

Environmental stochasticity in dispersal areas can explain the ‘mysterious’ disappearance of breeding populations

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We present the results of an individual-based simulation model, showing that increasing the mortality of non-breeding dispersers within settlement areas can lead to the extinction of species and (meta)populations in a subtle way. This is because the areas where dispersers settle are generally unknown or difficult to detect. Consequently, fewer efforts are devoted to the conservation of these sites than to the conservation of breeding territories. Additionally, high mortality rates affecting the floater sector of a population become evident in the breeding sector only after several of years, when it is too difficult or too late to halt the decline. As a result, because most conservation projects on endangered species and populations mainly focus on breeding areas, many current efforts may be wasted in locations other than those in which conservation would be really necessary and effective.

Keywords: extinction; decline; survival; persistence; floaters; settlement areas

1. INTRODUCTION

Understanding *how* and *why* animal populations fluctuate, decrease and disappear is a central theme in population ecology and conservation (Pimm *et al.* 1988). Recently, projections of population trajectories into the future have attracted much attention from scientists, decision-makers and the general public. Habitat loss and human interference with natural processes, as well as occurrence of natural catastrophes, have been claimed to increase species vulnerability and extinction rates well above background levels (Pimm *et al.* 1995; Owens & Bennet 2000; Woodruff 2001; Balbontin *et al.* 2005). However, the real causes of species and (meta)population extinction are sometimes difficult to interpret (Soulé 1983). As stated by Moulton & Sanderson (1999), ‘...with increasing frequency, we hear and read about mysterious decreases in or disappearances of living organisms’.

Owing to the current dramatic loss of biodiversity (Leakey & Lewin 1995; Pimm *et al.* 1995), increasing attention is being devoted to rapid and efficient identification of species and populations at risk, to early warning signals and causes of decline, as well as to accurate models yielding reliable predictions of future species and population trends (Fagan *et al.* 2001; Ferrer *et al.* 2003; O’Grady *et al.* 2004). For this reason, many aspects of species life histories and population dynamics have been increasingly explored. Depending on the taxa, habitats and regions considered, a large body of literature has shown the importance of the spatial context in which individuals or populations interact for their stability and persistence (Gates & Donald 2000; Matter 2001; Bascompte *et al.* 2002; Ovaskainen *et al.* 2002).

Because the best predictors for determining species and population trends should encompass indicators of both deterministic and stochastic risks (Woodroffe & Ginsberg 1998), such predictors should consider the whole of a population (e.g. breeders and floaters). This means not only understanding *how* and *why* animal populations fluctuate, decrease and disappear, but also *where* are the factors leading to extinction.

About one-third of the threatened bird species in the world are at risk of extinction as a result of human persecution and predation from introduced species, whereas two-thirds are primarily threatened by habitat loss (Beissinger 2000). In most studies published to date, the main ecological attributes that have been linked to the probability of a species, or (meta)population, extinction include various biological parameters of the breeding population (McKelvey 1996; Brook *et al.* 2000; Purvis *et al.* 2000; Rodrigues *et al.* 2000; Sæther *et al.* 2000; Donald & Greenwood 2001). Therefore, most authors have focused on the mortality of the breeding sectors of populations, and on the impact of persecution and habitat loss on the dynamics of breeding communities (Pimm *et al.* 1988; Beissinger 2000; Tworek 2003).

On the contrary, the temporary settling zones used during dispersal by non-breeders (i.e. settlement areas) are usually unknown for most species, and the dynamics of dispersers within them are poorly studied. Therefore, the effects of habitat loss, mortality rates, extinction probability and environmental stochasticity have been considered as less important, if not ignored, for settlement areas. Consequently, such sites are typically less protected than breeding territories, which may lead to increased risk of mortality for dispersing individuals. In addition, because dispersal displaces individuals across unfamiliar

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terrain, losses during dispersal are probably considerable. As a result, habitat destruction and decline in survival rates within settlement areas could be critical factors affecting the persistence of the whole population. This may make the species more vulnerable to extinction by demographic and environmental stochasticity (Hill *et al.* 2002).

