Thesis
3439

UNIVERSITY OF STIRLING
INSTITUTE OF BIOLOGICAL SCIENCES

TEMPORAL DYNAMICS AND SPATIAL PATTERNS OF GALLIFORM BIRDS IN TRENTINO - ITALY

Thesis submitted for the degree of Doctor of Philosophy

Isabella M. C. Cattadori

March 1999

06/00

ProQuest Number: 13916341

All rights reserved

INFORMATION TO ALL USERS
The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript
and there are missing pages, these will be noted. Also, if material had to be removed,
a note will indicate the deletion.

ProQuest 13916341

Published by ProQuest LLC (2019). Copyright of the Dissertation is held by the Author.

All rights reserved.
This work is protected against unauthorized copying under Title 17, United States Code
Microform Edition © ProQuest LLC.

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 – 1346

STATEMENT OF ORIGINALITY

I hereby acknowledge that this Ph.D. dissertation is solely based upon original work carried out by myself and has no been submitted for consideration previously for a higher degree at this or any other University. Any references henceforth used have been appropriately acknowledge.

Isabella M. Cattadori

March 1999

Acknowledgement

The first day in which this experience started it is still very clear in my mind. We were at the Centro di Ecologia Elpina and a man was keeling on the floor kissing a pile of papers saing: "***You have a treasure***!" That man was Peter, and the treasure was 30 years of data on gamebirds in Trentino. I have learnt a lot in these three years during which Peter has introduced me to three main things. First, an enthusiasm for biology and an understanding of the mechanisms in nature, I had always wanted to study biology and I can't imagine myself doing anything else. The second big experience was the hard work of a builders mate when I learnt to dig a floor with a pneumatic drill and fit panels to the wall. My hands were sore and my back stiff after the weekends but what a great pleasure to see the changes we had made to Peters steading ! I now think I could put my name towards the "Changing rooms" programme! The third important thing I was introduced to was the myth of Van Morrison and his distinctive way to sing and more important the stochastic rhythm that provided the background to this study.

So the first person I would like to thank, and it's never enough, is Peter. He is a great person, and he knows this! but I must stop before I come too boring. There are many other people I would like to thank. First must be Annapaola, I have to admit that sometimes she drives me crazy but that is Annapaola and one can not forget her easily once you have met her. I also would like to thank Gianni Nicolini, the director of the Centro di Ecologia Alpina who gave me the opportunity to do this Ph.D. and to work with a good group of people in a nice place. Big thanks to all my other colleagues at the Centro with whom I spent most of these three years and they never stopped supporting and encouraging my work. The colleagues, their gossip, their arguments and their friendship provided a good atmosphere and I have fond memories of the many good times we spent together.

Special thanks to Sandro, a great friend, how can I forget the hours spent together talking of everything and nothing, being trivial and getting cross or supporting each other during bad moments? Also, how can I ever thank Mary enough, she made me welcome in her house and she convinced me that the British cuisine is much better than an Italian expected! I also want to mention Tom who introduced me to Manchester United and the new English bands and Kitty who was so full of warmth, generosity and let me use her bathroom. All of them have been wonderful to me, a great family.

Last but least I want to thank my family (well I'm Italian how can I forget about THE FAMILY?). They always joke about my work and never take it seriously but now here is a good opportunity to sit down and read this thesis!? A special warm thanks to my mother who was always worried about me, my health and my work (another quality of the mamma italiana!) and who never stopped to looking after me, even through she always had an adventorous spirit herself.

Thanks again to everyone and all the many people I met during these three years, both in Italy and in Scotland.

ABSTRACT

This study examines the population dynamics of 5 species of closely related galliform birds in the Dolomites, north-east Italian Alps. The aim was to assess the dynamics of these populations at the edge of their European distribution and to investigate the patterns of spatial synchrony. Three main types of data sets were used in the analysis. First, the hunting statistics collected from 210 hunting areas between 1965 and 1994 for each of the 5 galliform species. Second, rock partridge count data from 29 sample areas during the period 1994 to 1998. Third, guts helminths collected from rock partridge shot between 1995 and 1998.

Tetraonid populations at the edge of their southern European distribution exhibited a weak tendency to cycle. These cycles only showed significant negative autocorrelation at half the cycle period and were classified as phase-forgetting quasi-cycles contrasting with the more regular oscillations recorded in the same species in Finland. Cycles were not found in time series of black grouse *Tetrao tetrix* or capercaillie *Tetrao urogallus*. Rock partridge *Alectoris graeca saxatilis* exhibited a higher tendency to fluctuate.

Rock partridge populations declined between 1965 and 1975 with populations in the western province declining earlier. Total winter loss and spring to summer loss of adults were the most important population parameters influencing the year to year change in numbers. There was some compensation to hunting mortality.

The hypothesis that macroparasites may be of significance in destabilising partridge abundance and generating cyclic oscillations was examined by investigating the intensity of parasite infection in cyclic and non cyclic populations. *Ascaridia compar* and *Heterakis tenuicauda* were prevalent in the rock partridge populations and significantly greater in cyclic populations than non-cyclic populations.

There were large variations in synchrony both within and between species and only weak negative relationships between synchrony and distance. Species in neighbouring habitats were more likely to be in synchrony than species separated by several habitats. A detailed spatial analysis on rock partridge populations found an increase in synchrony with scale from the population to meta-population level. Rock partridge clustered in two groups DRY and WET and synchrony was stronger in populations in the same habitat with populations in the dry habitat showing a higher tendency to cycle. The modelling of the long term dynamics of spatially structured populations indicated that environmental stochasticity was the main cause of synchrony although there is also some dispersal between populations and the importance of this varied between species.

Population viability analysis of the grey partridge *Perdix perdix* in populations in Britain between 1930-1960 and the "declining" continental populations from 1970 to 1994 confirms that the UK populations prior to 1960 were more resilient than the continental populations. Even very small harvesting cannot be tolerated by the present continental populations and this may indicate that the persistence of hunting activity, although with a limited effort, has contributed to the extinction of many sub-populations and is critically threatening the remaining ones.

CONTENTS

GENERAL INTRODUCTION

Many animal species are distributed in spatially structured populations as opposed to a large, continuos inter-breeding population. These structured populations are commonly termed metapopulations and their persistence in the natural environment occurs as a balance between extinction and colonisation through dispersal (Hanski & Gilpin 1991, 1997). The rate of extinction is determined by a combination of environmental stochastic perturbations and demographic stochasticity (Wiens 1997). Balancing this extinction is dispersal that plays a central role in the cohesion of populations in a fragmented landscape, and has important implication both demographically and in the maintenance of genetic diversity (Stancey et al. in Hanski & Gilpin 1997, Hedrick 1985).

The metapopulation concept can be defined broadly as a series of inter-connected, structured populations. What ever the definition, the ecological theory of metapopulation has developed faster than field studies and there is now a need for empirical studies to undertake detailed investigations that can test the theory. Questions of spatial dynamics in a heterogeneous landscape, and synchrony in species-specific or non-specific populations are of fundamental importance to the conservation of single species and to the design of nature reserves and managed population.

The galliform birds have been identified as suitable bioindicators for monitoring variations in the quality of the alpine habitat (Brendel 1994). Because of their high turnover rate, these species are likely to react very fast in response to natural factors, human disturbance or management activities and provide the benefit of being easy to monitor with both temporal and spatial data. In particular, rock partridge and rock ptarmigan have been considered as the most important species that reflect changes in the alpine environment because their distribution is restricted to the open habitat of the alpine prairies and rocky plateaux, respectively (Brendel 1994). Other gamebirds are also found in the alpine environment but are not restricted to a single habitat, for example black grouse, capercaillie and hazel grouse are all woodland species but inhabit a range of woodland types that vary in species association and structural composition. The Alps represent a good area for investigating the galliform birds since it is the southern range of the distribution of several grouse species and the northern extreme end of the rock partridge range. Thus, the study of the spatial and temporal patterns of these species at the edge of their European distributions provides an opportunity to examine two aspects of population dynamics. The first aspect we can investigate is if species at the southern edge of their European distributions exhibit similar temporal pattern and density dependent structure compared to species in the northern part of their range. Second, using these closely related species with distinct altitudinal distributions within each mountain groups we can investigate the tendency of synchronous dynamics within and between species and see if we can identify the role of stochastic environmental events in influencing the synchronous patterns between populations. In reality, all these species are influenced by anthropogenic factors, and habitat fragmentation while exhibiting similar life histories but inhabiting different habitats.

BROAD AIMS

The principal aim of this thesis was been to examine the spatial structure and the temporal dynamics of the galliform species in Trentino that include most of the Dolomites (north-east Italy) and to compare the patterns observed with those recorded in other populations in various parts of Europe. I selected the rock partridge as a central species to study since basic count data has been obtained, historic bag records of species abundance could be collected, spatial distribution patterns are available and information on parasite abundance was being carried out by colleagues at the Centro di Ecologia Alpina. Comparative spatial and long term temporal analysis were also undertaken on the four grouse species found in the Dolomites in an attempt to identify the common mechanisms responsible for the dynamics observed.

STRUCTURE OF THE THESIS

This thesis is divided into 10 independent chapters that represent single papers, published or in manuscript, on different aspects of the population dynamics of galliform birds. A final general discussion brings together the main interesting findings of each chapter. Each chapter has been done by myself in collaboration with Peter Hudson and other chapters include a number of other colleagues. Chapters 6 and 7 include parasitological analysis by

Annapaola Rizzoli while my contribution was the long-term analysis of population dynamics in rock partridge. In chapter 10, my contribution to the work done by Giulio De Leo was to carry out the basic demographic analysis using statistical tools.

The first two chapters are an overview of existing knowledge on the pattern of spatial synchrony in the animal populations and a description of the main mechanisms that influence this process. Chapter 1 investigates in details the main mechanisms causing spatial synchrony, developing aspects of the Moran effect using a basic modelling approach. Chapter 2 is a review of the Moran Effect and its role in synchronous populations of sheep in the St. Kilda Archipelago. The next five chapters investigate in detail the population dynamics of rock partridge. In particular, chapter 3 synthesises the relationship between species and habitat and suggests a multivariate model to single out the principal environmental variables affecting the presence of rock partridge in the fifties. Chapter 4 examines the population dynamics of rock partridge using long term hunting statistics and count data in different habitats of Trentino in an attempt to identify the general pattern of the populations in the last 30 years and single out the key factors influencing annual variation in abundance. Chapter 5 investigates the temporal dynamics of rock partridge populations and examines the cyclic dynamics and the spatial pattern of synchronous population fluctuations using hunting statistics. Chapter 6 and 7 describe the intestinal helminth comunity of rock partridge and relate the prevalence and abundance of the different species with the spatial pattern and the temporal dynamics of the species. The temporal dynamics of grouse species in the southern edge of their European distribution is investigated in chapter 8 using hunting statistics of 4 grouse species from the province of Trentino and applying the approach used for rock partridge in chapter 5. In chapter 9 the spatial pattern of synchrony of rock partridge and grouse species within and between species are examined in more detail using a modelling approach to identify the relative importance of dispersal and common stochastic events in causing spatial synchrony. Finally, in chapter 10 a population viability analysis of grey partridge in Europe is performed by means of stochastic demographic models, that explicitly accounts for variability in the vital rates and dispersal of the juveniles.

THE TRENTINO AND THE DOLOMITES

Trentino (6250 km²) is an autonomous province that include most of the Dolomitic Alps in north-east Italy. Altitude ranges from 65 m to 3750 m a.s.l. and more than 70% of the province is above 1000 m a.s.l. (Anon. 1992). The mountains fall into 18 discrete mountain groups that can be clustered into 3 different areas: a west and east area mainly characterised by volcanic and metamorphic rocks and wide central area with limestone mostly of which are calcareous rocks. Obvious valleys with anthropocentric activities and arable land separate the mountain groups (see figure 1 in chapters 3, 4, 5 8 and 9).

The climate of Trentino is dominated by two rainfall patterns. First, the annual precipitation that divides the province into three distinct areas: an eastern and a western wet zone where the rain exceed 1000 mm per annum, and a central dry zone with less than 1000 mm of rain per annum (Boato et al. 1988). Second, the seasonal distribution of the precipitation which divides the southern, pre-alpine, sub-continental area with an equinoctial peak in rainfall, from a northern area with continental conditions and a summer peak in rainfall (Gafta 1994). The combination of these two patterns determines 11 macro-climates.

Vegetation is well correlated with the climate and altitude, and despite the complexity of the environment, 4 distinct altitudinal associations can be identified. A sub-mediterranean zone with common species such as *Olea europaea, Cupressus semprevirens, Quescus ilex* and *Nerium oleander*, a sub-continental zone between 1200-1300m with species like *Castanea sativa, Fagus sylvatica* and *Abies alba*, a continental zone between 1600-1800m with *Pinus sylvestris, Picea excelsa, Larix decidua,* and *Pinus cembra*, and an alpine zone between 1800-1900m which shrubs of *Rhododendron* and *vaccinium* and open prairies and alpine meadows (Anon. 1989, 1992).

GENERAL INTRODUCTION TO THE GALLIFORM BIRDS IN THE ITALIAN ALPS AND TRENTINO

There are five common galliform species in the Italian Alps and Trentino maintains the most significant populations of rock partridge and grouse species of the Italian Alps (De Franceschi 1988, De Franceschi 1992a, b, c, d, Priolo & Bocca 1992, Artuso 1994). There are small populations of pheasant (*Phasianus colchicus*) and grey partridge (*Perdix perdix*) in the valleys but this study concentrates on the mountain species (Table 1 and Fig. 1a, b, c, d, e).

All five species are distributed throughout the Italian Alps and were found in most of the Alps between France and Slovenia until the end of the nineteenth century. During the first decades of this century the range of these species started decreasing and has continued up to present. At the end of 1950s, capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) disappeared from the western mountain groups and most of the central alpine and prealpine districts (De Franceschi 1992a, d, De Franceschi 1994a, b and Fig. 1d, e). Black grouse (*Tetrao tetrix*) decreased in abundance but colonised new areas favoured by the increase of woodland at lower altitudes and in areas previously used for agricultural and pastoral activities (De Franceschi 1992c, De Franceschi 1994c and Fig. 1c). Rock partridge (*Alectoris graeca saxatilis*) abundance fluctuated around quite stable densities over time during the first half of this century but dramatically collapsed in the last 40 years (Priolo & Bocca 1992, Bernard Laurent & De Franceschi 1994, Fig. 1b). A general decline in abundance was also observed in rock ptarmigan (*Rock ptarmigan*) inhabiting the mountain plateaux although no changes in the habitat were observed (De Franceschi 1992b) (Fig. 1a).

CAUSES OF POPULATION CHANGES: A REVIEW

Identifying the principal factors that cause population changes requires detailed long term monitoring of a range of population parameters and the collection of a representative range of environmental and biological variables that relate to requirements of the species. Probability of persistence depend on the interaction between the density dependent and density independent processes, influencing the population birth, death and dispersal rates. Despite growing knowledge on the galliform species within the Italian Alps the causes of their decline are not yet clear. Ever so, most authors agree that there are three main causes:

1. habitat changes or destruction,
2. anthropogenic activities
3. natural enemies: predation or infectious diseases.

To provide background to the thesis and the fact that most of the previous publications are in Italian I shall now review each of these in detail.

1 - *Habitat changes.* Changes in agricultural land use are considered the most important factor that has caused the contraction of range in the rock partridge and in the woodland grouse. On mountain areas, crops of cereals and scattered open patches for cattle grazing at low and medium altitude were abandoned and invaded by thick shrubs and natural broad-leaves trees (Fig. 2). In parallel, reforestation occurred supported with planting and the conversion of coppice to dense and old stands of woodlands not suitable for reproduction or refuge (De Franceschi 1994a, b, c). At present, the "natural" management of the woodland tends to maintain the heterogeneity and the complex structure of the forests, preserving the habitats with local species and improving natural regeneration of the wood. Other habitat changes have been associated with tourism, with an increase in mountain roads and skiing developements.

Climatic change has been considered another possible factor that has affected the habitat structure and led to a decrease in abundance of the galliform in the Alps. No long-term studies are available to confirm the direct effect of climate on population dynamics although it is generally accepted that there have been increased extreme conditions in both winter and summer climate. There is evidence that severe meteorological conditions during the hatching period or the winter season can affect abundance (Ramponi 1928, Glutz et al. 1973, Müller 1974b, Schroder et al. 1982a, Bernard Laurent 1990, Bernard Laurent 1992). Gluz Von Blotzheim et al. (1973) found a positive relationship between the climatic fluctuations and the oscillations in abundance of rock partridge at the beginning of the 1900s and De Franceschi (1994d) showed a negative relation between the mean daily temperature in late June and early July and the brood size of black grouse in Trentino. As such, it is possible that increased frequency of repeated cold and rainy seasons associated with changes in the habitat have resulted in the small and isolated populations suffering a greater mortality.

2 - *Anthropogenic activities.* This heading include disturbance from tourism, agro-silvicultural activities and hunting pressure. Tourism and the management of woods and

arable lands have had a high impact on galliform reproductive period (Klaus & Bergmann 1994). Nest desertion or its destruction, disturbance of the brood and young dispersal have all been influenced by anthropogenic factors (Anon. 1990, 1991, De Franceschi 1994a, b, c). Disturbance in winter on ski areas could be fatal for grouse species when the energy budget is reduced and the risk of predation increased (Müller 1977, Marti 1985, Klaus et al. 1989). An increase in ski areas and internal roads has been observed in the past 20 years in Trentino (Anon. 1989, 1992) and they are used during the critical periods of the species in winter or during reproduction in summer. Disturbance by cattle or sheep is restricted to small areas around the scattered farm buildings and do not seem to directly reduce the local galliform density. However, the decrease in the cattle abundance since the II World War has contributed to increased woodland succession into the alpine prairies and this has impacted rock partridge populations. Pesticides use and intensive agricultural technology have been restricted to the valleys and they impact has been low on the mountain galliforms species.

In the past, hunting pressure caused few problems in terms of persistence of the galliform populations. In general, hunters had to walk though mountains to hunt and invariably were only able to hunt relatively small areas. The increased accesses with mountain roads and the patchiness of suitable habitat has changed the situation so hunting is thought to have been responsible for the decrease of some species in some alpine districts. Hunting has been restricted in various parts of the Italian Alps and Trentino continues to restrict hunting to local people. Whether or not the hunting pressure caused the decrease in abundance of the galliform species is difficult to say, however it is evident but not demonstrated that hunting has had a high impact on isolated populations at low density.

3 - *Predation and disease*. Few data are available about predation on alpine galliform birds in Italy. There are some records concerning predation on nests and individuals of grouse by raptors (*Accipiter gentilis, Aquila chrysaetos, Buteo buteo*) and corvids (*Corvus corone cornix* and *corax*). In the Maritime Alps predation caused 85% of the natural mortality in rock partridge (Bernard Laurent 1989). Predation has also been identified recorded as one of the main causes affecting the breeding production in grey partridge and red grouse in Britain (Potts 1986, Hudson 1992, Hudson et al. 1996).

Previous workers have proposed that parasitic infections may have been the main cause of reduction of rock partridge abundance in the Italian Alps during the seventies although no empirical studies were carried out to confirm this hypothesis (Salvini & Colombi 1983). Meneguz and Rossi (1988) in Italy and Belleau and Leonard (1991) in France thought the abundance of parasites in rock partridge was not important. In contrast, Rizzoli et al. (1997) have found evidence of parasite induced reduction in rock partridge host fecundity. However, macroparasites such as the gut helminths are unlikely to cause declines in species. This is more likely to be caused by a series of epidemic outbreaks of microparasites but again, no data exist to test this hypothesis.

REFERENCES

Anon. 1989. Rapporto sullo stato dell'ambiente. 1 Assessorato al Territorio Ambiente e Foreste, Provincia Autonoma di Trento.

Anon. 1990. Censimento Tetraonidi, Gallo cedrone e Forcello. Provincia Autonoma di Trento, Servizio Foreste, Caccia e Pesca. Ufficio Caccia e Pesca.

Anon. 1991. Censimento Tetraonidi, Gallo cedrone e Forcello. Provincia Autonoma di Trento, Servizio Foreste, Caccia e Pesca. Ufficio Caccia e Pesca.

Anon. 1992. Rapporto sullo stato dell'ambiente. 2 Assessorato al Territorio Ambiente e Foreste, Provincia Autonoma di Trento.

Artuso I. 1994. Progetto Alpe. F.I.d.C., U.C.Z.A.

Bellau E. & Leonard P. 1991. Le parasitisme digestif automnal chez la Perdix bartavelle (*Alectoris greaca saxatilix*) le Lagopéde alpin (*Lagopus mutus*), le Tétras-lyre (*Tetrao tetrix*) dans le dépatement des Hautes-Alpes. Gibier Faune Sauvage. 8:161-173.

Bernard Laurent A. 1989. Importance de la prédation sur une popolation de Perdix rochassières (*Alectoris greaca saxatilix* x *Alectoris rufa rufa*) des Aples Méridionales. Rev. Ecol. (Terre Vie) 45: 321-344.

Bernard Laurent A. 1990. Biologie de reproduction d'une popolation de perdix rochassière *Alectoris greaca saxatilix* x *Alectoris rufa rufa* dans les Aples Méridionales. Gibier Faune Sauvage 45: 321-344

Bernard Laurent A. 1992. Densité en période de reproduction de la Perdix bartavelle *Alectoris greaca saxatilix* dans le massif des Ecrins. Rapport interne Parc National des Ecrins.

Bernard Laurent A. & De Franceschi, P.F. 1994. Statut, évolution et facteurs limitant les populations de perdrix bartavelle (*Alectoris graeca*): sinthèse bibliographique. In: Plans de restauration pour quelques galliformes européens: la gelinotte des bois, le grand tétras, le tétras-lyre et la perdrix bartavelle. Gibier Faune Sauvage, Game Wildlife 11. Hors série Vol. 1. Office Natl. Chasse, Paris: 267-304.

Boato S., Arrighetti A. & Osti F. 1988. Parchi e riserve naturali del Trentino. Temi Trento.

Brendel U., Mingozzi T. & D'Oleire Oltmanns 1994. Evolution of alpian avifauna. FUTURALP final report.

De Franceschi P.F. 1988. La situazione attuale dei galliformi in Italia. Ricerche recenti o ancora in corso. Problemi di gestione e prospettive per il futuro. In Spagnesi M. & Toso S. (eds.) Atti I Conv. Naz. Biol. Selvaggina. Suppl. Ric. Biol. Selvaggina XIX: 165-180.

De Franceschi P.F. 1992a. Francolino di monte (*Bonasa bonasia*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 697-708.

De Franceschi P.F. 1992b. Pernice Bianca (*Lagopus lagopus*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 708-721.

De Franceschi P.F. 1992c. Gallo Forcello (*Tetrao tetrix*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 721-739.

De Franceschi P.F. 1992d. Gallo Cedrone (*Tetrao urogallus*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 740-756.

De Franceschi P.F. 1994a. Statut, distribution géographique et facteurs limitant de la gelingotte de bois (*Bonasa bonasia*) in Italie. In: Restoration plans for some European galliformes: hazel grouse, capecaillie and black grouse. Gibier Faune Sauvage, Game Wildlife 11. Hors série Vol. 2. Office Natl. Chasse, Paris: 141-160.

De Franceschi P.F. 1994b. Statut, distribution géographique et facteurs limitant du gran tétras (*Tetrao urogallus*) in Italie. In: Restoration plans for some European galliformes: hazel grouse, capecaillie and black grouse. Gibier Faune Sauvage, Game Wildlife 11. Hors série Vol. 2. Office Natl. Chasse, Paris: 161-184.

De Franceschi P.F. 1994c. Statut, distribution géographique et facteurs limitant du tétras-lyre (*Tetrao tetrix*) in Italie. In: Restoration plans for some European galliformes: hazel grouse, capecaillie and black grouse. Gibier Faune Sauvage, Game Wildlife 11. Hors série Vol. 2. Office Natl. Chasse, Paris: 185-206.

De Franceschi P.F. 1994d. Black grouse Tetrao tetrix population on Mount Baldo (Verona, Italy), 1985-90. Atti 6^ Convegno Italiano di Ornitologia, Museo Regionale di Scienze Naturali, Torino.

Gafta D. 1994. Tipologia, sinecologia e sincorologia delle abetine nelle Alpi del Trentino. Braun-Blanquetia, Review of Geobotanical Monographs vol. 12.

Glutz Von Blotzheim U.N., Bauer K.M. & Bezzel E. 1973. Handbuch der Vögel Mitteleuropas. Band 5:Galliformes und Gruifomes. Frankfurt am Main.

Hanski I.A. & Gilpin M.E. 1991. Metapopulation dynamics: brief history and conceptual domain. Biol. J. Linnean Society, Academy Press.

