



The decline of the grey partridge in Europe: comparing demographies in traditional and modern agricultural landscapes

Giulio A. De Leo^{a,*}, Stefano Focardi^b, Marino Gatto^c, Isabella M. Cattadori^d

^a Dipartimento di Scienze Ambientali, Università degli Studi di Parma, Parco Area delle Scienze 33A, Parma 43100, Italy

^b Istituto Nazionale per la Fauna Selvatica, Bologna, Italy

^c Dipartimento di Elettronica e Informazione, Politecnico di Milano, Milano, Italy

^d Department of Biology, Mueller Lab, Penn State University, University Park, PA 16802, USA

Received 17 July 2002; received in revised form 10 November 2003; accepted 23 November 2003

Abstract

Count data were collected from available studies on the European grey partridge (*Perdix perdix*) populations with at least 3 years of consecutive data. According to habitat characteristics, the period of study and the management practice the data were combined in two main subsets: the British populations from 1930 to the end of the 1960's and the "declining" continental populations from 1970 to the present. The latter populations are located in areas where the traditional landscape has been severely modified by important changes in agricultural practices. The goal of this work is: (a) to compare demographies of the two sets of populations; (b) to design and calibrate a stochastic demographic model on the basis of available data; (c) to use it to assess the risk of extinction under different management alternatives; (d) to test some of the most credited hypotheses on the grey partridge decline. Population dynamics are investigated via regression analyses of different factors on demographic rates. Spring-to-summer rate of increase and autumn to winter survival are shown to be density dependent in both UK and continental populations. Over-winter losses in UK prior to 1970 are positively correlated with the young-to-adult ratio, suggesting an important role of dispersal. Reproduction and survival rates were systematically larger in the traditional UK populations. Based on the regressions, stochastic demographic models were then built to assess the probability of extinction under various harvesting and management conditions, and the possibility of developing conservative hunting strategies. The stochastic modelling confirms that the UK populations prior to 1970 were intrinsically much more resilient than the continental populations in recent decades. Even very low rate of harvesting cannot be tolerated by the present continental populations, suggesting that the persistence of hunting activity, although with a limited effort, has probably contributed to the extinction of many sub-populations and is critically threatening the remaining ones. We show that the introduction of stochasticity into the model is fundamental for assessing the real extinction risk for partridge populations under different management scenarios. The comparison of UK and continental demographies does not provide evidence of a single main bottleneck for the continental populations, but the viability of continental populations is endangered by the concurrent deterioration of reproduction and survival rates.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Density dependence; Dispersal; Extinction risk; Harvesting; Stochastic demographic models; Population viability analysis; *Perdix perdix*

* Corresponding author. Tel.: +39-0521-905619; fax: +39-0521-905402.

E-mail address: deleo@dsa.unipr.it (G.A. De Leo).

¹ Agenzia Regionale per la Protezione dell'Ambiente della Lombardia, Via Restelli 1, Milano 20124, Italy.

1. Introduction

Stochastic simulations have proven to be a very effective tool to analyse the probability of persistence and the projected range of population abundance under different management scenarios (Possingham et al., 1993; Beissinger and Westphal, 1998). This technique, commonly known as population viability analysis (PVA; Boyce, 1992), has been successfully used in ecological studies concerning extinction risk assessment of several bird species such as orange-bellied parrot (*Neophema Chrysogaster*) (Drechsler et al., 1998), spotted owl (*Strix occidentalis*) (Lamberson et al., 1992), helmeted honeyeater (*Lichenostomus melanops cassidix*) (McCarthy, 1996; Akçakaya et al., 1995), great tit (*Parus major*) (Sæther et al., 1998), Hawaiian stilt (*Himantopus mexicanus knudseni*) (Reed et al., 1998) and capercaillie (*Tetrao urogallus*) (Marshall and Edward-Jones, 1998).

On the other hand, the outcome of these stochastic analyses can be strongly affected by the specific assumptions made on model parameters and model structure (Todd et al., 2001). Kangas and Kurki (2000), for instance, have shown that the results of PVA of the capercaillie *Tetrao urogallus* in different regions in Finland can drastically change if density dependence in adult and juvenile mortality rate is included or, conversely, not accounted for-in the model. Similar conclusions have been previously derived in general terms by Ginzburg et al. (1990) and for the grizzly bear by Mills et al. (1996).

The problem of parameter estimation and model structure is exacerbated by the fact that ecological analysis at all levels is usually plagued by lack of reliable data. This is particularly true in conservation biology, as models of population viability analysis are usually derived for rare or endangered species that often characterized by a substantial lack of field data to estimate the basic vital rates or a lack of comprehensive knowledge of the species basic ecology (Todd et al., 2001). As a consequence, even for species that have attracted remarkable attention (Kangas and Kurki, 2000), researchers have to conduct viability studies by performing stochastic analyses on the basis of a-priori assumptions or even best-guess trials on the expected value and variance of otherwise unknown demographic parameters (Ferson et al., 1989; Mangel and Switzer, 1998). The use of

powerful, user-friendly and cost-effective software such as ALEX (Possingham and Davies, 1995) or VORTEX (Lacy, 2000) strongly simplifies the numerical approach to risk assessment thus encouraging the user to overparameterize the model with respect to available data and thus to formulate a number of a-priori assumptions on the magnitude of unknown parameters and the shape of their probability distributions (Marshall and Edward-Jones, 1998; Bearlin et al., 1999). While the pressure for answers and the urgency to implement conservation measures for endangered species usually leaves the applied ecologist with no other alternatives to this practical approach-as extensive field experiments are costly, require skilled workers and rarely produce significant results in the short run, scenario analyses based on weak assumptions eventually cast doubts on the effectiveness and usefulness of PVA studies (Harcourt, 1995; Brook et al., 1997; Vucetich and Waite, 1998). In these cases, sensitivity analysis needs to be performed with respect to uncertain parameters and model structure (Lindenmayer and Lacy, 2002; Lindenmayer et al., 2003) as advocated by Reed et al. (1998); Kangas and Kurki (2000) and Todd et al. (2001).

In this work, we present a PVA of the grey partridge (*Perdix perdix* L. 1758) in which the possibility for density dependence and for correlations between vital rates has been carefully tested on available data. We show that, by keeping model structure simple enough, as recommended by Vucetich and Waite (1998), there is no need for making unsupported assumptions on parameter values and on their functional dependency and, thus, all demographic parameters and their variances can be strictly estimated from available data. Therefore, as our data driven approach allows us to explicitly include uncertainty in parameter estimation due to environmental noise or errors in data sampling (Parysow and Tazik, 2002), the demographic projections fully reflect the available information embedded in the data gathered in the field.

The grey partridge, a typical game bird of open arable landscapes, is a very interesting species to show the effectiveness of the data driven approach to PVA because of its great conservation relevance. In fact, *P. perdix* was mostly affected, along with a variety of bird species in agricultural ecosystems, by the changes in land use that occurred in the majority of European and North American countries from the 1950s

(Fuller et al., 1995; Baillie et al., 1997; Dobson et al., 1997; Siriwardena et al., 1998; Sotherton, 1998). Grey partridge probably established originally in the Eastern part of the Euro-Mediterranean sub-region and spread into Europe following the diffusion of agriculture (Toso and Cattadori, 1993). After world war II, the European populations underwent an impressive decline, as clearly documented by seminal book (Potts, 1986). As a consequence of a generalised and persistent trend of decreasing abundance in Europe, the grey partridge has been listed among the species with an unfavourable conservation status (Hagemeijer and Blair, 1997).

The causes for population decline are manifold (Rands, 1986; Potts, 1990; Sotherton and Robertson, 1990; Sotherton et al., 1992; Aebischer et al., 1994; Tapper et al., 1996; Borg and Toft, 2000) and can be summarized as follows: (a) reduced availability of chick food supplies, such as caterpillars, plant bugs and beetles, due to increased use of pesticides and herbicides on farmland; (b) loss of suitable nest sites such as hedge bottoms and rough grassland due to agricultural intensification; (c) nest destruction caused by early sowing and other farm machinery operations; (d) reduction in predation control due to the decline in the number of game-keepers. In particular, the modelling of the Sussex population dynamics by Potts (1986) and Potts and Aebischer (1991, 1995) showed that the effect of agrochemicals on partridge density could indeed lead to a quasi-extinction demography in absence of predation control. Recently, (Tompkins et al., 2000a,b) have suggested also a non-mutually exclusive hypothesis: parasite mediated competition between pheasant and grey partridge has probably spread parasites from an increasing numbers of released pheasants, thus contributing to the decline of wild grey partridge populations in the UK in the past 50 years. This phenomenon could have played a synergistic role in reducing UK populations.

The decline of the grey partridge has been even more remarkable in continental Europe. The attempt to prevent the partridge decline by extensive re-stocking was apparently insufficient to reconstruct viable populations—as argued also by Birkan (1977a); Birkan and Damange (1977); Mazzoni della Stella (1990) and Dowell (1991) and no self-sustaining populations are left in Italy (Prigioni et al., 1977; Zacchetti et al., 1989; Cattadori and Zacchetti, 1991;

Mazzoni della Stella and Burrini, 1993). In Eastern Europe, chick mortality was lower than in Britain and Western Europe and agrochemicals might not have affected chick mortality as much as in Britain (Chlewski and Panek, 1988).

Demographic parameters estimated for a number of European populations show a high degree of variation at both spatial and temporal scales (Middleton, 1934; Panek, 1992; Potts and Aebischer, 1995; Aebischer and Potts, 1998). Despite this variability, attempts to model the population dynamics of grey partridge have been based on deterministic models (Potts, 1980, 1986; Panek, 1992; Potts and Aebischer, 1995) with no explicit use of a stochastic simulation procedure (Shaffer, 1981; Akçakaya, 1992; Boyce, 1992; Reed et al., 1998). Deterministic models can describe only population trends of specific areas but do not account for the variability of demographic parameters and the effect of random events. Only recently, Bro et al. (2000) have published a comprehensive demographic study of 10 grey partridge populations in North–Central France explicitly including environmental and demographic stochasticity. Their analysis has shown that even when the Malthusian deterministic model (no density dependence included) predicts a viable population (finite population growth rate greater than 1), the stochastic version of the simulation model predicts a risk of extinction ranging between 5 and 10% over 10 years under the current shooting policy.

The aim of this study, is to investigate the decline of the grey partridge in Europe on the basis of available demographic data. The viability of grey partridge populations will be assessed using fairly simple stochastic models that explicitly account for density dependence and variability in vital rates. The analysis has been performed on published studies on grey partridge population dynamics in Europe and two sets of raw data drawn from the scientific literature have been used to estimate model parameters: the “traditional” British populations between 1930 and 1970 and the “declining” Continental populations from 1970 to 1993. Accordingly, we have developed two stochastic models that have been used to assess:

- (i) the relative importance of the demographic rates characterising the partridge life cycle;
- (ii) their dependence upon partridge density;

- (iii) the probability of extinction under various hunting policies; and
- (iv) the possibility of developing conservative management strategies aimed at increasing survival or reproductive success, or decreasing the harvesting rate.

As recommended by Reed et al. (1998), the model parameters and their variances have been estimated from the two data sets and hence closely reproduce the form of density dependence and the level of dispersal and environmental stochasticity observed in the field. Therefore, our demographic models, strictly calibrated on field data, realistically mimic the dynamics of our populations under different management scenarios (Ludwig, 1999). The results of our analysis are finally compared with the Sussex (Potts and Aebischer, 1995) and French studies (Bro et al., 2000).

