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SMR.940 - 4

## *THIRD AUTUMN WORKSHOP ON MATHEMATICAL ECOLOGY*

*(14 October - 1 November 1996)*

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# "Population Viability Analysis of gamebird populations: The black grouse and the grey partridge"

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# POPULATION VIABILITY ANALYSIS

**PVA** is a procedure to assess the likelihood that a population will become extinct within a certain time and under different management options.

## Factors that can cause extinction

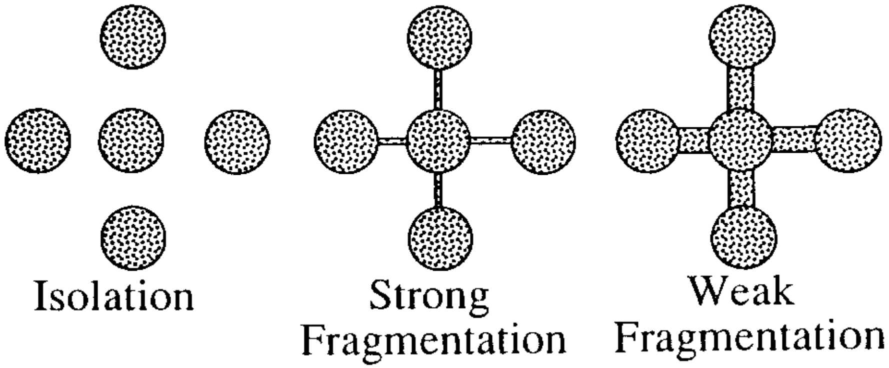
1. Endogenous
    - Random demographic changes
    - Social and/or behavioral dysfunction
    - Genetic drift and inbreeding

2. Exogenous
    - Chronic environmental factors such as habitat alteration, increased predation and competition, disease
    - Acute environmental stress or catastrophes such as fires, floods, epidemics

**In practice PVA is performed by running suitable simulation models of the population dynamics**

# KEY CONCEPTS IN PVA

- Probability of extinction within a certain time, median extinction time, distribution of extinction times
- Demographic stochasticity (the size of small populations must be treated as an integer number) vs. environmental stochasticity
- Quasi-extinction defined via a threshold below which the fate of the population is very uncertain due to inbreeding, Allee effect, demographic stochasticity, etc.
- Geographic structure in terms of metapopulations of differently connected local populations



# MODELLING BLACK GROUSE POPULATIONS IN NORTHERN ITALY

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## ABSTRACT

Black grouse populations were censused in 6 areas of Lombard Alps. Based on these data a stochastic demographic model is built, which takes into account density-dependence for the reproductive success. Harvesting policies are then included in the model. We search for optimal policies using two criteria: 1) maximization of the average annual bag with a constraint on minimal population size; 2) multiobjective optimization in the space of three performance indices: average annual catch, relative catch variability and minimum adult density.

## Introduction

Black grouse (*Tetrao tetrix*) is widely distributed in the Italian Alps and represents an important species for game hunting. The increasing fragmentation of its habitat due to the construction of roads, ski facilities, etc., together with hunting pressure, may pose a threat to many populations of this tetraonid. We have, thus, conducted a study in Lombardy (Northern Italy) to estimate the actual demographic parameters of black grouse and to evaluate the relative merits of different shooting policies.

It is worth while to give some general information concerning the biology and habits of black grouse. *Tetrao tetrix* is quite similar to its better known congener, the capercaillie (*Tetrao urogallus*), although smaller in size and with different plumage. The habitat also is different: while capercaillie prefer conifer woods, black grouse occupy areas at higher elevations where vegetation is sparser (usually just above the timberline). In Lombardy black grouse is concentrated in the Alpine and Prealpine zone between 900 and 2,000 m elevations. In late spring, at the beginning of the reproductive period, cocks congregate to particular open areas (called arenas or leks) where they sing, fight and display in a ritualized way to attract females. This behavior lasts from

April to June. Females, few at a time, come to the leks and copulate with the chosen male, but stay in the arenas only for a brief period. In fact, as soon as a hen is fertilized, she leaves the arena and, all alone, takes care of nesting, brooding and subsequently feeding the newly hatched chicks. Cocks, after all the females have come to the arena, will be solitary for the whole summer. Each hen produces 6-10 eggs and the brooding takes 4 weeks. Juveniles stay with the mother for about 60-70 days until September, when the chickens gradually become independent. During the winter, black grouse may form groups (usually of one sex) and migrate to more favorable sites to search for food. Most of natural mortality is concentrated in this season.

**Available data**

The data that will be used in the present work have been collected in six study areas. These were chosen, because they were considered as representative of the different features that characterize Lombard populations[1]. A list of these areas is given in Table 1. Census methods are described in detail by Scherini et al.[2]. In summary, displaying cocks and reproductive females in the arenas were counted by several observers in the springs 1983-85, while juveniles (# of broods and size of each brood) were censused with the aid of pointing dogs in the late summer of 1983 and 1984. Data relevant to our study are shown in Table 2.

While the number of males counted on the arenas is reliable and representative of one-year-old and older cocks, this is not true of females whose presence on the arenas is only sporadic. In fact, the number of counted females is often lower than the number of broods that will be found later in the same area. As for the late summer census, it should be remarked that *b* and *J* are not to be confused with, respectively, number of nests and clutch size. The census was performed at least two months after hatching when the chicks had already been struck by heavy infant mortality. One should remark the wide variability of data between areas and from year to year: 1983 is considered a "good" year, while 1984 is in the average.