Hanski I.A. & Gilpin M.E. 1997. Metapopulation Biology. Ecology, Genetics and Evolutions. Academic Press.

Hedrick P.W. 1985. Genetics of Populations. Jones & Bartlett, Boston.

Hudson P. J. 1992. Grouse in Space and Time. Game Conservancy Trust. Fordingbridge.

Hudson P. J., Newborn D. & Robertson P.A. 1996. Geographical and seasonal pattern of mortality in red grouse *Lagopus lagopus scoticus* populations. Wildlife Biology 2: 79-87.

Klaus S., Andreev A.V., Bergmann H.H., Müller F., Porkert J. & Wiesner J 1989. Die Auerhühner. Die Neue Brehm-Bücherei. Ziemsen, Wittemberg, Lutherstadt.

Klaus S., Bergmann H.H. 1994. Distribution, status and limiting factors of Capercaillie (*Tetrao urogallus*) in central Europe, particularly in Germany, including an evauation of reintroductions. In: Restoration plans for some European galliformes: hazel grouse, capecaillie and black grouse. Gibier Faune Sauvage, Game Wildlife 11. Hors série Vol. 2. Office Natl. Chasse, Paris: 57-80.

Marti C. 1985. Unterschiede in der Winterökologie von Hahn und Henne des Birkhuhns (*Tetrao tetrix*) in Aletschgebiet (Zentralalpen). Orn. Beob. 82:1-30.

Meneguz P.G. & Rossi L. 1988. Indagine parassitologica sulla fauna minore di montagna oggetto di prelievo venatorio: risultati preliminari. In Spagnesi M. & Toso S. (eds) Suppl. Ric. Biol. Selvaggina 14: 639-640.

Müller F. 1974b. Hahn in Ruh. Pirsch 26: 50-52.

Müller F. 1977. Wieviel Störung vertragen unsere Rauhfushühner? Nationalpark 13: 9-13.

Potts R.G. 1986. The Partridge. Pesticides, Predation and Conservation. Collins

Priolo A. & Bocca M. 1992. Coturnice (*Alectoris graeca*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 766-777.

Ramponi S. 1928. I Tetraonidi. - Biblioteca Venatoria vol II, Monauni Trento.

Rizzoli A., Manfredi M.T., Russo F., Rosà R., Cattadori I. & Hudson P.J. 1997. A survey to identify important macroparasites of rock partridge (*Alectoris graeca saxatilis*) from Trentino. Parasitologia 39: 331-334.

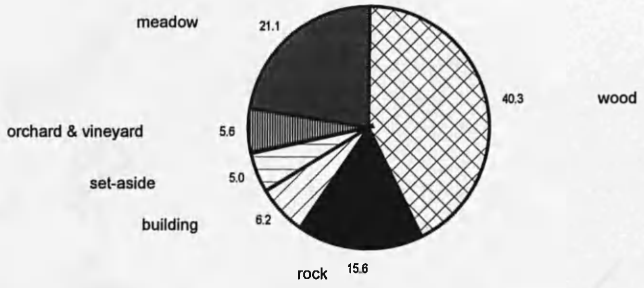
Salvini G.P. & Colombi G.C. 1983. La Coturnice. Studi sulla popolazioni della Coturnice delle Alpi Unione Nazionale cacciatori Zona Alpi.

Schröder W., Schröder J & Scherzinger W 1982a. Über die Rolle der Witterung in der Popolationsdynamik des Auerhuhns (*Tetrao urogallus*) J. Orn. 123: 287-296.

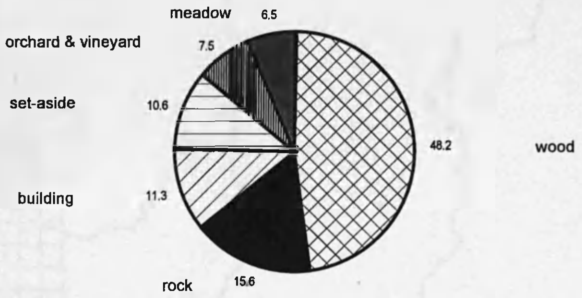
Wiens J.A. 1997. Metapopulation Dynamics and Landscape Ecology. In: Hanski I.A. & Gilpin M.E. (eds). Metapopulation Biology. Ecology, Genetics and Evolutions. Academic Press.

SPECIES	Average Altitudinal Range (m)*	Suitable Habitat	Clutch size (juv./brood)	Brood size (juv./brood)	Trend in Trentino
Rock partridge (*Alectoris graeca saxatilis* B)	800-1900	Alpine prairies, meadows	8-10°	5.5-7.5°	- & 4-8
Rock ptarmigan (*Lagopus mutus helveticus* T)	2000-2400	Plateaux	5-9^	1.5-4.5^	- & 5
Black grouse (*Tetrao tetrix* L)	1400-1900	Timberline	7-9^	3.4-5.5^	-
Capercaillie (*Tetrao urogallus* L)	1100-1500	Broad leaf and coniferous wood	6-9^	1.5-3.1^	-
Hazel grouse (*Bonasa bonasia* L)	700-1200	broad leaf wood	7-10^	2-3.7^	- & 6

Table 1. Basic populations characteristics on galliform birds in the Italian Alps. * Artuso 1994, ^ De Franceschi 1992a, b, c, d, ° Priolo & Bocca 1992.



1950's



1990's

Figure 2. Pie charts showing the proportion of habitats types in Trentino during the two decades of the fifties and nineties

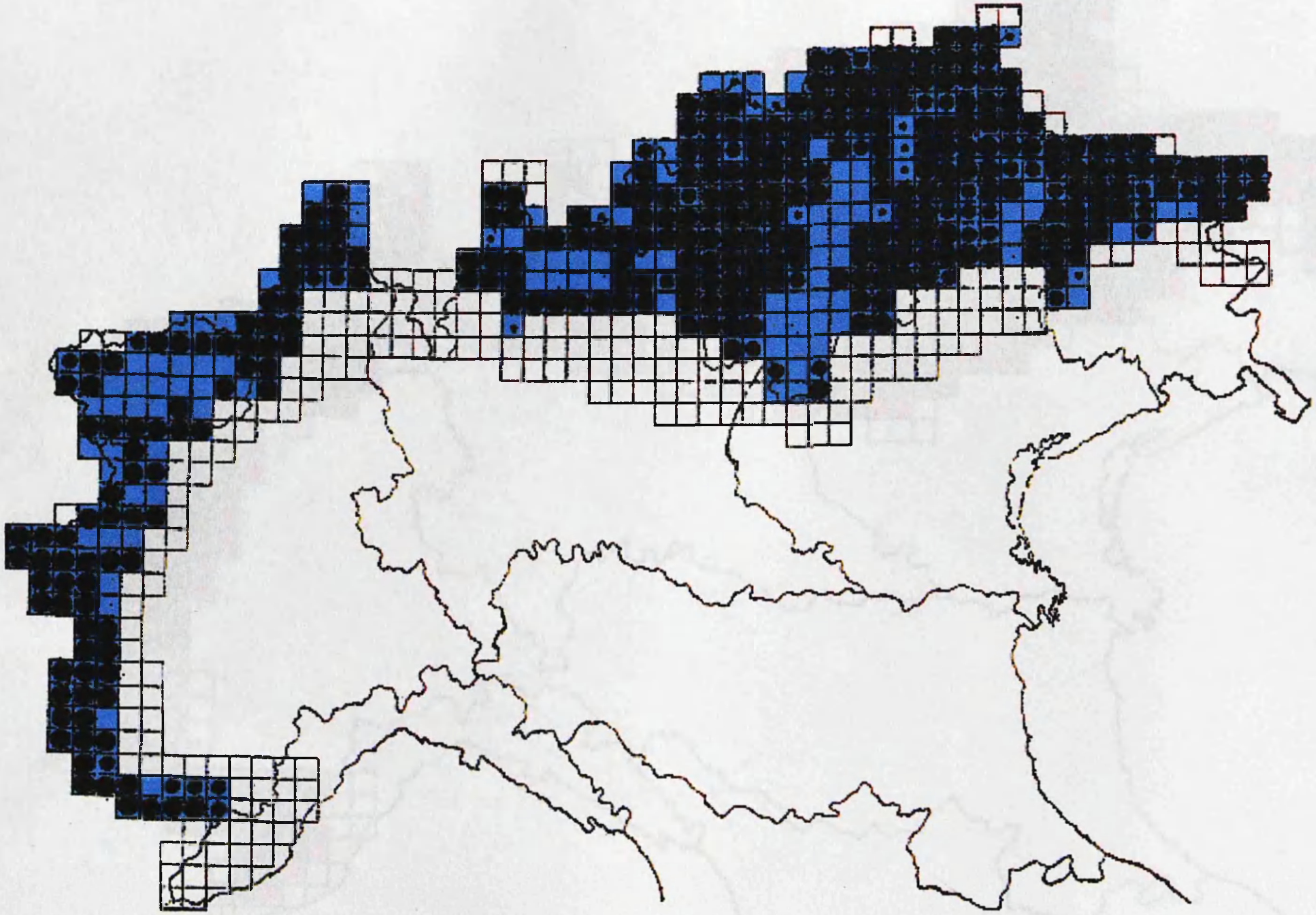


Figure 1a. Distribution map of the Rock ptarmigan in the Italian Alps during the 1980's (from Artuso 1994, modified).

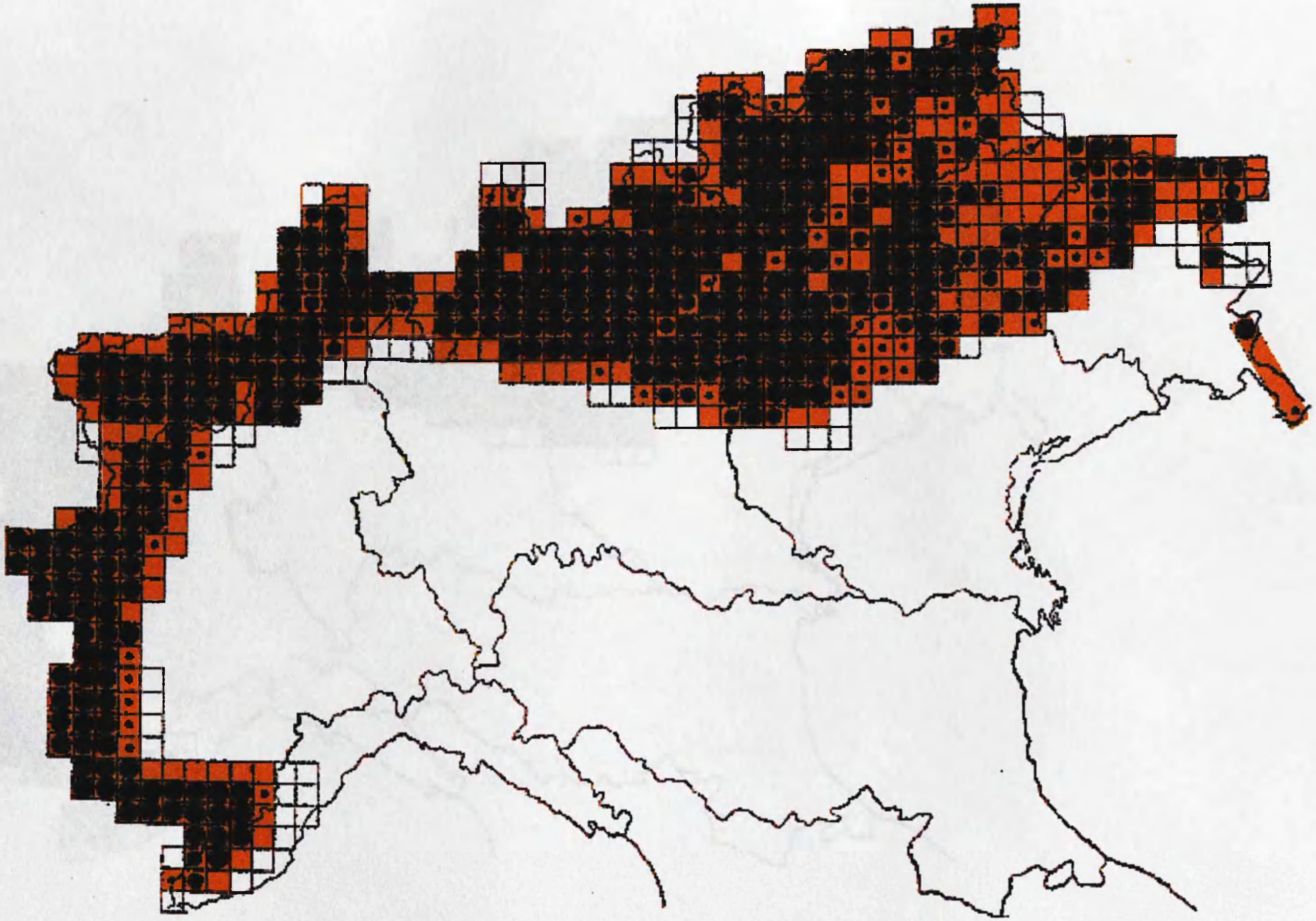


Figure 1b. Distribution map of the Rock partridge in the Italian Alps during the 1980's (from Artuso 1994, modified).

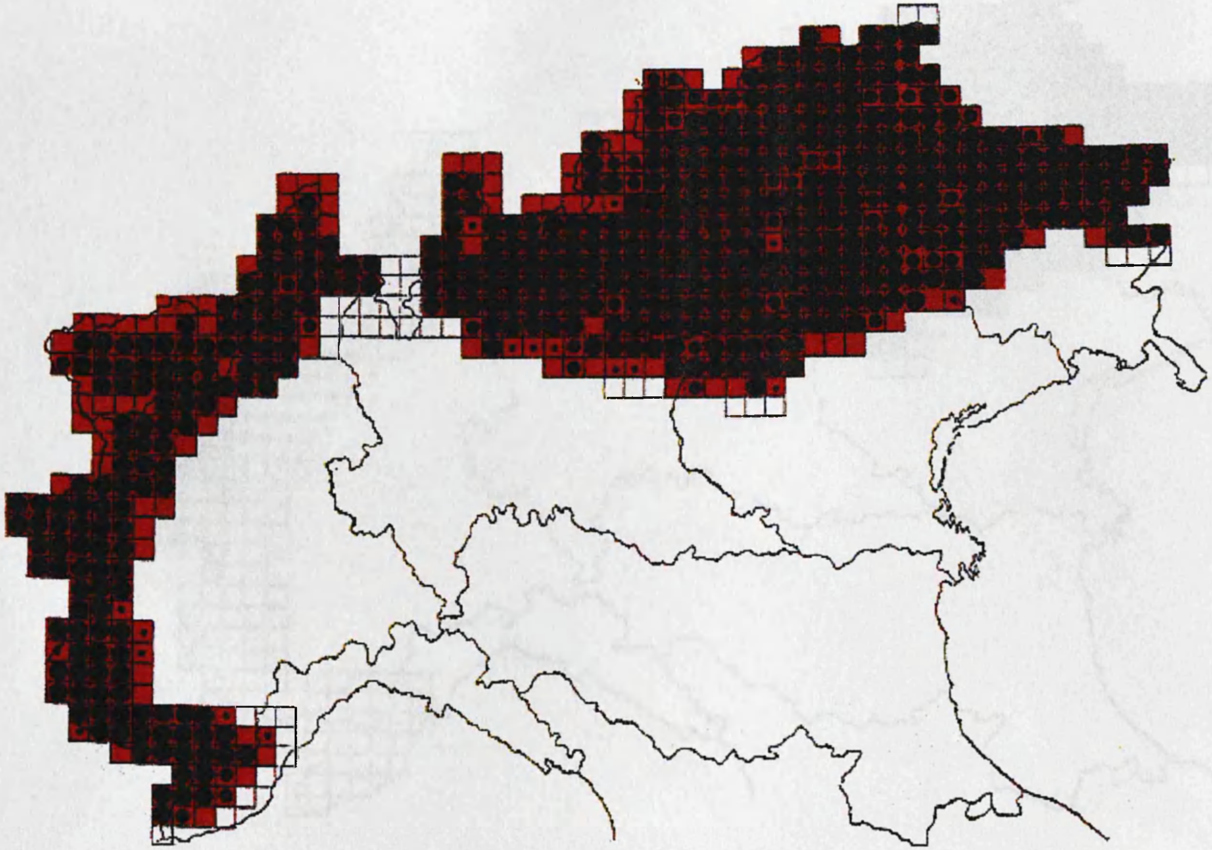


Figure 1c. Distribution map of the Black grouse in the Italian Alps during the 1980's (from Artuso 1994, modified).

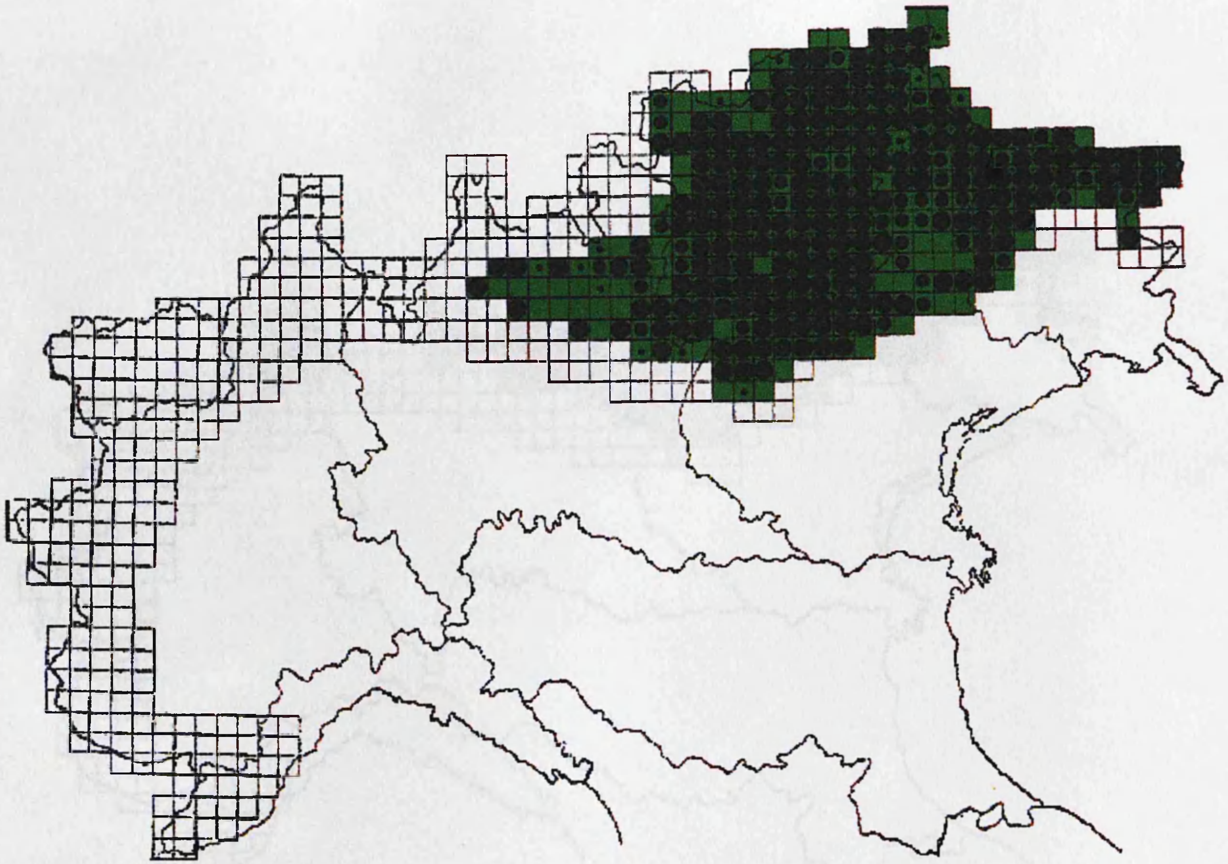


Figure 1d. Distribution map of the Capercaillie in the Italian Alps during the 1980's (from Artuso 1994, modified).

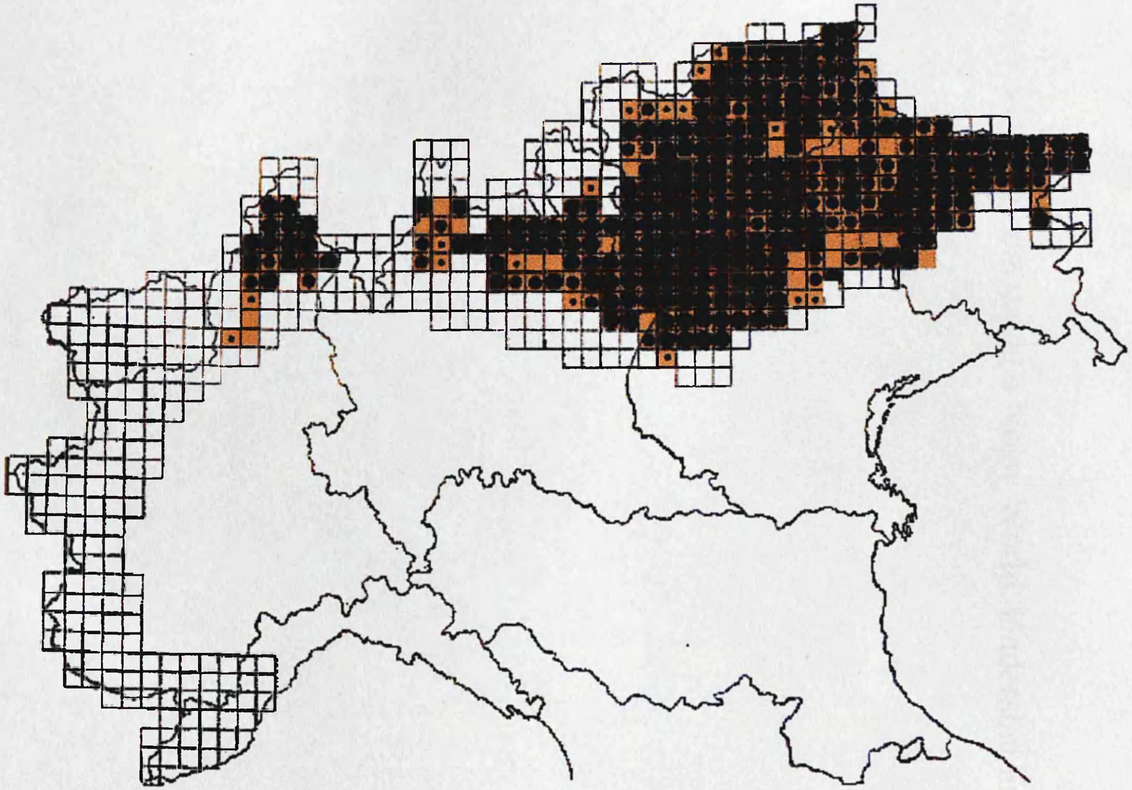


Figure 1e. Distribution map of the Hazel grouse in the Italian Alps during the 1980’s (from Artuso 1994, modified).

CHAPTER 1

Population Synchrony in a Noisy World: Understanding the Moran Effect

POPULATION SYNCHRONY IN A NOISY WORLD: UNDERSTANDING THE MORAN EFFECT

Isabella M. Cattadori & Peter J. Hudson

This paper summarises the existing knowledge on the pattern and causes of spatial synchrony in the animal populations. Synchronous fluctuations in abundance were initially recorded in cyclic populations but have now been observed in a range of other species that do not exhibit cyclic fluctuations. Three main hypotheses have been proposed to explain synchrony: (1) dispersal between populations, (2) common stochastic events, often referred to as the Moran effect and (3) large-scale predator-prey interaction. This study explores how these processes operate and undertakes a more detailed analysis of the role of the Moran effect in causing synchrony.

The traditional approach to population dynamics has been to investigate the temporal changes in spatially unstructured populations and to capture their dynamics through simplified deterministic models. In general, many of the early workers ignored the spatial structuring of populations and assumed that emigration and immigration were in balance and that populations were essentially homogenous unit. In reality, such assumptions are false and populations usually exhibit a spatial structuring with interactions at a range of scales. May (1994) pointed out that the majority of field studies are undertaken in a time frame much less than the life expectancy of the species studied and within a spatial area equivalent to less than the home range of the average individual. Consequently, while studies on temporal dynamics have been revealing they have been limited and at times probably drawn wrong conclusions without incorporating estimates of dispersal in and out of populations. This has become more evident with the emergence of the concept of metapopulation dynamics and landscape ecology (Wiens 1995a, Hanski & Gilpin 1997).