We used an individual-based simulation model to show how species and (meta)populations can be predicted to become extinct when individual dynamics within settlement areas are taken into account in theoretical studies (e.g. assessment of extinction risks) and their applications (e.g. conservation plans). We based our work on a century-long time-series on a metapopulation of the Spanish imperial eagle *Aquila adalberti*, the most endangered bird of prey in Europe (with less than 150 pairs worldwide) and one of the most threatened raptors in the world, for which extinction has been forecasted within the next 200 years (Ferrer 2001).

2. MATERIAL AND METHODS

(a) Empirical and theoretical basis of the model

The Spanish imperial eagle population of Doñana (south-western Spain) consists of a maximum of 16 pairs. This species is a large (2500–3500 g), sedentary and territorial bird of prey, characterized by low reproductive rates (on average 0.75 chicks per pair per year), a density-dependent immature phase of 3–5 years (most frequently 5) and a maximum longevity of 21–22 years. Juvenile unpaired eagles are not territorial, and move during the dispersal period through a series of temporary settlement areas (areas known for the Doñana population through extensive radio-tracking data; Ferrer 1993a,b).

The dataset on the species in Doñana is, to our knowledge, one of the most long-running for vertebrate species (data collection started in 1890). Such a dataset represents a unique source of information and a strong basis for understanding small population dynamics and the building of realistic predictive models as a tool for conservation. This is because: (i) during approximately 15 years of research (1986–2000), 60% of the whole breeders and floaters of this population were marked with radio tags (Ferrer 2001) and (ii) long-lived species such as this eagle are usually more sensitive to human persecution and small perturbations, which makes them more susceptible to extinction (Bennett & Owens 1997; Beissinger 2000; Owens & Bennet 2000).

When studying species (such as birds), in which the processes affecting populations are characterized by temporally (reproduction versus dispersal) and spatially (breeding versus settlement areas) disjunct locations, we should consider the influence of environmental stochasticity (changes in the physical or biological environment) on the different sectors of a population. Consideration should also be given to the potential effects attributable to the synchronous or asynchronous way in which biotic and abiotic factors may act (Matter 2001; Johst & Drechsler 2003). In previous analyses (Penteriani *et al.* 2005), we showed that: (i) the survival of dispersing individuals is highly dependent on the number of available settlement areas, mediated by the time that their main prey, the rabbit (*Oryctolagus cuniculus*) takes to modify its behaviour so as to avoid predation and (ii) environmental stochasticity has a stronger influence on the whole population when variations in environmental

conditions occur in a synchronous way (i.e. in both the settlement and breeding areas at the same time). For this reason, the following simulations were performed under the less adverse scenario (i.e. when the variations in environmental conditions occur in an asynchronous way). The results shown here are thus considered conservative and those found under the more adverse, synchronous scenario are expected to be even more extreme.

The model was built to assess the consequences of increasing floater mortality in settlement areas (ranging from 5 to 30%) on the stability of the breeding portion of the population. Such a mortality increase could be a result of the occurrence of environmental stochasticity (e.g. occurrence of natural catastrophes or habitat destruction caused by human activities) or human-induced deaths (e.g. poisoning, electrocution). Understanding the influence of such types of disturbances is of paramount importance for conservation because of their potentially severe impact on population stability (Casagrandi & Gatto 2002). Because the main objective of this simulation was to assess the effect of a mortality increase within settlement areas on the breeding population, we did not separate the effects induced by environmental disaster and those caused by human alterations (Casagrandi & Gatto 2002).

Our model included density-dependent compensation, individual effects and individual \times area interactions. All simulations started at time $t=0$ with 15 eagle pairs and 15 floaters (to simulate the real average population size). We ran 100 simulations (each of them of 100 years) and, at the end of each series of 100 simulations, the model generated the means of number of pairs and productivity (fledged young) for the 100 years of each simulation.

