Floater mortality within settlement areas can explain the Allee effect in breeding populations

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ABSTRACT

The Allee effect (the positive relationship between population growth rate and population size) is a constraint of some animal populations at low numbers, which increases their likelihood of extinction because of a decrease in reproduction and/or survival. We were able to demonstrate that the Allee effect can be the result of a mortality increase affecting floaters (i.e. dispersing individuals able to enter as breeders in the reproductive population when a breeding territory or a potential mate – owner of a suitable breeding territory – becomes available). Previously, potential mechanisms underlying Allee effects were always related to the breeding portion of a population only. In contrast, our understanding of or solutions to population declines due to the Allee effects can reside elsewhere, away from breeding territories.

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1. Introduction

Without attempting a comprehensive explanation, let us spell out the three essential features that main portray the Allee effect in animal populations (Courchamp et al., 1999; Stephens et al., 1999; Dennis, 2002). Firstly, the Allee effect denotes a scenario in which populations at low numbers are affected by a positive relationship between population growth rate and population size, which increases their likelihood of extinction because of a decrease in reproduction and/or survival. Secondly, the numerous factors associated with such an effect can be classified into three main categories: (a) genetic inbreeding and loss of heterozygosity; (b) demographic stochasticity (including sex-ratio fluctuations); and (c) reduction in cooperative interactions among conspecifics when there are fewer individuals (including sexual reproduction, i.e. shortage of receptive mate encounters during the mating period when density is too low). Finally, there exists a critical density below which the aggregation unit considered (e.g. population, colony or social group) is prone to extinction.

The increasing interest for the Allee effects in animal populations (examples of Allee effect have been described

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for most animal taxa; Møller and Legendre, 2001; Dennis, 2002) is largely due to its importance as strong selective forces in evolution (Dennis, 1989), as well as to the significance of his consequences on coloniality (Serrano et al., 2005), the theory of population dynamics (especially when studying small metapopulations), establishment/eradication of species, predator prey cycles and conservation (Courchamp et al., 1999; Stephens and Sutherland, 1999; Dennis, 2002; Engen et al., 2003; Bessa-Gomes et al., 2004). As for this latter, species/(meta)population can be dramatically impacted by Allee effect (Lande, 1988), being more predisposed to catastrophic collapses with only a slight increase in mortality (Courchamp et al., 1999). Such an interest in conservation biology is increased by the fact that, in the past, many conservation programs focused on extinction risks and minimum population size without take into consideration the Allee effect. Knowing that a given species/(meta)population is under the risk of an Allee effect would be of much help to reverse the fate of the population collapse by reducing or eliminating the cause/s that conducted the species/(meta) population close to, or below, its critical threshold. As an end result, more systematic investigation on the Allee effect in endangered populations were evoked to better understand their dynamics and efficiently protect them (Courchamp et al., 1999), the causes of decline of many populations still remaining a puzzle (Courchamp et al., 1999; Penteriani et al., 2005a).

In a time when human disturbances on natural systems lead to even smaller population size, the question posed by Allee (1938, p. 107) "…*what minimal numbers are necessary if a species is to maintain itself in nature?*" continue to be of an awesome and contemporary actuality. However, after more than a half a century on research on how the Allee effect works on animal population, we think that an additional question arises: *if the Allee effect is a consequence of population decrease, what generate and where is determined such a decrease? Or, in other words, where does the Allee effect originate?*

We previously showed that factors affecting the survival of floaters (i.e. dispersing individuals able to enter as breeders in the reproductive population when a breeding territory or a potential mate – owner of a suitable breeding territory – becomes available) have the potential to directly influence the dynamics of the whole population due to their effects on the breeding segment of the population in reproductive areas (Penteriani et al., 2005b). What is more, an increase in floater mortality within settlement areas can both explain puzzling declines or extinctions of breeding populations (Penteriani et al., 2005a) and patterns of density-dependence fecundity (Penteriani et al., 2006). The strong relationship between floaters and breeders of a same population suggests that individual dynamics within settlement areas may be at the origin of the density-dependence properties of a (meta)population. Consequently, mortality rates of dispersers have the potential to be one of the (overlooked) ecological mechanism by which the population size can affect demographic rates, leading to the Allee effect. Clearly defining the portion of the population (e.g. floaters) that shapes density-dependent patterns may help to solve some of the puzzling extinction processes, allowing us to focus our conservation effort on the right direction (e.g. reduction of mortality rates within settlement areas). In fact, whereas the phenomenon of the Allee effect is today

clearly defined and described, the main mechanisms at the basis of the Allee effects are still unclear (Møller and Legendre, 2001; Engen et al., 2003).