The original view of a metapopulation was of a “population of populations” that suffered periodic extinction and colonisation events and appeared as “blinking lights in the dark"(May 1994). More recently the definition has been widened to incorporate most spatially structured populations that experience immigration and emigration. The concept has allowed us to view populations as a series of inter-linked entities rather than part of a continuous and homogeneous population. The metapopulation concept emphasises the importance of landscape structure so we now view the habitat as a mosaic of different components with boundaries and connections that allow individuals to disperse between subpopulations and interact with habitat structure. Parallel with the development of the metapopulation concept and the more explicit field of landscape ecology, there has been an increasing interest in the processes that link spatially structured populations. In particular an interest in the spatial patterns of populations and the mechanism that cause synchrony in the fluctuations in abundance.

Synchrony was initially recorded in cyclic Canadian lynx (*Lynx canadensis*) populations (Moran 1953b) but has now been reported in a wide range of species that do not necessary exhibit cyclic changes in abundance (Ranta et al. 1995a, 1997a, b, c, Heino et al. 1997). Identifying the cause of this pattern and the mechanism that operate at different spatial scales is of fundamental importance to our understanding of how animal populations persist and hence for the conservation of species (Heino et al. 1997, Heino 1998, Palmqvist & Lundberg 1998). In fact, if populations are spatially isolated then stochastic perturbations, be they demographic or environmental, may drive some of these scattered populations to extinction. On the other hand if populations are linked then local extinction will be followed by rapid recolonisation of the empty habitat.

This review summarises the existing knowledge on the patterns of synchrony observed in animal taxa and investigates the modelling used to explain the possible mechanisms involved before taking a more detailed examination of the Moran effect and how it operates.

Estimating Synchrony

Synchrony between populations is usually estimated by cross correlation analysis at time lag 0 using the standard product-moment correlation coefficient. In some instances workers look for time delays in synchrony and have examined correlation coefficients with time lag $\neq 0$. A major assumption of serial correlations and cross correlations is that data at year t are independent of data at year $t-1$. This is not the case although this assumption is rarely respected. A second problem of independence arises when we correlate more than one pair of time series. When there is a significant correlation between population A and population B and between population B and population C then out of necessity there will be a correlation between A and C and yet this correlation is not independent of the other two correlations (Pollard 1991, Hanski & Woiwod 1993, Sutcliffe et al. 1996). As such, in a cross correlation analysis between 10 populations only 17 correlations are independent, 9 correlations from the first population and 8 form the second and all subsequent relationships can be derived from the previous correlations. A simple and effective method to overcome the non independence of the data and avoid Type I errors is to produce a null hypothesis and test against this using the bootstrapping method (Efron 1992, Efron & Tibishirani 1993, Ranta et al. 1995a, b). This involves choosing a pair of populations, undertaking a random resampling of the original data and generating new "null time series". These null time series can then be used to estimate the expected correlation coefficient and its confidence limits.

Patterns of Synchrony

Seasonal synchrony in the pattern of reproduction by females is a well-known phenomenon in a large number of species that lead to seasonal changes in abundance between populations (Iason & Guinness 1985, McShea 1989, Labin 1993). However this strong seasonal correlation in breeding activity will not lead to annual synchrony unless year to year variation in breeding production is synchronised through some environmental factor and populations are regulated by similar density dependence. In general the null hypothesis is there will be no synchrony between populations or, with a cyclic species fluctuating with a period n, at the very least a n^{-1} probability of being in synchrony. In this respect we say "at least" since populations slightly out of perfect synchrony may still appear statistically in synchrony. In fact, synchrony between populations has now been well documented in a wide range of species of different taxa (Table 1).

Synchrony may vary with the scale of the process. For example, some workers have found close synchrony at both local and regional scales but not at intermediate scales (Thomas 1991, Sutcliffe et al. 1996). This could come about through different mechanisms operating at different scales. Three clear patterns commonly emerge when the cross correlation is plotted against distance between populations. First, and the more frequent of cases, a decrease in synchrony with distance, second little or no decay in the strength of synchrony over distance and third large variation in synchrony between populations falling to little synchrony at greater distances.

At local scale where distances between the populations is relatively short, dispersal is likely to be the principal cause of correlated population dynamics and will produce a decrease in synchrony with distance (Ranta et al 1995a, b). The mobility of the individuals and the fragmentation of the habitat affect the general pattern of the spatial correlogram, so that for less mobile species or species in a more fragmented habitat, synchrony breaks down beyond a relatively short distance. At the regional scale, local environmental heterogeneity is averaged out and correlated environmental perturbations become the driving force of synchrony. The pattern this produces is a relatively constant synchrony with distance (Myers 1998, Cattadori et al. 1999). Since the movement of individuals is restricted over such large distances the similarities in the intrinsic dynamics of the populations associated with variations in habitat and environmental characteristics will be more important to the synchrony. As such, populations with the same linear density dependent structure, usually in the same habitat type, will be more in synchrony that populations with different density dependent structure associated with different habitats.

The patterns generated by environmental variation are determined by two stochastic elements, first the total year to year variation and second the error of this variation between localities, and they are termed regional and local stochasticity, respectively (Ranta et al. 1995a, b, 1997a, Heino et al. 1997). When the local stochasticity is relatively small then populations can be in synchrony over large areas at a relatively constant level but when the local stochasticity is high then we can observe large variations between populations and a weak and negative fall in synchrony with distance. Even so, differences in the slope and shape of the density dependence can have profound effects on the patterns of synchrony.

Mechanisms of Synchrony

Since synchrony was initially identified in cyclic species, workers assumed that the two were linked and the factor that caused the cycles would also be the cause of synchrony. Subsequently this led to a search for global causes such as forest fire cycle and sunspots or ozone cycles (Royama 1992, Sinclair et al. 1993). Moran (1953b) later pointed out that the mechanism that caused synchrony may well be independent of those causing regular oscillations. This was then confirmed by other studies that found that non-cyclic populations could exhibit synchronous fluctuations to the same intensity (Ranta 1995a, Cattadori et al. ms). Recently, alternative hypotheses have been proposed and it is generally accepted that the following three are the more parsimonious.

1- Dispersal between populations (Maynard Smith 1974).
2- The stochastic effect of common environmental events on populations with the same density dependence; commonly referred to as the Moran effect (Moran 1953b, Hanski 1991, Royama 1992).
3- Large scale trophic interactions, usually through synchronised levels of predation (Ydenberg 1987).

These mechanisms are not mutually exclusive and their relative importance seems likely to depend on the scale of the process.

1. Dispersal

Density dependent or density independent dispersal of individuals between populations can drive two populations asymptotically to synchrony. Maynard Smith (1974) defined the dispersal between two neighbouring populations as either being conservative, that is all dispersing individuals survive, or not conservative in which a proportion of the dispersing individuals die. When dispersal is conservative then populations will fluctuate in synchrony with the same amplitude, while if dispersal is not conservative or a fraction of individuals disperse to different populations then synchrony will be observed but the amplitude of the oscillations in the systems will be reduced (Maynard Smith 1974). The amplitude will remain the same when there is dispersal between two populations with different dynamics although a gradual change in phase will be observed in the weaker population that will move in synchrony with the other. Non conservative dispersal with mortality during dispersal will tend to stabilise the dynamics of population and its fluctuations (Ruxton et al. 1997). Moreover, migration alone can prevent global extinction when the populations are isolated and with a chaotic dynamics (Ruxton 1994). In this case dispersal has a stabilising effect in the fact that temporally maintain the persistence of the metapopulation.

At the local scale we may expect dispersal between neighbouring populations to be relatively high although the actual rate will depend on relative population densities, distribution of individuals, species mobility and the connectance between the populations. Connectance will to some extent be determined by habitat patterns, if the habitat is homogenous and continuos most of the movements will be diffusive and will decrease exponentially with distance. However, if the habitat is fragmented the movements will be more affected by the density of the original population, the amplitude of its fluctuations and how the species use the discrete habitat patches as stepping stones between populations. Numbers and rate of dispersal may increase with density and in relatively mobile species synchrony will be greater between neighbouring than distant populations. If the fragmentation of the habitat is greater than the dispersal distance, populations isolated but in phases will be driven apart by asynchronous events.

Dispersal is believed to be the main cause of synchrony at local scale in many populations of invertebrate (Pollard 1991, Thomas 1991, Hanski & Woiwod 1993, Sutcliffe et al. 1996) and vertebrate (Heino et al. 1997). However there have been no clear experiments on natural populations that have manipulated dispersal in a controlled manner. Dispersal has also been proposed as the driving force of synchrony for grouse populations and a variety of other animal species over large geographical areas in Finland and for the lynx and snowshoe hare in Canada (Lindström et al. 1996, Ranta et al. 1995a, b, 1997 a, b, c and Fig. 1). While most of these species could cover long distances (Cramp & Simmons 1980, Johnsgard 1983) the hypothesis that dispersal is the cause of synchrony between distant populations is not likely. In contrast it is possible that the populations have been combined from areas that tend to reflect political boundaries rather than ecological divisions or that the wide spread correlations between the environmental perturbations slowly break down due to the gradual change in the uniform environmental conditions.

2. The Moran Effect

The effect of correlated environmental factors on the synchronous dynamics of widespread populations was first described by Moran (1953b). Investigating the long temporal series of the lynx data from the fur trade of the Hudson's Bay Company, Moran concluded that if two populations with the same density dependence structure were influenced by spatially correlated environmental stochastic factors, they would exhibit synchronous fluctuations in abundance. However this does assume that the density dependence structure of the populations is linear. When a similar linear density dependence is observed the cross correlation between populations will be equal to the correlation between the stochastic events that influence the populations. In the description of the temporal pattern of the lynx data, Moran used a simple environmental stochastic process to avoid any cyclic effect of the model (Moran 1953a) and it consisted of a second order linear autoregressive function that incorporated a stochastic, density independent event. The autocorrelation generated by this process closely represented the 10 years cycle with the random component maintaining the oscillations and synchronising the fluctuations between populations. To investigate the role of environmental stochasticity on synchrony Moran analysed the effect of some climatic variables on the number of furs collected and observed that the two data sets were correlated both at time t and at time $t-1$. He dismissed the possibility that the pattern could be generated by the trapping efficiency or by the effect of weather on the trappers and proposed the more plausible hypothesis that the weather was acting directly or indirectly on the populations but not through the trapping efficiency. Moran did not demonstrate that weather was the driving force that synchronised the lynx cycle over the whole of Canada although his final results suggested that the lynx-hare relationship determined the cyclic fluctuations and the weather affected the synchrony.

While the Moran theorem was first proposed at the beginning of the fifties, only in the last decade the interest in this process has increased (Fig. 2). This has probably arisen because of the emerging interest in spatial processes and it is worth noting that reference to the

Moran effect has exponentially increased in parallel with reference to the concept of metapopulation (Hanski & Gilpin 1997 and Fig. 2)

More recently Royama (1992) examined Moran's approach and confirmed the validity of his hypothesis. Royama simulated random time series with similar autoregressive parameters and varied strength of the stochastic terms. The time series demonstrated that the populations with the same structure and correlated stochastic perturbations exhibited synchrony while there was no synchrony between those without common stochasticity (Royama 1992 Fig. 2.22).

The effect of wide spread and common environmental perturbations have been proposed as the principal driving force of synchrony between populations at regional scale (Hanski & Woiwod 1993, Sutcliffe et al. 1996, Myers 1998, Cattadori et al. 1999, Cattadori et al. ms). Much of this work has been unable to demonstrate the importance of common stochastic events since testing empirically this hypothesis at the population level is logistically difficult. However, recently Grenfell and co-workers (1998) demonstrated how stochastic climatic events could synchronise the unstable dynamics of populations of sheep in the St Kilda Archipelago. Investigating the dynamics of populations inhabiting different islands, where dispersal between islands is prevented by the lethal Atlantic swell, they demonstrated that the synchronous periodic crashes of the populations were caused by March gales acting on high density populations. The population exhibited non-linear density dependence and the impact of the gales was greater but more varied above a specific threshold. The synchrony observed is in fact a tension between the synchronising effects of the gales and the desynchronising effects of the non-linear density dependence.

3. Predator-Prey Interaction

When predation pressure varies between years and is correlated between prey populations this can lead large scale synchronised predation that will generate synchrony between prey populations. What is more, if the density dependence in the prey populations is similar then occasional periods of heavy predation, similar to the occasional environmental perturbations, can lead to large-scale synchrony in the prey populations. An example of this is the occasional large changes in the abundance of raptors seen in parts of Canada when climatic conditions or the collapse of the rodent populations leads to a southerly migration of raptors. Generally speaking we can expect nomadic predators such as the raptors to be important in causing synchrony in this manner. This has been supported by studies on rodents in Northern Fennoscandia (Korpimaki & Norrdahl 1989a, Ydenberg 1987, Ims & Steen 1990) that found nomadic raptors determining the synchronous dynamics in the populations of rodent over wide spread areas. Heikkilä et al. (1994) carried out a survey on populations of rodents from a number islands and proposed that local large-range carnivores had a major role in causing synchrony of vole populations from different islands. There was insufficient data to examine this hypothesis in detail although the results seem quite clearly to suppose that the semi-generalist predator, the stoat, produced offspring that dispersed to other islands where able to synchronise populations of prey at a regional scale. One possible conclusion is that predators with different hunting strategies determine similar density dependence regulation on the prey and consequently a synchronous pattern both within and between species. As expected predators may also cause synchrony between populations of the same species by moving between them to exploit periods of prey abundance and thus smoothing the differences between populations and bringing them in phase (Ydenberg 1987, Ims & Steen 1990, Steen et al. 1990, Heikkilä et al. 1994, Norrdahl & Korpimaki 1996).

Modelling the Moran Effect – Current Situation

Royama (1992) re-examined the concept formulated by Moran and called it "The Moran effect" emphasising its significance in studies of persistence and conservation. More recently Ranta and colleagues (1995a, b) have investigated the relative importance of dispersal and the Moran effect in causing spatial synchrony within species. They simulated the dynamics of a number of Finnish species by applying a range of statistical models based on the Ricker equation. Again, the results clearly showed that the Moran effect is capable of causing synchrony between populations over large distances while dispersal generated a decrease in synchrony with distance. Moreover, superimposing the Moran effect on dispersal retained the general pattern of a decrease in synchrony with distance. The relationship between synchrony and distance did not vary significantly between a first and second order logistic model or even a Ricker function with age-structured dynamics. Ranta et al. (1997a) further modified the Ricker model by incorporating delayed density dependent regulation according to Turchin (1990) and Kaitala et al. (1996a, b). In this instance the Moran effect was more likely to produce synchrony in a broad spectrum of environmental events. As Moran (1953b) noted and then Ranta (1997a) confirmed, the cause of the population cycle and synchrony are two independent processes although the mechanism driving the cycle could also cause synchronous fluctuations in populations with the same density dependence structure. Indeed Hudson & Cattadori (unpublished) have demonstrated that the Moran effect can reduce synchrony when the populations exhibit year to year variations in the strength of their density dependence structure. Synchrony may also occur when the assumption of linearity is violated, in fact while non-linear density dependence will tend to accentuate the differences between populations (Grenfell et al. 1998), non-linear processes can still be in synchrony if a low correlation between the residuals occur in a uniform environment (Moran 1953b).

From a mathematical point of view the delayed density dependent model presented by Turchin (1990) and modified by Kaitala et al. (1996a, b) is severely restricted. To produce consistent results the model must have a positive equilibrium and the autoregressive parameters with negative values, while it is in contradictions when positive values are selected (Royama 1992, p. 154). When the relative strength of the autoregressive parameters is explored using the bi-dimensional space represented by Royama‘s triangle (Royama 1992 and Fig. 3), the region investigated by the Turchin model is restricted to the areas IV and IV’ that describe a population dynamics with damped oscillations and a delayed density dependent regulation. If this model is used to reproduce the temporal dynamics it will induce a cyclic tendency in the dynamics of the populations and thus confounding effects when the pattern of synchrony of these populations is investigated.

Haydon and Steen (1997) investigated the stochastic effects as a combination of local and regional environmental perturbations. Basically, they viewed regional stochastic effects as environmental factors that operate over a whole area, while local stochasticity are the small scale variations in these environmental perturbations. They investigated the relative importance of these two components on synchrony and recorded that synchrony by the

Moran effect is not generated by extreme large-scale environmental conditions but by variation in these conditions. What is more their analyses showed that it was the coefficient of variation of local and global events that determined the synchrony and not the shape of their distributions. In particular if the stochastic events have the same intensity (coefficient of variation) they will affect the populations with the same synchronising effect, independently of the shape of their distributions.

In all these studies stochasticity was expressed through a range of values that were suppose to represent the real environmental perturbations. In a recent paper Cattadori et al. (in ms) quantitatively investigated the Moran effect and dispersal in closely related gamebirds populations in the Dolomites using environmental data from the sample area and two different approaches. In the first simulation they identified *a priori* the environmental event that may affect the dynamics of populations from a range of climatic variables selected during the breeding period. The variable was then used to reproduce the basic procedure proposed by Ranta et al. (1995a, b) and the dispersal rate and range were estimated for each species. In the second approach they estimated the relative effect of environmental perturbations and the rate of dispersal using the populations' time series and estimating function method following the approach by Lele et al. (1998). In general the two approaches produced similar results that singled out the importance of environmental perturbations in affecting synchrony within species, while dispersal had less impact but still contributed to cause the pattern of synchrony in some species.

These studies have clarified what the Moran effect is and the mechanism involved in this process. To understand more in detail how the Moran effect operates and its relative contribution on populations of different dynamics, three questions need to be addressed:

- Does the method used to define the Moran effect influence synchrony between populations?
- Are species with more variability more synchronous?
- Does synchrony change with the temporal pattern of the populations?

A clearer understanding of the process can be obtained by undertaking simple modelling simulations and to use the graphical representation to compare the results from different models.

A series of recent studies have investigated the effect of environmental stochasticity and the risk of extinction on the spatial dynamics of synchronous populations and clearly demonstrated that the dynamics are strongly influenced by the manner in which the stochastic events are introduced into the model (Heino 1998, Palmqvist & Lundberg 1998, Ranta et al. 1998). In fact, while different patterns of synchrony are observed in populations with different dynamics (Ranta et al. 1998), similar results can be achieved by incorporating environmental stochasticity in different ways in the model (Heino 1998). These analyses were carried out including both the stochastic event and dispersal patterns into the modelling. In the following simulations we shall investigate the effect of stochastic noise on the pattern of synchrony assuming that no dispersal links the populations.

Basic Modelling Approach

- *Does the method used to define the Moran effect influence synchrony between populations?*

We generated time series using the basic Ricker model and the stochastic perturbation was modelled in two different ways:

1- Stochasticity has a multiplicative effect on the growth rate (Allen et al. 1993):

$$x_{i(t+1)} = x_{it} * \exp(r(1+u_{it})(1-x_{it})) \qquad (1)$$

where x_{it} is the population size at time t in the ith patch, r is the maximum reproductive rate and u_{it} is the stochastic event in the ith patch and is assumed to be an independently and identically distributed (i.i.d.) random variable.

2- Stochasticity has an additive effect on the growth rate. We used an extension of the Ricker model with a delayed density dependence effect (Turchin 1990, Kaitala 1996a, b):

$$x_{i(t+1)} = x_{it} * \exp(r + a_1 x_{it} + a_2 x_{i(t-1)} + u_{it}) \qquad (2)$$

where a_1 and a_2 are constant parameters and represent the direct and delayed density dependence population regulation, respectively. This model was considered in two forms, when $a_2=0$, the function was comparable to equation (1), and $a_2 \neq 0$ where the combined effect of direct and delayed density dependence regulation was investigated.

We used a spatial structure of 10 patches, in the first patch we considered a population of species x and a population of species y, while in the remaining 9 patches a population of species y. Time series of independent random number were generated for each population. Synchrony between the two species was measured using zero lag cross correlation, $r_{xy}(0)$, and the coefficient of variation, CVm (Sokal & Rohlf 1981), was used to measure the variation of the population and of the perturbation in each patch. We assumed spatial stochastic correlations between patch (x,y) and the yth patches. Environmental stochasticity was generated from identically independent random number (i.i.d.) and 3 distributions were considered: Uniform $[-u_i, u_i]$, Uniform [0, 1] and Normal [0, 1]. We generated time series 200 generations long and the last 150 cross correlation coefficient were used. The parameters values were: r=2, a_1=-0.6 and a_2=-0.7 and stochasticity was assumed to have all the possible values ranging in the distribution selected.

No consistent differences were observed in the spatial pattern of synchrony when the Moran effect was measured as an additive effect or as a multiplicative effect on growth rate (Fig. 4A, B). In general, the two models exhibited similar results for each stochastic distribution used. When stochasticity was assumed to have a U[0,1] distribution the variation in the population (CVpop) was positively correlated with the environmental variation of its patch (CVpat) and synchrony between populations directly increased with synchrony between the stochastic event of the patches (Fig. 4A, B). Moreover, increasing the CVpat synchrony between populations showed a tendency to a logistic increase. The adding of a delayed density dependence factor to the model (2) did not increase the strength of synchrony between the populations and a similar spatial pattern was observed with a direct or a delayed density dependence regulation (Fig. 4B). When stochasticity was assumed to have a normal N[0,1] distribution or a uniform U[-1,1] distribution the descriptive capabilities of the models included negative and positive values with a wider range of possibilities. Again, the two models exhibited similar results. A clear symmetrical pattern was detected between the CVpat and the CVpop, and no increase in synchrony of populations was observed increasing the environmental synchrony between the patches

(Figure 4A, B). Large variation in the relationship of population synchrony with environmental synchrony was observed in model (2) compared to model (1) using both N[0,1] and U[-1,1] distributions for the environmental stochasticity (Fig. 4B).

These results demonstrate that the way stochasticity is applied to population growth rate seems to have a weak effect on the spatial pattern of synchrony. In contrast, the distribution and range of environmental stochasticity does affect synchrony. Synchrony between populations was linearly related to environmental synchrony when a Uniform [0,1] distribution was used while no apparent pattern was observed using a Normal or an Uniform [-1,1] distribution. Model 2 with additive stochasticity showed a reduction in the variation of synchrony between populations compared to model 1 with multiplicative stochasticity .

These results are in general agreement with previous studies that identified how the pattern of population synchrony can be different according to the way in which stochasticity is incorporated into the model (Heino 1998, Ranta et al. 1998). While these studies considered both dispersal and the stochastic effect in the population dynamics the general conclusions remain quite the same.

- *Are species with more variability more synchronous?*

We generated time series using a non-linear second order autoregressive model with stochastic perturbation u_{it} (Royama 1992):

$$x_{i(t+1)}=x_{it}+1-exp(-a_1x_{it}-a_2x_{i(t-1)})+u_{it} \qquad (3)$$

where a_1 and a_2 are direct and delayed density dependence parameters, respectively, and u_{it} is the environmental stochasticity at time t in the ith patch. The autoregressive parameters were estimated using the co-ordinates of the points in figure 2.9 from Royama (1992, and points 1 to 8 and 12 in fig. 3) where four general density dependent patterns are described: logistic, damped or diverging oscillations and neutral equilibrium. u_{it} was assumed to be an independent identically distributed random number with N[0, 0.04] distribution. We generated two independent populations (x, y) 200 generations long from random time series where each pair exhibited similar autoregressive parameters but different environmental stochasticity. The procedure was iterated 15 times fixing the parameters and changing the intensity of environmental stochasticity and the cross correlations were calculated using the last 150 values.

Synchrony between populations exhibited different patterns in relation to the density dependent structure of the populations (Fig. 5). In general, populations with large variation showed a tendency to be more in synchrony than populations with less variation. Populations with a divergent equilibrium (point 2) or increasing oscillations (point 4) exhibited more variation and a tendency to be more in synchrony while populations with damped oscillations of short period (points 3, 5 and 6) or a pattern converging to equilibrium (point 1) showed less variations and weak or no synchrony. When the period was longer but still exhibiting damped oscillations (points 7 and 8) a large variation in the perturbation corresponded to a large variation in the synchrony. In fact when the variation is high the correlation is positive and strong while it decreases with a reduction of variation or with damped oscillations. With neutral stable equilibrium (point 12) the populations with low variation in abundance exhibited large variation in synchrony.

- *Does synchrony change with the temporal pattern of the populations?*

We used the Ricker model as in equation (1) and changing the values of the growth rate we generated the following patterns:

1) Logistic growth r=1.8
2) Cyclic fluctuations: r=2.5
3) Random dynamic with rare and occasional stochastic perturbations r=3.5
4) Random dynamic with stochastic cyclic fluctuations r=3.5.

Stochasticity u_{it} was assumed to be an independent identically distributed random variable with N[0, 0.04] distribution. In case 3, we generated two occasional and synchronous high intensity perturbations while in case 4 the stochasticity was autocorrelated in the time of an order t=1 so that $u_{it}{}^*=(u_{it}+bu_{it-1})$ where b is a constant variable. Two cases were investigated, b=1 that generated long period of stochastic fluctuations, and b=-1 that produced short period of stochastic fluctuations (Royama 1992). We generated two independent populations (x, y) from random time series 200 generations long and each pair was similar in the autoregressive parameters but different in the environmental stochasticity. The procedure was iterated 15 times, fixing the parameters and changing the stochasticity; the cross correlations were calculated using the last 150 values.