Table 1 - Information on the six study areas

| Area | District | Hectares | Hunting |
|---|---|---|---|
| A Lema | Varese | 697 | No |
| B Valvarrone | Como | 585 | Yes |
| C Zandila | Sondrio | 647 | No |
| D Aprica | Sondrio | 728 | No |
| E Vivione | Bergamo | 808 | Yes |
| F Puria | Brescia | 847 | No |

**Data analysis and the demographic model**

We now proceed to elaborating the data in order to build a stochastic demographic model of the male population. The restriction to one sex is due both to the fact that female counts are unreliable and to the fact that hunting is exerted only on males. The model is based on the following assumptions:

- Mortality is concentrated in winter.
- Population is divided in two classes: juveniles (born in the same year of late summer counts) and adults (older).
- All adult males are counted as displaying cocks in spring. This is a simplification with respect to reality. It is known that some individuals may take more than one year to become sexually mature.
- Sex ratio at birth is 1:1.
- Overwinter mortality is the same for juveniles and adults. In fact, separate estimates of juvenile and adult survivorships do not yield significantly different results[3].

The structure of the model is schematically represented in Fig. 1.

Table 2 - Data from the spring and late summer censuses

Spring census

| | 1983 | | | 1984 | | | 1985 | | |
|---|---|---|---|---|---|---|---|---|---|
| Area | *M* | *F* | $M/km^2$ | *M* | *F* | $M/km^2$ | *M* | *F* | $M/km^2$ |
| A | 7 | 6 | 1.00 | 13 | 2 | 1.87 | 13 | 2 | 1.87 |
| B | 8 | 0 | 1.37 | 5 | 3 | 0.85 | 3 | 3 | 0.51 |
| C | 13 | 7 | 2.00 | 16 | 3 | 2.47 | 24 | 4 | 3.70 |
| D | 16 | 6 | 2.20 | 28 | 11 | 3.85 | 19 | 2 | 2.61 |
| E | 21 | 9 | 2.60 | 10 | 5 | 1.24 | 16 | 2 | 1.98 |
| F | 13 | 1 | 1.53 | 17 | 4 | 2.01 | 22 | 3 | 2.60 |

*M*: # of males *F*: # of females

Late summer census

| | 1983 | | | | 1984 | | | |
|---|---|---|---|---|---|---|---|---|
| Area | *b* | *J* | *J/b* | $J/km^2$ | *b* | *J* | *J/b* | $J/km^2$ |
| A | 5 | 21 | 4.20 | 3.0 | 4 | 15 | 3.75 | 2.1 |
| B | 6 | 33 | 5.50 | 5.6 | 6 | 31 | 5.17 | 5.3 |
| C | 6 | 21 | 3.50 | 3.2 | 3 | 10 | 3.33 | 1.5 |
| D | 14 | 48 | 3.43 | 6.5 | 6 | 25 | 4.17 | 3.4 |
| E | 11 | 51 | 4.64 | 6.3 | 8 | 39 | 4.88 | 4.8 |
| F | 4 | 18 | 4.50 | 2.1 | 3 | 14 | 4.67 | 1.6 |

*b*: # of broods *J*: # of juveniles

As for survival during winter, only areas without hunting were considered. No significant density dependence was detected. The assumed relationship between one year and the next is therefore

$$M_{t+1} = \sigma \delta_t (M_t + J_t/2)$$

where

$M_t$ = # of adult males per km$^2$ in year $t$

$J_t$ = # of juveniles per km$^2$ in year $t$

$\sigma$ = average overwinter survival

$\delta_t$=multiplicative environmental noise;assumed lognormally distributed with unitary mean value.

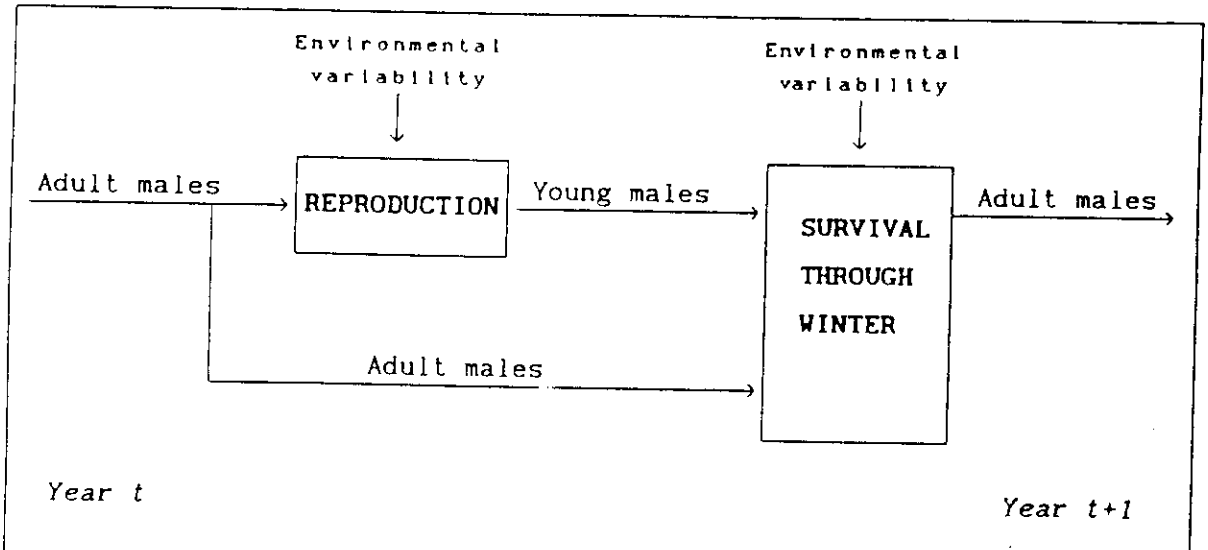

Fig. 1 - A block diagram of the model

By taking logarithms and performing a linear regression (see Fig. 2) one obtains the following estimates:

$\sigma$ = 0.735

95% confidence interval for $\sigma$ = [0.591,0.914]

Standard Deviation of $\ln \delta$ = 0.2612

The regression is significant at the 5% confidence level.