2. Materials and methods

2.1. Partridge life cycle and available count data

The grey partridge has been extensively studied in the last 60 years and its life cycle is well assessed. Pair formation usually occurs in February–March. Females lay 15–16 eggs on average and hatching occurs from the beginning of June. Further clutches may be

laid in the event of failure. Nestlings are subject to the highest mortality during the first 3 weeks of life, while hen mortality peaks during incubation. In late summer, young and adults combine together in large winter coveys that will break up in February–March when young birds disperse. Hunting mainly occurs in October and November.

The present study, is based on an extensive survey of published European data on grey partridge. Only censuses based on at least 3 years of consecutive data have been considered in the present study. For UK we have used the following studies: Middleton (1934, 1936, 1937); Jenkins (1961); Blank and Ash (1959); Blank et al. (1967); Potts (1973). For Continental Europe we have used: Panek (1992), and Chlewski and Panek (1988) for Poland; Birkan et al. (1975); Birkan (1985); Birkan (1977b); Serre and Reitz (1989) and Reitz (1992) for France; Montagna and Meriggi (1991) and Mazzoni della Stella and Burrini (1993) for Italy. In a few cases (Middleton, 1934, 1936, 1937; Blank and Ash, 1959; Blank et al., 1967) data of a number of sampling campaigns carried out on the same study area have been combined from different papers. From now on, we will use N^p , N^s , N^a , and N^w to indicate grey partridge density (ind. km⁻²) in spring (February–March), summer (late August), autumn (October–November after hunting) and winter (December–January), respectively (Fig. 1). H will indicate the harvest per unit area (we have assumed

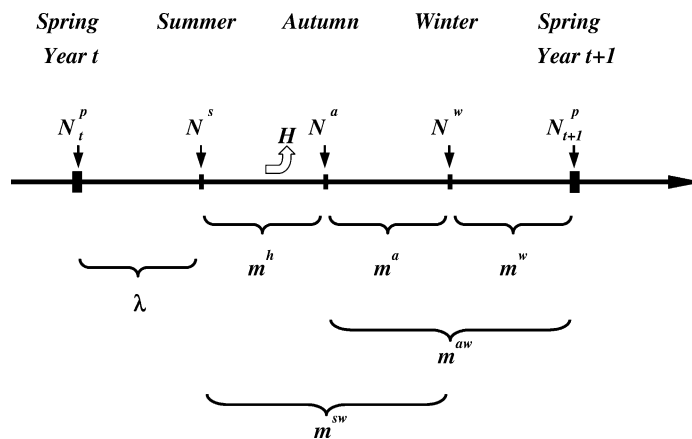


Fig. 1. Graphical description of the main population variables and demographic rates of the grey partridge used in this study. m are mortality rates (fractions of individuals that die in a given season), λ is the spring-to-summer population growth rate, H the number of partridges harvested during the hunting season. The fraction σ^i of individuals surviving during season i ($i = h, a, w, aw$) is equal to $1 - m^i$. See text for further details.

Table 1
Mean partridge densities (ind. km⁻²) and standard deviations in the two datasets

	Continental data set after 1965		UK data set before 1968	
	Mean density ± S.D.	Number of observations	Mean density ± S.D.	Number of observations
N^P	26.3 ± 22.6	84	42.8 ± 29.3	39
N^S	77.0 ± 54.8	60	156.1 ± 68.1	28
N^A	69.4 ± 46.0	64	108.9 ± 47.3	21
N^W	7.2 ± 10.4	5	111.2 ± 19.9	16

Continental densities are always significantly lower than in UK ($P < 0.01$). The UK data set refers to populations of the first half of the century before the use of pesticides and with predation control. In contrast, the continental populations of recent decades have been subject to little predation control and, possibly, to the detrimental effects of agrochemicals.

$N^S - H = N^A$), and (the ratio of young-to-adult birds in summer, when the two age classes are still distinguishable.

Data on partridge density are usually available in spring and autumn and, despite some methodological differences, the census techniques are comparable among different studies. Two rather homogenous subsets were clearly identified in the available data: (1) the UK censuses performed between 1933 and 1968, when partridge populations were still characterised by high density; and (2) the continental data set from France, Poland and Italy in the 1965–1993 period, mostly referring to declining populations. To our knowledge, no published data with 3 years of consecutive counts were available for continental populations before 1965. UK and continental data sets are indeed representative of quite different situations. First, herbicides and pesticides were not intensively used in the first half of the

tal populations were not subject to such a control. The differences between the data sets are apparent from a simple statistical investigation: partridge density in continental populations is significantly lower compared to that in UK before 1968 and continental populations are more variable in size and exhibit larger coefficients of variation (Table 1), which is per se an indicator of populations at a larger risk of extinction (Wright and Hubbel, 1983). Raw data used for the present analysis along with further information on the sampling period and area are reported in Appendix A.

2.2. Demographic parameters

The following demographic parameters have been computed as finite rates from the data reported in the various censuses (see Fig. 1):

$\lambda = N^S/N^P$	Population rate increases between spring and summer counts (λ includes both reproduction and mortality during spring)
$m^h = (N^S - N^A)/N^S$	Hunting mortality, i.e. the fraction of individuals harvested during the hunting season (the number H of harvested partridges is thus $m^h \times N^S$)
$m^a = (N^A - N^W)/N^A$	Autumn mortality
$m^w = (N^W - N_{+1}^P)/N^W$	Winter mortality, migration included (N_{+1}^P is the spring density in the following year)
$m^{aw} = (N^A - N_{+1}^P)/N^A$	Pooled autumn–winter mortality
$m^{sw} = (N^S - N^W)/N^S$	Summer to winter mortality (hunting mortality included)
$\sigma^i = 1 - m^i$	Fraction of individuals surviving during season i ($i = h, a, w, aw$)

century (UK data set), while intensive use of chemicals in agriculture has become a common practice afterward (continental data set). Second, population management was rather different: in UK an effective predation control was performed by game-keepers in the first half of this century, while on the continen-

2.3. Model structure and statistical methodology

The lack of an homogeneous data set is a limit to our demographic analysis. We utilised a demographic model based on four main periods: (i) spring to late summer; (ii) late summer to autumn; (iii) autumn to

beginning of winter; and (iv) beginning of winter to subsequent spring. For the Continental populations a single autumn–winter period was considered (point (iii) and (iv) combined together).

Two main phenomena need to be tested against available data to choose appropriate demographic models:

- (i) whether density dependence occurs at any point of the partridge life cycle;
- (ii) whether the loss of individuals during the winter period is due not only to natural mortality but also to juvenile dispersal.

The class of models used here relates the population N in year t to that in the following year N_{t+1}^p as follows:

UK	
$N_t^s = \lambda_t N_t^p$	Spring-to-summer survival and recruitment
$N_t^a = N_t^s - H_t$	Late summer to early autumn hunting
$N_t^w = \sigma_t^a N_t^a$	Autumn survival
$N_{t+1}^p = \sigma_t^w N_t^w$	Winter survival
Continent	
$N_t^s = \lambda_t N_t^p$	Spring-to-summer survival and recruitment
$N_t^a = N_t^s - H_t$	Late summer to early autumn hunting
$N_{t+1}^p = \sigma_t^{aw} N_t^a$	Autumn–winter survival

where λ_t and σ_t^a can be functions of partridge density in spring and autumn, respectively, while σ_t^w and σ_t^{aw} can be functions also of the young-to-adult partridge ratio ρ , where winter mortality includes juvenile dispersal.

Moreover, if reproduction is very successful, as evidenced by a large λ , we expect to have more young in the population (larger ρ). Therefore, it is reasonable to assume that ρ_t is an increasing function of λ_t . To sum up, the spring-to-summer population growth rate and the autumn-to-winter and winter-to-spring survivals are modelled as follows:

$$\lambda_t = \Delta(N_t^p) \varepsilon_t^p \tag{1.1}$$

$$\rho_t = \Phi(\lambda_t) \varepsilon_t^p \tag{1.2}$$

$$\sigma_t^a = \psi(N_t^a) \varepsilon_t^a \tag{1.3}$$

$$\sigma_t^w = \Gamma^w(N_t^w, \rho_t) \varepsilon_t^w \tag{1.4}$$

$$\sigma_t^{aw} = \Gamma^{aw}(N_t^a, \rho_t) \varepsilon_t^{aw} \tag{1.5}$$

where Δ , Φ , Ψ , Γ^w and Γ^{aw} are decreasing functions of their arguments and the ε 's are uncorrelated random factors that explicitly account for environmental stochasticity. Note that by using the summer ratio ρ we implicitly assume that hunting and natural mortality between summer and winter are not age-selective. Values for ε^p , ε^a , ε^ρ , ε^{aw} and ε^w are drawn according to a distribution function. A log-Normal distribution with unitary median and variance to be estimated from available data is the natural choice and is more appropriate than a Normal distribution since this may imply negative values for λ , ρ and the σ 's. The use of a multiplicative log-Normal noise in population ecology has been assessed on the basis of both empirical observations (Allen, 1973) and theoretical arguments (Walters and Hilborn, 1976) and is considered a standard assumption when testing for density dependence (see Royama, 1992; and Dennis and Taper, 1994 for a comprehensive review of the issue). Note that our model implicitly assumes no compensation between hunting related mortalities and autumn to winter losses, as Ψ and Γ^{aw} depend upon N_t^a only. Also, no compensation is assumed between autumn and winter mortality in UK, as Γ^a depends upon N_t^w and ρ only. Of course, both assumptions on compensation need to be tested against data by performing a correlation analysis.

As for Δ and Ψ we use the general expression (the subscript t will be omitted in the sequel when not necessary):

$$\alpha \exp(-\beta N), \quad \alpha > 0, \quad \beta \geq 0 \tag{2.1}$$

namely, a decreasing exponential function of population density that was first introduced by Ricker (1954) and widely used in demography since then (Dennis and Taper, 1994). This expression allows for a straightforward logarithmic transformation of (1.1) and (1.3) so that α and β and other relevant statistics can be estimated by means of a simple linear regression. A value of β significantly different from zero implies density dependence. The use of other functional forms (such as the Gompertz, suggested by Rotella et al., 1996) does not significantly change the results of the present study.

A similar expression is used for G^w and G^{aw} by assuming that the influence of r is analogous to that of N^w and N^a , respectively, but with a different weight, namely:

$$\Gamma^w(N^w, \rho) = \alpha_{\Gamma} \exp(-\beta_{\Gamma} N^w - \beta_{\rho} \rho) \tag{2.2}$$

$$\Gamma^{aw}(N^a, \rho) = \alpha_{\Gamma} \exp(-\beta_{\Gamma} N^a - \beta_{\rho} \rho) \tag{2.3}$$

we also need to test whether the young-to-adult ratio is related to the population rate of increase λ . The choice of the functional relationship Φ between ρ and λ requires a rather careful argumentation. In fact, given that $\lambda = FS_Y + S_A$, where F is the number of eggs, S_Y the juvenile survival and S_A the adult survival during spring, it is easy to ascertain that:

$$\rho = \frac{FS_Y}{S_A}$$

we reasonably assumed that young and adult survival during spring are affected by the same environmental stochasticity. However, as the young survival is more heavily affected by a bad season than the adult survival, we can hypothesise that S_Y is systematically smaller than S_A . A simple model is thus:

$$S_Y = k(S_A - b)$$

where b is the minimum adult survival corresponding to a vanishing survival of young partridges and k is a positive constant correlating the two survivals. Easy computations yield a hyperbolic relationship of the kind:

$$\Phi(\lambda) = \frac{a(\lambda - b)}{(1 + a)b + \lambda - b} \tag{2.4}$$

with $a = kF$.