Synchrony exhibited different patterns in relation to the temporal dynamics of the populations. Populations with a logistic growth exhibited strong synchrony with a positive correlation when the temporal dynamics were in phase and negative correlation when they were out of phase (Fig. 6). In this situation the strength of the stochastic event is of little importance compared to the starting values of the series. Two populations with a cyclic pattern still exhibited strong synchrony although this pattern was more affected by the strength of stochastic perturbations that destabilising the regular fluctuations occasionally reduced the synchrony between the populations (Fig. 6). Random perturbations with occasional but synchronous perturbations of the same intensity generated synchrony in populations that were not correlated (Fig. 6). The strong and synchronous stochastic variation increased the correlation between the populations that then fluctuated in phase for a short period. Cyclic stochastic fluctuations were able to synchronise populations with random dynamics (Fig. 6). Although this, synchrony exhibited large variation and moderate to weak cross correlations using cyclic perturbation with both a long or short cycle period.

Discussion

Spatial synchrony between populations is not uncommon in animal species and an increasing number of species have been identified to exhibit this pattern independently of the tendency to show a cyclic dynamics. A number of studies have examined the possible mechanisms that determine synchrony within and between populations and while the modelling clearly demonstrated that this pattern can occur among the natural populations no empirical experiments have been carried out to quantify the role of dispersal and environmental stochasticity in causing synchrony. The consequence of such process on local persistence and the relevance in the conservation of the species is important. There is a strong relationship between populations' synchrony and their extinction risk and generally global and local extinction increase with positive auto correlations among populations (Heino et al. 1997, Heino 1998). This relationship can become very complex

when the effect of environmental stochasticity and dispersal are considered. Dispersal generally reduces the extinction rate of the populations but when the fraction of migrating individuals is very high and weakly density dependent the extinction rate correspondingly increase (Heino et al. 1997). Stochastic events generate synchrony between populations and thus can severely affect the risk of extinction while non correlated perturbations generally reduce population synchrony. However, these results closely depend on the model details and how environmental noise and dispersal are incorporated into the function so that different qualitative conclusions can be obtained by the relationship between population synchrony and risk of extinction (White et al. 1996b, Heino et al. 1998). Our basic simulations, focused on environmental stochacticity, further demonstrate the possibility of observing different patterns in relation to the way the perturbations are introduced into the model. There is a conventional tendency to distinguish between catastrophes and environmental stochasticity in the narrow sense and, thus, the way of modelling their effects (Shaffer 1981). Catastrophes models usually consider a positive growth rate of population that became negative and often large when an unpredictable hurting event outbreaks (Mangel & Tier 1993b, Lande 1993). In the case of environmental stochasticity growth rate is constantly affected by the perturbation effects that assumes different intensities in relation to good, bad or indifferent years and the common pattern of growth rate follows a gaussian distribution. In general, when environmental stochasticity had a Normal [0, 1] or Uniform
[-1, 1] distribution there was a similar probability to generate population in synchronous phase or in opposite phase with a large variability in the cross correlation coefficients. If the stochastic events have a non-simmetrical distribution then synchronous environmental events positive affected synchrony between populations that resulted high and with low variation.

Different synchronous patterns can also be observed in populations with different dynamics but affected by similar environmental stochasticity. In this respect positive synchrony had a higher probability to occur in populations with a cyclic pattern or with a in-phase logistic growth, while populations with a random dynamics but in a synchronous environment exhibited large variation and low synchrony. In general populations with large variation or diverging fluctuations showed a higher tendency to fluctuate in synchrony.

From a conservation point of view populations in synchrony with the same density dependence structure but further apart distributions can be managed suggesting similar strategies of conservation, in contrast populations not spatially in synchrony need different approaches specific for each single case. Moreover, we can prevent the risk of extinction of threatened populations investigating the pattern of close related synchronous species that exhibit similar demographic patterns. When the populations are small or spatially isolated environmental stochasticity has a stronger effect but its effect is negligible when population's size reach the hundreds. Dispersal or migration are important in preventing extinction, in contrast they can increase the extinction rate in small and fragmented population with a tendency to migrate.

These studies emphasized the importance of accounting for two general important aspects in the study of population dynamics, first the spatial structure of the population and second, the modelling of their dynamics and the relative effect of demographic and environmental stochasticity. Spatial synchrony combines together long term temporal processes and spatial dynamics analysis over large geographical areas, and despite the previous extensive work focused on specific topics only recently these two general aspects of population dynamics have been associated and investigated together on a broad scale. Many of the problem to manipulate large amount of data of populations with complex spatial structures have been resolved developing *ad hoc* statistical techniques and using faster tools. However there are still many unsolved problems in the modelling and analyses of environmental stochasticity and in estimating the relative extintion parameters capturing these aspects in simplified general models.

REFERENCES

Allen J.C., Schaffer W.M. & Rosko D. 1993. Chaos reduces species extinction by amplifying local population noise. Nature 364: 229-232.

Baars M.A. & Van Dijk T.S. 1984. Population dynamics of two carabid beetles at Dutch heathland. 1. Subpopulation fluctuations in relation weather and dispersal. J. Anim. Ecol. 53: 375-388.

Cattadori I.M., Hudson P.J., Merler S. & Rizzoli A. 1999. Synchrony, scale and temporal dynamics of rock partridge (*Alectoris graeca saxatilis*) populations in the dolomites. J. Anim. Ecol. 68.

Cattadori I.M. & Hudson P.J. 1999. Temporal dynamics of grouse populations at the southern edge of their distribution: The Dolomitic Alps. Ecography 12.

Cattadori I.M., Merler S. & Hudson P.J. Mechanisms of synchrony in spatially structured gamebird populations (in ms).

Cramp S. & Simmons K.E.L. 1980. The birds of Western Palearctic. Vol. II, Oxford University press, Oxford.

Cristiansen E. 1983. Fluctuations in some small rodent populations in Norway 1971-1979. Holartic Ecology 6:24-31.

Efron B. 1982. The Jackknife, the Bootstrap and Other Resampling Plans. - CBMS-NSF Regional Conference Series in Applied Mathematics. Vol 38, SIAM.

Efron B. & Tibshirani R. J. 1993. An Introduction to Bootstrap. Chapmam & Hall Ltd., London.

Grenfell B.T.G., Wilson K., Finkenstädt B.F., Coulson T.N., Murray S., Albon S.D., Pemberton J.M., Clutton-Brock T.H. & Crawley M.J. 1998. Noise and determinism in synchronised sheep dynamics. Nature 394: 674-677.

Hanski I.A. 1991. Single-species metapopulation dynamics In: Gilpin M. & Hanski I.A. (eds) Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press.

Hanski I.A. & Woiwod I.P. 1993. Spatial synchrony in the dynamics of moth and aphid populations. J. Anim. Ecol. 62: 656-668.

Hanski I.A. & Gilpin M.E. 1997. Metapopulation Biology. Ecology, Genetics and Evolutions. Academic Press.

Heikkilä, J., Below, A. & Hanski, I. A. 1994. Synchronous dynamics of microtine rodent populations on islands in Lake Inari in northern Fennoscandia: evidence of regulation by mustelid predators. Oikos 70: 245-252.

Heino K., Kaitala V., Ranta E. & Lindström J. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. Proc. R. Soc. Lond. B 264: 481-486.

Heino M. 1998. Noise colour, synchrony and extinctions in spatially structured populations. Oikos 83: 386-375.

Hydon D. & Steen H. 1997. The effect of large- and small-scale random events on the synchrony of metapopulation dynamics: a theoretical analysis. Proc. R. Soc. Lond. B 264: 1375-1381.

Iason R.G. & Guinness F.E. 1985. Synchrony of oestrus and conception in red deer (*Cervus elaphus* L.) Anim. Behav. 33: 1169-1174.

Ims R.A. & Steen H. 1990. Geographical synchrony in microtine population cycles: a theoretical evaluation of the role of the nomadic avian predators. Oikos 57: 381-387.

Johnsgard P.A. 1983. The Grouse of the world. Croom Helm, London.

Kaitala V., Ranta E. & Lindström J. 1996a. Cyclic population dynamics and random perturbations. J. Anim. Ecol. 65: 249-251.

Kaitala V., Ranta E. & Lindström J. 1996b. External perturbations and cyclic dynamics in stable populations Ann. Zool. Fennici. 33 in press.

Korpimaki E. & Norrdahl K. 1989a. Avian predation on mustelids in Europe 2: impact on small mustelids and microtine dynamics - a hypothesis. Oikos 54:154-164.

Labin X. 1993. Determinants of the synchrony of reproduction in Townsend's voles, *Microtus townsendii*. Oikos 67: 107-113.

Labin X., Elston D.A., Petty S.J. & MacKinnon J.L. 1998. Spatial asynchrony and periodic travelling waves in cyclic populations of flied voles. Proc. R. Soc. Lond. B 65: 1491-1496.

Lande R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. An. Nat. 142: 911-927.

Lele S., Taper M.L. & Gage S. 1998. A spatial analysis of population dynamics in space and time using estimating functions. Ecology 79: 1489-1502.

Lindström J., Ranta E. & Lindén, H. 1996. Large scale synchrony in the dynamics of capercaillie, black grouse and hazel grouse populations in Finland. Oikos 76: 221-227.

Mangel M. & Tier C. 1993b. Dynamics of metapopultions with demographic stochasticity and environmental catastrophes Theor. Popul. Biol. 44: 1-31.

May R.M. 1994. The effect of spatial scale on ecological questions and answers. In: P.J. Edwards R.M. May & N.R. Webb (eds) Large-Scale Ecology and Conservation Biology. Blackwell Scientific Publications.

Marcström V., Höglund N & Krebs C. 1990. Periodic fluctuations in small mammals at Bota, Sweden from 1961 to 1988. J. Anim. Ecol. 59: 753-761.

Maynard Smith J. 1974. Models in ecology. Cambridge University Press, Cambridge.

McShea W.J. 1989. Reproductive synchrony and home range size in a territorial microtine. Oikos 56: 182-186.

Moran P.A.P. 1953a. The statistical analysis of the Canadian Lynx cycle. I Structure and prediction. Austral. J. Zool. 1: 163-173.

Moran P.A.P. 1953b. The statistical analysis of the Canadian Lynx cycle. II Synchronization meterology. Austral. J. Zool. 1: 291-298.

Myers J.H. 1998. Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect. Ecology 79: 1111-1117.

Norrdahl K. & Korpimaki E. 1996. Do nomadic avian predators synchronize population fluctuations of small mammals? A field experiment. Oecologia 107: 478-483.

Palmqvist E. & Lundberg P. 1998. Population extinctions in correlated environments. Oikos 83: 359-367.

Pollard E. 1991. Synchrony in population fluctuations: the dominant influence of widespread factors on local butterfly populations. Oikos 60: 7-10.

Ranta E., Lindström J. & Lindén H. 1995a. Synchrony in tetraonid population dynamics. J. Anim. Ecol. 64: 767-776.

Ranta E., Kaitala V., Lindström J. & Lindén H. 1995b. Synchrony in population dynamics. Proc. R. Soc. Lond. B 262: 113-118.

Ranta E., Kaitala V., Lindström J. & Helle E. 1997a. The Moran effect and synchrony in population dynamics. Oikos 78: 136-142.

Ranta E., Lindström J., Kaitala V., Hokko H., Lindén H. & Helle E. 1997b. Solar activity and hare dynamics: A cross- continental comparison Am. Nat. 149: 765-775.

Ranta E., Kaitala V. & Lindström J. 1997c. Dynamics of Canadian lynx populations in space and time. Ecography 20: 454-460.

Ranta E., Kaitala V. & Lundberg P. 1998. Population variability in space and time: the dynamics of synchronous population fluctuations. Oikos 83: 367-382.

Royama T. 1992. Analytical Population Dynamics. Chapman & Hall Ltd., London.

Ruxton G.D., Gonzalez-Andujar J.L. & Perry J.N. 1997. Mortality during dispersal stabilises local population fluctuations. J. Anim. Ecol. 66: 289-292.

Ruxton G.D. 1994. Low levels of immigration between chaotic populations can reduce system extintions by inducing asynchonous regular cycles. Proc. R. Soc. Lond. B 256: 189-193.

Shaffer M.L. 1981. Minimum population sizes for species conservation. BioScience 31: 131-134

Sinclair A.R. E., Gosline J.M., Holdsworth G., Krebs C.J., Boutin S., Smith J.N.M., Boonstra R. & Dale M. 1993. Can the solar cycle and climate synchronise the snowshoe hare cycle in Canada? Am. Nat. 141: 173-198.

Sokal R.R. & Rohlf F.J. 1981. Biometry Second Edition. W.H. Freeman and Company , New York.

Steen H., Yoccoz N. G. & Ims R. A. 1990. Predators and small rodent cycles: an analysis of a 79-year time series of small rodent population fluctuations. Oikos 59: 115-120.

Steen H., Ims R. & Sonerud G. A. 1996. Spatial and temporal patterns of small rodent population dynamics at a regional scale. Ecology 77: 2365-2372.

Stenseth N.C., Bjørnstad O.N. & Saitoh T. 1996. A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. Proc. R. Soc. Lond. B 263: 1117-1126.

Sutcliffe,O. L., Thomas C. D. & Moss D. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. J. Anim. Ecol. 65: 85-95.

Thomas C.D. 1991. Spatial and temporal variability in a butterfly population. Oecologia 87: 577-580.

Turchin P.1990. Rarity of density dependence or population regulation with lags? Nature 344 1990.

White A., Begon M. & Bowers R. 1996b. Explaining the colour of power spectra in chaotic ecological models. Proc. R. Soc. B Lond 263: 1731-1737.

Wiens J.A. 1995a. Landscape mosaics and ecological theory. In "Mosaic Landscapes and Ecological Processes. Eds. Hansson L., Fahrig L. & Merriam G. Chapman & Hall, London.

Ydenberg R.C. 1987. Nomadic predators and geographical synchrony in microtine population cycles. Oikos 50: 270-272.

Species	Period of Study	Study site	Scale	Synchrony (r)	Trend	Reference
Microtine Rodents	1988-1992	Finland	r		4-5	Heikkilä et al. 1994, Norrdahl & Korpimaki 199
Microtine Rodents	1962-1992	Japan	r		4-5	Stenseth et al. 1996
Fisher	1919-1957	Canada	r			Ranta et al. 1998
Snowshoe hare	1844-1991? 1849-1904	Canada	r		10	Sinclair et al. 1993 Ranta et al. 1997b
Lynx	1821-1939 1919-1957	Canada	r		10	Moran 1953b, Ranta et al. 1998
Butterfly	10 years	England	r/l			Sutcliffe et al. 1996
Butterfly	1932-1992	N. Emisphere	r			Myers 1998
Months & aphids	10 & 24	England	r			Hanski & Woiwod 1993
Soay Sheep	1955-1997	St. Kilda	r	0.68		Grenfell et al. 1998
Black grouse	1964-1983	Finland	r	0.27	6-7	Ranta et al. 1995a,b
Capercaille	1964-1983	Finland	r	0.41	6-7	Ranta et al. 1995a,b
Hazel grouse	1964-1983	Finland	r	0.27	6-7	Ranta et al. 1995a,b
Magpie	16 years	Finland	r	0.43	+	Ranta et al. 1995a,b
Mountain hare	21 years	Finland	r	0.42	r	Ranta et al. 1995a,b
Red squirrel	1964-1983	Finland	r	0.72	r	Ranta et al. 1997a
Willow grouse	21 years	Finland	r	0.48	4	Ranta et al. 1995a,b
Black grouse	1965-1994	Italy	r	0.33	-	Cattadori et al. ms
Capercaille	1965-1994	Italy	r	0.62	-	Cattadori et al. ms
Hazel grouse	1965-1994	Italy	r	0.18	- & 5	Cattadori et al. ms
Rock partridge	1965-1994	Italy	r/l	0.23	- & 4-7	Cattadori et al. 1999
Rock ptarmigan	1965-1994	Italy	r	0.21	- & 4-8	Cattadori et al. ms
Carabid beetle	1959-1980	Netherlands	l		3	Baars & Van Dijk 1984
Vole & lemming		Norway	r		c	Cristiansen 1983,
Bank vole	1990-1994	Norway	l		c	Steen et al. 1990, 1996
Vole & lemming	1961-1988	Sweden	r		3-4	Marcström et al. 1990
Voles	1984-1997	Scotland	l		c	Lambin et al. 1998
Fox	1919-1957	Canada	r			Ranta et al. 1998
Coyote	1919-1957	Canada	r		-	Ranta et al. 1998
Field vole	1919-1957	Canada	r		c	Ranta et al. 1998

Table 1. Representative population studies on synchrony. We reported, when citated, the trend: cyle with the period (CL), increasing (+), decreasing (–) and no apparent dynamics: (r=random). Spatial scale of the sudy: l= local, r=regional.

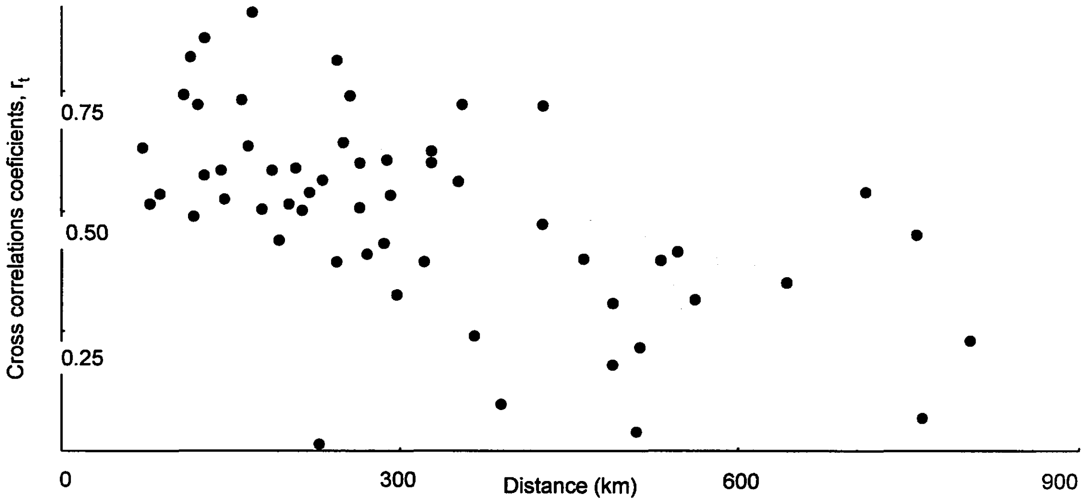


Figure 1 Pattern of synchrony on distance between populations of mountain hare (*Lepus timidus*) among 11 province in Finland during the period 1946-1984 (from Ranta et al. 1997d, modified).

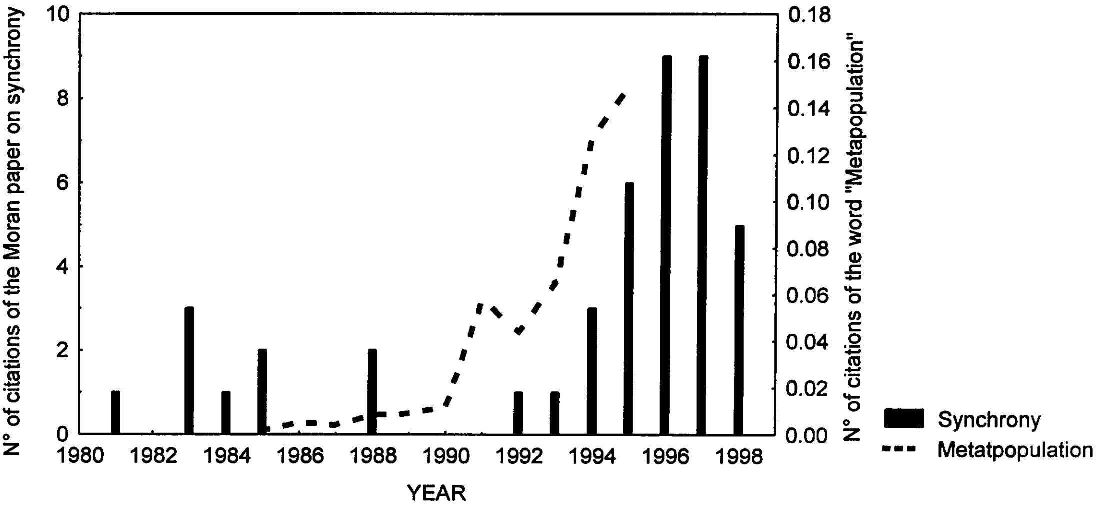


Figure 2. Number of citations of the paper *The statistical analysis of the Canadian Lynx cycle II. Synchronisation and meteorology* (Moran 1953b) and standardized number of citations of the key word 'Metapopulation' (from Hanski & Gilpin 1997 modified). Data available form BIOSIS data base between 1953-March 1998 for Moran's paper citation and between 1970-1995 for the citation of the word "Metapopulation".

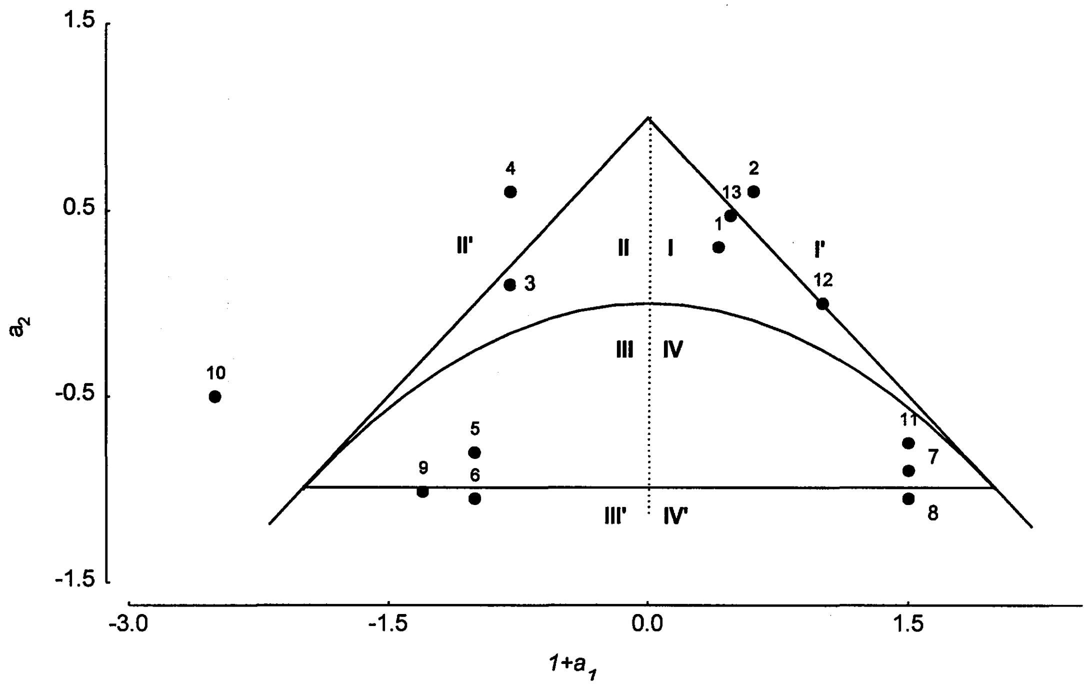


Figure 3 Royama's triangle representing the plane of the autoregressive parameters ($1+a_1$, a_2) from a non linear second order pure autoregressive process. The triangle is divided into 8 regions according to the values of the solutions of the autoregressive equation. We reported the points 1-8 and 12 as in figure 2.9 from Royama (1992) that represent different density dependence structure of population.