As for reproduction, we investigated several correlations between indices of reproduction and indices of grouse density, taking all study areas into account. The most significant relationship we found is the following that links reproductive success $J/M$ to male density

$$J_t/M_t = \varepsilon_t \; exp[a-bM_t]$$

where $\varepsilon_t$ is lognormally distributed with unitary mean value and $a$ and $b$ are positive parameters. By taking logarithms and performing a linear regression, which turns out to be 5% significant, one obtains the estimates

$a$ = 1.757

$b$ = 0.5757

Standard deviation of $\ln \varepsilon$ = 0.582.

The fit to data is shown in Fig. 3.

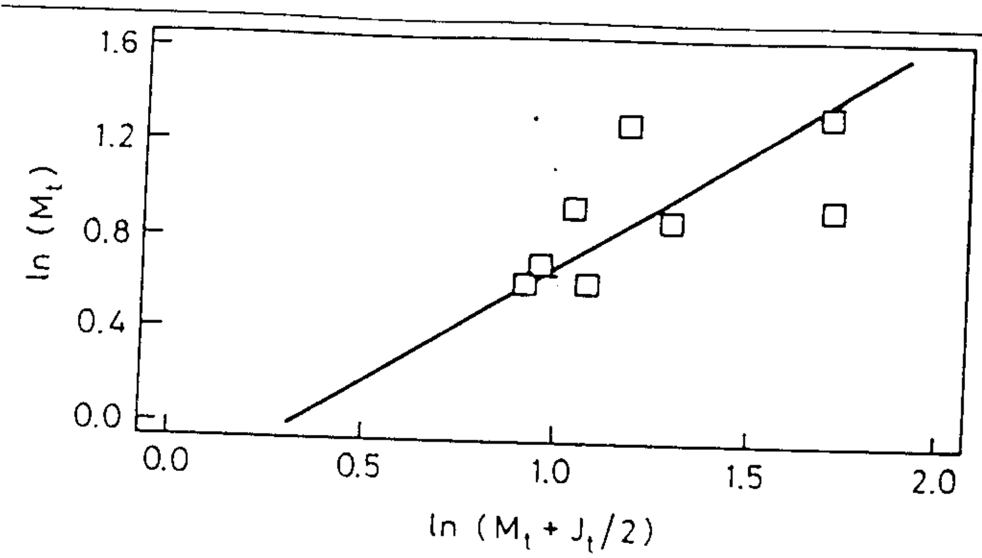

Fig.2 - Regression of $\ln(M_{t+1})$ vs. $\ln(M_t + J_t/2)$

By connecting the survival and the reproduction modules one finally gets the stochastic model, which is specified as follows

$$M_{t+1} = \sigma\, exp[G(0.2612)]\; M_t\; (1 + \frac{1}{2}\, exp[a-bM_t+G(0.582)])$$

where $G(s)$ is a casual number drawn from a normal distribution with zero mean and standard deviation equal to $s$. In the few cases when $\sigma exp[G(0.2612)]$ turns out bigger than unity, it is set equal to 1. A graphical representation of the stochastic model is given in Fig. 4a, where shadings of different intensity indicate higher or lower probability of obtaining $M_{t+1}$ for each given $M_t$. Fig. 4b displays a simulation of grouse dynamics for a period of 30 years. Notice that

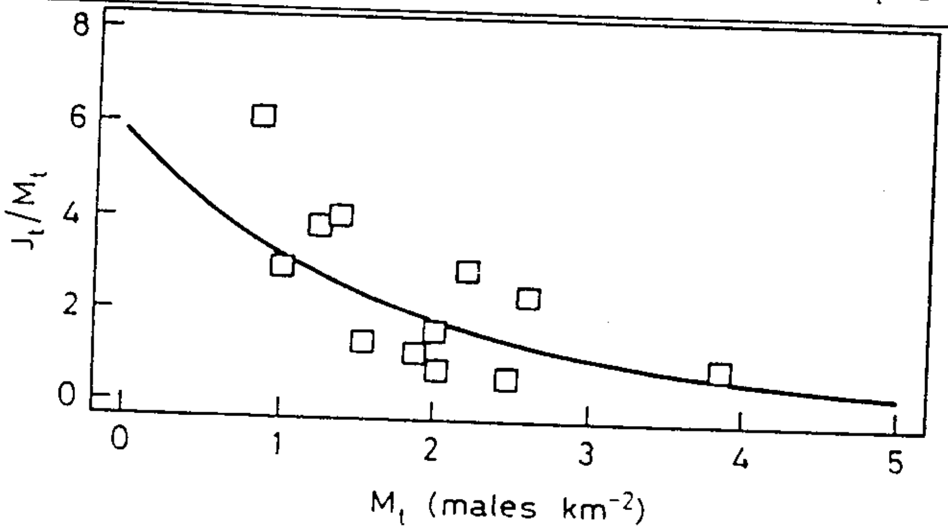

Fig.3 - Regression of $J_t/M_t$ vs. $M_t$

oscillations are originated by stochasticity, because the underlying deterministic model (described by the increasing curve shown in Fig. 4a) is purely compensatory.