Eight parameters were used to simulate the effects of the floater mortality in settlement areas on the breeding population:

- (i) Death timing: the productivity of a pair depends on the time of the year in which mortality occurs, especially in species characterized by a long breeding cycle (V. Penteriani, F. Otalora & M. Ferrer, unpublished results). For this reason, two different temporal sequences were selected at random in the simulation: 75% of the time, we ran the sequence *mating* \rightarrow *death* \rightarrow *reproduction* (productivity = 0), and 25% of the time, the sequence *death* \rightarrow *mating* \rightarrow *reproduction*, in which case productivity may or may not be zero.
- (ii) Productivity: productivity was modelled as density-dependent, relying on the population saturation. For a saturation threshold = 1 (population totally saturated), the probability of producing 0, 1, 2 or 3 young (based on the field data) is 47.62, 38.10, 9.52 and 4.76%, respectively. For a saturation threshold = 0, the probability is 20, 30, 30 and 20%. For intermediate values of saturation, this probability is calculated as the weighted average of the extreme values: $saturation \times productivity(1) + (1 - saturation) \times productivity(0)$;
- (iii) Mortality: the mortality was calculated as the combination of two probability distributions: (a) natural mortality, represented as a sigmoidal distribution centred on 30.0 and with exponent 10.0 and (b) accidental mortality, corresponding to a probability distribution with modal values of 60% (mortality for the first year of life), 6% (mortality of mated individuals) and a value of 30% for non-mated eagles

greater than 1 year old, based on observed values from our long-term dataset. Environmental stochasticity was represented as a normal stochastic variable of mean 1.0 and s.d. 1.0 that multiplies the probability of accidental death and changes from year to year;

- (iv) Sexual maturity: the age of first breeding was set at 3 years old;
- (v) Saturation: the saturation of the breeding territories, dependent on the characteristics of the breeding population, is represented by a sigmoidal distribution centred on 30.0 and with exponent 10.0;
- (vi) Sex ratio: it was set at a male : female ratio of 0.5;
- (vii) Mating probabilities: the probability that two non-mated, sexually mature individuals of the opposite sex become a pair was set as density-dependent and calculated as $1 - \text{saturation}$;
- (viii) Shuffle: we allowed aleatory rearrangement of the list of living individuals in each new simulation, which avoids possible uncontrolled correlations between individuals. Otherwise, there would be a risk of biased, age-related correlations because, after a few years, individuals end up sorted by age as new chicks are added only at the end of the list of individuals. This could introduce a bias in all density-dependent processes (e.g. mating), because the simulated events are evaluated iteratively over the list.

(b) Output analyses

When data were not normally distributed, they were transformed. If normalization was not possible, then we used non-parametric tests. In particular, we used the Kruskal–Wallis test to investigate changes in the parameters of the model outputs under different conditions of annual floater mortality. We employed the Mann–Whitney *U*-test to compare population parameters when mortality in settlement areas increased from 5 to 30%. All means are given with ± 1 s.d., all tests are two-tailed and statistical significance was set at $p < 0.05$.

3. RESULTS AND DISCUSSION

When floater mortality varied from 5 to 30% (figure 1), a significant change occurred for the mean number of pairs (for an age of first reproduction of 3 years old: $\chi^2 = 488.48$, $p = 0.0001$; 4 years old: $\chi^2 = 517.96$, $p = 0.0001$; 5 years old: $\chi^2 = 517.37$, $p = 0.0001$; $n = 600$, Kruskal–Wallis test), and for mean productivity (3 years old: $\chi^2 = 432.19$, $p = 0.0001$; 4 years old: $\chi^2 = 288.42$, $p = 0.0001$; 5 years old: $\chi^2 = 197.38$, $p = 0.0001$; $n = 600$, Kruskal–Wallis test). The most drastic decrease was observed when the floater mortality reached the threshold of 25–30% and the age of first reproduction of the breeding population was 5 years old (figure 1c). Under such circumstances, the extinction of the breeding population occurred approximately 100 years after the increase of mortality in the settlement areas. Early age of first reproduction acted as a buffer to balance high mortality rates within settlement areas, where population extinction occurs only when the age of first breeding is 5 years.

Because productivity is density-dependent in this population (Ferrer & Donazar 1996), this parameter was less sensitive to the initial increase in floater mortality, which reduced the saturation of the breeding population.

In fact, at the beginning, the decline in number of pairs did not affect productivity, successively starting a falling off as high as the combination of age at first reproduction–mortality.