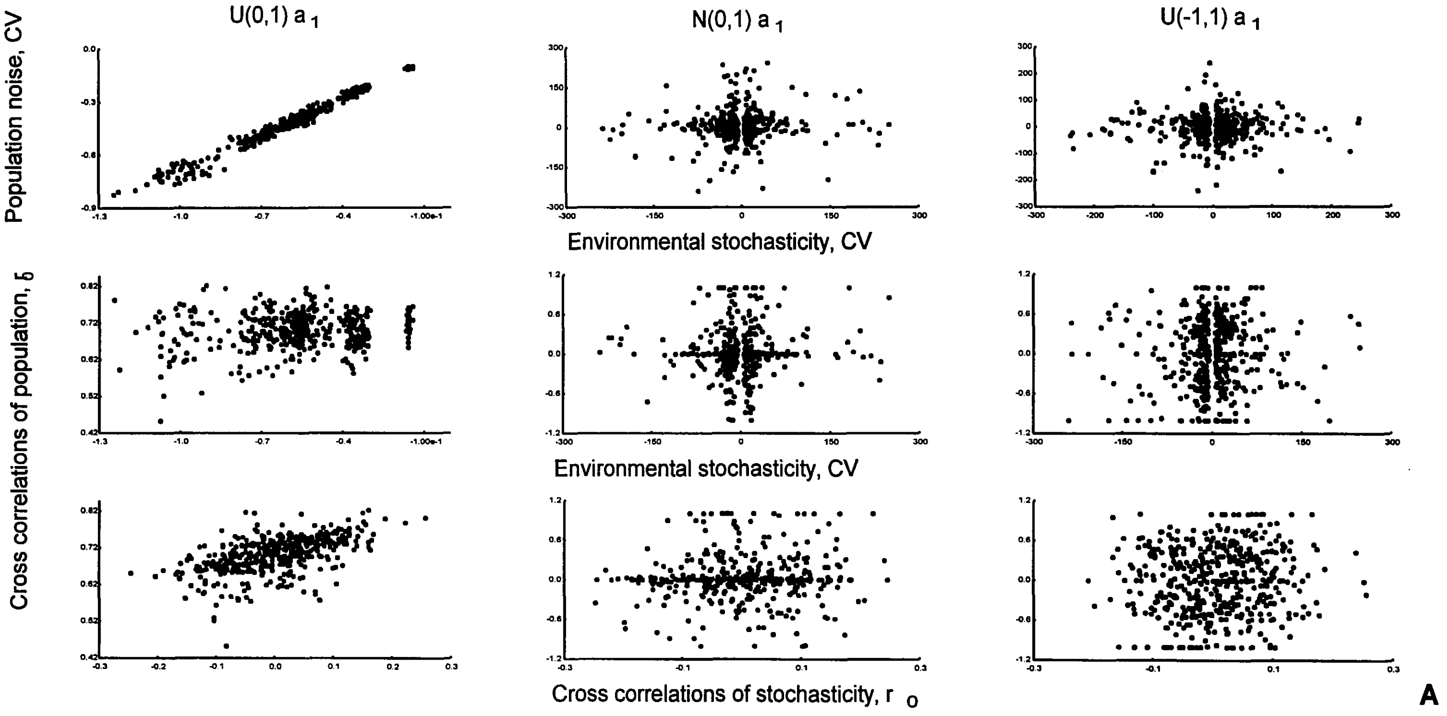


Figure 4. Relationship between variation in populations and in stochastic events, and between synchrony of populations and synchrony of environmental events using different modelling of environmental stochasticity:

A- moltiplicative stochasticity on growth rate with U(0,1)
N(0,1)
U(-1,1)

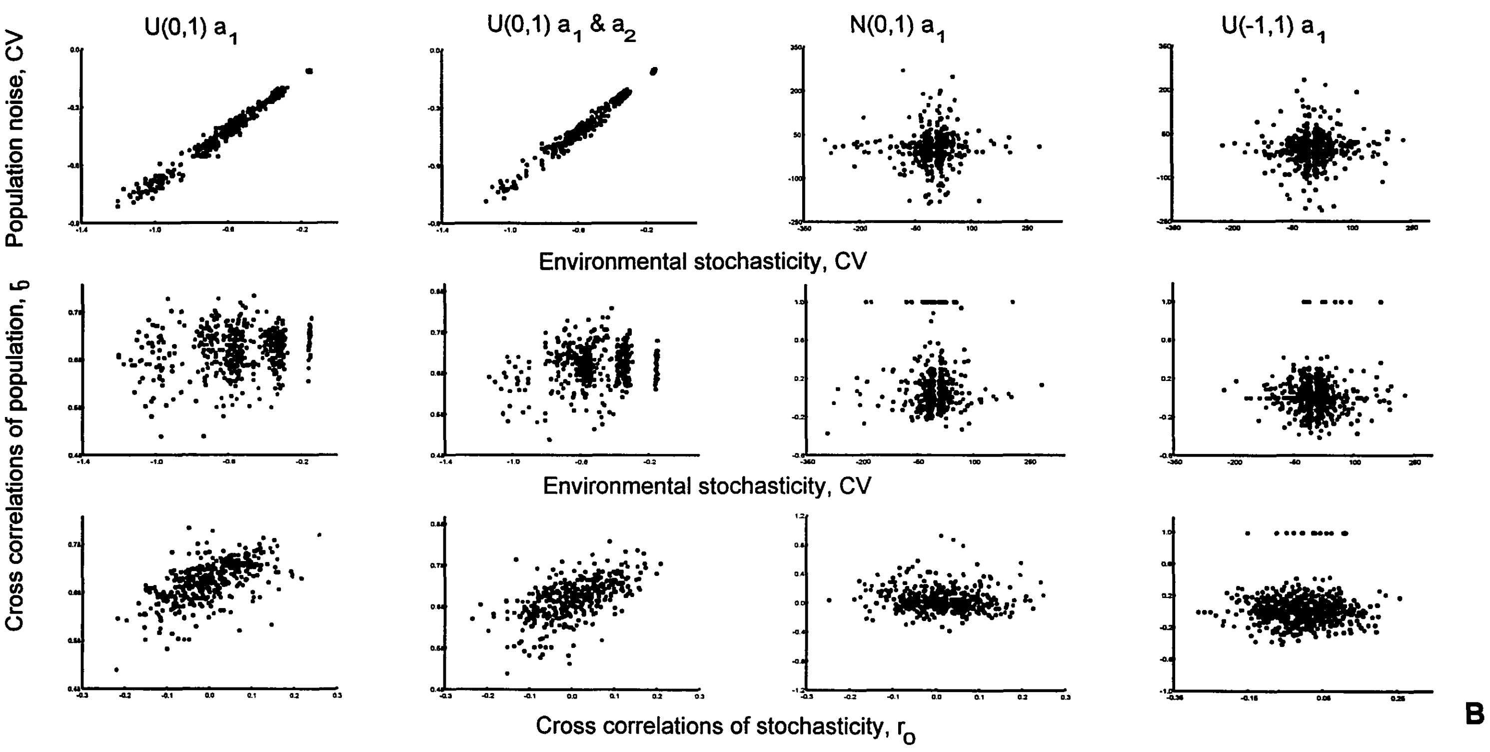


Figure 4. (second part) B - additive stochasticity on growth rate with: a2=0 and U(0,1)
a1 and a2≠0 with U(0,1)
a2=0 with N(0,1)
a2=0 with U(-1,1)

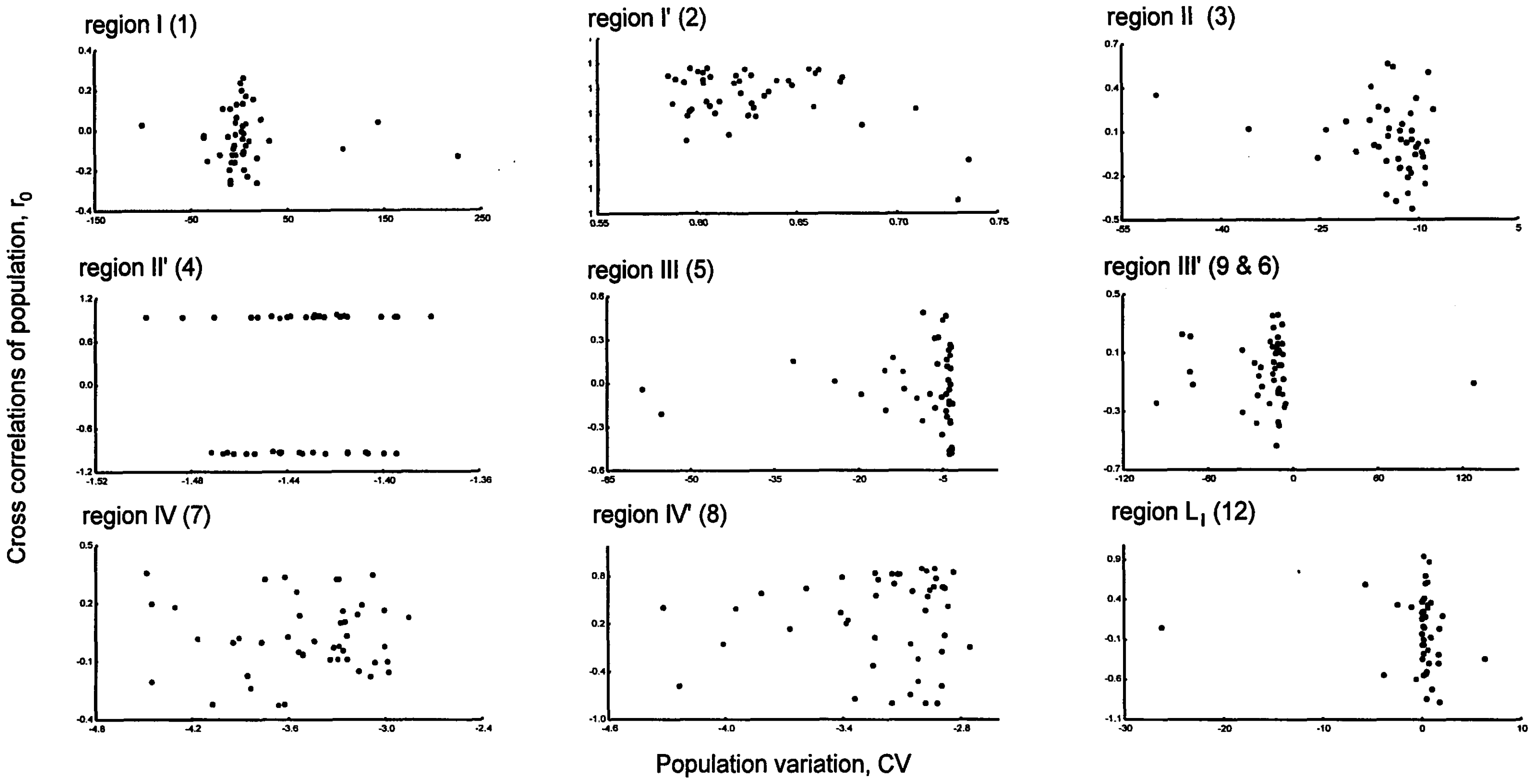


Figure 5 Pattern of synchrony on population variation using a non linear AR(2) model and different patterns of populations dynamics as represented in figure 3 by the points 1-9 and 12: region I, logistic growth, region I' exponential growth, region II, III and IV damped oscillations, region II', III' and IV' diverging oscillations line L_I neutral equilibrium.

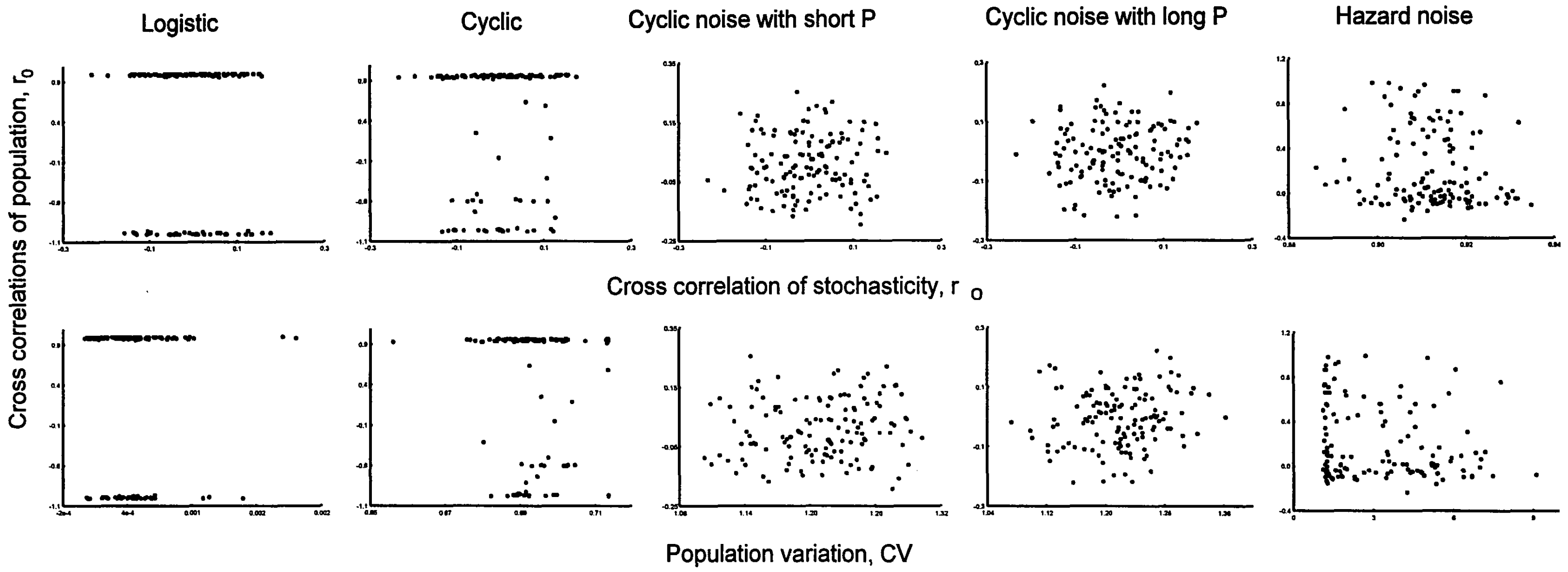


Figure 6 Pattern of synchrony on population variation and on stochastic perturbations using the Ricker model and simulating different patterns of population dynamics: logistic, cycle, random perturbation with synchronous intensive perturbation, cyclic perturbation with short period $u_{it}=(u_{it}-bu_{it-1})$, and cyclic perturbation with long period $u_{it}=(u_{it}+bu_{it-1})$.

CHAPTER 2

The Moran Effect: a Cause of Population Synchrony

P.J. Hudson[1] & I.M. Cattadori[1, 2] 1999

[1]Institute of Biological Sciences, University of Stirling
[2]Centro di Ecologia Alpina, Trento, Italy

Trends in Ecology and Evolution 1: 1-2

THE MORAN EFFECT: A CAUSE OF POPULATION SYNCHRONY

Peter J. Hudson & Isabella M. Cattadori

Progress in population ecology generally occurs through the continual synthesis of theory with empirical findings but occasionally a study acts as a beacon and guides the discipline into new and exciting areas of research. In the study of population fluctuations, Charles Elton's first description of the regular cycles in the fur returns of Canadian lynx (*Lynx canadensis*) to the Hudson's Bay Company[1] was arguably one of the most influential. His description has stimulated more than 70 years of theoretical and empirical investigation into the possible causes of population cycles, why population fluctuations are spatially synchronised and the relative importance of intrinsic and extrinsic mechanisms. While we still do not have clear experimental demonstration of the mechanism that generates cycles in any natural systems, a recent paper shows that there exists an interesting tension between the synchronising effects of extrinsic environmental stochasticity and the desynchronising effects of non-linear density dependence[2]. Random effects have a major role to play in a non-linear world and their influence is becoming increasingly recognised in ecological theory[15].

A series of studies published within the past five years have shown that spatial synchrony is a general phenomenon not restricted to vertebrates or to cyclic species[3,7,9,11]. The majority, though not all[4], have shown synchrony over a fairly wide geographical area with the degree of synchrony between populations decreasing with distance. However, identifying synchrony is just the first step, the more difficult task is to identify the mechanism that causes this pattern. Early workers assumed that the cause of population cycles would also be the cause of the synchrony so they looked for links with global events such as cycles in sunspot activity, ozone levels and forest fires[6]. However, Moran[5] dismissed the need for a single causation hypothesis and pointed out that, if two populations had the same density dependent structure, then correlated density independent factors (usually weather-induced) would bring the populations fluctuations into synchrony.

Royama[6] highlighted this in his synthesis of population dynamics and called it the "Moran effect".

The simplest model of synchrony between two uncoupled populations would be two linear auto-regressive equations with no density dependence but similar environmental variation. In this case, the correlation of the populations will asymptotically equal the level of correlation in the environmental variation. However, synchrony between populations will also depend on the nature of their density dependence[7] so that two asynchronous, uncoupled populations can only be brought into synchrony by environmental noise when their density dependence is similar. Introducing a time lag in density dependence that may generate cyclic fluctuations will also increase the probability of synchrony[7]. However, the Moran effect is not the only mechanism that may produce synchrony - dispersal tends to link sub-populations and thus leads to synchrony[3]. So we must ask which of the two mechanisms is dominant?

Distinguishing between the causal mechanisms is important because synchrony is strongly correlated with the probability of global extinction and hence is of particular concern in conservation[8,9]. If dispersal is the main cause of synchrony and a local population is wiped out, by something like a virulent epidemic, then the empty habitat will be recolonised. However, when the Moran effect is dominant and dispersal rare then empty habitat may not be subsequently repopulated. Even when a harsh environmental perturbation causes the global population to crash, large sub-populations may persist and can repopulate suitable habitat islands as long as there is some dispersal. Even so, dispersal is something of a double-edged sword since it not only facilitates persistence at the local scale but also leads to synchrony and an increased probability of global extinction. The same features that cause concern to conservationists are an aid to those attempting to control pest outbreaks. This is particularly important when the Moran effect dominates, since it may be possible to eradicate local pest and pathogen populations' knowing that re-colonisation is unlikely. However, the emergent spatio-temporal effects of control intervention also play a role. For example, recent work on measles has found that while vaccination reduces the size of epidemics it also desynchronises populations and promotes global persistence. A potential solution is to apply pulsed vaccination that will keep the populations synchronised and make elimination more likely[10].

Studies of synchrony have attempted to disentangle the Moran effect from those of dispersal. Generally speaking, both the models and the data suggest that scale is important[3,8]. At the local scale, dispersal may dominate over the Moran effect but at global scales the Moran effect will be dominant since dispersal range and rate will be rare. This is supported by studies on butterfly populations that identified synchrony at low spatial scales, similar to dispersal ranges, and again at large global scales, greater than dispersal range[11]. Nevertheless the two mechanisms are not mutually exclusive and both may be operating at smaller spatial scales so we can not really distinguish between the relative importance of each without an experiment or some sophisticated analyses.

Demonstrating synchrony requires the manipulation or elimination of one of the synchronising mechanisms. This was achieved during a recent study of the irregular population fluctuations of the sheep populations on the St Kilda archipelago[2]. More than 40 years of sheep count data from the two islands of Hirta and Boreray exhibited remarkable synchrony (r=0.68) and the role of dispersal was easily dismissed since 3.5 km of Atlantic swell provides a perfect barrier to sheep dispersal. However, the islands are so close together that they will be exposed to similar environmental conditions. The population data from Hirta show a clear non-linear reduction in population growth rate with density that probably comes about through intra-specific competition for food[12]. Grenfell and colleagues show that the consequence of this non-linear density dependence is to accentuate the differences in synchrony between populations - small differences in density between the populations will lead to large differences in the growth rate between the two populations leading to asynchrony. This occurs above a threshold that equates approximately to the point where the average growth rate falls to zero. Below the threshold the population invariably increases but above the threshold the environmental conditions determine if the population crashes or remains high. The paper explored the tension between these two features using a non-linear time series model that incorporated this threshold effect. The model shows that with the non-linear density dependence the environmental correlation must be high (in excess of 0.9) and quite a bit higher than we would expect if there were no density dependence (0.68). More specifically the environmental factors must result in the two populations crossing the threshold in the same year if the synchrony is to be maintained.

Environmental variations can play an important role in population ecology, not only in generating cyclic patterns of fluctuation[13,14] but also in causing synchrony. Although the Moran effect is the main factor synchronising the St Kilda sheep populations, it is too early to say that it is the dominant factor in most synchronised populations. Nevertheless these findings together with the work by Esa Ranta and colleagues[3,7,8] lead us to suspect that it could be very important in a number of systems. Ecologists are coming to grips with spatial population dynamics and have recognised that incorporating simple stochastic variations in models can generate interesting dynamics; further integration will lead to progress in the discipline[15].

Acknowledgements

We thank Bryan Grenfell, Pej Rohani, Ken Wilson, Tim Benton and Jan Lindström for discussion and comments.

References

1. Elton, C. (1924) **Fluctuations in the numbers of animals: their causes and effects,** *Br. J. Exp. Biol.* 2, 119-163
2. Grenfell, B.T. et al. (1998) **Noise and determinism in synchronised sheep dynamics,** *Nature (Lond.)* 394, 674-677
3. Ranta, E. et al. (1995) **Synchrony in population dynamics,** *Proc. R. Soc. Lond.* B 262, 113-118
4. Cattadori, I.M. et al. (1998) **Temporal and spatial dynamics of rock partridge (*Alectoris graeca saxatalis*) in the Italian Dolomites,** *J. Anim Ecol.* (in press)
5. Moran, P.A.P. (1953) **The statistical analysis of the Canadian lynx cycle. II Synchronization and meteorology,** *Aust J. of Zool.* 1, 291-298
6. Royama, T. (1992) *Analytical population dynamics,* Chapman and Hall. London
7. Ranta, E. et al. (1997) **The Moran effect and synchrony in population dynamics,** *Oikos* 78, 136-142
8. Heino, M. et al. (1997) **Synchronous dynamics and rates of extinction in spatially structured populations,** *Proc. R. Soc. Lond.* B 264, 481-486
9. Hanski, I. and Woiwod, I. P. (1993) **Spatial synchrony in the dynamics of moth and aphid populations,** *J. Anim. Ecol.* 62, 656-668
10. Earn, D.J.D., Rohani, P. and Grenfell, B.T. (1998) **Persistence, chaos and synchrony in ecology and epidemiology,** *Proc. R. Soc. Lond.* B 265, 7-10
11. Sutcliffe, O.L., Thomas, C.D. and Moss D. (1996) **Spatial synchrony and asynchrony in butterfly population dynamics,** *J. Anim. Ecol.* 65, 85-95
12. Clutton-Brock, T.H. et al. (1997) **Stability and instability in ungulate populations: an empirical analysis,** *Am. Nat* 149, 195-219
13. Potts, G.R. Tapper, S.C. and Hudson, P.J. (1984) **Population fluctuations in red grouse: analysis of bag records and a simulation model,** *J. Anim.Ecol.* 53, 21-36
14. Kaitala, V. Ranta, E., and Lindström, J. (1995) **Cyclic population dynamics and random perturbations,** *J. Anim. Ecol.* 62,249-251
15. Leirs, H. et al. (1997) **Stochastic seasonality and nonlinear density-dependent factors regulate population size in an Africa rodent,** *Nature* 389, 176-180

CHAPTER 3

A Model of Habitat Suitability for Rock Partridge (*Alectoris graeca saxatilis*) in the Trentino

I.M. Cattadori[1], V. Pandini[2], E. Cistoldi[2]. & A. Meriggi[2] 1998

[1]Centro di Ecologia Alpina, Trento, Italy
[2]Dipartimento di Biologia Animale, Universita' di Pavia

Gibier Faune Sauvage, Game Wildlife 4: 397-406

A MODEL OF HABITAT SUITABILITY FOR ROCK PARTRIDGE (*ALECTORIS GRAECA SAXATILIS*) IN THE TRENTINO ALPS: PRELIMINARY RESULTS

Isabella M. Cattadori, Valter Pandini, Elena Cistoldi & Alberto Meriggi

ABSTRACT

The historical distribution (1950's-1960's) of rock partridge (*Alectoris graeca saxatilis*) was examined in relation to habitat features in Trentino, Italy. The study aimed to describe distribution according to habitat variables in fifties and to construct a model of habitat suitability to compare with the habitat of the species at present in order to identify suitable habitat not occupied. The province of Trento was subdivided into sample squares of 400 ha, and within each 39 habitat variables were estimated from aerial photographs taken in 1954. Information about the distribution of the species were obtained from the Forestry Service and the Hunters Association.

Forward stepwise logistic regression analysis was used to model the presence-absence of rock partridge populations in relation to the habitat variables: 75% of all cases were classified correctly, of which 78% with presence of rock partridge and 72% without rock partridge. Seven variables entered into the model: suitability was positively influenced by increasing slope, southern exposure and habitat diversity, and negatively influenced with expansion of thick forests, lakes areas and developed areas. The fit of the model was satisfactory given the large study area and the historical nature of the data and provides a working hypotheses for future conservation programmes.

I. INTRODUCTION

The rock partridge (*Alectoris graeca saxatilis*) has decreased in abundance throughout a large part of the Italian Alps, and since the 1950s a clear contraction of its alpine range has been recorded (DE FRANCESCHI, 1988; PRIOLO and BOCCA in BRICHETTI, 1992; BERNARD-LAURENT and DE FRANCESCHI, 1994). Most authors agree that changes in habitat, in particular the expansion of forests and abandonment of cultivations, and disease (SALVINI and COLOMBI, 1983) have been the main reasons for the disappearance of rock partridges. These hypotheses have yet to be rigorously tested. Other possible hypotheses exist, such as over-hunting or potentially negative effects of restocking with other species of Alectoris partridge.