**Optimization of hunting**

Different harvesting policies can easily be included in the above model, which can be used to obtain predictions in probability on the effects of hunting. Each policy was evaluated by generating 20 fifty-years simulations. Two types of hunting regulations were considered: constant effort and constant escapement policies. With the first type annual harvest in fall is a constant fraction of males present in late summer, namely

$$H_t = p_M M_t + p_J J_t$$

where $H_t$ is the harvest in year $t$, while $p_M$ and $p_J$ are the percentages of respectively adults and juveniles shot during the hunting season. The second type of regulation is more complicated: harvest is determined, before the hunting season starts, in such a way that a constant number of males is allowed to escape. If the number of available males, as determined from spring and late-summer counts, is smaller than the target escapement, hunting is not permitted. Escapement, after the losses during the winter period, will become the new reproductive stock in spring. More precisely, let $S_a$ be the target escapement in fall (so that $S = \sigma S_a$ is the ensuing average reproductive stock in spring). Then, the allowed harvest is given by

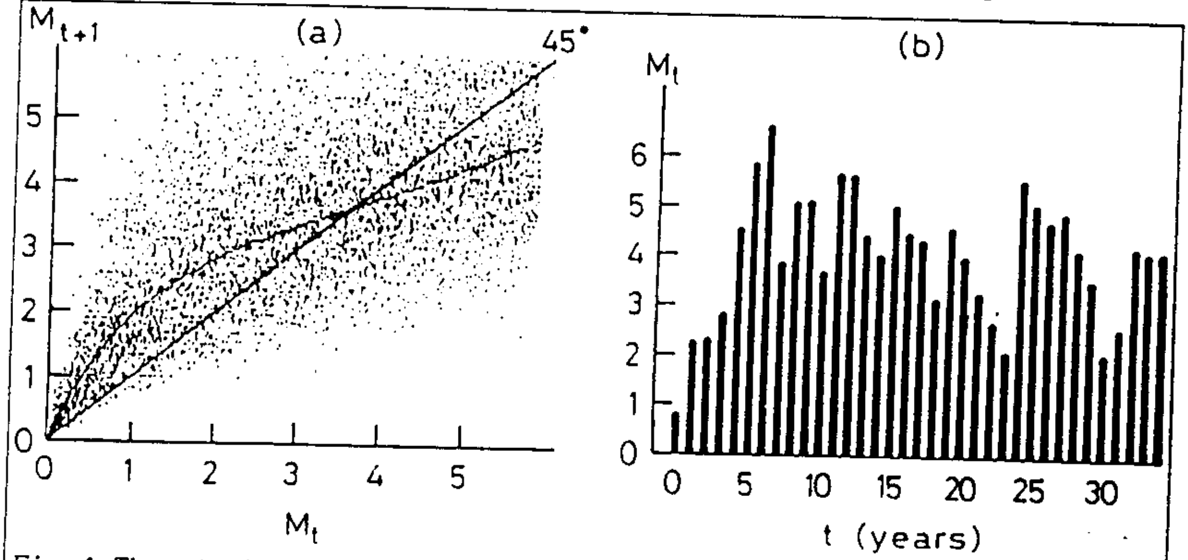

Fig.4-The stochastic model of black grouse dynamics. a) Representation of the model in the plane $M_t$-$M_{t+1}$; for explanation see text.
b) 30 years' simulation with initial adult male density equal to 0.8 individuals per km$^2$.

$$H_t = \begin{cases} M_t + \frac{1}{2} J_t - S_a & \text{if } M_t + \frac{1}{2} J_t > S_a \\ 0 & \text{if } M_t + \frac{1}{2} J_t \le S_a \end{cases}$$

As a case study, we considered a hunting area the size of the one in Sondrio district (39,000 ha) and ran the model to evaluate three performance indices for each policy: average annual catch, relative catch variability (i.e., the ratio between the standard deviation of catches and the average catch) and minimum adult density in spring. A first optimization criterion that has been considered is the maximization of the average annual bag (over the 20 fifty-years simulations) with the constraint that adult male density in spring never gets under a safe threshold (identified in 0.5 males $km^{-2}$). The result is that the best constant escapement policy ($S$ = 1.25 males $km^{-2}$) allows a greater harvest (633 males per year over the whole area) than the best constant effort policy (477 males per year obtained using the following percentages: $p_M$ = 20%, $p_J$ = 40%). This result is not unexpected, because it is known that constant escapement policies, under some general conditions, maximize expected harvest (see Gatto and Rinaldi[4], Reed[5]). It is also known, however, that constant escapement policies have the drawback of a higher catch variability. This is confirmed by our case, in which the best constant escapement policy is characterized by a higher standard deviation of catch (1.31 males $km^{-2}$) than the best constant percentage policy (0.5 males $km^{-2}$). In view of this, as a second optimization criterion, we have identified Pareto policies in the space of the three performance indices mentioned above (we remember that a Pareto policy is such that no other policy is better under all respects). Of course, expected harvest and minimum adult density should be maximized, while harvest variability should be minimized. The results from this analysis are shown in Figs. 5a and 5b, which display the projections of the Pareto boundaries (separately for the two types of policies considered) onto the planes (Average annual harvest - Minimal density) and (Minimal density - Harvest relative variability). It is interesting to remark that, if one took into account only mean harvest and minimum density, all constant-effort Pareto policies would be dominated by at least one constant escapement policy. On the other hand, if only minimum density and catch variability were considered, all constant-escapement Pareto policies would be dominated by a constant effort policy. Also, notice that minimal density and harvest variability are positively correlated for constant escapement policies, whereas they are negatively correlated for constant effort policies.