The outputs of our individual-based simulation models show how floater dynamics within settlement areas can be responsible for the Allee effect that we detect in animal (meta)populations.

2. Methods

2.1. The species and main population parameters

Our individual-based models were based on a century-long time series of the metapopulation of the Spanish imperial eagle *Aquila adalberti* of Doñana (south-western Spain), which consists on a maximum of 16 pairs. With less than 150 pairs, this large eagle is the most endangered bird of prey in Europe and one of the most threatened raptors in the world (Ferrer, 2001). The maximum population threshold of the Spanish imperial eagle population in Doñana consists 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 22 years. Typically, breeding pairs include two adults (which can remate over successive years), but some pairs may be mixed, that is one or both mates have not attained adult plumage (<5 years old). Survival probability is equal for males and females. Using the same procedures as in Penteriani et al. (2005a,b, 2006), we analysed the effects of floater mortality (ranging from 5 to 30%) within settlement areas on the relationships between mean number of pairs (the population size) and mean fecundity (i.e. the mean number of fledglings per year, averaged over all pairs in the population) within the breeding population. On the basis of the previous results (Penteriani et al., 2005a,b, 2006), we simulated two different scenarios: (i) when the age at first reproduction of the breeder population varied from 3 to 5 years; and (ii) for three different metapopulation size, i.e. 10, 15 and 20 breeding pairs. We explored these ranges of values for age at first reproduction and saturation levels of the population because they best reflect the real scenarios that we observed for the Spanish imperial eagle in Doñana. The values of floater mortality reflects the real range of possible values that we recorded in the field (Ferrer et al., 2004 reported an annual mortality of 0.26 ± 0.30 for unpaired eagles) after then 30 floaters (60% of the whole disperser population) were marked with radio tags over a period of approximately 15 years (Ferrer, 2001). The structure, parameters and initial values of our models were guided and set by the observed long-term (more than one century) eagle population dynamics, for which previous simulations proved the similarity between modelled patterns and empirical data (Ferrer and Penteriani, 2003; Ferrer et al., 2004).

2.2. Simulation algorithms and parameters

Because in previous analyses (Penteriani et al., 2005a,b, 2006) we highlighted that 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), the simulations were performed under the less adverse scenario, that is when the variations in environmental conditions occur asynchronously. An increase in floater mortality could be due to environmental stochasticity (e.g. natural catastrophes, habitat destruction and fragmentation) or human-induced deaths (e.g. poisoning, electrocution).

Our model included density-dependent compensation because models without density-dependent compensation inevitably lead to the demise or explosion of a population, as well as erroneous inferences about a population's responses to individual intra- and interspecific interactions (Emlen et al., 2003).

All the simulations start at time $t = 0$ with 15 eagle pairs and 15 floaters (to simulate real situations). We ran 100 simulations (each of them of 100 years) and, at the end of each series of 100 simulations, the model generated the mean of number of pairs and fecundity (fledged young) for the 100-year period for each simulation.

The output of a simulation contains statistics on the population census for each interaction (1 year). The population dynamics were simulated by individual-based evaluation of three main stochastic functions whose behaviour is driven by the internal status of the given individual.