When replacing expressions Eq. (2) into Eq. (1), we obtain (after a logarithmic transformation) the following relationships between demographic parameters and partridge densities:

$$\ln \lambda = -\beta_{\Phi} N^p + \ln \alpha_{\Phi} + \ln \varepsilon^p \tag{3.1}$$

$$\ln \rho = \ln \frac{a(\lambda - b)}{(1 + a)b + \lambda - b} + \ln \varepsilon^p \tag{3.2}$$

$$\ln \sigma^a = -\beta_{\Psi} N^a + \ln \alpha_{\Psi} + \ln \varepsilon^a \tag{3.3}$$

$$\ln \sigma^w = -\beta_{\Gamma} N^w - \beta_{\rho} \rho + \ln \alpha_{\Gamma} + \ln \varepsilon^w \tag{3.4}$$

$$\ln \sigma^{aw} = -\beta_{\Gamma} N^a - \beta_{\rho} \rho + \ln \alpha_{\Gamma} + \ln \varepsilon^w \tag{3.5}$$

these relationships must be tested against available data. The assumption of normality for residuals has been verified by means of a Kolmogorov–Smirnov test while predictions errors (which will be used to run Monte Carlo simulations of the demographic models) have been estimated according to Hines and Montgomery (1980). More precisely, if X is the independent variable and $Y = f(X)$, the predicted value y of the dependent variable Y has been computed as follows:

$$y = f(x) + \text{Norm}(0, \theta(x))$$

where $\text{Norm}(0, \theta)$ is a random number drawn from a Normal distribution with null mean and standard deviation equal to θ . $\theta(x)$ has been computed as follows (Hines and Montgomery, 1980):

$$\theta(x) = \text{SEE} \sqrt{1 + \frac{1}{N} + \frac{(x - E(X))^2}{\sum_i (x_i - E(X))^2}}$$

where SEE is the standard error of estimate, n is the number of observations (available data points), x_i is the i -th value of the independent variable ($i = 1, 2, \dots, n$), and $E(X)$ is the expected value of X .

2.4. Simulation of the stochastic model

The population dynamics can be summarised as a diagram in the $N_t^p - N_{t+1}^p$ plane along with the 45° line. The region above the line is characterised by a growing population, as $N_{t+1}^p > N_t^p$, and the region below the line by a decreasing population, as $N_{t+1}^p < N_t^p$. The deterministic model is simply represented by a curve relating partridge density in year t (N_t^p) to partridge density in the following year (N_{t+1}^p), while assuming the random factors ε_t set to one. Of course, any equilibrium point of the deterministic model lies on the intersection of the 45° line with the curve linking spring abundances in subsequent years. In the stochastic setting, to each partridge density N_t^p in year t there corresponds not just a single value in year $t + 1$, but a distribution of densities N_{t+1}^p . The dispersion of predicted partridge densities around the deterministic value is specified by upper and lower boundaries representing the 5th and the 95th percentile of the predicted densities. Percentiles have been computed by means of Monte Carlo simulations, that is, by randomly drawing 5000 values of N_{t+1}^p for any N_t^p .

The stochastic demographic models built on the two data sets are then used to assess extinction probability (Burgman et al., 1993). We run 1000 Monte-Carlo simulations, each 100 year long (Mace, 1994) for both the Continent and UK populations. For most endangered species, a risk of extinction smaller than 5% in 100 years is usually taken as a goal for species preservation from extinction (Seal and Lacy, 1990). To overcome the problems posed by phenomena such as inbreeding, Allee effect and demographic stochasticity, which are not accounted for by our model, the modelling has been performed with reference to quasi-extinction thresholds (Ginzburg et al., 1982): if a population density drops below such a threshold, it is considered extinct (or on the way to extinction) to all effects. When the density is below the threshold, the models here derived are no longer appropriate to describe the dynamics of the population. As partridges in the continent are typically restricted over preserved areas of 2–5 km², a threshold of 2–10 ind. km⁻² corresponds to an overall population of 5–50 individuals, which seems a realistic threshold for quasi-extinction. Since picking up a unique threshold would be highly debatable (Ludwig, 1999), we have computed the likelihood of extinction corresponding to different quasi-extinction thresholds, with simulation times ranging between 5 and 100 years.

3. Results

3.1. Preliminary statistical analysis

We performed *t*-tests to identify any significant difference between the demographic parameters of UK

and Continent subsets (Table 2). Autumn mortality m^a in the Continent populations in recent decades was significantly larger than in the UK populations of the first half of the century, while hunting mortality and spring-to-summer recruitment λ were slightly but significantly smaller. No consistent differences are observed between ρ and m^{aw} of the two data sets.

To investigate if compensation occurred in the autumn–winter period, the effect of hunting on natural mortality m^a was examined. Since the data for the continental populations were insufficient this has been tested for the UK populations only. The analysis showed that natural mortality m^a was not correlated to hunting mortality m^h ($r = 0.075$, $P \gg 0.05$). Moreover, a positive correlation (0.76 , $P \ll 0.01$) was observed between hunting mortality m^h and the overall autumn mortality-computed as m^{SW} (Fig. 1) suggesting that larger overall losses were expected at higher exploitation rate. Thus we concluded that there was no compensation between hunting activity and other sources of autumn–winter mortality. Some form of compensation between autumn mortality m^a and winter mortality m^w could not be ruled out in UK, but the correlation was weak ($r = -0.465$) and non significant ($P = 0.08$).

3.2. Estimation of model parameters

Regressions for λ , ρ , σ^a , σ^{aw} and σ^w given by Eq. (3) have been performed separately for UK and continental data sets (i) to test whether these regressions are indeed significant, (ii) to derive the functional shape of λ , ρ and the σ 's accordingly, and finally (iii) to estimate the variances of the random factors ε^p , ε^a , ε^ρ , and ε^w which have been subsequently used in the

Table 2
Means and standard deviations of the main demographic parameters of UK and Continental partridge populations

	Continent after 1965		UK before 1968		Difference between UK and Continent
	Mean \pm S.D.	Sample size	Mean \pm S.D.	Sample size	
ρ	3.14 \pm 1.6	41	2.73 \pm 1.3	34	n.s.
λ	2.82 \pm 1.4	56	3.56 \pm 1.3	28	*
m^h	14.8% \pm 21.3	51	25.3% \pm 20.6	21	*
m^a	80.9% \pm 27.6	5	11.1% \pm 14.2	16	**
m^w	–	–	39.4% \pm 12.3	15	–
m^{aw}	58.4% \pm 21.3	49	50.8% \pm 14.3	18	n.s.

A *t*-test was used to assess the significance of the difference between the means of the two data sets; n.s.: $P > 0.05$.

* $0.01 < P \leq 0.05$.

** $P \leq 0.001$.

Table 3

Results of regression between the main demographic parameters and partridge densities or young-to-adult ratio in the two data sets

Regression	Continent after 1965	UK before 1968
$\ln \lambda$ vs. N^P	$-0.00735 \pm 0.0026^{**}$ (d.f. = 49)	$-0.0118 \pm 0.002^{**}$ (d.f. = 26)
$\ln \rho$ vs. $\lambda^{(a)}$	n.s.	$a = 33.42 \pm 16.30^*$ $b = 0.885 \pm 0.036^{**}$ (d.f. = 20)
$\ln \sigma^a$ vs. N^a	n.s.	$-0.003 \pm 0.0011^{**}$ (d.f. = 19)
$\ln \sigma^w$ vs. N^w	No data available	n.s.
$\ln \sigma^w$ vs. ρ	No data available	$-0.175 \pm 0.056^*$ (d.f. = 8)
$\ln \sigma^{aw}$ vs. N^a	$-0.002 \pm 0.001^*$ (d.f. = 55)	n.s.
$\ln \sigma^{aw}$ vs. ρ	n.s.	n.s.

When significant, the regression coefficient β of Eq. (3) is reported along with its standard deviation and the degrees of freedom; n.s.: $P > 0.05$.

* $0.01 < P \leq 0.05$.

** $P \leq 0.01$.

^a Non-linear regression.

stochastic models. Results are reported in Table 3. The most interesting findings are summarised in Fig. 2. Population rate of increase λ decreases as density increases in both UK (Table 3, Fig. 2a) and Continental populations (Table 3, Fig. 2b). Moreover, for any density N^P , λ is systematically larger in UK in the first half of the century than in the Continent in recent decades (Fig. 2a and b). The regressions $\lambda - \ln \rho$ and $N^a - \ln \sigma^a$ are statistically significant only when tested on the UK data set. Winter survival σ^w depends on ρ only for UK (Fig. 2c), while in the continental case σ^{aw} depends on N^a only but not on ρ . Tests on residuals show that the normality assumption for $\ln \varepsilon$ is indeed valid. The resulting stochastic models for the two data sets and the parameter values are reported in the Appendix B.

3.3. Simulation of the stochastic model

The main dynamic properties of both the stochastic and the deterministic version of the model (i.e., with no variance of the demographic parameters) are reported in Fig. 3; the degree of dispersion around the deterministic values is indicated through the 5th and 95th percentile boundaries.

For the UK populations in the first half of the century there was a nontrivial stable equilibrium at $N^P = 93.9 \text{ ind. km}^{-2}$ (Fig. 3a). When stochasticity

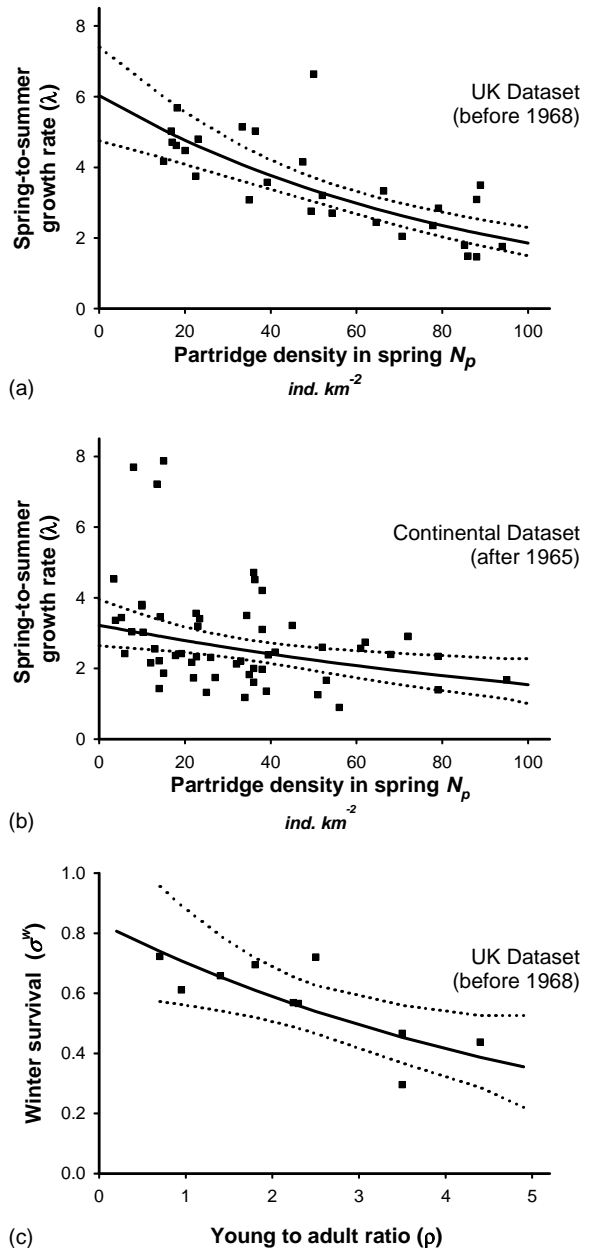


Fig. 2. (a) Spring-to-summer rate of increase as a function of partridge density in spring for UK populations; (b) same for continental population; (c) relationship between winter survival and young-to-adult ratio in UK. Black squares represent field data, while the solid line is the result of regression (see also Table 3). The dotted lines show the 95% confidence intervals for the regression.