In this paper we present the preliminary results of a three years study about the management and safeguard of the rock partridge in the Italian province of Trentino. More specifically we seeks to model the historical distribution of rock partridges based on habitat variables; our objectives were: (1) to describe the distribution of rock partridges between 1950 and 1960, (2) to identify habitat variables related to the presence of the species, (3) to obtain a qualitative model of habitat suitability predicting presence or absence of rock partridges.

The validation of the model on the historical data and the classification of the habitat quality at the present will be the next steps of our work.

II. MATERIAL AND METHODS

Trentino Province (5995 km^2) is a mountainous region located in north-east Italy, in the oriental side of the Alps (Fig. 1). The altitude range from 65 m to 3750 m, the 50% of the total surface is between 1000 m and 2000 m. The climate is sub-Mediterranean in the south and alpine in the centre and north. In the 1990s the provincial surface consisted of forests for the 49%, rocky and uncultivated areas for the 26%, arable land for the 14% and urbanised areas for the 11%; while in the 1950s the forests were 41%, rocky and uncultivated areas 22%, arable lands 30%, and urbanised areas 7%.

The distribution of rock partridge in the 1950s was established by a questionnaire survey sent in autumn to the Forest (n= 47) and Hunter (n= 210) Stations spread throughout all the Province. The information about presence and absence of the species was based on the bag records data in each reserve. A map making programme was employed to translate the information on a map.

For measuring habitat variables and to have a synthetic view of the presence or absence of the rock partridge, the province was subdivided into squares of 400 ha (2km x 2km tetrads). The dimension of the grid coincides with the squares of the Technical

Regional Card of the Trentino in scale 1:10.000 and this dimension was chosen in order to distinguish with a good resolution the areas with and without rock partridges, and to have a good statistic variability in the habitat variables. The grid was superimposed and fitted over historical aerial photos (1:66.000 scale) of the province taken by Military Aeronautic Service in 1954. The photos available for the habitat analysis covered a total of 414 squares, which was 28% (1656 km^2) of the whole Province. The Stelvio National Park was not included in the sample.

An aerophotogrammetric analysis was used to identify the habitat variables for each square unit. A total of 39 variables were recorded including 22 vegetation variables, 3 anthropocentric variables, 11 physical variables and 3 environment complexity variables (detail are provided in APPENDIX 1). We used the casual points method of MARCUM & LOFTSGAARDEN (1980) to estimate the surface area of each variable within each square.

Logistic regression analysis was employed to obtain a predictive model of habitat suitability of rock partridge. We used the function as follow:

$Y=(1+e^{-Z})^{-1}$

where:

Y = probability to have presence of rock partridges

Y' = 1-Y the probability to have absence of rock partridges

$Z = B_0+B_1X_1+......B_iX_i$

X_i = independent variable; B_i = coefficient estimated from the data

We used a forward stepwise procedure to select a best subset of variables to predict the probability of presence of rock partridges. We tested how well the model classifies the observed data with the -2 Log likelihood test, while to test how well the logistic model performs we used the -2 Log likelihood test with all the selected variables, the Goodness of Fit Statistic (Z^2) and Chi-square (X^2). The importance of each variable on the independent one is explain by the partial correlation value (R) and by the Esp(B), this last one defined as ratio Y/Y'. The improvement is the change of the -2LL between successive steps of building model.

The model derived is empirical and can be used, within limitations, to predict the potential distribution of rock partridges in relation to actual habitat features.

All statistical analysis was carried out using SPSS/PC (NORUSIS /SPSS, 1992).

III. RESULTS

The historical distribution (1950-1960) of rock partridges in Trentino covered an area of 48% of the Province (2854 km^2), corresponding to 56% of the arable and forest surface (Fig. 2). The distribution was fairly uniform and continuous from north to south and from east to west, except in the north-east of Trentino where the species was sparsely distributed.

The logistic regression model correctly predicted presence or absence of rock partridges in 75% of all sample squares, 78% of ones with presence and 72% of ones where the species was absent (Table I). Seven variables entered the model. The probability of the presence or absence of the species was determined, in order of entry, by: the difference in height, south exposure and Shannon index, which were positively related to presence; dense conifer forests, developed areas, area of lakes and number of forests, which were negatively related to presence.

IV. DISCUSSION

The selection of variables by logistic regression provides a synthetic view of the elements which define habitat quality for the rock partridge. The results confirm the hypotheses we find in the literature. Several authors (DE FRANCESCHI, 1988; BOCCA, 1990a and b; PRIOLO and BOCCA in BRICHETTI, 1992) have argued that forest expansion at high altitudes caused a decrease in the area of pastures and prairies which reduced habitat suitability, while open forests, such as those which were managed for wood some decades ago, are readily accepted by rock partridges (ZBINDEN, 1984). The growth of developed areas (urban and industrial areas, roads, etc.) is also cited by the same authors as a negative factor influencing the distribution of this species. Our analysis did not confirm the importance of pastures at middle altitudes and the production of crops at high altitudes (DE FRANCESCHI, 1988; JOHNSGARD, 1988).

The model provides a simplification of relationships between the presence of rock partridges and habitat components. Through the validation of the model on the historical data and afterwards its comparison with the habitat of the species at present, we should identify habitat where change may be related to the decrease of rock partridges in

Trentino. It is must be realised that regression techniques we have used do not demonstrate cause and effect, so subsequent work would need to test the fine scale relationships between habitat variables and partridge distribution, furthermore we need to evaluate additional factors that could influence density.

The fitting of the model appears satisfactory considering the real difficulties in defining the detailed distribution of the species thirty years ago. Similar predictive multivariate models have been proved useful for other species of Phasianidae (HILL and ROBERTSON, 1988; MERIGGI, 1990; MERIGGI *et al.*, 1992a; MERIGGI *et al.* 1992b) and also for large predators (MASSOLO and MERIGGI, 1994).

V. CONCLUSIONS

By comparison with currently occupied habitat for rock partridges, we intend to use the model predictively to identify area that are suitable but not yet occupied, for future management purposes. Indeed, the model provides a synthesis of relationships between habitat and partridges because of this it is of interest to public administrators and private managers in management projects. Manipulation of separate variables and evaluation of their effects on habitat suitability for rock partridges is also possible. That allows researchers to predict the consequences of certain type of management, and to minimise risks of failure in cases of attempted reintroductions.

ACKNOWLEDGMENTS

The authors thank the Forest and the Hunter Stations of the Trentino Province for their help in collecting data.

REFERENCES

BERNARD-LAURENT A. & DE FRANCESCHI P. (1994). - Status, trends, and limiting factors of rock partridge (*Alectoris graeca*) populations: a literature survey. Gibier Faune Sauvage, 11 : 267-308.

BOCCA M. (1990a). - La coturnice (*Alectoris graeca*) e la Pernice bianca (*Lagopus mutus*) in Valle D'Aosta. Regione Autonoma della Valle D'Aosta e Comitato Regionale Caccia, Aosta 76 p.

BOCCA M. (1990b). - La cartografia dell'areale potenziale della coturnice in Valle d'Aosta: problemi metodologici e finalità applicative. Atti V Conv. Ital. Ornit. Suppl. Ric. Biol. Selvaggina, XVII : 265-270.

DE FRANCESCHI P. (1988). - La situazione attuale dei galliformi in Italia. Ricerche recenti o ancora in corso. Problemi di gestione e prospettive per il futuro. *In*: M. Spagnesi & S. Toso eds. Atti I Conv. Naz. Biol. Selvaggina. Suppl. Ric. Biol. Selvaggina, XIX : 165-180.

HILL D. A. & ROBERTSON P. (1988). - The pheasant. Ecology, management and conservation. Blackwell Scientific, Oxford, 279 p.

JOHNSGARD P. A. (1988). - Rock Partridge. *In*: The Quails, Partridges and Francolins of the world. Oxford University Press, Oxford : 114-116.

MARCUM C. L. & LOFTSGAARDEN D. O. (1980). - A nonmapping technique for studying habitat preferences. J. Wildl. Manage., 44 : 963-968.

MASSOLO A. M. E. & MERIGGI A. (1994). - A new guideline for wolf management: a predictive model of presence in northern Apennines, Italy. Proceeding of the Congress "A Coexistence of Large Predators and man" October 1994 Bieszczady, Poland (in press).

MERIGGI A. (1990). - Criteri di analisi e valutazione ambientale: Galliformi e Lagomorfi. gestione e protezione del patrimonio faunistico. Atti I e II Corso di aggiornamento, Brescia 1990 : 103-118.

MERIGGI A., SAINO N., MONTAGNA D. & ZACCHETTI D. (1992a). - Influence of habitat on density and breeding success of Grey and Red-legged Partridges. Boll. Zool., 59 : 289-295.

MERIGGI A., GARIBOLDI B. & MAGNANI B. (1992b). - Habitat requirements of the bobwhite quail in northern Italy. Boll. Zool., 59 : 73-78.

NORUSIS /SPSS (1992). - SPSS/PC Advanced Statistic Manual. SPSS Inc., Chicago.

PRIOLO A. & BOCCA M. (1992). - Coturnice (*Alectoris graeca*). *In*: P. Brichetti P. De Franceschi and N. Bacetti eds., Fauna d'Italia XXIX Aves I. Calderini, Bologna : 766-777.

SALVINI G. P. & COLOMBI G. C. (1983). - La coturnice. Studi sulle popolazioni della coturnice delle Alpi. Unione Nazionale Cacciatori Zona Alpi, Italia 48 p.

SPANO' S. & BOCCA M. (1983). - Coturnice: *In*: P. Brichetti ed. Atlante degli uccelli nidificanti sulle Alpi italiane, II. Riv. It. Orn., 53 : 101-144.

ZBINDEN N. (1984). - Zur Verbreitung. Siedlungsdichte und Herbst-Winternahrung des Steinhuhns *Alectoris graeca* im Tessin. Or. Beob., 84 : 49-61.

Habitat Variables	Regression coefficent	S.E.	Level of significance	-2 Log likeliwood	Correlation coefficient	Esp(B)
Constant	-3,05	0,52	0,0001	533,41		
Difference in height	0,98	0,16	0,0001	488,29	0,25	2,66
S exposure	0,74	0,14	0,0001	455,05	0,22	2,10
Dense conifer forests	-0,98	0,17	0,0001	429,38	-0,25	0,37
Developed areas	-1,21	0,22	0,0001	403,73	-0,23	0,30
H'Shannon	0,89	0,17	0,0001	389,60	0,21	2,43
N° forests	-0,60	0,15	0,0001	370,91	-0,16	0,55
Lakes	-0,47	0,16	0,0027	360,51	-0,11	0,62
-2 Log Likelihood	360,60					
Goodness of Fit	323,86					
Chi-square	172,91		d.f.= 7	p=0,0000		
Improvement	10,40		d.f.= 1	p=0,0013		
Classification results						
Sample square without partridges		n=202 71,7%	correctly	classified		
Sample square with partridges		n=212 78,3%	correctly	classified		
Total		n=414 75,1%	correctly	classified		

Table 1. Logistic regression model for the presence or absence of the rock partridge (*Alectoris graeca*) in Trentino province in 1950-1960.

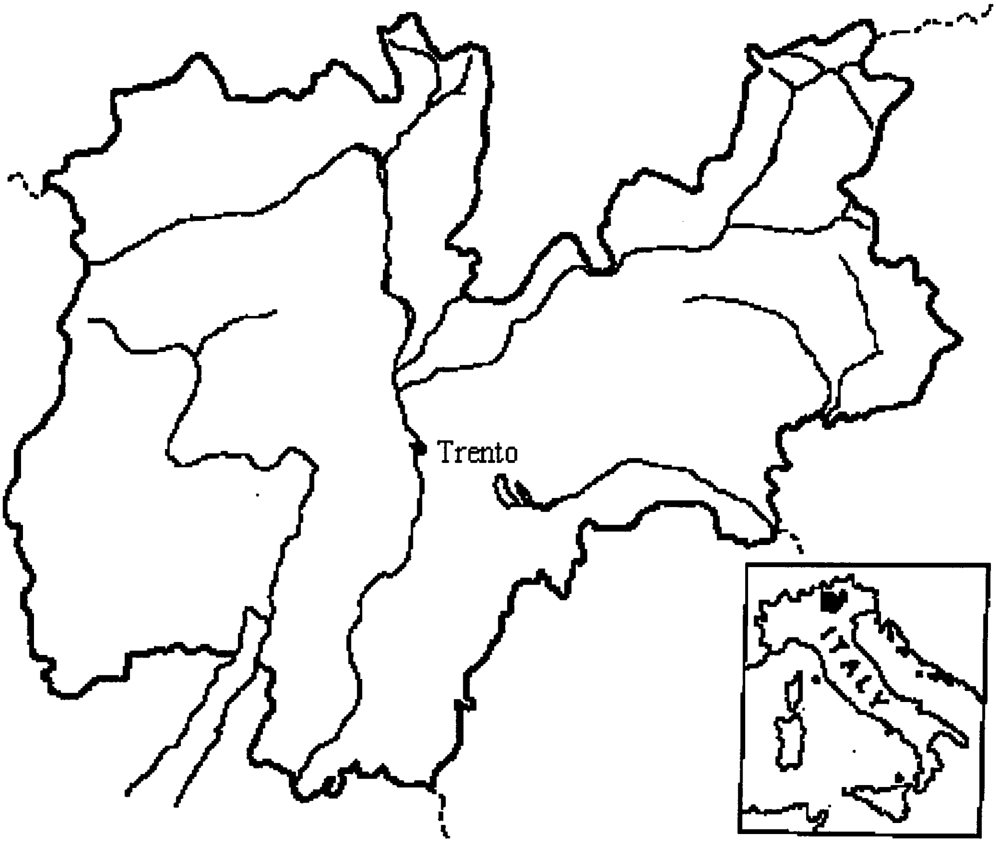


Figure 1: Map of Italy, showing the location of Trentino Province (5995 kmý) where rock partridge (*Alectoris greaca*) distribution was modelled.

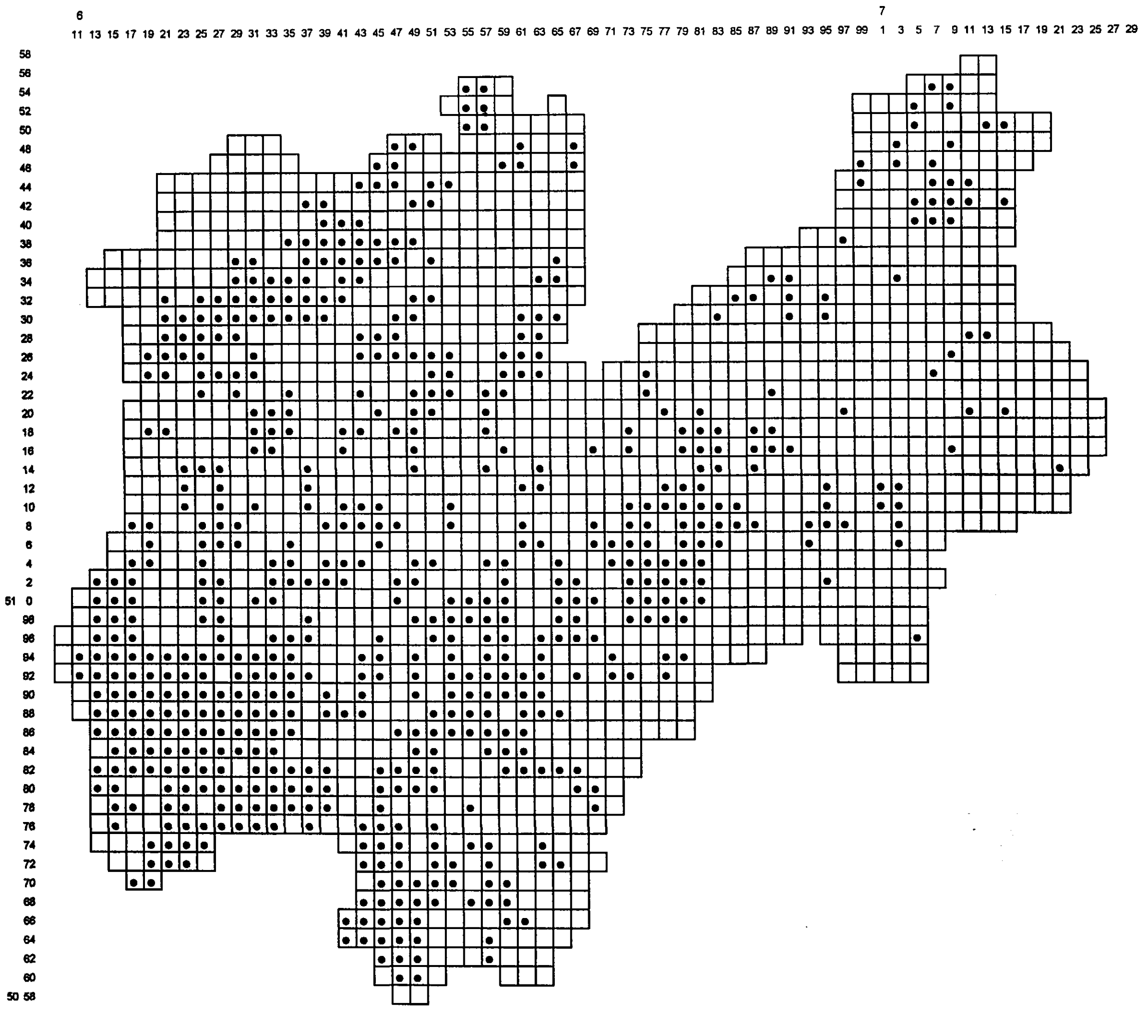


Figure 2: Distribution of the rock partridge (Alectoris graeca) in Trentino in 1950-1960. Each square represent 400 ha. The dotted square are the ones where rock partridges were present. On the left and on the top of the figure are marked the geographyical coordinates of the Technical Regional Card of the Trentino (scale 1:10.000) used for the localisation of the grid.

APPENDIX 1

Variables assessed from the aerial photos and the environmental maps of Trentino and used in the model

Vegetation Variables (surface in ha)

Dense conifer forest
Thick conifer forest
Dense broad-leaf forest
Thick broad-leaf forest
Dense mixed softwood-hardwood stand
Thick mixed softwood-hardwood stand
Rocky land
Shrubs
Prairies
Prairies with rocks
Prairies with trees and shrubs
Prairies with rocks, trees and shrubs
Pastures
Pastures with rocks
Pastures with trees and shrubs
Pastures with rocks, trees and shrubs
Orchards
Crops
River bed surface
Lakes
Urban and industrial areas
Mean forests size

Habitat Complexity Variables

Shannon index
Number of forests
Number of plots

Anthropocentric Variables

Number of scattered buildings
Number of villages
Roads length (m)

Physical Variables

In metres:
Maximum altitude
Minimum altitude
Difference in height

In hectares:
NW Exposure
N Exposure
NE Exposure
SW Exposure
SE Exposure
S Exposure
E Exposure
W Exposure

CHAPTER 4

Population dynamics of Rock Partridge (*Alectoris graeca saxatilis*) in the Dolomitic Alps

I.M. Cattadori[1,2], G. De Franceschi[3] & P.J. Hudson[1]

[1]Institute of Biological Sciences, University of Stirling
[2]Centro di Ecologia Alpina, Trento, Italy
[3]via Carlotti 2 Verona, Italy

Ibis, under review

POPULATION DYNAMICS OF ROCK PARTRIDGE *ALECTORIS GREACA SAXATILIS* IN THE DOLOMITIC ALPS

Isabella M. Cattadori, Giacomo De Franceschi & Peter J. Hudson

The population dynamics of rock partridge *Alectoris greaca saxatilis* were investigated in the Italian Dolomites using count data collected between 1994 and 1998. Breeding density was estimated in spring using the playback of a territorial call and breeding production was assessed using trained pointing dogs to locate the broods. *K* factor analysis and λ sensitivity analysis were performed to identify the demographic parameters responsible for the year to year changes in abundance. Long term temporal dynamics were examined using hunting statistics collected from 18 main mountain groups during the period 1965-1994. A high decrease in animal shot was observed between 1965 and 1975 and populations in the western part of the province exhibited an earlier decline. Significant differences were observed in the breeding density between years and mountain groups. Density of breeding birds plus young in summer was consistent between years, mountain groups, between cyclic and non-cyclic populations and in both western and eastern areas. Key factor analysis identified total winter mortality, k_{01}, and spring to summer loss, k_2, as the key factors in most populations. Total winter mortality, k_{01}, was confirmed as the most important variable influencing population changes, using λ contribution analysis. Hunting pressure varied significantly between mountain groups and there was evidence of compensation on winter loss. These results indicate that rock partridge populations have now stabilised at a low density and some hypotheses to explain this pattern are suggested.

A large number of species of conservation value are declining in abundance through direct or indirect anthropogenic effects although in the majority of cases the precise cause of this decline is not known. There are immense logistic problems in obtaining sufficient data to produce an insight into the demographic cause of the decline, particularly since species are usually at low densities and estimating survival and fecundity is difficult. The best approach is to gain data from replicated counts in different sample areas and to compare the temporal dynamics of the populations in relation to the environmental changes. Analytical tools are available for this analysis although the commonly used methods may not be relevant for declining species. In this paper we use demographic data on rock partridge *Alectoris graeca saxatilis* to investigate the cause of populations decline and to apply analytical procedures.

The majority of galliform species are declining within Europe, principally as a consequence of habitat change that has come about through agricultural intensification and a change in forestry management but also through an interaction with natural enemies such as predation, parasitism and hunting (Hudson & Rands 1988, Tapper 1992, AA.VV. 1994). Like most of galliforms, the rock partridge have exhibited both a decrease in density and a contraction in range since the fifties (Spanò & Bocca 1983, Priolo & Bocca 1992, Bernard Laurent & De Franceschi 1994, Meriggi *et al.* 1998). More recently, analyses of hunting statistics from the Dolomites has identified that the dynamics are unstable with a higher tendency to exhibit cyclic fluctuations in abundance in the drier habitats (Cattadori *et al.* 1999). The populations in the dryer habitat carry a higher infection of the caecal nematode *Ascaridia compar* (Rizzoli *et al.* 1997) and recent unpublished studies have found evidence of parasite induced reduction in host fecundity. Although this has yet to be tested experimentally, these data imply that parasites may be the causative agent in population cycles as recorded in red grouse (Hudson et al. 1992, Dobson & Hudson 1992, Hudson et al. 1998).

Separating which factors cause short-term cyclic declines in abundance compared with those influencing the long-term trend is not always simple but a good starting point is to obtain detailed demographic data. A traditional approach for answering these questions is to perform key factor analysis and identify the key factor that contributes most to the year to year total mortality using linear regression (Morris 1959, Podoler & Rogers 1975). Whilst this technique has been frequently performed in the analysis of life table data it has limitations and problems of interpretation (Manly 1990, Royama 1996). One of the problems is that key factor analysis only considers mortalities and net emigration and does not incorporate realistic variations in birth rates. Previous workers usually get around this problem by considering the maximum potential birth rate and subtracting this from the actual birth rate to give mortality before birth. However, since this difference can be very high it may appear an unnaturally high cause of mortality influencing changes in total mortality (Sibly & Smith 1998). Further problems concern the fact that continual declines in numbers cannot be analysed and that successive mortalities reduce the number of individuals such that abundance in the last age group before breeding can be very low but its contribution considered like the other age classes. In this situation the loss of just one or two individuals can have a large influence on mortality estimates. These issues provide serious problems in the analyses of threatened or declining populations. One way of avoiding some of these problems is to apply sensitivity analysis, a technique which evaluates the sensitivity of the growth rate λ to changes in the population parameters (Caswell 1989, Steen & Erikstad 1996, Sibly & Smith 1998). This approach examines the relative contribution of the mortalities and birth rates to the relative population growth rate. Since this technique is relatively new it has not been widely applied so in this paper we analyse the rock partridge count and present the findings using both key factor analysis and λ contribution analysis.

MATERIALS AND METHODS

Study sites and species

Detailed counts of rock partridge were undertaken in Trentino (6250 km^2), an autonomous province in the north-eastern Italian Alps that include a large proportion of the alpine population of rock partridge (Fig.1). Trentino consists of 18 discrete mountain groups separated by obvious valleys and with approximately 50% of the total surface between 1000 m and 2000 m of altitude. The climate is sub-Mediterranean in the south and sub-continental to alpine in the north although local macro climatic conditions dominate as consequence of two main rainfall patterns. Variation in the annual precipitation divides the province in two wide areas: a dry area where rainfalls does not exceed 1000 mm per annum and a wet area with rainfalls over 1000 mm the annum. Variation in the seasonal distribution of rainfall divides the province into a northern area with a peak in precipitation during the summer months and a southern area where rainfall peaks in spring and autumn (Boato *et al.* 1988, Gafta 1994, Cattadori et al. 1999).