Present hunting regulation is basically a constant effort policy. Since all hunters are amateurs, catch variability is likely to be perceived by the public opinion as less fundamental than the preservation of the grouse stock. In this sense, our study demonstrates that there might be an advantage in adopting a constant escapement policy.

## Acknowledgments

The work has been partially supported by the Italian Ministry for Universities and Scientific Research, Progetto MURST 40% "Dinamica dei Processi Ecologici".

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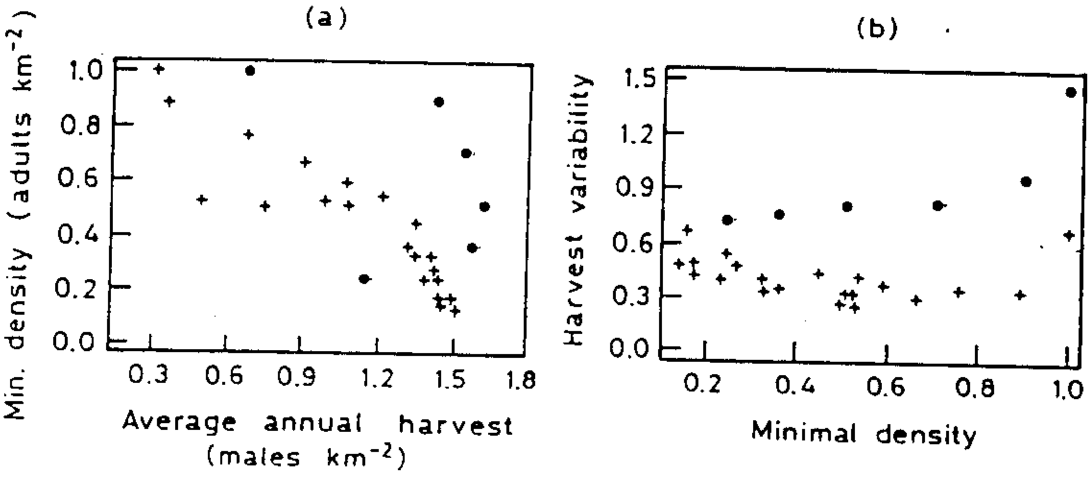

Fig.5 - Pareto policies for the black grouse harvesting problem. Each policy is represented by the triplet of the resulting performance indices. Constant effort policies are indicated by crosses (+), constant escapement policies by solid circles (•). a) Projection of Pareto policies onto the plane (Average annual harvest - Minimal density); b) projection of Pareto policies onto the plane (Minimal density - Harvest relative variability).

# A Population Viability Analysis of the grey partridge (*Perdix perdix*) in Europe

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## GLOBAL DENSITY TRENDS

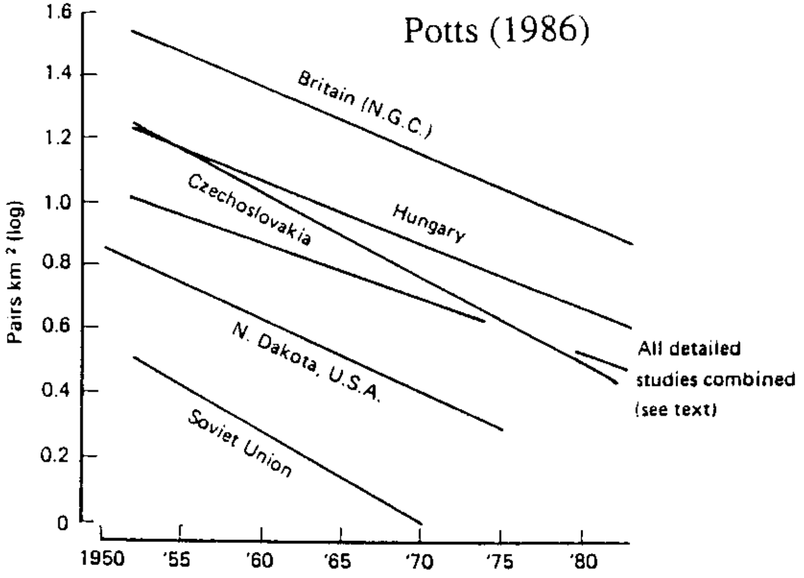
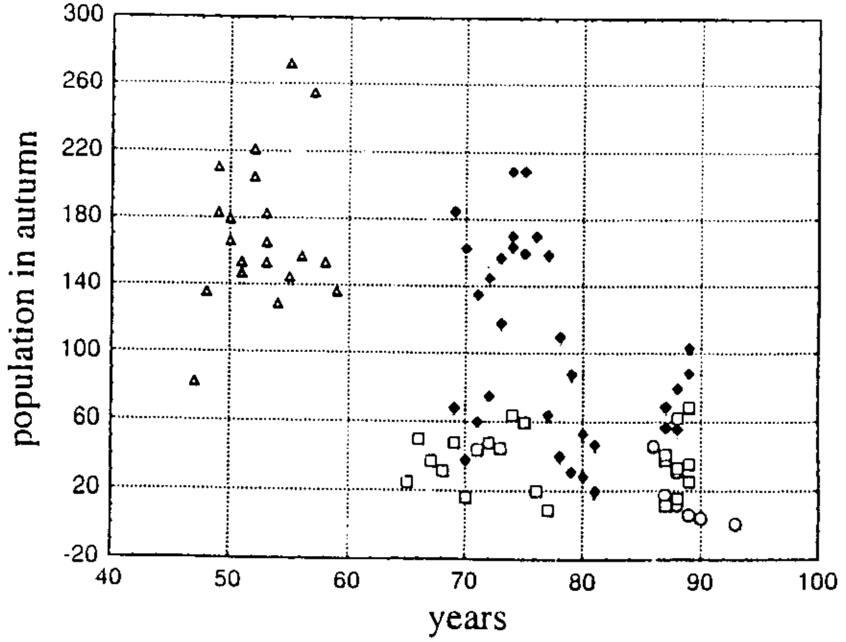