2.2.1. Function 1: death

Computes a Boolean value stating if the given individual will die during the current year. The value returned by this function is TRUE (the individual will die) if

$$r < A(a) + (1 - A(a))B(s)$$

where

- a is the age of the individual,
- s is the status (chick, floater, breeder) of the individual,
- r ($0 < r \leq 1$) is an uniformly distributed random deviate,
- $A(a)$ is a continuous probability distribution

$$A(a) = 1.0 - \left(\frac{1}{1 + (a/30)^{10}} \right)$$

describing the probability of death as a function of the age of the individual,

- $B(s)$ is a randomised discrete function

$$B(s) = knP(s)$$

describing the probability of accidental death as a function of the status of the individual (k and n are normally distributed random variates with mean 1.0 and standard deviation 1.0 and $P(s)$ is a discrete function returning 0.6 for chicks, 0.06 for breeders and a value in the range 0.05–0.30 for floaters (this value is a parameter of the simulation as described in the text). Finally, the expression

- $A+(1 - A) \times B$ implements the logic or operator for two probability distributions.

The value of the random deviate k is fixed for each year, representing "environmental stochasticity". The correlated or uncorrelated effect of stochasticity in breeders and floaters discussed in the paper is simulated by generating two different values of k, one for breeders and one for floaters (asynchronous stochasticity).

All numerical values conditioning the shape of the probability distributions have been estimated from actual data in the historic series.

2.2.2. Function 2: breed

Is evaluated for all breeder females, returning the number of chicks produced during the current year as a density-dependent distribution

$$N(c) = w(c)D_h + (1 - w(c))D_l$$

where

- w is a weighting term for the two discrete productivity functions D_h and D_l

$$w(c) = 1 - \left(\frac{1}{1 + (c/15)^{10}} \right)$$

this value can be though as the "saturation" of the population

- D_h is the high-w limit of the Percent Point Function (PPF) of the discrete productivity distribution E_h describing the probability of raising a given number of chicks as

No. chicks	Probability
0	0.48
1	0.37
2	0.10
3	0.05

A number of chicks is selected as the value of the PPF for an uniformly distributed random variable.

- D_l is the low-w limit of the productivity distribution Percent Point

Function of the discrete productivity distribution E_l describing the probability of raising a given number of chicks as

No. chicks	Probability
0	0.20
1	0.30
2	0.30
3	0.20

A number of chicks is selected as the value of the PPF for a uniformly distributed random variable.

The resulting number of chicks is added to the population as 0-year-old individuals.

All numerical values conditioning the shape of the probability distributions have been estimated from actual data in the historic series.

2.2.3. Function 3: couple

Computes a suitable partner for the current individual. If the individual is a non-breeder adult, it generates a list of all potential partners and randomly chooses one of them (if the list is not empty). Each candidate (non-breeder adult of the opposite sex) in the population is tested and included in the list with a density-dependent probability

$$C(c) = 1 - w(c)$$

function of the number of couples c in the population. If, eventually, a partner is found (i.e. the list is not empty), both the individual being evaluated and the chosen partner are tagged as breeders.

The simulation proceeds by iterative evaluation of the three functions each year for each individual in the population and updating accordingly the internal status of each individual.

Due to this iterative processing three subtle corrections were built into the simulation:

(a) *Individual shuffling*. As new chicks are append to the end of the population list, individuals end up sorted by age into the list, resulting in old individuals being evaluated before younger ones. During the loop that evaluates all individuals, some parameters of the population change, notably the "saturation" that has an effect in all density-dependent calculations. To avoid this effect, the list containing all individuals is shuffled at the beginning of each yearly update;

(b) *Events sorting*. The death of a breeding individual implies that either no young is produced by the couple during this last year (if the death function is evaluated before the breed function) or that all chicks are produced elsewhere. Obviously both situations are wrong. To account for this effect, the order in which these two functions are evaluated is randomly chosen with a 75% probability of being "death–breed" and a 25% probability for the reverse order. These probabilities were chosen because the success of raising a chick depends on parental care during 75% of the year;

(c) *Sex sorting*. When a breeding individual dies, his/her partner also loss his breeding status. This can lead to an artificially reduced productivity.

Having "Event Sorting" implemented, it is safe to evaluate females before males to account for this effect.

The model has been implemented using heavily Object Oriented techniques in the Python programming language (www.python.org).