Counts were undertaken between 1994 and 1998 as part of the Provincial Forestry and Wildlife Service's Galliform Monitoring Scheme. In this study we consider a total of 29 areas, 9 where both spring and summer counts were undertaken and 20 where just spring counts were carried out. Study sites were selected to represent a variation in habitat type and to provide representative data from the different mountain groups of the province. Not all the areas were counted each year and in this analyses we ignore the sites with less than 4 years of consecutive data. Each sample area was classified in relation to the mountain group in which it was located and the tendency of the population to cycle or not cycle as determined by previous analysis of long term hunting statistics (Cattadori *et al.* 1999 and Fig. 1).

We also included count data collected by Paolo F. De Franceschi and co-workers since 1990 from the Carnic Alps in the province of Udine where breeding density and production were counted on two sites.

Long Term Population Changes

The long term temporal pattern of rock partridge was investigated using the hunting statistics collected form 210 hunting areas between 1965 and 1994 and aggregated into the main 18 mountain groups of Trentino (Fig. 2). Time series with more than five missing values or more than five zeros were ignored while in the case of less than five missing data the points were interpolated averaging the neighbouring data values. A total of 14 time series were considered (details in Cattadori *et al.* 1999). We used a simple exponential model to describe the decline:

$$n_{t+1}=\lambda n_t \exp^{-an_t}$$

where n_t is population at time t, λ is the finite rate of population increase and a a constant. The parameters λ and a from each population were estimated by applying natural logarithms:

$$\log(n_{t+1}/n_t)=\log(\lambda) - an_t$$

and regressing $\log(n_{t+1}/n_t)$ on n_t. The estimated parameters were then used to generated time series 30 years long and with the initial population size equal to the original time series.

The spatial pattern of long term population dynamics was investigated using K-mean cluster analysis selecting the method that maximise variability between and minimise variability within clusters. The analysis was repeated for 4, 3 and 2 clusters using the standardised time series that removed the species-specific effect and the specific differences between the mountain groups but maintained the specific strength of fluctuations and the general population decline characteristic of each site.

Recording demographic data

Breeding density was estimated between the first week of May and the middle of June as the number of males that responded to the playback of a recorded territorial call (Bernard Laurent & Laurent 1984, Sutherland 1996). Playbacks were carried out during the five hours immediately after dawn along pre-defined line transects that provided a total acoustic cover of the whole study area as tried and tested by previous workers (Bernard Laurent & Laurent 1984, Meriggi 1989, Bocca 1990). Playbacks were repeated on 3 different days and the location of all males mapped. The number of calling males regularly recorded was taken as breeding density of males and we assumed that each calling male was paired to a female (Bernard Laurent & Laurent 1984). Summer counts were undertaken in 9 of the spring sites with the aid of trained pointing dogs that quartered the whole area, located and then flushed broods so all birds could be counted and aged.

In Trentino the counts were performed in areas where hunting was undertaken, except two sites that were in protected areas. The hunting season generally runs from the middle of September to the middle of December and hunting is restricted to the local people with a maximum number of animals shot per area. Data on the sex, age and location of each animal shot were obtained from most of the hunting areas and from 18 areas it was possible to estimate the hunting mortality k_0 (Cattadori et al. 1999). In the two sites of the Carnic Alps hunting was stopped after 1991.

Key factor analysis

Key factor analysis was carried out on numbers of female partridges using the count data from Trentino. Since it was not possible to distinguish between juvenile females and males we assumed an equal sex ratio in broods (Paganin, unpublished). The count data were used to measure the annual population changes and to estimate the k mortalities or losses. The variables were then transformed to natural logarithms [log(n+1) where n is the abundance at time t] since some populations went locally extinct and were recolonized. The following k-mortalities were recorded:

k_0	shooting mortality (number of females shot during the hunting season)
k_1	winter loss (number of females before hunting season, minus the number shot, minus the spring number of females the following year); it include natural winter loss and spring dispersal
k_{01}	k_0+k_1 total winter mortality
k_2	adult loss from spring to summer (female in spring minus adult female in summer)
k_3	nest loss (females in summer minus breeding females in summer)
k_4	chick loss (potential production of hen minus number of young females raised)
k_{breed}	k_3+k_4 total breeding mortality
k_{tot}	$k_0+k_1+k_2+k_3+k_4$ total annual mortality

The maximum potential clutch size was taken as 12 and sex ratio at hatching as 1:1 (Priolo & Bocca 1992).

Linear regression was performed between each key mortality and k_{tot} and the mortality with the regression coefficient closest to unity was selected as the variable having made the greatest contribution to year to year changes in total mortality (Podoler & Rogers 1975). Key factor analysis was carried out on each of the 9 sample areas with the spring and summer counts from 5 mountain groups.

λ contribution analysis

To ensure that key factor analyses did not bias the conclusions of this study we also undertook sensitivity analysis on the demographic parameters. Sensitivity coefficients can be scaled multiplying the log-transformation of the sensitivity coefficient by the coefficients of variation (CV) (actual elasticity coefficient, Steen & Erikstad 1996) or multiplying the sensitivity coefficient by the deviance of its demographic parameter (λ contribution analysis, Sibly & Smith 1998). Both these approaches weight each demographic parameter more appropriately examining the relative effect of the mortality and birth parameters on population growth rate, λ. For our investigation we used λ contribution analysis (Sibly & Smith 1998). The contributions of each parameter is expressed as the partial derivative of λ with respect to the parameter itself ($\partial\lambda/\partial p_i$, where p_i is the i^{th} parameter) keeping all others parameters fixed. The sum of the changes of each parameter, $\Sigma\partial\lambda/\partial p_i * \delta p_i$, is the total of the perturbations of growth rate, $\delta\lambda$, and thus of the population's change (for more detail see Sibly & Smith 1998). Note that in this analysis all the parameters causing changes are weighted in relation to the annual growth rate.

To make the analysis comparative with the key factor analysis the rock partridge data were analysed using the number of females. The mortality parameters k_0, k_1, k_{01}, k_2 and k_3 were estimated as in the previous key factor analysis and the birth parameters were measured as:

b birth rate (number of young females in summer/number adult females in summer) *l* survivor from birth to 60 days assuming maximum number of females hatched to be 6.

Simple linear regression was undertaken between each mortality and birth parameter and total growth rate, λ_{total}, to identify the parameter that contributes most to the year to year change in population's abundance.

RESULTS

Long term population changes

Total bag records for the whole of Trentino showed a decline in the relative abundance from 1965 and the present and the period of fastest reduction of animal shot was observed between 1965 to 1975. The modelling of the long term temporal dynamics on the populations of each mountain group reflected the decrease in abundance between 1965 to 1971 and a quite stable pattern or slow decrease in abundance in the following years. The variance explained by the models was generally low (R^2 for all: from 0.01 to 0.22) probably because of the annual fluctuations in the abundance that characterise most of the populations especially during the period 1965-1975. To avoid the effect of these initial years, the simulations were repeated using the initial year of decline from the last peak of abundance (Table 1 and Fig. 2). The new simulations improved the fit of the model and the variance explained generally increase (R^2 for all: from 0.06 to 0.29) although the relative values were still low. Mean decline rate *a* from the complete time series was 0.12 (± 0.016) and no significant difference was observed between the cyclic and non-cyclic populations (Table 1).

In general, k-mean cluster analysis on the standardised time series aggregated the populations in two clear clusters whose composition did not change fundamentally when 2, 3 and 4 clusters were examined. Group 1 aggregated the mountain groups 3, 4, 5, 6, 8, 9, and 17 mostly in the western side of Trentino and group 2 aggregated mountain groups 1, 2, 7, 10, 12 and 14 mostly in the eastern side of the province (Fig. 1). The analysis of the long term population dynamics of the combined data in East and West group, showed a tendency of the West cluster to a stronger decline rate *a* (0.0006 in the West and 0.0004 in the East group). When we fitted the improved exponential model to the two time series, a similar decline rate was observed and a no consistent difference was found in the starting time of decline between the populations in the eastern and the western side of the province (Mann-Whitney U test Z=-0.214 P=0.830 Table 1 and Fig. 2).

Demography of the populations

Mean breeding density from the 29 spring areas of Trentino was 2.32 (±1.894) pairs/km² (Table 2). In the majority of study areas (66%) the density was consistently less than 3 pairs/km² while in only 34% of sites did the densities rise above 3 pairs/km². There were significant differences in breeding density between years (Kruskall-Wallis ANOVA $\chi^2{}_4$= 12.47 $P<0.05$) and between mountain groups (Kruskall-Wallis ANOVA $\chi^2{}_9$= 21.852 $P<0.05$). Populations in the west area of the province exhibited a consistently higher breeding density compared to sample areas in the east (Mann-Whitney U test Z= -2.197 $P<0.05$) while no difference was observed between cyclic and non-cyclic populations.

Mean density in summer (adults plus juveniles) from the 9 sample areas was 3.47 (± 3.910) birds/km², mean brood density was 0.42 (± 0.526) broods/km² and the mean number of juveniles per successful brood was 5.01 (± 1.791; Table 2). Total density in summer was similar between years, mountain groups (Kruskall-Wallis ANOVA for all: $P>0.05$), and between cyclic and non-cyclic populations or western and eastern area (Mann-Whitney U test for all: $P>0.05$). Number of successful broods varied significantly between mountain groups (Kruskall-Wallis ANOVA $\chi^2{}_4$= 13.067 $P<0.05$). Number of juveniles per brood was consistently different between the years (Kruskall-Wallis ANOVA $\chi^2{}_4$= 9.833 $P<0.05$) and a higher proportion of juveniles was observed in the populations in the western side of the province (Mann-Whitney U test Z=-1.988 $P<0.05$).

Mean population growth rate ($r= n_{t+1}/n_t$, where n_t= pair density in spring) from the spring areas was 1.01 (±0.937) and no consistent differences were observed between years, or cyclic and non- cyclic populations or west and east areas. Growth rate tended to fall exponentially as spring population size increased. There was a positive relationship between growth rate and breeding production (defined as juvenile per hen: r=0.46 n=22 $P<0.05$). While the count data were from a much shorter and more recent period, the long term dynamics indicates that breeding density has now stabilised at a low density and of the 24 count areas 79% showed a decrease and 21% an increase over the five years of study.

Mean breeding density from the 2 spring areas of the Carnic Alps was 2.26 (± 0.905) pairs/km². Mean brood density was 0.05 (± 0.007) broods/km² and the mean number of juveniles per brood was 4.67 (± 1.366). Mean growth rate was 1.08 (± 0.721). No significant differences were observed in the population variables between years or mountain groups (for all: $P>0.44$). There were no statistical differences in the population variables between Carnic Alps and the population data from Trentino.

Hunting effect

The proportion of rock partridge shot in each area varied significantly between mountain groups (Kruskall-Wallis ANOVA $\chi^2_7 = 17.301$ $P<0.05$). A higher proportion of animals were shot in the cyclic than the non-cyclic populations (Mann-Whitney U test $Z=2.106$ $P<0.05$) while no differences where detected between the eastern and western populations or between years. Growth rate exhibited a negative but not significant relationship with the number of rock partridge shot during the winter season. When we investigated the effect of hunting in winter, using the k-mortalities, there was a positive but not significant association between hunting mortality and total winter mortality (k_{01} $r=0.25$ $n=8$ $P=0.554$), as well, there was a negative but not significant relation between natural winter loss and the hunting mortality (k_1 $r=-0.15$ $n=8$ $P=720$, Fig. 3). While these samples size were too small to identify any significant relationship these results and the observation that breeding density was similar in unshot versus shot areas suggest the possible effect of compensation of hunting mortality on total winter mortality. As expected, number of animal shot was positively correlated with breeding success in the prior breeding season but again no significant relationship ($r=0.42$, $n=8$, $P=0.297$).

Key factor analysis

All populations exhibited fluctuations in abundance that permitted the application of key factor analysis. Key factor analysis form the 9 sites identified total winter mortality, k_{01} and spring to summer adult loss, k_2 as the k factors causing year to year changes in abundance. Total breeding loss, k_{breed} was important in two populations and hunting mortality, k_0 in one sample area. The variables entered the model invariably explained a high variance (R^2 = 43% to 97%) although only 2 of the 9 cases exhibited a significant relationship with k_{tot}. The spatial pattern of the most important key mortalities was investigated and k_{tot} was consistently different between years (Kruskall-Wallis ANOVA $\chi^2 4$= 10.722 P<0.05) but not between mountain groups, while k_{breed} k_2, and k_{01} did not exhibit significant differences.

In general, positive correlations were observed between k_{total} and spring to summer adult loss, k_2, and k_{total} and breeding mortalities (k_3, k_4 and k_{breed}). Negative correlations were observed between shot mortality, k_0 and winter loss, k_1 and between winter mortalities (k_1 and k_{01}) and spring to summer adult loss, k_2. Chick mortality, k_5 was negatively correlated with egg loss, k_4 and nest loss, k_3 (Tab. 3a).

λ contribution analysis

λ contribution analysis identified total winter mortality, k_{01} as the most important contributing factor in 6 out of 9 sample areas. Total breeding loss, k_{breed} was important in 2 populations while spring to summer adult loss, k_2 was the main factor in one population. As with key factor analysis the parameters explained a high variance of the model (R^2 from 0.48 to 0.98) in all but one case (R^2=0.09) and only 44% were significant. λ_{total} was positively correlated with the winter mortalities, k_{01} and k_1 and total breeding mortality, k_{breed}. Winter loss, k_1 was negatively correlated with hunting mortality, k_0 and total winter mortality, k_{01} was positively correlated with winter loss, k_1 (Tab. 3b).

DISCUSSION

The decline of rock partridge numbers in the Dolomites reflects the more wide spread decline of the species in other Alpine districts where has been observed in the majority of the populations since the fifties and where populations have now stabilised at low densities (Bernard Laurent & De Franceschi 1994). There were variations in the decrease of populations within different parts of Trentino but at present, populations in the western side exhibit higher densities. Cyclic fluctuations appears to have increased the rate of decline (mountain groups 5, 8 and 9).

Many hypothesis have been suggested to explain the cause of the decline in rock partridge and a recent study on rock partridge distribution in Trentino in the last 40 years demonstrated that a reduction and a fragmentation of the suitable habitat, especially the increase in woodland at medium to low altitudes, may have lead to a contraction of the range and the extinction of small, isolated populations (Meriggi et al. 1998). While the factors that caused the reduction of rock partridge distribution seem to be identified in the land use changes, the mechanism that determined the collapse in abundance was probably a combination of factors. Salvini and Colombi (1983) suggested that one of the main causes was a parasite infection both in adults and juveniles that started in the eastern Italian Alps in the fifties and affected the western regions in the seventies. No empirical demonstrations were carried out to support this hypothesis, however, recent analyses on rock partridge have found evidence that guts helminths can reduce the reproductive rate of captive birds and thus potentially affect the abundance of natural populations (Rizzoli et al. 1997). However, macroparasites such as these helminthis cause morbidity rather than mortality and epidemics caused by microparasites would be more likely to have caused the decline in abundance. However, the tendency of this infection to spread from east to west of the Alps does not seem to have occurred in Trentino and an analysis on parasites in rock partridge shot during the hunting season singled out a significantly higher abundance of *Heterakis gallinarum* in the eastern population (Man-Whitney U test $Z=2.625$ $P<0.001$) where a consistent lower breeding density and offspring production was recorded. Moreover, the tendency of the western, cyclic populations to a higher decline rate could be caused by the effect of *Heterakis gallinarum* associated with *Ascaridia compar*, which was found more abundant in the cyclic populations (Rizzoli et al. 1997). We do not refute the possible role of parasite in causing the collapse in rock partridge stocks during the sixties although such a decline may have been caused by a microparasite rather than a helminth. Parasites had a low impact (9%) on the annual mortality of a natural population of hybrid partridges (*Alectoris graeca saxatilis* x *Alectoris rufa rufa*) in the French Alps while predation during the winter months was the principal factor of mortality (85%; Bernard Laurent 1989). While predators can reduce the abundance of a prey, this does not mean predators are important in regulating the prey population. In fact, there is a little evidence to suppose that predators are important in regulating prey density (Crawley 1992). Predators can only regulate the prey population when there is a density-dependent relationship in the predator-prey system, which was yet to be investigated in the Trentino (Crawley 1992). In contrast, over-hunting seems a more possible cause of collapse in rock partridge abundance in the Italian Alps (Priolo & Bocca 1992, De Franceschi 1998). We know that the hunting in the Italian Alpine districts is regulated giving a total maximum number of animals to shoot and only local people are allowed to hunt in their own reserve (Bocca & Grimod 1989, Cattadori et al. 1999). The restriction on hunting is relatively recent so prior to this regulation it is possible that hunting pressure was strong enough to cause a reduction of stocks during the sixties. However, there is some evidence for partial compensation in this study but no consistence of an increase in total winter mortality with the number of animals shot.

Rock partridge densities exhibited a tendency to decline over the past 5 years although annual fluctuations in abundance were observed. These densities were consistent with the low densities recorded in other Italian provinces (Spanò & Bocca 1983, De Franceschi 1980, Rossi et al. 1988 Bocca & Grimod 1989, Bocca 1990) and other alpine countries (Glutz et al. 1973, Bernard Laurent 1984, 1987, 1990, 1992, Zbinden 1984). A weak positive relationship was observed between the growth rate and the offspring production implying that breeding production could be a weak density dependent mechanism of regulation in rock partridge. However, at these low densities the populations are probably more affected by the stochastic effects of environmental perturbations.

This study demonstrated that the factors responsible for the annual variation in rock partridge populations in Trentino were principally total winter mortality and secondly winter to summer adult loss. Total winter mortality increased with hunting mortality and despite the relatively low density of the populations hunting mortality was partially compensated for reduced winter loss. In fact, while hunting was stronger in the cyclic populations, located in the drier part of the province, total winter mortality was not different between the mountain groups. The causes of mortality were not known although deaths from starvation during heavy snowfall have been reported to be important in the wet areas (Gossow et al. 1992). Death from starvation represented only 3% of the annual natural mortality in the French Alps although very heavy deep snow at low altitudes can cause an increased number of deaths (Bernard Laurent 1988, 1989). Spring to summer adult mortality was another important component of annual population's variation and studies in Maritime Alps have identified that this is caused principally by predation (Bernard Laurent 1989). However, because this mortality was estimated using the abundance of female, it is possible that their higher vulnerability during the breeding period over estimated the relative importance of this cause of mortality.

In general, key factor analysis and λ contribution analysis provided similar results. Both the methods identify similar main parameters that occurred with similar proportions. This conclusion is in accordance with Sibly & Smith (1998) that arrived at the same result after using the two approaches to examine the population dynamics of deer population on the island of Rhum. However, λ contribution analysis is to be preferred since better estimates the importance of each population parameter weighting its variation according to the annual growth rate and thus overcoming many of the general problems of the k factor analysis.

In summary rock partridge have declined in Trentino over the past 40 years and most of the collapse occurred between 1965-1975. At present the populations exhibit a general low density and hunting pressure probably played some role in keeping these abundances at these low levels.

Acknowledgement

We would like to thank the Forestry and Wildlife Service of the Autonomous Province of Trentino that provided some of the data used in this study. Special thanks to the forestry guards involved in the field work. Annapaola Rizzoli kindly supplied the data on parasites and Paolo De Franceschi improved the manuscript by his constructive criticisms. This research was founded by the Centro di Ecologia Alpina.

REFERENCES

AA.VV. 1994. In: Plans de restauration pour quelques galliformes européens: la gelinotte des bois, le grand tétras, le tétras-lyre et la perdrix bartavelle. *Gibier Faune Sauvage, Game Wildlife* 11. Hors série Vol. **1, 2** Office Natl. Chasse, Paris.

Bernard Laurent, A. & Laurent, J.L. 1984. Mèthode de recensement des perdix bartavelles (*Alectoris graeca saxatilis* BECHSTEIN 1805) au printemps. Applications dans les Alpes-Maritimes. *Gibier Faune Sauvage* **4**: 69-85.

Bernard Laurent, A. 1987. Démographie comparée d'une popolation de perdix bartavelle *(Alectoris greaca saxatilix)* et d'une population d'hybrides *(A. g. saxatilix* x *A. r .rufa)* dans les Alpes-Maritimes. *Rev. Ecol. (Terre Vie)* suppl. **4**: 189-199.

Bernard Laurent, A. 1988. Les déplacements en automne et en hiver de perdix rochassières *(Alectoris greaca saxatilix* x *Alectoris rufa rufa)* dans les Aples Méridionales et leurs déterminants. *Gibier Faune Sauvage* **4**: 171-186.

Bernard Laurent, A. 1989. Importance de la prédation sur une popolation de Perdix rochassières *(Alectoris greaca saxatilix* x *Alectoris rufa rufa)* des Aples Méridionales. *Gibier Faune Sauvage* **6**: 361-382.

Bernard Laurent, A. 1990. Biologie de reproduction d'une popolation de perdix rochassière *Alectoris greaca saxatilix* x *Alectoris rufa rufa* dans les Aples Méridionales. *Rev. Ecol. (Terre Vie)* **45**: 321-344.

Bernard Laurent, A. 1992. Densité en période de reproduction de la Perdix bartavelle *Alectoris greaca saxatilix* dans le massif des Ecrins. Rapport interne Parc National des Ecrins.

Bernard Laurent, A. & De Franceschi, P.F. 1994. Statut, évolution et facteurs limitant les populations de perdrix bartavelle (*Alectoris graeca*): sinthèse bibliographique. In: Plans de restauration pour quelques galliformes européens: la gelinotte des bois, le grand tétras, le tétras-lyre et la perdrix bartavelle. *Gibier Faune Sauvage, Game Wildlife* 11. Hors série Vol. **1**. Office Natl. Chasse, Paris: 267-304.

Boato, S., Arrighetti, A. & Osti, F. 1988. *Parchi e riserve naturali del Trentino.* Temi Trento.

Bocca, M. 1990. La coturnice (*Alectoris graeca*) e la Pernice bianca (*Lagopus mutus*) in Valle D'Aosta. Regione Autonoma della Valle D'Aosta e Comitato Regionale Caccia, Aosta.

Bocca, M. & Grimod I. 1989. Note sulla gestione venatoria in Valle d'Aosta. Museo Regionale di Scienze Naturali di Saint-Pierre, St. Pierre, Aosta.

Caswell, H. 1989. Analysis of life table response experiments I. Decomposition of effects on population growth rate. *Ecological Modelling* **46**: 221-237.

Cattadori, I.M., Hudson, P.J., Merler, S. & Rizzoli, A. 1999. Synchrony, scale and temporal dynamics of rock partridge (*Alectoris graeca saxatilis*) populations in the Dolomites. *J. Anim. Ecol.* **68**.

Crawley, M. J. 1992. *Natural Enemies. Population Biology of Predators, Parasites and Diseases*. Blackwell Scientific Pubblications.

De Franceschi, P.F. 1988. La situazione attuale dei galliformi in Italia. Ricerche recenti o ancora in corso. Problemi di gestione e prospettive per il futuro. In Spagnesi M. & Toso S. (eds.) Atti I Conv. Naz. Biol. Selvaggina. Suppl. *Ric. Biol. Selvaggina* **XIX**: 165-180.

De Franceschi, P.F. 1980. Coturnice delle Alpi e Pernice bianca: alcune considerazioni. *Caccia e Pesca* **11**: 28-30.

Dobson, A. P. & Hudson, P. J. 1992. Regulation and stability of a free living host-parasite system: *Trichostrongylus tenuis* in red Grouse. II. Population models. *J. Anim. Ecol.* **61**: 487-498.

Gafta, D. 1994. Tipologia, sinecologia e sincorologia delle abetine nelle Alpi del Trentino. Braun-Blanquetia, *Review of Geobotanical Monographs* vol. **12**.

Glutz Von Blotzheim, U.N., Baue,r K.M. & Bezzel E. 1973. Handbuch der Vögel Mitteleuropas. Band 5:Galliformes und Gruifomes. Frankfurt am Main.

Gossow, H., Hafner, F., Pseiner-Petrjanos, S., Vonkilch, G. & Watzinger, G. 1992. The status of grey partridge (*Perdix perdix)* and rock partrige (*Alectoris graeca saxatilis)* populations in relation to humanland use in Austria: a review. Birkan M., Potts G.R., Aebischer N.J. & Dowell S.D. (eds.) Perdix VI, First Int. Symp. On Partridges, Quails and Francolins, *Gibier Faune Sauvage* **9**: 515-521.

Hudson, P. J & Rands, M.R.W. 1988. *Ecology and management of gamebirds*. B S P Professonal Books.