The effects of high mortality in the settlement areas became appreciable in the breeding sector of the population only after more than 20 years (figure 1c), when the declining trend accelerated. Interestingly, when considering the more extreme scenarios (age of first breeding = 5 years and floater mortality = 25 and 30%), there is a positive correlation between number of pairs and productivity (25%: $r = 0.948$, $p = 0.0001$; 30%: $r = 0.918$, $p = 0.0001$; $n = 100$), which could explain the high time of latency before the definitive decline of breeding performance, when the high mortality in the settlement areas makes pair formation increasingly difficult because of the lack of new individuals potentially available to replace a lost mate.

Overall, a mortality increase within the settlement areas, when the age of first reproduction was 5 years (the most common in the studied species) was sufficient to determine the extinction of a small population with density-dependent productivity. When mortality in the settlement areas was low, the demographic contribution of dispersers compensated for breeder mortality, which reduced the risk of extinction.

Because of density-dependence, productivity was less sensitive at the beginning of an increase in floater mortality. This meant that at the beginning of a population decline resulting from an important loss of floaters, the relatively stable breeding performance could generate the false impression that the population is healthy, even if some breeding territories are lost. However, because the less frequently occupied, and the earliest deserted, territories are generally the low quality ones (Liberatori & Penteriani 2001; Sergio & Newton 2003), such an early warning signal could easily go unobserved. This implies that it could be dangerous to monitor only the breeding portion of a population because of the potential delay in decline detection, and thus the underestimation of decline extent and overestimation of recovery levels (Kokko & Sutherland 1998; Kenward *et al.* 2000).

Generally, because the areas where dispersers settle are unknown or difficult to detect, fewer efforts are devoted to the conservation of these sites than to breeding territories, which can result in less effective conservation plans and action. Population studies, analyses of population viability and extinction risk assessments that ignore the dynamics of dispersers within settlement areas may fail to understand how and why animal populations decrease and where to plan conservation action. In the specific case of the Spanish imperial eagle, dispersers frequently use areas in which high levels of anthropogenic disturbance result in high mortality rates (Ferrer & Harte 1997). Therefore, because conservation efforts targeting endangered species or populations focus on breeding areas or nesting sites, conservation programmes planned for breeding territories can be ineffective if the real problem is located in the settlement areas. As a result, human and economic efforts are wasted in locations other than those in which conservation measures are really necessary. In fact, declines in breeding population size could divert our attention from the real problem (e.g. by increasing conservation efforts in breeding areas). Likewise, the creation of reserves to ensure