2.3. Sensitivity analysis of the model

A visual debugging of our simulations was performed to prevent that some errors in the model could generate false outputs (Grimm, 2002; Grimm et al., 2006). Such a sensitiv-ity analysis of the model showed that: (1) the main observed effect (i.e. positive density dependence of fecundity) was really due to the floater availability along the time of the simulation. When we looked at simulations run again, as well as the population structure year by year during the visual debugging of our model, we mainly observed that: (a) once a breeder dies, floaters quickly fill in the vacant position (in the year later) and the population is always at its saturation level. However, this occurred only for high floater availability (i.e. low floater mortality). In such a scenario the mean productivity is constant and low (due to the density-dependent fecundity, see features of the *function 2_breed* of the model); (b) an increase in floater mortality determines a corresponding decrease of the floater availability and, consequently, lower floater numbers cannot allow to replace all the vacancies in the breeding population (i.e. decrease in the recruitment process) because in our model there is a specific probability that determines new pair formation (again the *function 2_couple* of the model). For low numbers of floaters the probability of formation of a new pair is very low too. In fact, our simulation is not deterministic (e.g. each time a breeder dies there is a replacement of the lost mate by an adult floater of the same sex), but mating is under a probability constraint and difficulties in pair formation can also appear when the number of floater is not $n = 0$ (see also the *function 2_couple*); (c) as a consequence of the density dependence of fecundity, all the changes in the population saturation levels are reflected in the fecundity values that we recorded in the simulated population. Under scenarios of high floater mortality, extinctions can occur, but the extinct populations do not contribute in the calculation of the mean fecundity. In other words, there are no artefacts in the model and its computation of fecundity; and, finally, (d) the decrease in floater numbers and, consequently, its reduced availability as potential mates able to fill vacancies in the breeding territories, determines an increase in the age of breeders and, accordingly, in the probability of death of a breeder before the end of the breeding cycle, due to its older age (see both the *function 1_death* and *Events Sorting*). This breeder mortality before fledging is a secondary effect that, even determined by the highest levels of floater mortality, contributes to the decrease of the population's fecundity.

3. Results and discussion

By analysing the effect of an increasing mortality of floaters within the settlement areas that they use during dispersal, we contemporaneously observed the appearance of the Allee effect in the breeding population. In fact, when floater mortality reached the 30% threshold (Fig. 1), the number of pairs decreased (for the small populations of 20 and 10 individuals, A and B) and fecundity showed a positive density-dependent pattern, which is typical of the Allee effect. That is, when population size decreases (before extinction) the population shows inverse density dependence (the Allee effect strictly refers to inverse density dependence at low population numbers, Courchamp et al., 1999).

As predicted by the Allee effect (Henle et al., 2004), its consequences were more severe for the smallest population (Fig. 1B). Moreover, in the smallest population (10 breeding