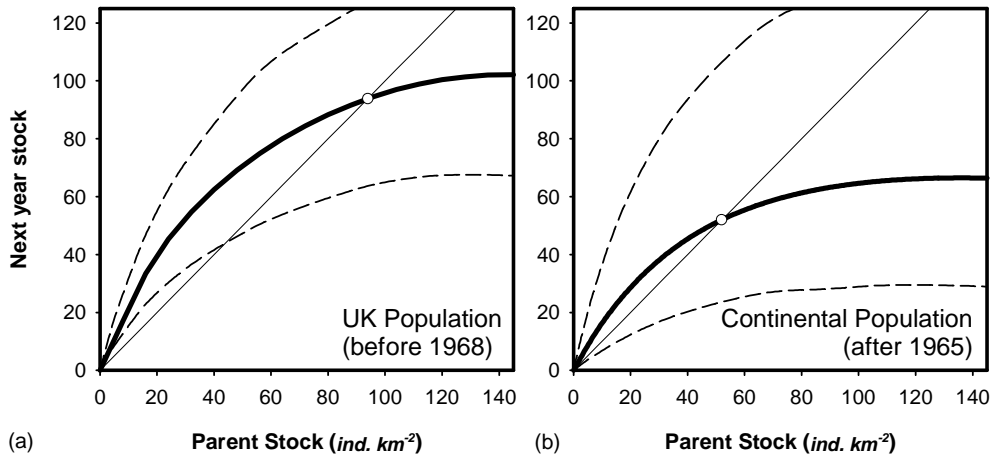


Fig. 3. Relationship between the partridge spring populations in two subsequent years for UK (a) and continental Europe (b). The solid line represents the deterministic model and gives N_{t+1}^p as a function of N_t^p . The dashed lines represent the 5th and 95th percentiles of the resulting stock as predicted from the parental stock via the stochastic model. The 45° line divides the plane in two regions: the upper region is characterised by a growing population, as $N_{t+1}^p > N_t^p$, the lower one by a decreasing population, as $N_{t+1}^p < N_t^p$. Circles indicate stable equilibria for the deterministic model.

was not included, the population could have sustained a maximum yield of 73.35 ind. km⁻², obtained by harvesting 47% of the autumn population. The stochastic formulation of the model shows that the non-harvested population used to have a negligible probability of ending up in the declining region when $N_t^p < 40$ ind. km⁻², while chances would increase at larger densities.

The graphic representation of the model for the continental populations in recent decades is reported in Fig. 3b. The deterministic model has a non-trivial equilibrium at a density considerably lower than in the UK populations, namely $N^p = 52$ ind. km⁻². Compared to the UK case, a substantially smaller fraction of the autumn population (that is, 28%) could be sustainably harvested every year to maximise the yield (8.7 ind. km⁻²) with no random fluctuations included. Even though the equilibrium point of the deterministic model is stable, environmental stochasticity has produced a great impact on the demography of the continental populations: as shown in Fig. 3, the dispersion of year-to-year density N_{t+1}^p resulting from a given parental stock N_t^p is very large (coefficient of variation 50% in the average, versus 20% for UK). As the 5th percentile boundary is well below the 45° line (where $N_{t+1}^p < N_t^p$), there is a substantial probability that the continental population decreases to low den-

sity values, as also observed by Bro et al. (2000) for 10 grey partridge populations in France.

Not surprisingly, UK populations before 1968 and continental populations after 1965 are characterised by quite different extinction probabilities, as shown in Fig. 4. This figure reports the interval extinction risk for different harvesting rates, namely the probability that partridge density falls below a given threshold at least once during the simulation time (Ginzburg et al., 1982). Our analysis suggests that with no hunting activity the extinction probability in UK, under the conditions in which these populations were faring in the first half of the century before the intensive use of agrochemicals and with predation control, would be practically negligible even if the extinction threshold were assumed to be as high as 25 birds km⁻². On the contrary, Continental populations are characterised by high extinction probabilities even for low thresholds and no harvesting activity. There is a 5% extinction risk for a threshold density as small as 5.5 ind. km⁻². The threshold corresponding to the same extinction probability in UK is remarkably larger, namely 39 ind. km⁻².

The effect of harvesting is obviously quite different for UK and continental populations (Fig. 4). The UK population, could have endured substantial harvesting rates. Even with a harvesting rate set to 47%, so as

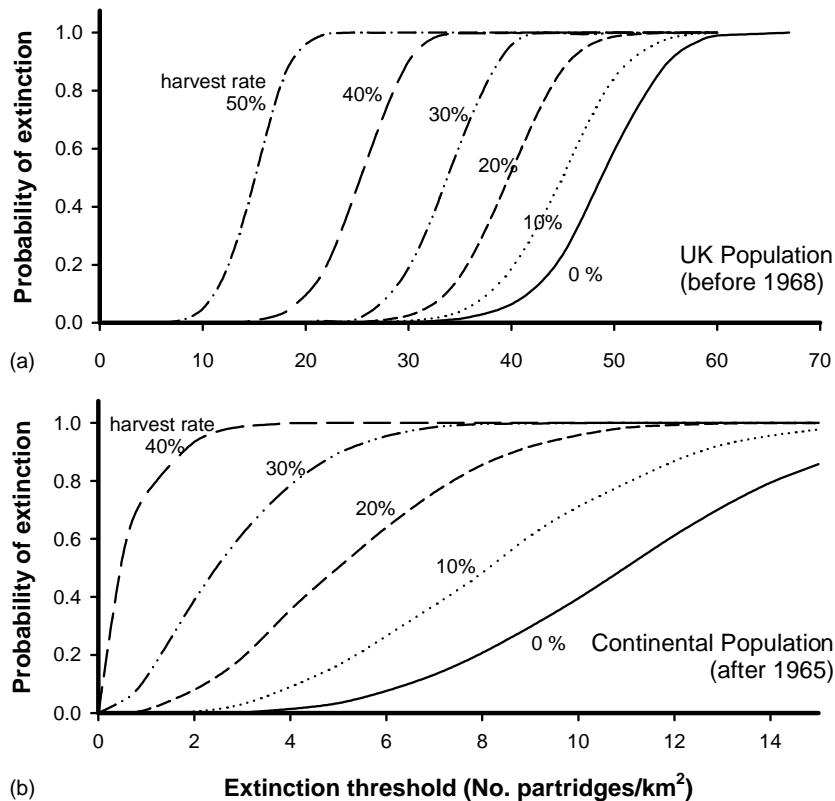


Fig. 4. Interval extinction risks, for a protected population and five levels of harvesting rate, evaluated as a function of quasi-extinction threshold for the UK (a) and continental populations (b). Probabilities have been estimated from 100 year simulations, replicated 1000 times.

to maximise the deterministic yield, extinction probability does not exceed 5% even for thresholds as high as 13 ind. km⁻². On the contrary, the effect of hunting on the fragile continental populations may be dramatic: a 30% harvesting rate (which is slightly more than that required to maximise the autumn harvest in the deterministic case) would extinguish the population in 100 years with probability one for a threshold of 8 ind. km⁻², while a harvest as small as 10% of the total population caused a 5% likelihood of pushing the population below 3.2 ind. km⁻².

The probability of extinction as a function of time in the continental case is reported in Fig. 5 for three different thresholds 2, 5 and 10 ind. km⁻², respectively, and two harvesting policies—a prudent hunting rate (15%, Fig. 5a), and an intensive hunting rate (30%, Fig. 5b). The extinction probability quickly increased with time for high threshold densities (i.e., 10 ind. km⁻²), however an intensive harvest would se-

riously threaten the viability of the population also for a quasi-extinction threshold as low as 2 ind. km⁻² (Fig. 5b). As the probability of a 90% decline over 50 years (from 52 to 5 ind. km⁻²) exceeds 30% when one third of the autumn population is harvested (Fig. 5b, extinction threshold = 5), the population can be classified as *critically endangered* according to Akçakaya (1992). Even for hunting rates as low as 15%, the population is still vulnerable, as the probability of a 90% decline is about 13% over 50 years (Fig. 5a).

When the replicates in the continental populations declined below a given quasi-extinction threshold, we have computed the first-passage-time, i.e., the first year when the population drops below that threshold (Fig. 6). By increasing the harvesting rate from 0 to 30% the mean time for the population to drop below 5 ind. km⁻² would decrease from 55 years (with a 5% likelihood of decline) to 37 years (with a 90% likelihood of decline).

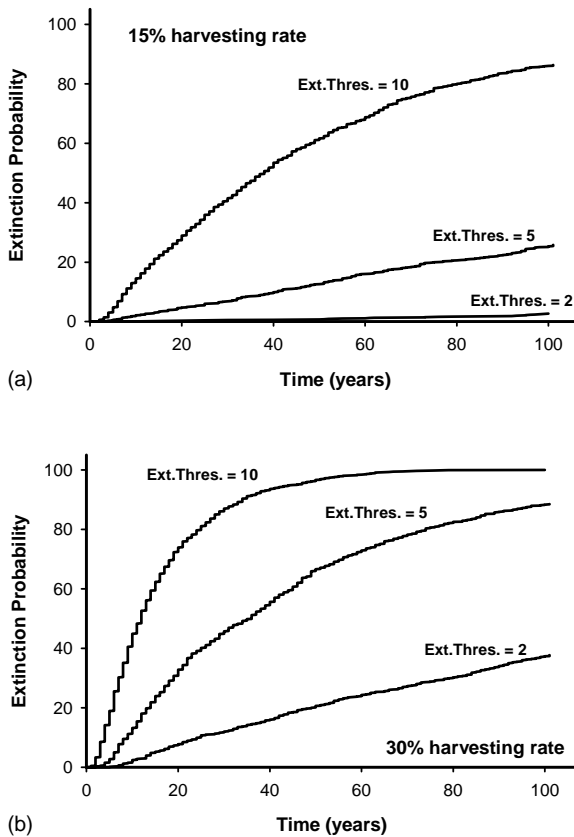


Fig. 5. Likelihood of extinction for the continental populations as a function of time elapsed from the beginning of the simulation, for three threshold densities and a 15% (a) and 30% (b) harvesting rate. Probabilities have been estimated from 100 year runs of the stochastic model, replicated 1000 times.