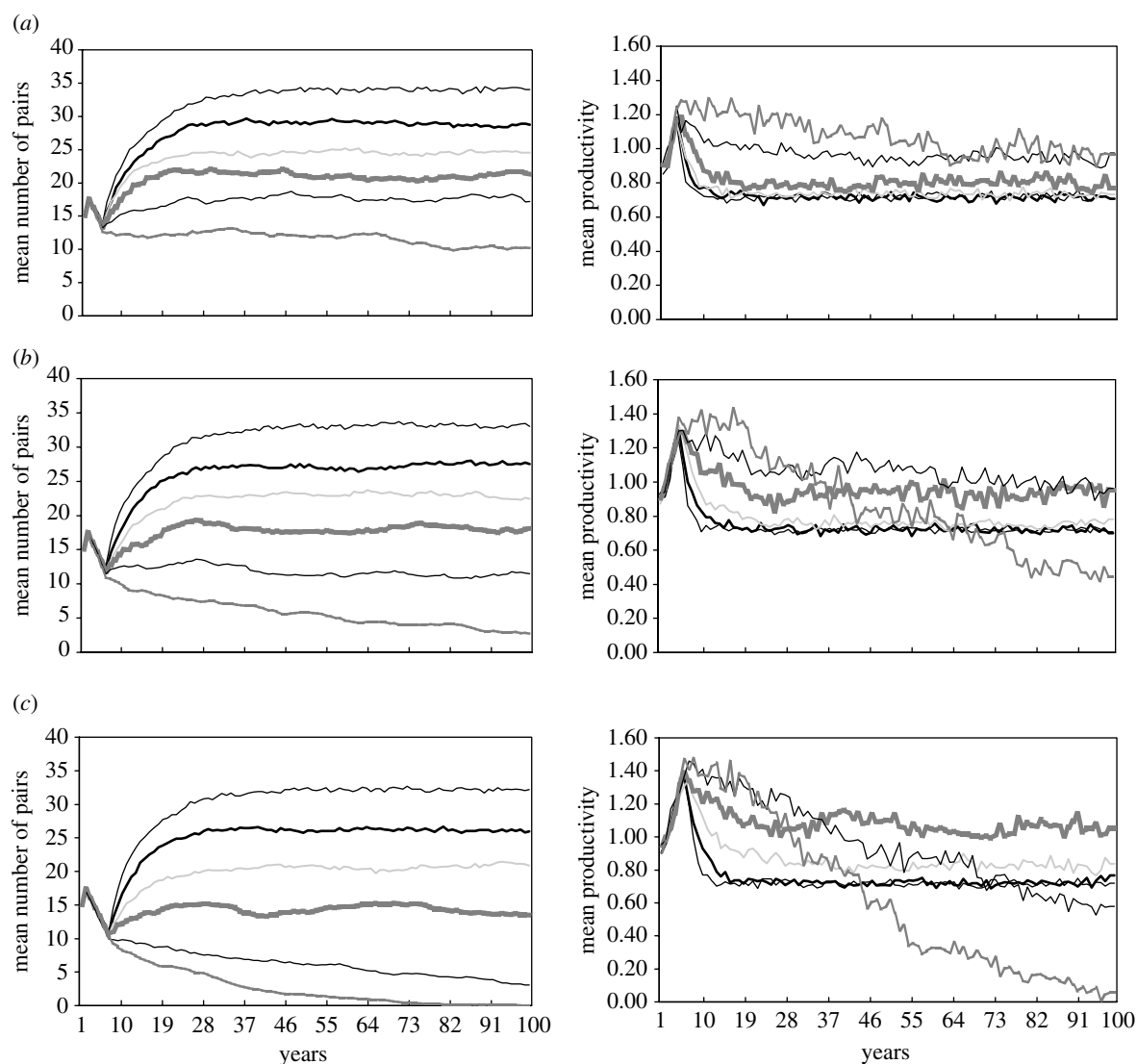


Figure 1. When floater mortality within settlement areas increases (e.g. from 5 to 30%), the number of pairs and productivity within the breeding sector of a population show a delayed decline. Such a decline can determine (meta)population extinction when the age of first breeding is late (e.g. 5 years old). We present the simulation outputs under three different ages of first reproduction: 3 (a), 4 (b) and 5 (c) years old, where 5% floater mortality = black line; 10% floater mortality = bold black line; 15% floater mortality = grey line; 20% floater mortality = bold grey line; 25% floater mortality = tiny black line; and 30% floater mortality = soft line. The sudden fluctuation right after the start of the simulations is an artefact owing to the unavoidable misfit between the initial fixed structure imposed to the population and its equilibrium structure, which depends on the simulation dynamics.

species and population persistence has usually focused on the areas occupied by breeders only (e.g. [Rodrigues *et al.* 2000](#); [Araújo *et al.* 2002](#)). However, reserve design theory has been recently developed for wildlife corridors and migratory species too, thus highlighting the critical role of non-breeding habitat to landscape-scale persistence of species (e.g. [Williams 1998](#); [Malcolm & ReVelle 2002](#)). In conclusion, when animal populations are characterized by both breeders and floaters sectors, we are confronted by a dichotomous dilemma. On the one hand, because of the increasing global loss of biodiversity, risk assessments should not be delayed, which justifies the use of simple indicators of the level of risk of species/population extinction (i.e. counts of breeding population size; [O'Grady *et al.* 2004](#)). On the other hand, we risk underestimating the threat when the main problem affecting a species/population is not located in its breeding territories, where the effects of floater mortality only appear dozens of

years after they have begun. Therefore, the absence of information on the location of settlement areas and on the dynamics of individuals within them (as for the majority of species) means we are unprepared to halt population declines. Despite its difficulty, it is time to devote more attention to floaters and settlement areas within the conservation arena. The solution to small- and declining-population paradigms ([Caughley 1994](#); [Norris 2004](#)) may reside here.

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