POPULATION THRESHOLDS OF 20 (A) AND 10 (B) BREEDING PAIRS

AGE AT FIRST REPRODUCTION OF 3 (C) AND 5 (D) YEARS-OLD
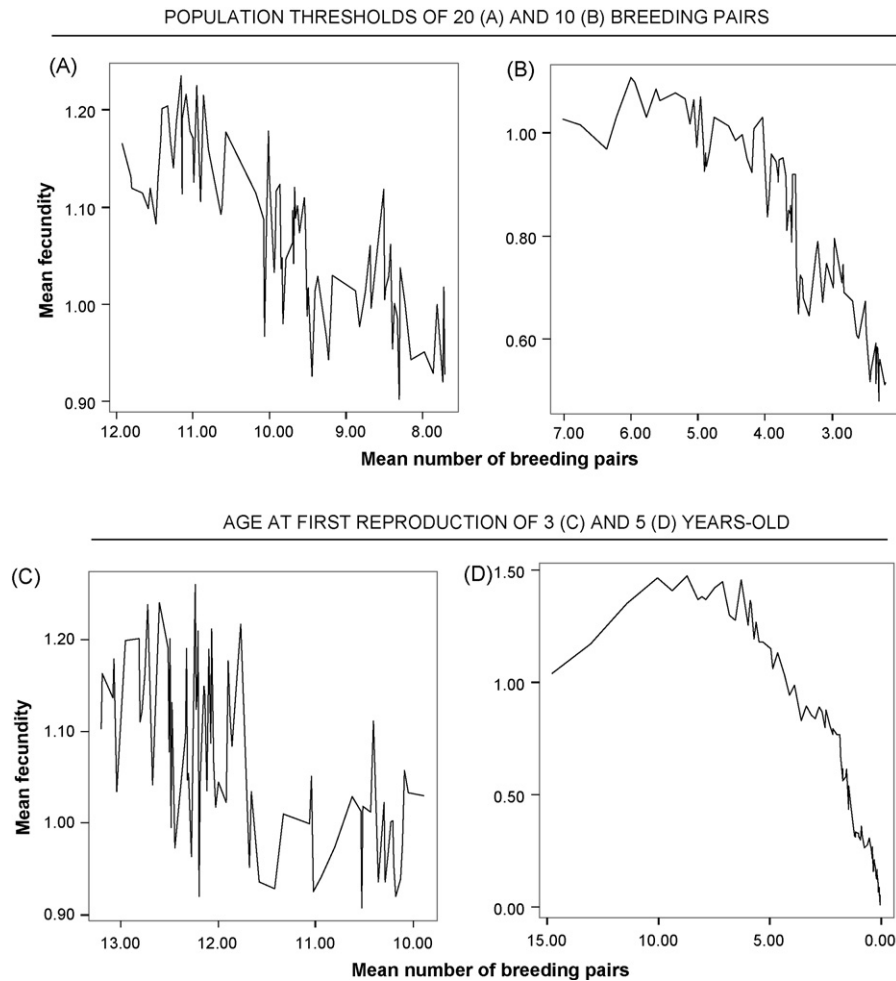
Fig. 1 – When floater mortality within settlement areas reach a threshold of 30%, the breeding population (i.e. number of pairs) decrease (for both a small population of 20 and 10 individuals, A and B) due to the scarcity of available mates and fecundity shows a positive density-dependent pattern (i.e. Allee effect). The Allee effect, as expected, is highest for the smallest size population (B). In the smallest population (population size = 10 breeding pairs), an age at first reproduction of 3 years old (C) buffers the floater mortality, whereas the same population become extinct at his most common age of first reproduction of 5 years old (D).

pairs), extinct occurs when an early age at first reproduction did not buffer (Ferrer et al., 2004) the increasing floater mortality (Fig. 1D). The extinction process started when the scarcity of available mates, because of the high mortality in settlement areas, made pair formation more and more difficult due to the lack of new individuals potentially available to replace a lost mate. The difficulty of finding a partner represents the most frequently mentioned cause of the Allee effect (McCarthy, 1997; Amarasekare, 1998; Courchamp et al., 1999; Stephens et al., 1999; Stephens and Sutherland, 1999; Engen et al., 2003; Lande et al., 2003).

Because of the density dependence of fecundity, for relatively low floater mortalities we observe an increase in the breeding performance due to the reduced saturation of the breeding population (Fig. 2, for a value of floater mortality ranging between 5 and 20%). When this occurs, the breeding territories of low quality (which when inhabited by breeding pairs lead to reduced mean breeding output of populations; Ferrer and Donázar, 1996; Krüger and Lindström, 2001;

