conservació de les espècies o poblacions analitzades (Kéry and Schaub 2011), doncs la imprecisió en les estimes de les taxes vitals pot comprometre les decisions de maneig basades en evidències científiques (Williams et al. 2002). Els avenços metodològics que redueixen els biaixos causats per l'heterogeneïtat individual i l'incertesa d'estat (capítol 3) i l'ús de models amb paràmetres explícits de detecció i recaptura ha ajudat a augmentar la fiabilitat de les taxes vitals estimades en aquesta tesi.

Per fer prediccions fiables sobre l'estat futur i les dinàmiques dels sistemes biològics cal un coneixement previ dels factors ecològics responsables de les dinàmiques observades. La confusió sobre els descriptors més adequats i la falta de coneixement sobre les relacions entre factors externs i processos biològics minva la fiabilitat de les prediccions dels models degut a l'existència d'aquestes fonts d'incertesa (Williams et al. 2002). En aquesta tesi he demostrat que tant les eines de captura-recaptura com els models d'ocupació permeten investigar la resposta de sistemes biològics complexos als canvis ambientals per mitjà de la formulació d'hipòtesis sobre els factors responsables dels canvis en les taxes vitals via la incorporació de variables externes en els models. La modelització amb covariables ha representat una part significativa de la meua recerca enfocada a la identificació dels models més parsimònics entre múltiples hipòtesis

alternatives. Per cada cas d'estudi, en comptes de realitzar anàlisis exploratòries amb totes les possibles combinacions d'efectes, vaig limitar la construcció de models a un conjunt d'hipòtesis biològiques concretes basades en el coneixement previ sobre l'espècie i les variables ambientals que, segons la seva biologia, tindrien una major rellevància per a les seves dinàmiques poblacionals. La selecció de models es va basar sempre en el criteri d'informació d'Akaike (AIC), cercant un equilibri entre l'ajustament del model i la precisió de les estimes per tal de seleccionar el model més parsimònic.

La modelització amb covariables duta a terme en aquesta tesi ha generat evidències empíriques sobre respostes poblacionals als canvis ambientals en un ampli rang de tàxons, permetent la identificació d'espècies, poblacions o estadis vitals vulnerables als canvis en les condicions ambientals. Aquests resultats proporcionen informació útil per la direcció d'esforços de conservació i el desenvolupament de plans de gestió; per exemple, en el cas de les papallones (capítol 4), accions com la protecció de les serralades mediterrànies podria beneficiar les poblacions d'espècies sedentàries de papallones degut a que la major variació topogràfica d'aquests indrets redueix el seu risc d'extinció. De manera similar, els resultats obtingut pel que fa a l'efecte del paisatge en colonització indiquen que l'execució d'accions encaminades a augmentar la permeabilitat del paisatge podria beneficiar a comunitats senceres de papallones, la qual cosa resulta essencial per a la conservació de la biodiversitat.

La identificació de lligams entre les taxes vitals i el medi ambient extern permet augmentar el realisme en les projeccions poblacionals i avaluar les conseqüències que diferents escenaris ambientals futurs poden tenir en el destí d'aquestes poblacions. Les projeccions poblacionals amb estocasticitat ambiental realitzades en el cas de la tortuga mediterrània (capítol 1) revelaren taxes de creixement poblacional baixes i riscos d'extinció més alts a les zones situades als extrems Est i Oest de la seva àrea de distribució mundial, on s'esperen condicions més seques en el futur, un resultat alarmant si tenim en compte que a moltes d'aquestes àrees, les poblacions de tortuga també pateixen mortalitat causada per agents no climàtics. Aquest PVA demogràfic es va basar en estimes de taxes vitals i relacions predictor-resposta que es varen obtenir per mitjà de models CJS amb estructura d'edats. En aquest cas, un robust diagnòstic de conservació va ser possible gràcies a la combinació d'eines analítiques de captura-recaptura i models

de matrius poblacionals, però tot i això, els resultats obtinguts poden ser considerats “optimistes”, doncs l'estocasticitat demogràfica i els efectes densodependents en les taxes vitals no van ser integrats en la modelització poblacional.

Malgrat que els models sempre són representacions molt simplificades de sistemes biològics reals, es requereix d'aquest tipus d'enfocament científic en conservació, docs moltes vegades l'alternativa a l'anàlisi quantitativa són opinions sense una base sòlida o decisions polítiques motivades per una escala de prioritats (Morris and Doak 2002). En general, en aquesta tesi he pogut fer inferències fiables sobre els diferents processos ecològics i els factors causals que afectaven les seves dinàmiques per mitjà d'un enfoc transversal, aplicant un conjunt d'eines per a l'anàlisi i modelització de dades recollides en diverses poblacions animals. Totes les quantitats demogràfiques i els efectes ambientals mostrats estan basats en l'evidència empírica i proporcionen una font d'informació útil per als professionals de la conservació. A mesura que noves eines d'anàlisi es van desenvolupar i integrar dins la caixa d'eines de l'anàlisi poblacional, aquesta tesi representa un treball en progrés que espero seguir contribuint en el futur.