4. Discussion

Recent advances on bird conservation in Europe clearly pointed out that modification in the agricultural landscape is one of the most relevant causes of declining bird numbers in Europe (Tucker and Heath, 1994; Sotherton, 1998). Nearly 60% of the species in agricultural landscapes declined and their distribution contracted. The grey partridge is one of the main lowland species that exhibited this pattern. Our comparison between UK and continental populations using a stochastic model showed quantitatively that the process seems to evolve towards a non-return direction. Year-to-year variation of partridge density in UK between 1933 and 1968, as predicted by the stochastic

model, is substantially smaller than in the populations of the Continent in the recent decades, namely 20% in the average versus 50%. Accordingly, we estimated that, given the demography prevailing at that time, the UK population had an almost negligible probability of dropping below 10 ind. km⁻². As well, a harvest rate as high as 50% was still sustainable. In contrast, the present continental populations cannot tolerate even very small harvests. Thus, the persistence of the hunting activity, although with a reduced effort, may have contributed to the extinction of many sub-populations and is critically threatening the remaining ones (Potts, 1986). In fact, the likelihood of dropping below 5 ind. km⁻², a realistic quasi-extinction threshold for fragmented populations, is dramatically high even under a low hunting pressure. The problem of harvesting is compounded by the fact that no compensation between hunting and autumn–winter mortality seems to be present in the grey partridge.

Over-winter survival significantly decreased in UK with increasing young-to-adult ratio, and this suggests that dispersal may play an important role when hunting reserves are small or the suitable habitat is fragmented and populations are hardly connected. Unfortunately, quantitative data about dispersal are rather scant and an explicit incorporation of dispersal in our demographic model was not possible (see Aufradet and Birkan, 2001 for continental populations and Jenkins, 1961; Potts, 1986; Reynolds et al., 1991 for UK populations).

The comparison of UK and continental demographies did not show a single main bottleneck for the continental populations. A concurrent reduction in the reproduction and in the spring-to-summer survival and autumn survival is probably the cause of the decline of continental partridges, as also suggested by Potts (1980) for the Sussex populations and by Rotella et al. (1996) for US populations. In fact, by running further simulations, we have found that if the continental model is modified by replacing the spring-to-summer rate of increase or spring-to-summer survival or autumn survival with the corresponding UK parameter (along with its density dependences), the viability of continental populations would in any case substantially increase. Our simulations show that, by implementing any of these modifications, continental populations could potentially reach densities quite close to those recorded in UK before the starting of

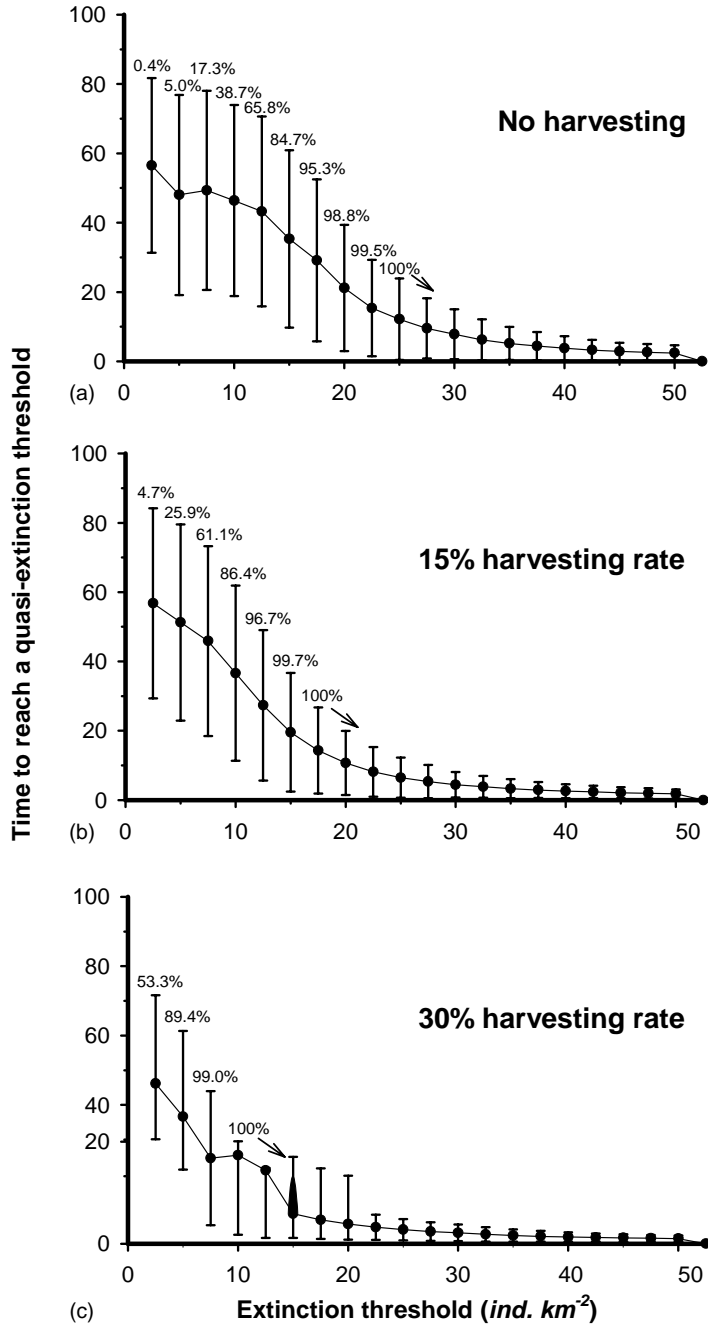


Fig. 6. Average time (computed from 1000 replicates of a 100 year simulation) to fall below a quasi-extinction threshold density for three different harvesting rates in the continental populations. Standard deviations are represented by error bars, while the percentages reported above the bar are the probabilities of dropping below each threshold.

the widespread decline. Nevertheless, as suggested by Bro et al. (2000), safe conservation strategies should be aimed at improving more than one demographic parameter.

Our analysis is also relevant to the decline of UK populations in recent decades, although the UK data we used come from studies prior to the start of this decline. Potts and Aebischer (1995) reported that a 33% reduction of chick survival as a consequence of herbicide use and lack of nest predation control should be sufficient to explain such a decline. We have incorporated these hypotheses in our UK model and run the simulation. These further simulations showed that even a 50% reduction of spring-to-summer rate of increase λ could decrease the population at the deterministic equilibrium from 93.9 to 69.2 ind. km⁻² however, the probability for the population to drop below a threshold as high as 20 ind. km⁻² was still negligible. Thus, we are inclined to believe that herbicide use and lack of nest predation control are undoubtedly the main causes of population decline in UK, but alone may be insufficient to fully explain this trend. Quite likely, all the rest being equal, the density dependent feedbacks operating during autumn and winter should be sufficient for the population to compensate, at least partially, for the increase of chick mortality. As already pointed out, changes in landscape and specifically the loss of over-wintered stubbles and nest sites (such as hedge bottoms and rough grassland) caused by a agricultural intensification, early mowing and other machinery operations may also have played an important role. Moreover, field experiments and modelling approaches have demonstrated that when grey partridge and pheasant in the same location are infected by the parasite *Heterakis gallinarum*, the impact of the parasite will be sufficient to cause the exclusion of the grey partridge population but not of the pheasant one (Tompkins et al., 2000a,b). The pheasant maintain the parasite in the system and indirectly compete, via the parasite, with the grey partridge. Thus, the UK grey partridge decline observed in the last 50 years and a possible explanation to our results may be partly due to the apparent competition with pheasant (Tompkins et al., 2000b).

Our results on the UK populations are consistent with the findings by Bro et al. (2000) for French populations, the only one risk analysis so far performed on the grey partridge in a truly stochastic framework.

They showed that only a simultaneous decrease of over-winter survival rate, hen survival rate, hatching of first clutches and chick survival rate would produce an unsustainable population.

In contrast to Bro et al. (2000) formulation, our model explicitly includes a density dependence in some demographic parameters. The data gathered by Bro et al. (2000) did not provide evidence of significant density-dependencies in model parameters-with the exception of shooting pressure, whose dependence upon density, anyway, was not included in their final model-while we have detected such dependencies in our dataset for various model parameters. This difference can be explained by the fact that density dependent phenomena do not occur at the low densities experienced by the populations analysed by Bro et al. (2000). In our study, while density-dependencies were recorded also in the low density continental populations, a more clear and significant pattern was observed in the high density UK populations.

Our analysis is not exempt from criticism. In particular, we were conscious that combining data from different European populations inhabiting different areas and in different years could produce confounding effects (Lebreton and Clobert, 1991). Yet, the choice of considering no more than two data sets in this study was constrained by the availability of reliable data: indeed, we have tried to perform a detailed analysis on single, isolated populations, as done by Bro et al. (2000) for the French populations, but the paucity of data prevented us from obtaining significant and reliable estimates of all the demographic rates for the full life cycle. Thus, we pooled the data in two sets that exhibited some degree of homogeneity and in general sufficient information on how the demographic rates respond to density. The aim of this study was to investigate the grey partridge decline at a large scale and to single out the main and most common mechanisms causing this dramatic decrease in abundance. Our models were not designed to explain the dynamics of each single population and thus, we are not able to explain in detail for which specific reason (limited use of chemicals in agriculture? limited habitat alteration? efficient predation control? low anthropogenic disturbance during breeding season? all of them?) there are still some cases of self-sustaining populations in continental Europe (Reitz, 1992). As Potts and Aebischer (1995) have already stressed, fur-

ther investigation and field analyses are needed in this area.

Despite these reservations, we are confident that our models, calibrated rigorously on field observations, are a useful and effective tool for analysing the causes of the grey partridge decline and investigating the impact of different harvesting scenarios (Ludwig, 1999). Some variability obtained by pulling together data from different continental populations has allowed us to estimate the dependence of vital rates upon a sufficiently wide range of partridge density.

With respect to other risk analyses based on untested assumptions on model parameters or on values of demographics rates simply pulled together from different published studies (Mangel and Switzer, 1998; Marshall and Edward-Jones, 1998; Bearlin et al., 1999; McKenna, 2000), our model has been tightly calibrated on available data thus reflecting the type of variability observed in the field. This data-driven modelling approach allows an increase of prediction power with respect to more general and user-friendly computer packages for population viability analysis, such as VORTEX (Lacy, 2000) or RAMAS (Lindenmayer et al., 1995). The advantages provided by the great generality of such computer software, namely the possibility to quickly analyse a broad range of scenarios by using user-friendly and cost-effective software tools that require no computer programming skill and very little modelling expertise, may be counterbalanced by the reduction in flexibility to closely match the structure of the model and, hence, the input parameters it requires with the actual data gathered in the field (Lindenmayer et al., 2000). In our case, the assumptions on the specific functional form of survival or fertility or young-to-adult ratio and on the relationship between model parameters has not been confined to a fixed set provided by the computer package. As discussed in Ginzburg et al. (1990) and Kangas and Kurki (2000), the use of well tuned demographic models substantially improves the understanding of the crucial role of density dependent factors and how they interact among themselves and with density independent factors. We have shown here that the effect of these density dependent and independent mechanisms is not always straightforward and often the outcome can be predicted only through numerical simulation. This is particularly important because, as reported by Potts and Aebischer

(1995), less than 2% of scientific papers relating to game bird research make use of models that are at all realistic.