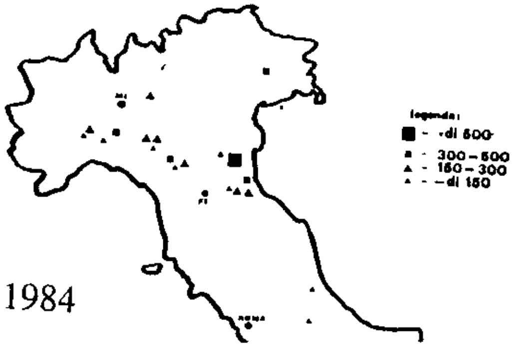
*Fig. 2.5* The trend in density of breeding pairs km$^{-2}$ over the period 1952 to 1985 for various regions of the world range.



## THE ITALIAN SITUATION

(Matteucci & Toso 1985)

Before WWII



1984

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## CAUSES OF DECLINE IN SUSSEX

Potts (1986) published the results of a long-term study conducted by the Game Conservancy in Sussex. The decline seems to be caused by

- **Increased chick mortality** due to the use of pesticides that kill prey which are **absolutely necessary** for survival during the first weeks after hatching
- **Lower predator control** by the gamekeepers
- Reduced protection against predators due to **removal of hedges**

## AIM OF THIS WORK

- To model the population dynamics of grey partridge for those populations not included in Potts' study (both UK and continental Europe populations)

- To determine whether there are important differences in the demographic parameters that characterize the different populations

- To include habitat fragmentation in the model

- To suggest management policies that can possibly counteract the grey partridge decline

## DATA ANALYSIS
(22 papers)

- The **life cycle** has been divided into two periods
    - **spring-summer** (reproduction)
    - **autumn-winter** (hunting, natural mortality, juvenile dispersal)
- We have searched for **correlations** among different variables to
    - evidence **density dependence**
    - estimate **environmental stochasticity**

### Main results

a) **spring-summer**
No density dependence in continental Europe
Density dependence in UK

b) **autumn-winter**
Density dependence in continental Europe
No density dependence in UK

## CONTINENTAL MODEL

$$N_{at} = \varepsilon_t R N_{st}$$
$$N_{wt} = N_{at} - h_t$$
$$N_{s,t+1} = \delta_t S_o \exp(-\beta N_{wt}) N_{wt}$$

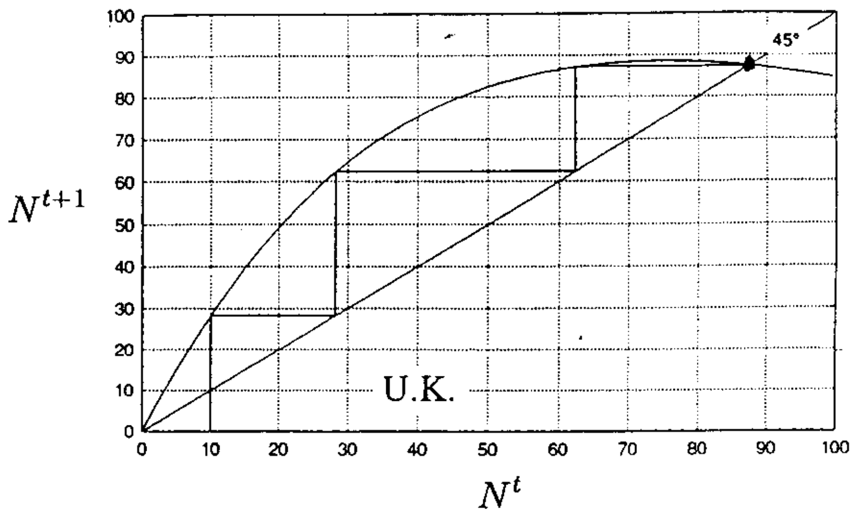
**where**

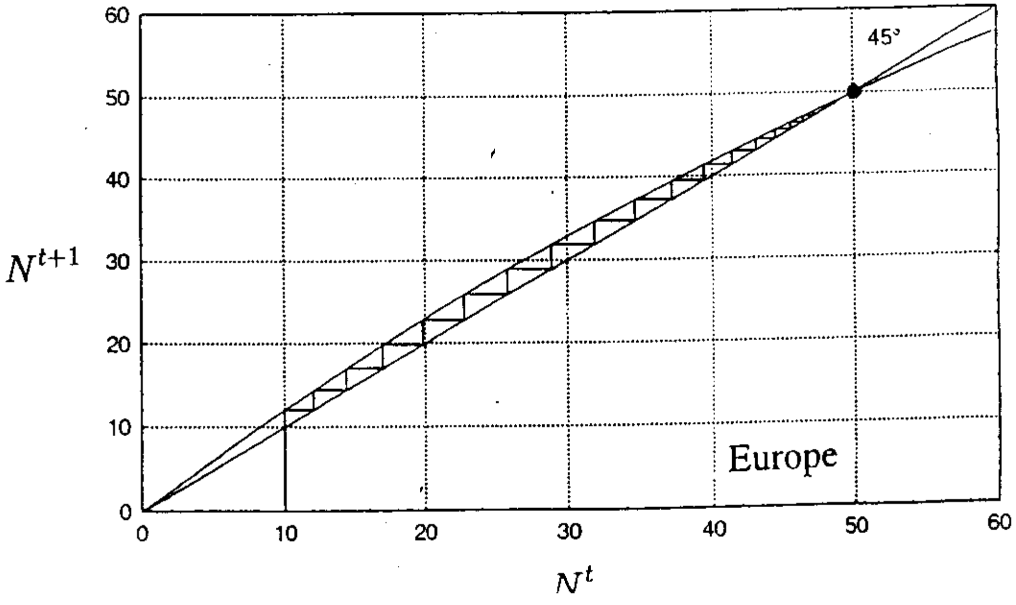
$N_{st}$ = Spring population at year t (# km-2)
$N_{at}$ = Autumn population
$N_{wt}$ = Winter population
$h_t$ = Harvest in autumn of year t
R = Finite rate of increase during spring-summer