Penteriani et al., 2004), disappear earlier than the high quality territories. In fact, best breeding territories generally show higher rate of occupancy than poor territories due to strong mate survival and site fidelity (Liberatori and Penteriani, 2001; Sergio and Newton, 2003). As an end result, the lost of poor territories determines an increase of the mean breeding performance of the population. The fact that the increased usage of poor territories in situation of high density decreases per capita breeding performance (Ferrer and Donázar, 1996; Both, 1998) is also known as site-dependent population regulation (Rodenhouse et al., 1997) or Habitat Heterogeneity Hypothesis (Ferrer and Donázar, 1996; Ferrer et al., 2006). In a scenario of not saturated populations, and until the population density does not approach the saturation again (e.g. reduced floater mortality in the settlement areas), we will detect an increase in the mean fecundity. But an increase in floater mortality (Fig. 2, for a value of floater mortality ranging between 25 and 30%) immediately gets the breeding population under the Allee effect. When the (meta)population felt below its critical
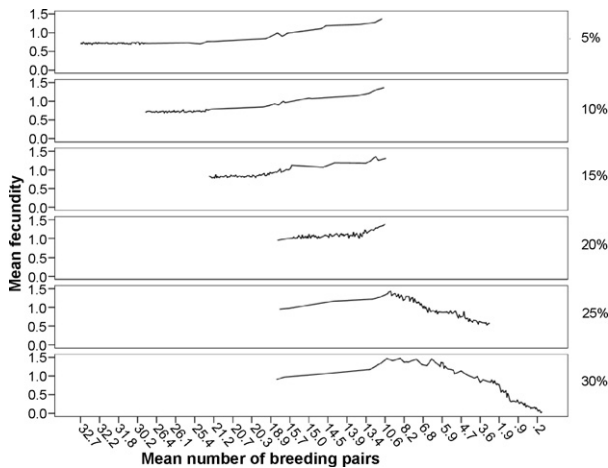
Fig. 2 – Appearance of the Allee effect in a breeding population (characterised by an age at first breeding of 5 years old and population threshold of 10 breeding pairs), when floater mortality within settlement areas shift from 5 to 30%. At the beginning of an increase in floater mortality (from 5 to 20%), because of density-dependent fecundity, we observe an increase in the breeding performance due to the reduced saturation of the breeding population. However, when the (meta)population goes below its critical threshold (from 25 to 30%), a positive relationship between population growth rate (i.e. fecundity) and population size (number of breeding pairs) determines extinction because of a decrease in reproduction (i.e. Allee effect).

threshold, the appearance of a positive relationship between population growth rate (i.e. fecundity) and population size (number of breeding pairs) determined its extinction.

To our knowledge, this is the first time that the Allee effect is explained in terms of floater dynamics. Potential mechanisms underlying Allee effects, as reduced availability of mates, sexual selection and foraging efficiency or increased risk of predation (see review in Møller and Legendre, 2001; Dennis, 2002; Lande et al., 2003), as well as the factors determining such effects at low population densities, always related to the breeding portion of a population only. In contrast, our understanding of or solutions to population declines due to the Allee effects can reside elsewhere, away from breeding territories. Taking into account or not the Allee effect in conservation programs or analyses of extinction risk is not our unique priority: WHERE to focus our attention to stop an extinction process (e.g. settlement areas) is the new and more urgent question now. Only knowing that a given species/(meta)population is prone to an Allee effect or that an Allee effect is threaten a population could not be of much help to reverse its fate. More importantly, we should exactly know where to direct protection effort to increase the species/(meta)population density, being population numbers one of the most useful criterion of endangerment in conservation programmes (Courchamp et al., 1999).

An animal population under the Allee effect can be considered as a living being infected by a flu or a virus, that is the disease affecting his survival (the Allee effect) is due to external causes, i.e. it is originated out of its body (i.e. in the settlement areas). That is, the effects that we observe in an animal population can be the result of external causes. Floaters, the "invisible" component of animal populations, represents their "foundations" and become "visible" by the Allee effect when environmental stochasticity reduces their number during dispersal and settlements previous to the incorporation as breeders. In conclusion, we do not should ever search for the causes of an observed pattern in the location in which it is visible, detectable or produced. The truth is out there.