The stochastic approach utilised in this study represents a further improvement with respect to the deterministic models that were used in previous studies (Potts, 1986; Panek, 1992; Potts and Aebischer, 1995). The introduction of stochasticity is not a mere theoretical and mathematical embellishment, but is fundamental for assessing the real extinction risk for partridge populations. This is especially true for continental populations, for which the deterministic model would lead to unreliable results, because it would predict a stable positive equilibrium whereas the stochastic model shows that extinction is very likely to occur. In addition, the model is an effective instrument that can be used by wildlife managers to assess the likelihood of success of various policies, such as re-stocking, habitat restoration and shooting plans. We can easily calculate the extinction risk as well as other management parameters (average harvest, expected time of recovery to a specified density, etc.) under the assumption that managers can monitor fluctuations in vital rates and act to modify those demographic parameters that we have shown to be critical for population viability.

Acknowledgements

The authors are grateful to Andy Dobson, Peter Hudson and Mike Crawley for their valuable suggestions on a first draft of this work. The study was partially supported by Istituto di Ingegneria Biomedica, CNR, Milano.

Appendix A. The database

The Tables A.1 and A.2 are shown below.

Appendix B. The Demographic models

As a result of the statistical analysis, the model describing the dynamics of the grey partridge population in UK is given by the equations:

$$(i) N_t^S = \lambda_t N_t^P$$

Table A.1
Data used in the analysis

Country	Area	Year	Surface (ha)	N^P	h	N^S	N^A	N^W	r
I	1	84	2400	12.00	0.00	0.00	0.00	0.00	0.00
I	1	85	2400	6.00	0.00	0.00	0.00	0.00	0.00
I	1	86	2400	13.00	0.00	33.20	45.20	0.00	2.70
I	1	87	2400	10.00	0.00	38.10	16.90	13.60	3.10
I	1	88	2400	10.00	0.00	37.70	30.20	22.60	0.00
I	1	89	2400	15.00	0.00	0.00	0.00	0.00	0.00
I	1	90	2400	4.00	0.00	0.00	3.60	0.00	2.10
I	1	93	2400	1.00	0.00	0.00	0.00	0.00	0.00
I	2	84	9500	5.20	0.00	17.90			4.30
I	2	85	9500	3.80	0.00	12.80			3.15
I	2	86	9500	3.40	0.00	15.40			6.20
I	3	87	175		0.00		17.10		
I	3	88	175	9.20	0.00		11.40		3.00
I	3	89	175	4.60	0.00		5.70		3.10
I	3	90	175	3.40	0.00		5.10		1.90
I	4	87	380	0.00	3.00	2.90	0.00	0.00	0.00
I	4	88	380	0.00	8.00	10.80	0.00	0.00	0.00
I	4	89	380	0.00	8.00	12.90	0.00	0.00	0.00
PL	5	65	610		0.00		24.90		
PL	5	66	610	8.00	0.00		49.60		
PL	5	67	610	33.00	0.00		37.20		
PL	5	68	610	17.80	0.00	42.10	31.30		3.30
PL	5	69	610	23.40	0.00	79.80	47.70		4.10
PL	5	70	610	8.00	0.00	61.60	16.40		4.40
PL	5	71	610	13.50	0.00	97.50	43.40		4.90
PL	5	72	610	15.00	0.00	118.20	47.70		5.10
PL	5	73	610	23.00	0.00	73.60	44.20		4.40
PL	5	74	610	28.00	0.00		63.80		
PL	5	75	610	35.00	7.00	63.80	52.50		3.30
PL	5	76	610	25.00	3.00	33.00	16.70		1.40
PL	5	77	610	12.00	0.00	25.90	9.10		1.20
PL	5	78	610	4.00	0.00				
PL	5	79	610	3.00	0.00				
PL	5	80	610	2.30	0.00				
PL	5	81	610	2.10	0.00				
PL	5	82	610	1.80	0.00				
PL	5	83	610	2.60	0.00				
PL	5	84	610	3.30	0.00				
PL	5	85	610	4.50	0.00				
PL	13	87	1010	6.00		14.50	11.50		
PL	13	88	1010	7.60		23.10	15.30		
PL	13	89	1010	10.20		30.90	25.40		
PL	13	90	1010	15.30					
PL	14	87	870	14.20		49.20	37.50		
PL	14	88	870	22.60		80.50	62.10		
PL	14	89	870	39.40		93.90	68.30		
PL	14	90	870	41.00					
PL	15	87	800	22.70		52.80	40.50		
PL	15	88	800	19.20		46.40	32.90		
PL	15	89	800	21.60		46.90	35.50		
PL	15	90	800	19.90					
F	6	69	380	79.00	14.00	185.00	171.00		
F	6	70	380	68.00	39.00	163.00	124.00		

Table A.1 (Continued)

Country	Area	Year	Surface (ha)	N^P	h	N^S	N^A	N^W	r
F	6	71	380	52.00	54.00	135.00	81.00		
F	6	72	380	45.00	26.00	145.00	119.00		
F	6	73	380	61.00	46.00	157.00	111.00		
F	6	74	380	72.00	38.00	209.00	171.00		
F	6	75	380	72.00	69.00	209.00	140.00		
F	6	76	380	83.00					
F	6	77	380	95.00	5.00	159.00	154.00		
F	6	78	380	79.00	2.00	110.00	108.00		
F	6	79	380	53.00	7.00	88.00	81.00		
F	6	80	380	39.00	4.00	53.00	49.00		
F	6	81	380	27.00	0.00	47.00	47.00		
F	6	82	380	12.00					
F	7	69	310	32.00	4.00	68.00	64.00		
F	7	70	310	22.00	3.00	38.00	35.00		
F	7	71	310	26.00	0.00	60.00	60.00		
F	7	72	310	38.00	2.00	75.00	73.00		
F	7	73	310	38.00	6.00	118.00	112.00		
F	7	74	310	36.00	32.00	170.00	138.00		
F	7	75	310	38.00	5.00	160.00	155.00		
F	7	76	310	62.00	30.00	170.00	140.00		
F	7	77	310	51.00	1.00	64.00	63.00		
F	7	78	310	34.00	5.00	40.00	35.00		
F	7	79	310	14.00	3.00	31.00	28.00		
F	7	80	310	15.00	4.00	28.00	24.00		
F	7	81	310	14.00	0.00	20.00	20.00		
F	18	73	2300		13.70				3.60
F	18	74	2300		10.60				4.30
F	18	75	2300		8.30				3.70
F	18	76	2300		6.30				3.80
F	19	73	424	34.40	55.00	120.50			3.10
F	19	74	424	36.30	69.00	163.80			3.70
F	19	75	424	63.70					
F	25	86	830		22.00	62.00	37.00		5.70
F	25	87	830	33.00	19.00	73.00	51.00		4.90
F	25	88	830	41.00	37.00	101.00	58.00		6.90
F	26	86	430	56.00	3.50	50.00	46.00		3.60
F	26	87	430	36.00	0.00	58.00	58.00		3.50
F	26	88	430	36.00	7.70	72.00	63.00		4.20
F	24	69	2000		15.90				1.47
F	24	70	2000		16.00				1.34
F	24	71	2000		21.20				1.45
F	24	72	2000		13.60				1.90
F	24	73	2000		57.10				1.93
F	24	74	2000		39.20				3.15
F	24	75	2000		28.70				2.57
F	24	76	2000		0.88				2.24
UK	10	53	256	94.00	23.40	165.60		140.60	0.95
UK	10	54	256	86.00	19.10	128.10		121.80	0.70
UK	10	55	256	88.00	46.10	272.30		147.70	2.24
UK	10	56	256	84.00					1.00
UK	16	47	1400	16.80	1.20	84.50		84.10	3.50
UK	16	48	1400	39.20	30.90	140.30		122.90	3.50
UK	16	49	1400	36.40	70.30	183.10		118.90	4.40

Table A.1 (Continued)

Country	Area	Year	Surface (ha)	N^P	h	N^S	N^A	N^W	r
UK	16	50	1400	52.00	51.00	166.70		95.90	2.30
UK	16	51	1400	54.30	39.00	147.05		95.40	1.80
UK	16	52	1400	66.30	73.00	221.01		108.00	2.50
UK	16	53	1400	77.80	24.00	182.80		133.70	1.40
UK	16	54	1400	88.00	12.00	129.10		110.10	
UK	16	55	1400	70.60	20.00	144.80		102.40	
UK	16	56	1400	64.60	26.00	157.60		115.10	
UK	16	57	1400	79.10	87.00	225.08		114.90	
UK	16	58	1400	85.20	42.00	153.70		76.40	
UK	16	59	1400	49.40	26.00	136.40		92.10	
UK	17	68		13.20					0.90
UK	17	69		12.00					1.50
UK	17	70	6500	11.40					2.40
UK	17	71	6500	11.60					1.70
UK	17	72	6500	14.20					0.70
UK	17	73	6500	11.80					1.60
UK	B2	33	800	20.00		89.60			3.48
UK	B2	34	800	22.50		84.38			2.75
UK	B2	35	800		129.13				3.74
UK	B2	36	800	35.00		107.80			2.08
UK	C1	33	360	33.33		171.33			4.14
UK	C1	34	360	50.00		332.00			5.64
UK	C1	35	360		592.78				5.61
UK	C1	36	360	88.89	323.33	311.11			2.50
UK	C5	33	1040						
UK	C5	34	1040	23.08		110.77			3.80
UK	C5	35	1040						
UK	C5	36	1040						
UK	D2	33	2000		29.05				3.07
UK	D2	34	2000		32.00				2.74
UK	D2	35	2000		27.80				2.01
UK	D2	36	2000		20.25				
UK	D4	33	400						
UK	D4	34	400	47.50		197.13			3.15
UK	D4	35	400						
UK	D4	36	400						
UK	F1	33	2000	14.00	14.35				
UK	F1	34	2000	17.00	17.70	80.07			3.71
UK	F1	35	2000	18.00	18.65	83.16			3.62
UK	F1	36	2000	15.00	7.95	62.55			3.17
UK	H1	33	680	20.59					
UK	H1	34	680	20.59	16.32				
UK	H1	35	680	19.12	16.32				
UK	H1	36	680		3.97				
UK	L1	33	440	18.18	35	103.27			5
UK	L1	34	440	23.64	54.55	115.82			3.90
UK	L1	35	440						1.44
UK	L1	36	440						2.47
UK	L2	33	800	25.00	40.13	148.25			4.93
UK	L2	34	800	31.25	49.00	110.63			2.54
UK	L2	35	800	28.75	37.13	115.29			3.01
UK	L2	36	800	27.50	35.00	92.40			2.36

Table A.1 (Continued)

Country	Area	Year	Surface (ha)	N^p	h	N^s	N^a	N^w	r
UK	M1	33	332	24.10	93.67				
UK	M1	34	332	42.17	62.05	193.98			3.60
UK	M1	35	332	39.16	85.24	164.46			3.20
UK	M1	36	332	39.16	35.84	172.68			3.41
UK	O1	33	2000		89.30				3.80
UK	O1	34	2000		148.20				3.51
UK	O1	35	2000		103.05				2.75
UK	O1	36	2000	61.60	47.05	138.60			1.25
UK	S1	33	4400	29.55	40.18	89.23			2.02
UK	S1	34	4400	43.18	54.50	107.09			1.48
UK	S1	35	4400	50.00	91.07	146.00			1.92
UK	S1	36	4400		59.11				1.16
UK	S3	33	800						2.90
UK	S3	34	800						1.07
UK	S3	35	800		39.63				1.13
UK	S3	36	800						
UK	W1	33	560		25.89				3.01
UK	W1	34	560	53.57	239.46	200.89			2.75
UK	W1	35	560	125.00	357.32	573.75			3.59
UK	W1	36	560	182.14	217.86	582.86			2.20
UK	W11	33	560						
UK	W11	34	560	39.29		191.32			3.87
UK	W11	35	560						
UK	W11	36	560						
UK	W6	33	800	22.50	10.25				
UK	W6	34	800	25.00	8.13	117.25			3.69
UK	W6	35	800	37.50		150.00			3.00

The identification of the area is reported in the references listed in Table A.2. The countries are Italy (I), France (F), Poland (PL) and Great Britain (UK).