$S_o \exp(-\beta N_{wt})$= Density dependent survival during winter

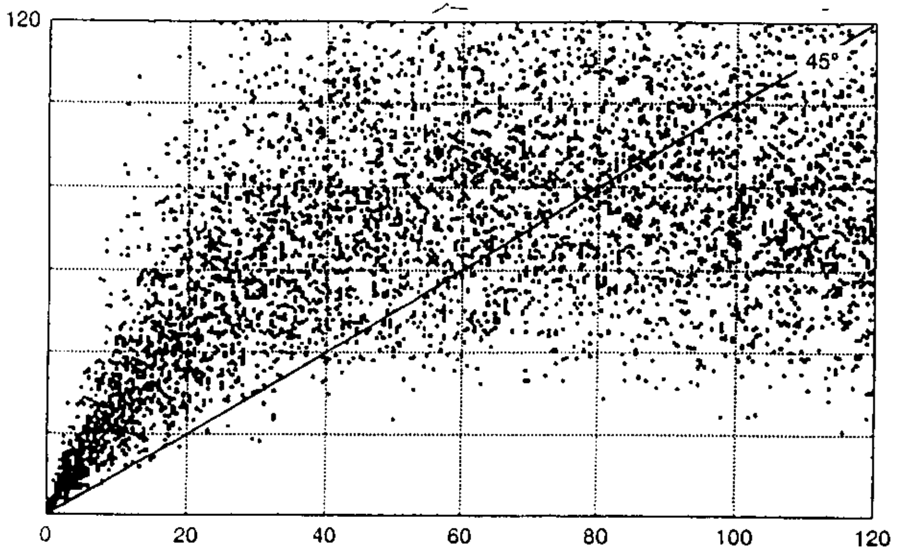
$\varepsilon_t$ , $\delta_t$ = multiplicative noises (unitary median)