Acknowledgements

REFERENCES

Allee, W.C., 1938. The Social Life of Animals. Norton.
Amarasekare, P., 1998. Allee effects in metapopulation dynamics. Am. Nat. 152, 298–302.
Bessa-Gomes, C., Legendre, S., Clobert, J., 2004. Allee effects, mating systems and the extinction risk in population with two sexes. Ecol. Lett. 7, 802–812.
Both, C., 1998. Density dependence of clutch size: habitat heterogeneity or individual adjustment? J. Anim. Ecol. 67, 659–666.
Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect. Trends Ecol. Evol. 14, 405–410.
Dennis, B., 1989. Allee effects: population growth, critical density and the chance of extinction. Nat. Res. Model. 3, 481–538.
Dennis, B., 2002. Allee effects in stochastic populations. Oikos 96, 389–401.
Emlen, J.M., Freeman, D.C., Kirchhoff, M.D., Alados, C.L., Escos, J., Duda, J., 2003. Fitting population models from field data. Ecol. Model. 162, 119–143.
Engen, S., Lande, R., Sæther, B.-E., 2003. Demographic stochasticity and Allee effect in population with two sexes. Ecology 84, 2378–2386.
Ferrer, M., Donázar, J.A., 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. Ecology 77, 69–74.
Ferrer, M., 2001. The Spanish Imperial Eagle. Lynx Ed., Madrid.
Ferrer, M., Penteriani, V., 2003. A process of pair formation leading to assortative mating: passive age-assortative mating by habitat heterogeneity. Anim. Behav. 66, 137–143.
Ferrer, M., Otalora, F., García-Ruiz, M., 2004. Density-dependent age of first reproduction as a buffer affecting persistence of small populations. Ecol. Appl. 14, 616–624.

Ferrer, M., Newton, I., Casado, E., 2006. How to test different density-dependent fecundity hypotheses in an increasing or stable population. J. Anim. Ecol. 75, 111–117.

Grimm, V., 2002. Visual debugging: a way of analyzing, understanding, and communicating bottom-up simulation models in ecology. Nat. Res. Model. 15, 23–38.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huseg, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent based models. Ecol. Model. 198, 115–126.

Henle, K., Sarre, S., Wiegand, K., 2004. The role of density regulation in extinction processes and population viability analysis. Biodiv. Conserv. 13, 9–52.

Krüger, O., Lindström, J., 2001. Habitat heterogeneity affects population growth in goshawk *Accipiter gentilis*. J. Anim. Ecol. 70, 173–181.

Lande, R., 1988. Genetics and demography in biological conservation. Science 241, 1455–1460.

Lande, R., Engen, S., Sæther, B.-E., 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, Oxford.

Liberatori, F., Penteriani, V., 2001. A long-term analysis of the declining population of the Egyptian vulture in the Italian peninsula: distribution, habitat preference, productivity and conservation implications. Biol. Conserv. 101, 381–389.

McCarthy, M.A., 1997. The Allee effect, finding mates and theoretical models. Ecol. Model. 103, 99–102.

Møller, A.P., Legendre, S., 2001. Allee effect, sexual selection and demographic stochasticity. Oikos 92, 27–34.

Penteriani, V., Delgado, M.M., Gallardo, M., Ferrer, M., 2004. Spatial heterogeneity and structure of bird populations: a case example with the eagle owl. Popul. Ecol. 46, 185–192.

Penteriani, V., Otalora, F., Sergio, F., Ferrer, M., 2005a. Environmental stochasticity in dispersal areas can explain the "mysterious" disappearance of breeding populations. Proc. R. Soc. Lond. B 272, 1265–1269.

Penteriani, V., Otalora, F., Ferrer, M., 2005b. Floater survival affects population persistence. The role of prey availability and environmental stochasticity. Oikos 108, 523–534.

Penteriani, V., Otalora, F., Ferrer, M., 2006. Floater dynamics can explain positive patterns of density-dependence fecundity in animal populations. Am. Nat. 168, 697–703.

Rodenhouse, N.L., Sherry, T.W., Holmes, R.T., 1997. Site-dependent regulation of population size: a new synthesis. Ecology 78, 2025–2042.

Sergio, F., Newton, I., 2003. Occupancy as a measure of territory quality. J. Anim. Ecol. 72, 857–865.

Serrano, D., Oro, D., Ursúa, E., Tella, J.L., 2005. Colony size selection determines adult survival and dispersal preferences: Allee effect in a colonial bird. Am. Nat. 166, E22–E31.

Stephens, P.A., Sutherland, W.J., 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol. Evol. 14, 401–405.

Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect? Oikos 87, 185–190.