Table A.2

The references used to compile the Table A.1

References	Area code	Note
Cattadori and Zacchetti (1991)	1	
Montagna and Meriggi (1991)	2	
Mazzoni della Stella and Burrini (1993)	3	ρ estimated in autumn
Mazzoni della Stella (1990)	4	
Chlewski and Panek (1988)	5	
Birkan (1985)	6, 7	
Jenkins (1961)	10	
Reitz (1992)	11, 12	
Panek (1992)	13, 14, 15	N^a is obtained between autumn and winter
Blank et al. (1967); Blank and Ash (1959) for the years 1947–48	16	ρ is from Blank and Ash (1959)
Potts (1973)	17	
Birkan (1977a, b)	18	
Birkan et al. (1975)	19	
Birkan (1977a,b)	24	Depurated from the data for <i>Alectoris</i>
Serre and Reitz (1989)	25, 26	
Middleton (1934, 1936, 1937)	All study areas with an alphanumeric code	

Note that some area code is missing since the study has been later excluded by the work.

where

$$\lambda_t = \exp\{1.797 - 0.0118N_t^p + \text{Norm}(0, \theta_p)\}$$

and

$$\theta_p = 0.260\sqrt{1 + \frac{1}{28} + \frac{(N_t^p - 51.29)^2}{2.001 \times 10^4}}$$

$$(ii) N_t^a = (1 - m_t^h)N_t^s$$

$$(iii) N_t^w = \sigma_t^a N_t^a$$

where

$$\sigma_t^a = \exp\{-0.003N_t^a + 0.25 + \text{Norm}(0, \theta_a)\}$$

and

$$\theta_a = 0.134\sqrt{1 + \frac{1}{16} + \frac{(N_t^a - 127.94)^2}{1.549 \times 10^4}}$$

$$(iv) N_{t+1}^p = \sigma_t^w N_t^w$$

where

$$\sigma_t^w = \exp\{0.175\rho_t + 0.179 + \text{Norm}(0, \theta_w)\}$$

$$\theta_w = 0.199\sqrt{1 + \frac{1}{10}}$$

$$\rho_t = \frac{33.42(R_t - 0.885)}{R_t + 29.56} \exp(\text{Norm}(0, \theta_\rho))$$

and

$$\theta_\rho = 0.125\sqrt{1 + \frac{1}{22}}$$

As for continental populations we have:

$$(i) N_t^s = \lambda_t N_t^p$$

$$\lambda_t = \exp\{1.172 - 0.00734N_t^p + \text{Norm}(0, \theta_p)\}$$

and

$$\theta_p = 0.423\sqrt{1 + \frac{1}{56} + \frac{(N_t^p - 32.43)^2}{2.629 \times 10^4}}$$

$$(ii) N_t^a = (1 - m_t^h)N_t^s$$

$$(iii) N_{t+1}^p = \sigma_t^{aw} N_t^a$$

where

$$\sigma_t^{aw} = \exp\{-0.0021N_t^a + 0.55 + \text{Norm}(0, \theta_a)\}$$

and

$$\theta_a = 0.3196\sqrt{1 + \frac{1}{57} + \frac{(N_t^a - 60.26)^2}{1.118 \cdot 10^5}}$$

References

- Aebischer, N.J., Potts, G.R., 1998. Spatial changes in grey partridge (*Perdix perdix*) distribution in relation to 25 years of changing agriculture in Sussex, U.K. *Gibier Faune Sauvage*. Numéro spéciale, Tome 1. 15, 293–308.
- Aebischer, N.J., Blake, K.A., Boatman, N.D., 1994. Field margins as Habitats for Game. BCPC Monograph 58, pp. 95–104.
- Akçakaya, H.R., 1992. Population viability analysis and risk assessment. In: McCullough, D.R., Barrett, R.H. (Eds.), *Wildlife 2001: Populations*. Chapman and Hall, New York, USA, pp. 148–157.
- Akçakaya, H.R., McCarthy, M., Pearce, J.L., 1995. Linking landscape data with population viability analysis: management options for the helmeted honeyeater *Lichenostomus melanops cassidix*. *Biol. Conserv.* 73, 169–176.
- Allen, K.R., 1973. The influence of random fluctuations in the stock-recruitment relationship on the economic return from salmon fisheries. *Conseil International pour l'Exploration de la Mer Rapport* 164, 351–359.
- Aufradet, D., Birkan, M., 2001. Comportement et devenir de Perdrix grises (*Perdix perdix*) célibataires en Seine-et-Marne, France. *Game Wildl. Sc.* 18 (3–4), 403–410.
- Baillie, S.R., Gregory, R.D., Siriwardena, G.M., 1997. Farmland bird declines: patterns, processes and prospects. In: Kirkwood, R.C. (Ed.), *Biodiversity and Conservation in Agriculture*. In: BCPC Symposium Proceedings No. 69: British Crop Protection Council, Farnham, UK, 1997, pp. 65–87.
- Bearlin, A.R., Burgman, M.A., Regan, H.M., 1999. A stochastic model for seagrass (*Zostera muelleri*) in Port Phillip Bay, Victoria, Australia. *Ecol. Model.* 118 (2–3), 131–148.
- Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. *J. Wildlife Man.* 62, 821–841.
- Birkan, M.G., 1977a. Lachers de perdix grise d'élevage, *Perdix perdix* L., valeur pour le repeuplement. I Les lachers de jeunes perdix en été. *Bull. Off. Nat. Chasse*, num. spec., pp. 47–83.
- Birkan, M.G., 1977b. Analyse de tableaux de chasse de Perdix. Structure et dynamique de population. In: Pesson, P., Birkan, M.G. (Eds.), *Ecologie du Petit Gibier et Aménagement des Chasses*. Gauthier-Villars, Paris, France, pp. 55–77.
- Birkan, M.G., 1985. Dynamique de population et relation avec l'occupation du milieu par la Perdix grise (*Perdix perdix*). In: De Crombrugge, S.A. (Ed.), *In: Proceedings of the XVII Congress International Congress of Game Biologists Brussels, Belgium*, pp. 927–934.
- Birkan, M.G., Damange, J.P., 1977. Lachers de perdix grise d'élevage, *Perdix perdix* L., valeur pour le repeuplement. II Les lachers de subadultes en novembre-décembre et d'adultes en mars. *Bull. Off. Nat. Chasse*, num. spec., pp. 55–77.
- Birkan, M.G., Oliver, J., Aubineau, J., 1975. Dynamique de population chez la perdix grise (*Perdix perdix*) et plan de chasse sur un territoire aménagé (Vaubéron, Aisne). In: *Proceedings of the XII International Congress of Game Biologists*, pp. 63–69.
- Blank, T.H., Ash, J.S., 1959. A population of Partridges (*Perdix p.* and *Alectoris r. rufa*) on Hampshire Estate. *ICI Game Research Station*, pp. 424–427.

- Blank, T.H., Southwood, T.R.E., Cross, D.J., 1967. The ecology of the Partridge I.-outline of population processes with particular reference to chick mortality and nest density. *J. Anim. Ecol.* 36, 549–556.
- Borg, C., Toft, S., 2000. Importance of insect prey quality for grey partridge chicks (*Perdix perdix*): a self selection experiment. *J. Appl. Ecol.* 37, 557–563.
- Boyce, M.S., 1992. Population viability analysis. *Annu. Rev. Ecol. Syst.* 23, 481–506.
- Boyce, N.S., 1992. Population viability analysis. *Ann. Rev. Ecol. Syst.* 23, 481–506.
- Bro, E., Sarrazin, J., Clobert, J., Reitz, F., 2000. Demography and decline of the grey partridge *Perdix perdix* in France. *J. Appl. Ecol.* 37, 432–448.
- Brook, B.W., Lim, L., Harden, R., Frankham, R., 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen *Tricholimnas sylvestris* (Sclater). *Biol. Conserv.* 82, 119–128.
- Burgman, M.A., Ferson, S., Akçakaya, H.R., 1993. Risk Assessment in Conservation Biology. Chapman and Hall, London, UK.
- Cattadori, I.M., Zacchetti, D., 1991. Dinamica e Biologia riproduttiva di una popolazione di starni (*Perdix perdix*) in un sistema ad agricoltura intensiva della pianura padana orientale. *Suppl. Ric. Biol. Selvaggina* 19, 609–612.
- Chlewski, A., Panek, M., 1988. Population dynamics of partridge on hunting grounds of Czempin, Poland. In: Pielowski, Z. (Ed.), In: Proceedings of the Common Partridge (*Perdix perdix* L.) International Symposium on Polish Hunting Association, Warsaw, pp. 143–156.
- Dennis, B., Taper, M.L., 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecol. Monogr.* 64, 205–224.
- Dobson, A.P., Rodriguez, J.P., Roberts, W.M., Wilcove, D.S., 1997. Geographic distribution of endangered species in the United States. *Science* 275, 550–553.
- Dowell, S.D., 1991. Problems and pitfalls of gamebird reintroduction and restocking: an overview. *G. Faun. Sauvage* 9, 773–780.
- Drechsler, M., Burgman, M.A., Menkhorst, P.W., 1998. Uncertainty in the population dynamics and its consequences for the management of the orange-bellied parrot *Neophema chrysogaster*. *Biol. Conserv.* 84, 269–281.
- Ferson, S., Ginzburg, L.R., Silvers, A., 1989. Extreme event risk analysis for age-structured populations. *Ecol. Model.* 47, 175–187.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conserv. Biol.* 9, 1425–1441.
- Ginzburg, L.R., Ferson, S., Akçakaya, H.R., 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conserv. Biol.* 4 (1), 63–70.
- Ginzburg, L.R., Slobodkin, L.B., Johnson, K., Bindman, A.G., 1982. Quasi extinction probabilities as a measure of impact on population growth. *Risk Anal.* 21, 171–181.
- Hagemeijer, W.J.M., Blair, M.J., 1997. The EBCC Atlas of European Breeding Birds. Their Distribution and Abundance. Published for the European Bird Census Council. Poyser, London, UK.
- Harcourt, A.H., 1995. Population viability estimates: theory and practice for a wild gorilla population. *Conserv. Biol.* 9, 134–142.
- Hines, W.W., Montgomery, D.C., 1980. Probability and Statistics in Engineering and Management Science. J. Wiley and Sons, New York, USA.
- Jenkins, D., 1961. Population control in protected partridges (*Perdix perdix*). *J. Anim. Ecol.* 30, 235–258.
- Kangas, A., Kurki, S., 2000. Predicting the future of capercaillie (*Tetrao urogallus*) in Finland. *Ecol. Model.* 134, 73–87.
- Lacy, R.C., 2000. Structure of the vortex simulation model for population viability analysis. *Ecol. Bull.* 48, 191–203.
- Lamberson, R., McKelvey, R., Noon, B., Voss, C., 1992. A dynamic analysis of spotted owl viability in a fragmented forest. *Biol. Conserv.* 6, 505–512.
- Lebreton, J.D., Clobert, J., 1991. Bird population dynamics, management and conservation; the role of mathematical modelling. In: Perrins, C.M., Lebreton, J.D., Hiron, G.J.M. (Eds.), Bird population Studies, Relevance to Conservation Management. Oxford University Press Oxford, UK, pp. 105–125.
- Lindenmayer, D., Lacy, R.C., Pope, M.L., 2000. Testing a simulation model for a population viability analysis. *Ecol. Appl.* 10, 580–597.
- Lindenmayer, D.B., Lacy, R.C., 2002. Small mammals, patches and PVA models: a field test of model predictive ability. *Biol. Conserv.* 103, 247–265.
- Lindenmayer, D.B., Burgman, M.A., Akçakaya, H.R., Lacy, R.C., Possingham, H.P., 1995. A review of the generic computer programs alex, ramas/Space and vortex for modelling the viability of Wildlife metapopulations. *Ecol. Model.* 82, 161–174.
- Lindenmayer, D.B., Possingham, H.P., Lacy, R.C., McCarthy, M.A., Pope, M.L., 2003. How accurate are population models? Lessons from landscape-scale tests in a fragmented system. *Ecol. Lett.* 6 (1), 41–47.
- Ludwig, F., 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80, 298–310.
- Mace, G.M., 1994. Classifying threatened species: means and ends. *Phil. Trans. R. Soc. London B.* 344, 91–97.
- Mangel, M., Switzer, P.V., 1998. A model at the level of the foraging trip for the indirect effects of krill (*Euphausia superba*) fisheries on krill predators. *Ecol. Model.* 105 (2–3), 235–256.
- Marshall, K., Edward-Jones, G., 1998. Reintroducing capercaillie (*Tetrao urogallus*) into southern Scotland: identification of minimum viable populations at potential release sites. *Biol. Conserv.* 7, 275–296.
- Marshall, K., Edward-Jones, G., 1998. Reintroducing capercaillie (*Tetrao urogallus*) into southern Scotland: identification of minimum viable populations at potential release sites. *Biol. Conserv.* 7, 275–296.
- Mazzoni della Stella, R., 1990. La reintroduzione della starna in un ambiente tipico della provincia di Siena. Amministrazione Provinciale di Siena, Servizio Risorse Faunistiche, Siena, Italy.