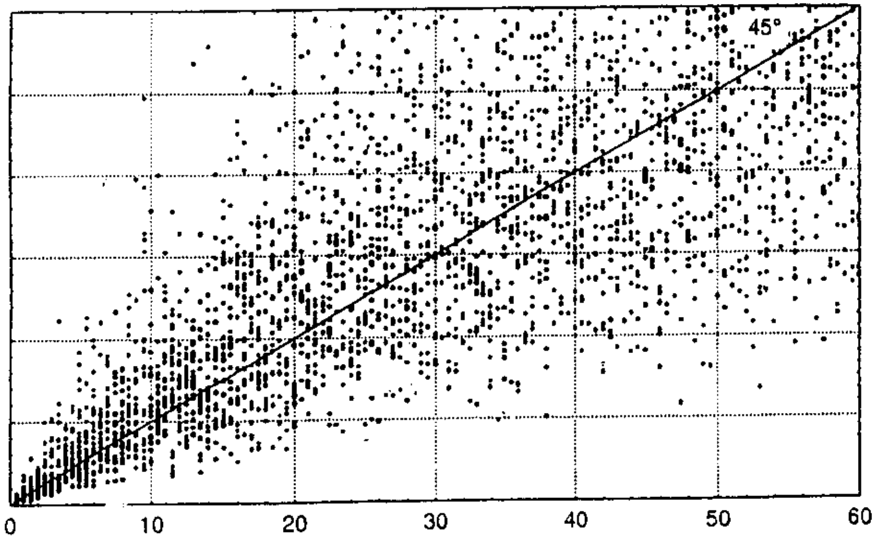
## MORAN DIAGRAMS





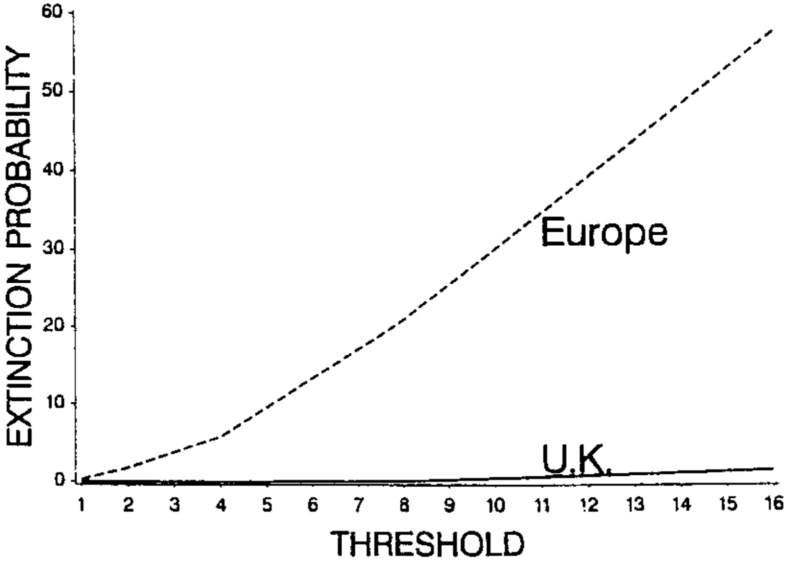
## Stochastic models





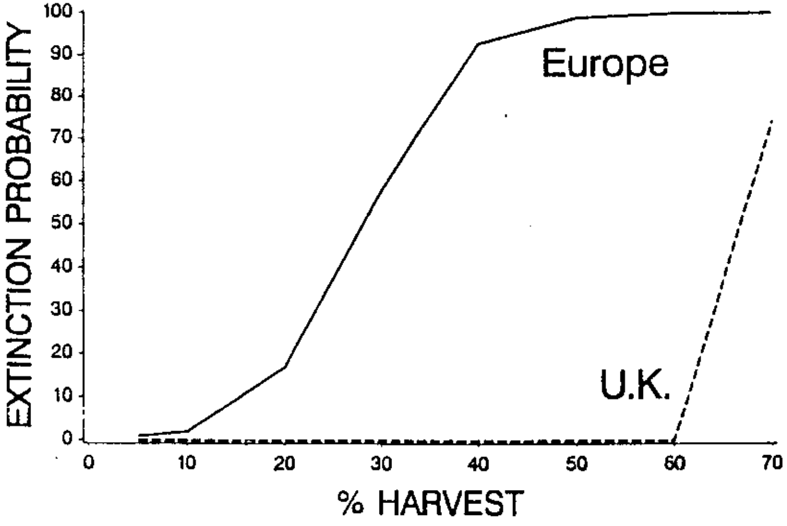
## 22 YEARS SIMULATIONS

No harvesting



Harvesting

threshold = 1



# JUVENILE DISPERSAL AND AREA OF THE PRESERVE

- Previous demographic models have been calibrated on study areas that average 600 ha
- Winter survival is comprehensive of juvenile dispersal

## What is the effect of the preserve area on grey partridge viability?

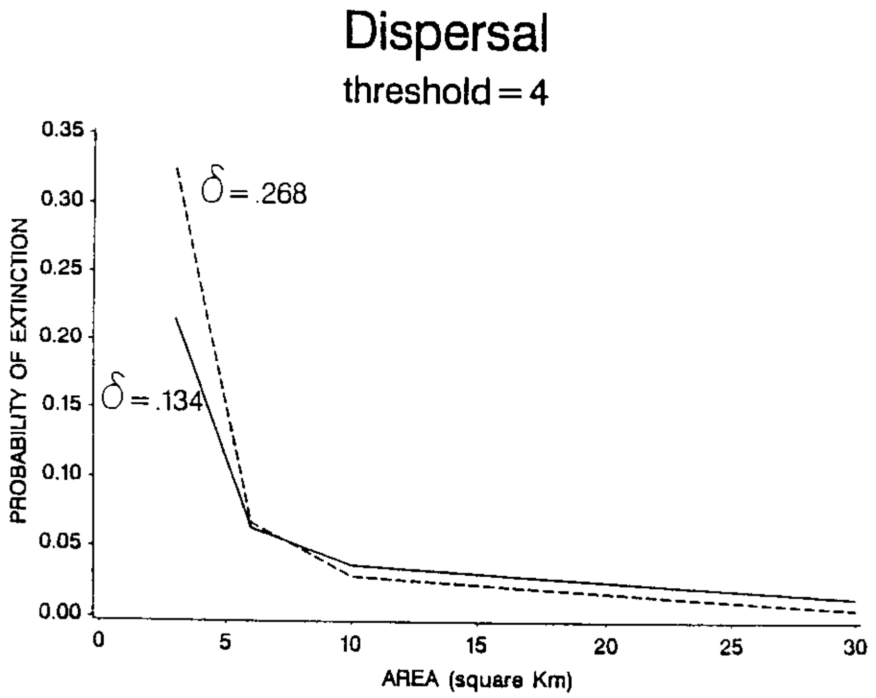
*Assumptions*
*1) Because of habitat fragmentation there is no immigration into local populations and juveniles that disperse are lost at all effects*
*2) Juveniles disperse randomly in any direction according to Brownian diffusion. We calculate*

$P_\delta(A)$ = *probability of dispersal outside area A for a juvenile characterized by diffusion coefficient* $\delta$

*With the hypothesis that juveniles are uniformly distributed over a square of area A at the beginning of the dispersal period*

$$P_\delta(A) = \frac{8\sqrt{\delta T}}{\sqrt{A}} \int_0^w cnorm(\xi)d\xi - \frac{16\delta T}{A}\left(\int_0^w cnorm(\xi)d\xi\right)^2$$

$w = \frac{\sqrt{A}}{2\sqrt{\delta T}}$ $T$ = *dispersal period* *cnorm* = *cumulated normal*



## CONCLUSIONS

- UK and continental Europe populations have different demographies
- Grey partridge is at high risk of extinction in continental Europe
- Continental Europe populations are not suitable for harvesting
- Larger preserve areas could effectively decrease the chance of extinction
- Our study is preliminary. More detailed management options such as setting up corridors connecting the preserves or reintroducing hedges necessitate a spatial and behavioral model to be evaluated