CONCLUSIONS

- 1) L'anàlisi poblacional basat en dades de seguiment longitudinal i la seva aplicació transversal al llarg de múltiples tàxons i escales de complexitat ecològica, permet abordar un ampli rang de qüestions biològiques que permeten també integrar els camps de l'ecologia, l'evolució i la conservació en la recerca científica.
- 2) En aquesta tesi, l'alta qualitat de les dades i l'ús de models de captura-recaptura i ocupació que tenen en compte els errors de detecció, va reduir els problemes analítics i augmentà la fiabilitat de les estimes dels paràmetres. En el cas de grans conjunts de dades de captura-recaptura, els models multievent van oferir un marc ideal per controlar heterogeneïtats de recaptura en les dades de camp.

- 3) L'ús de covariables en els models de captura-recaptura i ocupació és clau per abordar qüestions sobre les respostes dels sistemes ecològics a canvis en l'hàbitat i el clima que són problemes de conservació rellevants. La modelització amb covariables va reduir la confusió sobre els factors externs que influenciaven les dinàmiques poblacionals de les espècies analitzades.
- 4) L'aplicació dels models de captura-recaptura a l'anàlisi d'històries de seguiment individuals oferí estimes robustes de supervivència, dispersió i creixement i va permetre abordar qüestions específiques sobre aquests processos biològics. Les estimes de taxes vitals i les relacions predictor-resposta obtinguts es varen traduir en simulacions més realistes i prediccions més robustes sobre la viabilitat de les poblacions.
- 5) Els models d'ocupació aplicats a l'anàlisi de dades de seguiment de la biodiversitat va permetre la investigació simultània de les dinàmiques de múltiples poblacions a escala espacial i temporal altes. Els models d'ocupació dinàmica, enllaçant les taxes d'extinció i colonització a variables externes, varen proporcionar una manera alternativa d'avaluar la vulnerabilitat de les espècies als canvis ambientals.
- 6) Com és d'esperar en espècies de vida llarga, les taxes de supervivència adulta per la tortuga mediterrània i la gavina corsa van resultar altes i invariables i a més, en el cas de les gavines, molts similars entre poblacions. En la truita comuna, la supervivència per estats varià en el temps i entre poblacions, sent els individus del rierol més petit els únics que no mostraren diferències de supervivència entre estats. La supervivència juvenil de la tortuga mediterrània mostrà una variabilitat temporal influenciada per la precipitació mentre que la supervivència de les truites del riu més petit es va veure explicada en gran part per la severitat de l'hivern.

- 7) Les projeccions poblacionals amb estocasticitat ambiental realitzades sota escenaris de precipitació per al segle XXI pronosticaren tendències negatives i situacions de quasi-extinció a les poblacions de tortuga mediterrània situades als extrems Est i Oest de l'àrea de distribució de l'espècie degut a la baixa supervivència juvenil esperada en aquest indrets. Aquests resultats destaquen la importància del reclutament en la persistència a llarg termini d'aquesta espècie i la necessitat d'implementació d'estratègies de conservació que tinguin en compte els efectes del canvi climàtic.

- 8) Les transicions de creixement examinades en l'anàlisi multiestat aplicat a les poblacions de truita comuna varen confirmar la plasticitat de l'espècie en els seus trets d'història de vida i revelaren patrons de maduració contrastats entre rierols, possiblement com a resultat de diferències en la qualitat dels hàbitats.

- 9) L'examen del procés de dispersió reproductora en la gavina corsa va confirmar l'elevada fidelitat dels individus adults a la colònia de cria, la qual minvà en situacions de deteriorament de l'hàbitat. Les gavines en dispersió varen escollir per a l'assentament zones amb poblacions denses, fent servir el nombre d'individus com a indicador de la qualitat de l'hàbitat local. El moviment desde les colònies grans i la dispersió cap a zones fora de l'àrea d'estudi pot haver contribuït a l'expansió recent de l'espècie per la Mediterrània.

- 10) L'anàlisi de dades del CBMS destacà la importància de les variables deterministes en el recanvi poblacional de les espècies analitzades. Els models revelaren un efecte negatiu de l'àrea d'hàbitat en les probabilitats d'extinció i un efecte positiu de la permeabilitat del paisatge en colonització que s'ajusta a les prediccions de la teoria metapoblacional. En el cas de les espècies sedentàries, una major variabilitat topogràfica es traduí en un risc d'extinció més baix. Aquests resultats poden ser utilitzats per a implementar estratègies de maneig per al manteniment de la biodiversitat de papallones en paisatges humanitzats.

BIBLIOGRAFIA (veure secció corresponent en llengua anglesa)