- Mazzoni della Stella, R., Burrini, L., 1993. L'ultima popolazione di starna della provincia di Siena. *La Provincia di Siena* 1, 1–4.
- McCarthy, M.A., 1996. Extinction dynamics of the helmeted honeyeater: effects of demography, stochasticity, inbreeding and spatial structure. *Ecol. Model.* 85, 151–163.
- McKenna Jr., J.E., 2000. FITPOP, a heuristic simulation model of population dynamics and genetics with special reference to fisheries. *Ecol. Model.* 127 (1), 81–89.
- Middleton, A.D., 1934. The population of partridges (*Perdix perdix*) in 1933 and 1934 in Great Britain. *J. Anim. Ecol.* 4, 137–145.
- Middleton, A.D., 1936. The population of partridges (*Perdix perdix*) in Great Britain during. *J. Anim. Ecol.* 5, 252–261.
- Middleton, A.D., 1937. The population of partridges (*Perdix perdix*) in Great Britain during. *J. Anim. Ecol.* 6, 318–321.
- Mills, L.S., Hayes, S.G., Baldwin, C., Wisdom, M.J., Citta, J., Mattson, D.J., Murphy, K., 1996. Factors leading to different viability predictions for a grizzly bear data set. *Biol. Conserv.* 10 (3), 863–873.
- Montagna, D., Meriggi, A., 1991. Population dynamics of grey partridge (*Perdix perdix*) in northern Italy. *Bull. Zool.* 58, 151–155.
- Panek, M., 1992. Mechanisms determining population levels and density regulation in polish grey partridges (*Perdix perdix*). *G. Faun. Sauvage* 9, 325–335.
- Parysow, P., Tazik, D.J., 2002. Assessing the effect of estimation error on population viability analysis: an example using the black-capped vireo. *Ecol. Model.* 155, 217–229.
- Possingham, H.P., Davies, I., 1995. ALEX: a population viability analysis model for spatially structured populations. *Biol. Conserv.* 73, 143–150.
- Possingham, H.P., Lindenmayer, D.W., Norton, T.W., 1993. The role of PVA in endangered species management. *Pacific Conserv. Biol.* 1, 39–45.
- Potts, G.R., 1973. The Grey Partridge: Problems of Quantifying the Ecological Effects of Herbicides. In: Kjerner, I., Bjurholm, P. (Eds.), In: Proceedings of the XI International Congress of Game Biologist on National Swedish Environment Protection Board. Stockholm, Sweden, pp. 405–413.
- Potts, G.R., 1980. The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Ad. Ecol. Res.* 11, 1–79.
- Potts, G.R., 1986. The Partridge: Herbicides, Predation and Conservation. Collins, London, UK.
- Potts, G.R., 1990. Causes of Decline of Partridge Populations and Effect of Insecticide Dimethoate on Chick Mortality. In: Lumeij, J.T., Hoogeveen, Y.R. (Eds.), The future of wild Galliformes in the Netherlands. Organisatiecommissie Nederlandse Wilde Hoenders, Amersfoort, Netherlands, pp. 62–71.
- Potts, G.R., Aebischer, N.J., 1991. Modelling the population dynamics of the Grey Partridge: Conservation and management. In: Perrins, C.M., Lebreton, J.D., Hirons, G.J.M. (Eds.), Bird Population Studies: their relevance to conservation management. Oxford University Press, Oxford, UK, pp. 373–390.
- Potts, G.R., Aebischer, N.J., 1995. Population Dynamics of the Grey Partridge *Perdix* 1793–1993: Monitoring, Modelling and Management. *Ibis* 137 (supplement), pp. S29–S37.
- Prigioni, C., Meriggi, A., Fasola, M., Bogliani, G., Barbieri, F., 1977. Ripopolamento di starna (*Perdix perdix* L.) in provincia di Pavia: primi dati sull'inanellamento. In: Cacucci, E. (Ed.), Atti del VII Simposio Nazionale sulla Conservazioni della Natura. Bari, Italy, pp. 77–85.
- Rands, M.R.W., 1986. Effect of hedgerow characteristics on partridge breeding densities. *J. Appl. Ecol.* 23, 479–487.
- Reed, J.M., Elphick, C., Oring, L.W., 1998. Life-history and viability analysis of the endangered Hawaiian stilt. *Biol. Conserv.* 84, 35–45.
- Reed, J.M., Murphy, D.D., Brussard, P.F., 1998. Efficacy of population viability analysis. *Wildl. Soc. Bull.* 26, 244–251.
- Reitz, F., 1992. Adult survival and reproductive success in abundant populations of grey partridge (*Perdix perdix*) in north-central France. *G. Faun. Sauvage* 9, 313–324.
- Reynolds, J., Dowell, S., Brockless, M., Blake, K., Boatman, N., 1991. Tracking partridge predation. *Game Conservancy Rev.* 1994 23, 60–62.
- Ricker, W.E., 1954. Stock and recruitment. *J. Fisheries Res. Board Can.* 11, 559–623.
- Rotella, J.J., Ratti, J.T., Reese, K.P., Taper, M.L., Dennis, B., 1996. Long-term population analysis of grey partridges in Eastern Washington. *J. Wildl. Manage.* 60, 817–825.
- Royama, T., 1992. Analytical Population Dynamics. Chapman and Hall, London, UK.
- Sæther, B.-E., Engen, S., Islam, A., McCleery, R., Perrins, C., 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *Am. Nat.* 151 (5), 441–450.
- Seal, U.S., Lacy, R.C., 1990. Florida Panther Viability Analysis and Species Survival Plan. Captive Breeding Specialist Group, Species Survival Commission IUCN, pp. 264.
- Serre, D., Reitz, F., 1989. Démographie de la Perdix grise en Beauce. Etude de deux cas tres différents. *Bull. Off. Nat. Chasse* 139, 5–9.
- Shaffer, M.L., 1981. Minimum population sizes for species conservation. *Bioscience* 31, 131–134.
- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H., Wilson, J.D., 1998. Trends in the abundance of farmland birds: a quantitative comparison of smoothed common bird census indices. *J. App. Ecol.* 35, 24–43.
- Sotherton, N.W., 1998. Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. *Biol. Conserv.* 83, 259–268.
- Sotherton, N.W., Robertson, P.A., 1990. Indirect impacts of pesticides on the production of wild gamebirds in Britain. In: Church, K.E., Warner, R.E., Brady, S.J. (Eds.), In: Proceedings of the Perdix V: Gray Partridge and Ring-Necked Pheasant Workshop. Kansas Department of Wildlife and Parks, Emporia, KS, pp. 84–102.
- Sotherton, N.W., Robertson, P.A., Dowell, S.D., 1992. Manipulation of pesticide use to increase the production of wild game birds in Britain. In: Church, K.E., Dailey, T.V. (Eds.), Quail III National quail symposium, Kansas Department of Wildlife and Parks, Pratt, Kansas, USA, pp. 92–101.
- Tapper, S.C., Potts, G.R., Brockless, M.H., 1996. The effect of an experimental reduction in predation pressure on the breeding

- success and population density of grey partridges *Perdix perdix*. J. Appl. Ecol. 33, 965–978.
- Todd, C.R., Inchausti, P., Jenkins, S., Burgman, M.A., Ng, P.J., 2001. Structural uncertainty in stochastic population models: delayed development in the eastern barred bandicoot. Ecol. Model. 136, 237–254.
- Tompkins, D.M., Draycott, R.A.H., Hudson, P.J., 2000b. Field evidence of apparent competition mediated via the shared parasites of two gamebird species. Ecol. Letters 3, 10–14.
- Tompkins, D.M., Greenman, J.V., Robertson, P.V., Hudson, P.J., 2000a. The role of shared parasites in the exclusion of Wildlife hosts: *Heterakis gallinarum* in the ring-necked pheasant and the grey partridge. J. Anim. Ecol. 69, 829–840.
- Toso, S., Cattadori, I.M., 1993. La starna (*Perdix perdix* L.) in Italia: analisi dell'origine e della presenza storica di una specie influenzata dalle attività antropiche. Suppl. Ric. Biol. Atti del VII Convegno dell'Associazione A. Ghigi per la Biologia e la Conservazione dei Vertebrati (Eds.) Spagnesi, M., Randi., E.), Selvaggina XXI, 175–186.
- Tucker, G.M., Heath, M.F., 1994. Birds in Europe. Their conservation status. Birdlife Conservation Series No 3, Birdlife International Cambridge, UK.
- Vucetich, J.A., Waite, T.A., 1998. On the interpretation and application of mean times to extinction. Biol. Conserv. 7, 1539–1547.
- Walters, C.J., Hilborn, R., 1976. Adaptative control of Fishing Systems. J. Fisheries Res. Board Can. 33, 145–159.
- Wright, S.J., Hubbel, S.P., 1983. Stochastic extinction and reserve size: a focal species approach. Oikos 41, 466–476.
- Zacchetti, D., Montagna, D., Matteucci, C., 1989. Analisi comparata della dinamica e produttività di due popolazioni di starna (*Perdix perdix*) dell'Italia settentrionale. Suppl. Ric. Biol. Selvaggina XIV, 197–205.