Hudson, P.J., Newborn, D. & Dobson, A.P. 1992. Regulation and stability of a free-living host-parasite system: *Tricostrongylus tenuis* in red grouse I Monitoring and parasite reduction experiments. *J.Anim. Ecol.* **61**: 477-486.

Hudson, P. J., Dobson, A. P. & Newborn, D. 1998. Prevention of population Cycles by Parasite Removal. *Science* **282**: 2256-2258.

Manly, B.F.G. 1990. *Stage-Structured Populations: Sampling, Analysis and Simulation.* Chapman & Hall, London.

Meriggi, A. 1989. Analisi critica di alcuni metodi di censimento della fauna selvatica (Aves Mammalia). Aspetti teorici ed appplicativi. *Ric. Biol. Selvaggina* **83**:1-59.

Meriggi, A., Pandini, V., Sacchi, O., Ziliani, U. & Ferloni, M. 1998. Factors affecting the presence and population dynamics of rock partridge (*Alectoris graeca saxatilis*) in Trentino (Northern Italy). Centro di Ecologia Alpina *Report 15*, Trento.

Morris, R.F. 1959. Single factor analysis in population dynamics. *Ecology* **40**: 580-588.

Podoler, H. & Rogers, D. 1975. A new method for the identification of the key factors from life-table data. *J. Anim. Ecol.* 44: 85-115.

Priolo, A. & Bocca, M. 1992. Coturnice (*Alectoris graeca*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 766-777.

Rizzoli, A., Manfredi, M.T., Russo, F., Rosà, R., Cattadori, I.M. & Hudson, P.J. 1997. A survey to identify important macroparasites of rock partridge (*Alectoris graeca saxatilis*) from Trentino. *Parasitologia,* **39**: 331-334.

Rossi L., Meneguz, P.G. De Meneghi, D. 1988. Piano territoriale Faunistico della provincia di Torino. Assessorato Caccia e Pesca Zona Alpi, Torino.

Royama, T. 1996. A fundamental problem in key factor analysis. *Ecology* 3: 129-135.

Salvini, G.P. & Colombi, G.C. 1983. La Coturnice. Studi sulla popolazioni della Coturnice delle Alpi. Unione Nazionale cacciatori Zona Alpi.

Sibly, R.M. & Smith, R.H. 1998. Identify key factors using λ contribution analysis. *J. Anim. Ecol.* 67: 17-24.

Steen, H.& Erikstad, K.E. 1996. Sensitivity of willow grouse Lagopus lagopus population dynamics to variations in demographic parameters. *Wildlife Biology* 1: 27-35.

Sutherland, W.J. 1996. *Ecological Census Tecnhiques, a handbook.* Cambridge University Press.

Spano', S. & Bocca, M. 1983. Coturnice, *Alectoris graeca*: in Brichetti P. (ed) Atlante degli uccelli nidificanti sulle Alpi italiane, II. *Riv. It. Orn.* **53**: 101-144.

Tapper, S.C. 1992. Game Heritage: An ecological review from shooting and gamekeeping records. Fordingbridge, Hampshire: Game Counservacy Ltd.

Zbinden, N. 1984. Zur Verbreitung. Siedlungsdichte und Herbst-/Winternahrung des Steinhuhns *Alectoris graeca* im Tessin. *Ornithol. Beob.* **84**: 49-61.

Mountain group	**Cyclic/non Cyclic**	**East/West**	**Exp. Decline rate, *a* (30 years)**	**Time of Decline, *T* (years)**	**Best fit Exp. Decline rate, *a* (starting year)**
1	C	E	0.003	3	same
2	C	E	0.002	3	0.003 (1970)
3	N	W	0.002	3	0.003 (1967)
4	N	W	0.007	3	0.008 (1967)
5	C	W	0.022	8	0.031 (1968)
6	N	W	0.005	2	0.008 (1967)
7	N	E	0.006	3	same
8	C	W	0.018	3	0.019 (1969)
9	C	W	0.010	3	0.020 (1969)
10	N	E	0.023	3	same
12	N	E	0.002	3	0.005 (1970)
14	N	E	0.001	4	0.005 (1970)
15	N	*	0.006	3	0.006 (1972)
17	N	W	0.063	3	0.069 (1970)
WEST			0.0006	2	0.0007 (1966)
EAST			0.0004	3	0.0008 (1970)

*not included in the K mean cluster analysis

Table 1. Decline rate, *a*, from the long term analysis of rock partridge population using an exponential model fitted to the full time series (30 years) and using the initial year of decline from the last peak of abundance; the year is shown in parenthesis.

Demography of populations	**1994**	**1995**	**1996**	**1997**	**1998**
Breeding pair	2.64 ±1.607	2.78±1.769	2.72±2.010	1.87±2.116	1.67±1.717
(pair/km²)	(25)	(28)	(29)	(29)	(29)
Broods in summer	0.57±0.5640	0.72±0.480	0.37±0.643	0.15±0.255	0.31±0.500
(ind./km²)	(8)	(9)	(9)	(9)	(9)
Juvenile in summer	6.17±2.444	4.75±1.477	4.21±1.583	5.50±0.707	4.75±2.217
(juv./nid)	(5)	(8)	(4)	(2)	(4)
Total in summer	6.81±3.887	4.97±3.870	3.26±4.396	1.33±1.766	1.90 ±3.284
(ind./km²)	(8)	(9)	(9)	(9)	(9)
Growth rate		1.30±1.208	1.05±0.529	0.77±0.971	0.98±0.937
(n_{t+1}/n_t)		(25)	(28)	(29)	(29)

Table 2. Rock partridge population densities in the province of Trentino, mean and St. Dev. during the five years of sudy 1994-1998. In parenthesis number of cases.

Key factors	K_0	K_1	K_{01}	K_2	K_3	K_4	K_{breed}
K_0							
K_1	(**)						
K_{01}		**					
K_2		(*)	(**)				
K_3							
K_4					(*)		
K_{breed}		(*)	(*)		**		
K_{total}				*	**		**

3a

λ contribution	K_0	K_1	K_{01}	K_2	K_3	K_{breed}
K_0						
K_1	(**)					
K_{01}		**				
K_2						
K_3						
K_{breed}						
λ_{total}		*	*			**

3b

Table 3. Matrix of correlation between the parameters of population using: a) key factor analysis and b) λ contribution analysis; *= $P<0.05$, **= $P<0.01$, in patenthesis the negative correlations.

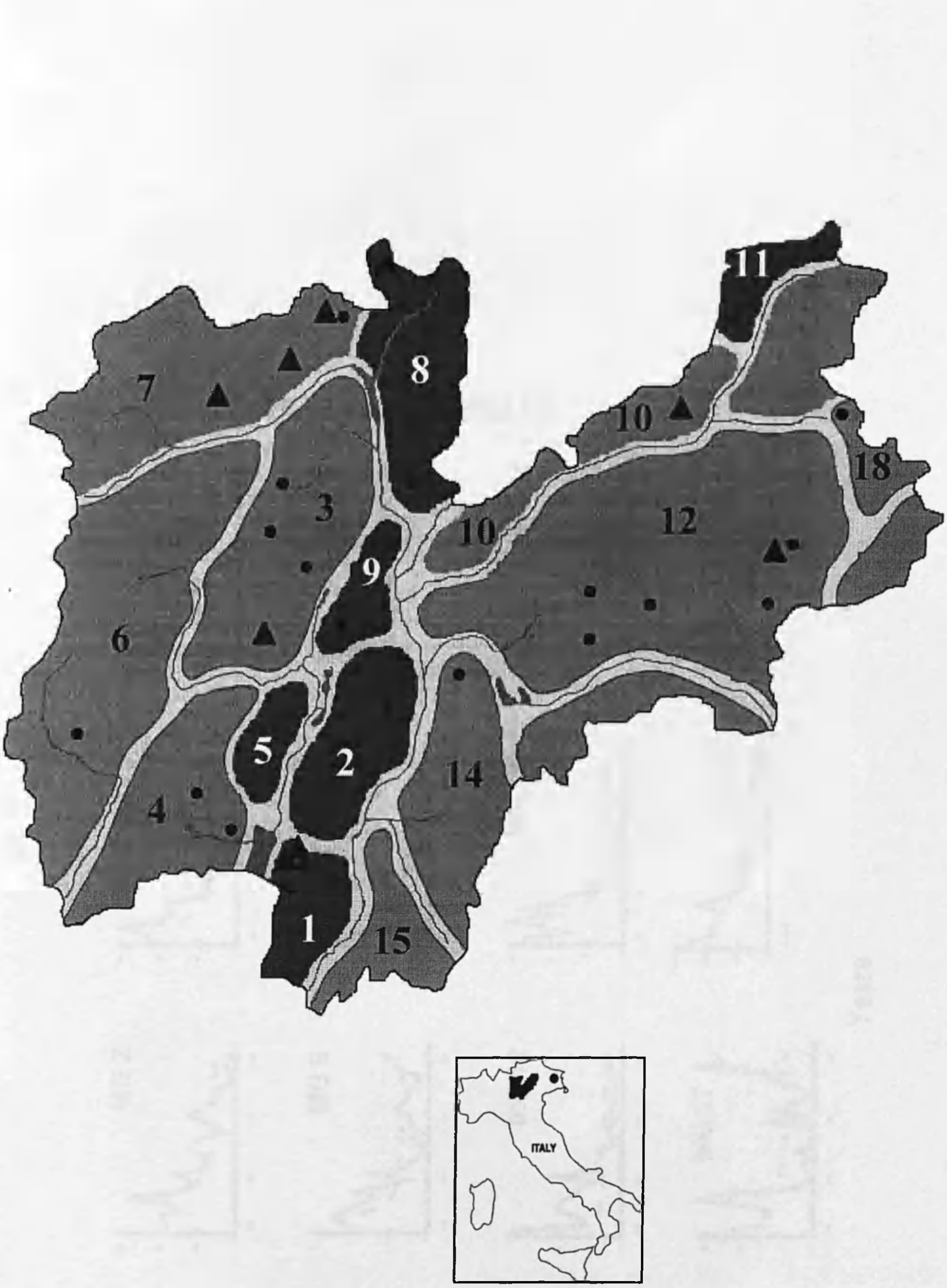


Figure 1. Map of the Province of Trentino showing the 18 major mountain groups and where the populations cycle (dark) and not cycle (clear). In dots the 20 areas used for the spring count and in triangle the 9 areas used for the spring and summer count.

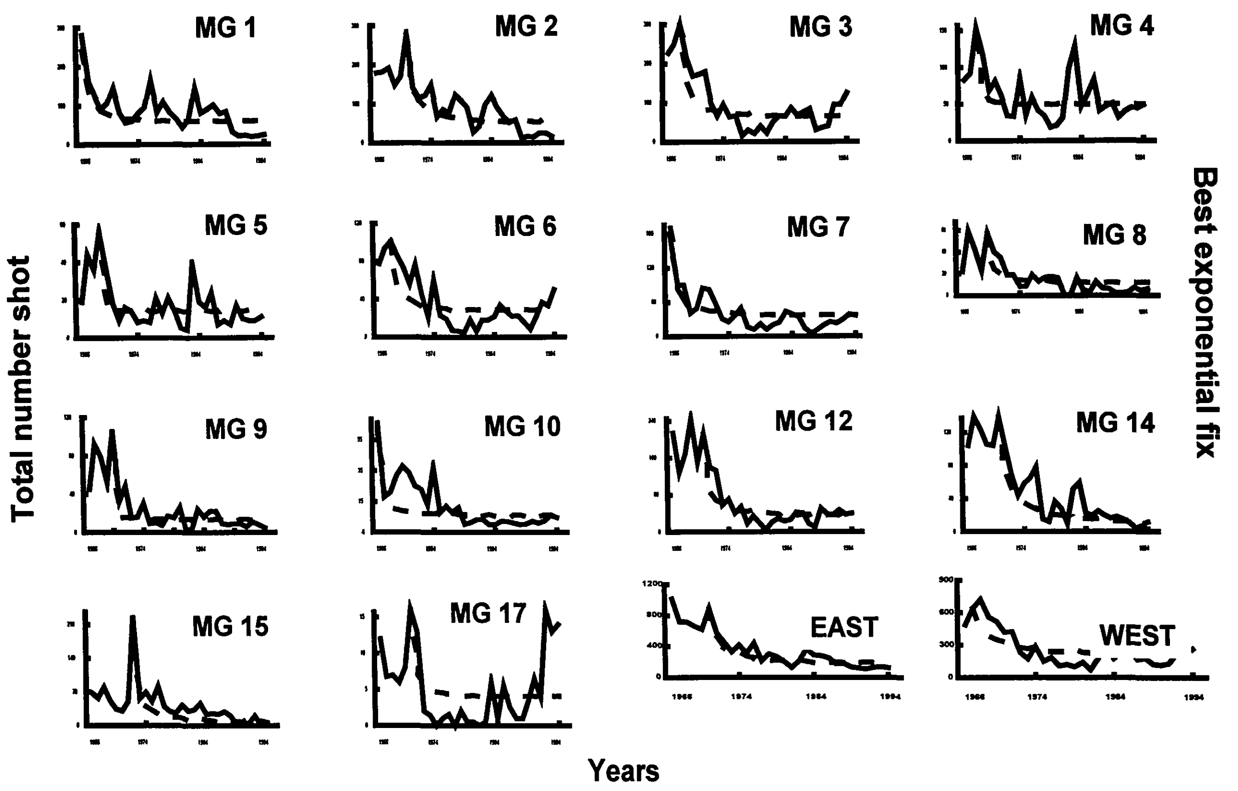


Figure 2. Number of rock partridge shot by mountain groups from 1965 to 1994 in Trentino (solid line), and negative exponential model fitted to the data starting from the year with the last peak of high abundance (dotted line).

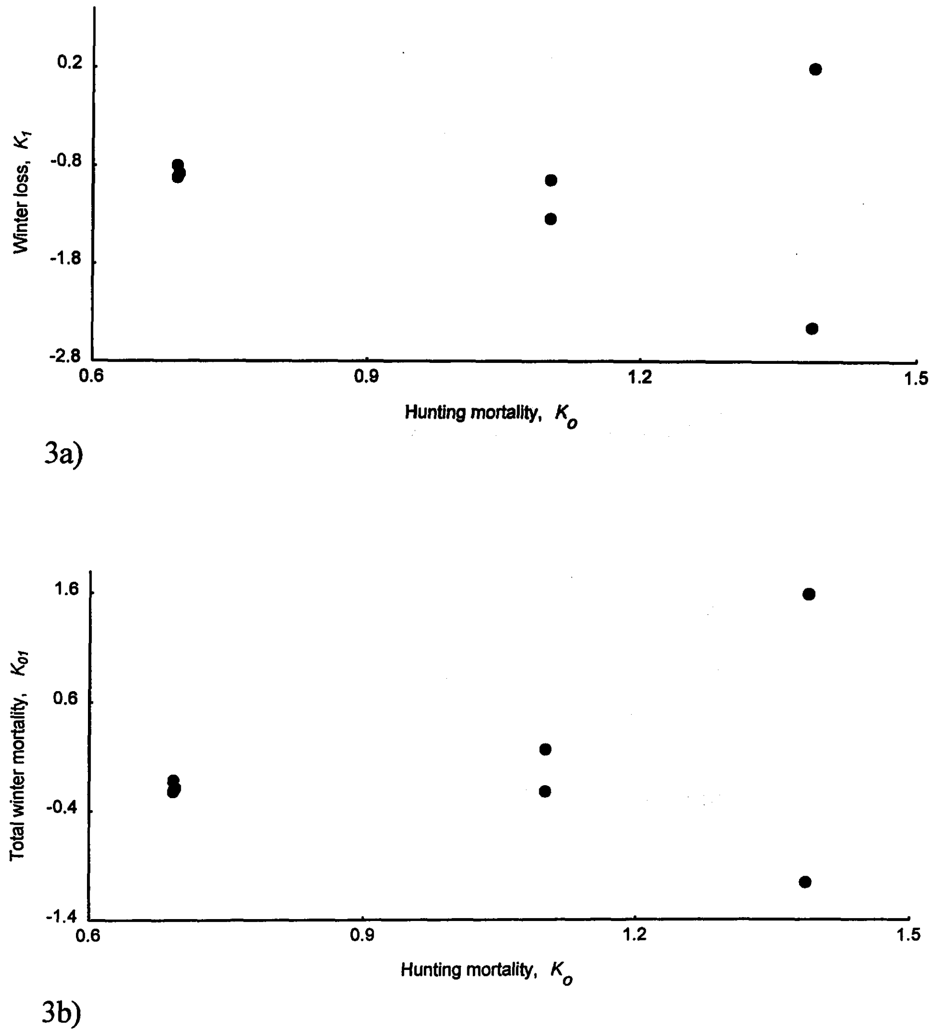


Figure 3 Relation between hunting mortality and a) total winter mortality and b) winter loss from the summer sample areas where it was possible to estimate number of rock partridge shot.

CHAPTER 5

Synchrony, Scale and Temporal Dynamics of Rock Partridge (*Alectoris graeca saxatilis*) Populations in the Dolomites

I.M. Cattadori[1,2], P.J. Hudson[1], S. Merler[2] & A. Rizzoli[2] 1999

[1]Institute of Biological Sciences, University of Stirling
[2]Centro di Ecologia Alpina, Trento, Italy

Journal of Animal Ecology 68, in press

SYNCHRONY, SCALE AND TEMPORAL DYNAMICS OF ROCK PARTRIDGE (*Alectoris graeca saxatilis*) POPULATIONS IN THE DOLOMITES

Isabella M. Cattadori, Peter J. Hudson, Stefano Merler & Annapaola Rizzoli

Summary

1. We examine harvesting records of rock partridge (*Alectoris graeca saxatilis*) to first identify the presence of cycles in a species with a southern European distribution and then examine synchrony between populations at a range of scales.

2. Hunting records from 1965 to 1994 were obtained from 210 hunting areas and analysed at three spatial scales: sub-population, population and metapopulation scale. Rock partridge exhibited cyclic fluctuations in about 40% of the time series with a period of 4 - 7 years. The results did not change with spatial scale. The density dependent structure of the populations showed that most populations exhibited damped oscillations.

3. The proportion of populations that were in synchrony increased with scale from the population to metapopulation level. There was no decline in synchrony with distance but a large variation between populations irrespective of distance.

4. The populations clustered into dry and wet habitats, with those in the dry habitat being more cyclic. We suggest the lack of spatial synchrony with distance but greater synchrony within habitats may reflect the influence of stochastic events operating on populations with different density dependence structures.

Introduction

A series of recent studies have found that animal populations exhibit large-scale spatial synchrony in population fluctuations (Moran 1952; Pollard 1991; Hanski & Woiwod 1993; Ranta *et al.* 1995a, b, 1997a, b; Steen *et al.* 1996; Heino *et al.* 1997). In general, workers have identified a fall in synchrony with distance but this relationship can vary with scale. For example, butterfly populations exhibit large scale synchrony across south east England and parts of Holland and even at local scales but this pattern is lost at intermediate scales, possibly through the effects of environmental heterogeneity (Pollard *et al.* 1986, 1991, 1993; Thomas 1991; Sutcliffe *et al.* 1996, 1997). To identify synchrony requires temporal data, which exhibits variability. Some of the best time series come from disease incidence data such as measles records from cities (Grenfell *et al.* 1995), or hunting statistics such as snowshoe hares and grouse species (Keith 1963; Krebs *et al.*1986; Hudson 1992; Sinclair *et al.* 1993; Lindström *et al.* 1995). Populations that show cyclic dynamics have advantages since they exhibit large variability in abundance, the order of density dependence can be easily estimated and the dynamics can be captured within simple population models. Indeed, spatial synchrony was first investigated in cyclic species and is now seen as a characteristic of many northern mammal species (Krebs & Myers 1974; Heikkilä *et al.* 1994; Grenfell *et al., in press*) and northern gamebirds (e.g. Ranta *et al.* 1995a, b; Lindström *et al.* 1996) but has not been recorded from species with a southern distribution.

We have been studying the population dynamics of rock partridge *Alectoris graeca saxatilis* B, within the province of Trentino in northern Italy and have mapped the extent of populations within well-defined environmental boundaries. Temporal abundance data in the form of hunting records from each population was used to address three questions in this paper:

1. Does a species with a southern European distribution, exhibit population cycles?
2. Are population fluctuations spatially synchronised?
3. Does synchrony vary with scale?

Methods

STUDY AREA AND SPECIES

Trentino (6250 km^2) is an autonomous province of north-east Italy. The area is mountainous with an altitude ranging from 65 m to 3750 m. a.s.l. and about 50% of the land surface between 1000 m and 2000 m. The mountain areas within the province can be classified into three distinct areas as determined from annual rainfall, altitude, geology and vegetation maps (Boato *et al.* 1988). The western area is a high altitude, alpine area characterised by igneous, siliceous and calcareous rocks with a continental/alpine climate and a rainfall that exceeds 1100 mm per annum with peaks of over 1500 mm per annum. The central area is characterised by relatively low altitude and is based on a mix of calcareous and sedimentary rocks; the climate is sub-continental to sub-Mediterranean because of the influence of the large Lake Garda with rainfall usually less than 1000 mm per annum. The eastern area is similar to the western block with high altitude mountain groups, igneous siliceous rocks, a continental/alpine climate and rainfall exceeding 1000 mm per annum.

The rock partridge is distributed from the Alps in France through to Slovenia and inhabits prairies and the rocky meadows. The abundance and distribution of this species has decreased in the last 40 years throughout most of the Italian Alps (De Franceschi 1988; Priolo & Bocca 1992; Bernard-Laurent & De Franceschi 1994) but good numbers remain within discrete populations in the Dolomites. Harvesting data from Trentino province were examined at three 3 spatial levels:

1. *Sub-population*: 210 hunting areas that represent administrative boundaries of each town and the minimum scale at which rock partridge hunting statistics were collected.
2. *Population scale*: 57 separate rock partridge populations were determined from known maps of rock partridge distribution (Meriggi *et al.* 1998).
3. *Metapopulation scale*: 18 discrete mountain groups separated by obvious valleys with a significant break in suitable rock partridge habitat but incorporating several populations (Fig. 1).

HUNTING STATISTICS

The 210 administrative hunting areas of Trentino province maintain a traditional hunting strategy whereby local hunting associations within each village control and record hunting statistics for ungulates and galliform birds. There is no limit on the number of licences produced each year to local people. The result of the annual harvest from each hunting area is forwarded to the Province Department of Wildlife and these data, from 1965 to 1994, are the basis of the current analyses. Rock partridge are hunted during autumn, from September to the middle of December, and the number of days available for hunting each year is set by the Department of Wildlife. During the period of this study, these varied between 22 and 36 days per annum; before 1992, there was no restriction on the number of birds that could be harvested by each hunter but since 1992 the Department has assigned a maximum number per season in each hunting area. While this change in procedure may influence the hunting bag statistics, we have included the data for 1992 to 1994 since the maximum was rarely reached and numbers harvested were not lower after 1992 (Fig. 2). Excluding these years did not influence the conclusions reached.

Data were available on the number of hunters and the number of days of hunting each year for 20 of the 30 years (from 1974 to 1994). From these data, the harvest per unit effort was estimated as the number shot/ hunter*days. The two types of data set, number shot and number shot/unit effort were used for the subsequent time series analysis and the results compared to evaluate the effect of hunting on bag records.

TIME SERIES ANALYSES

Each time series at each of the three spatial scales were transformed to natural logarithm [$\ln(X+1)$]. The time series with more than 5 missing values were ignored while missing values in the other time series were interpolated from the neighbouring data points. Since most of the time series exhibit a downward trend, this trend was removed by fitting a third order polynomial model ($X_t = b_0 + b_1 t + b_2 t^2 + b_3 t^3$) and the residuals used for the time series analysis.

Autocorrelation function analysis (Kendall 1984) was undertaken on each time series and displayed graphically within a correlogram, plotting autocorrelations with respect to time lag. Correlograms often produced negative autocorrelations at time lags of 2, 3 or 4 years, if these were larger than 2 standard errors of the white noise (Barlett's band) then we considered the series exhibited a tendency to oscillate. We classified the cyclic fluctuations according to the definitions by Nisbet & Gurney (1982) as either phase-remembering quasi-cycles (sustained autocorrelations), phase-forgetting quasi-cycle (damped autocorrelations) or were non-cyclic. The period of the population cycles were determined using spectral analyses with the fast fourier transform algorithm and the Hamming spectral density estimate (Monro & Branch 1976; Chatfield 1996). The order of density dependence was determined using partial autocorrelation function analysis (Box & Jenkins 1976; Royama 1992). Although we examined the first 4 lags we concentrated our attention on the density dependence order at lag 2, the structural order that is important in causing the 4 to 10 year cyclic fluctuation in the dynamics of vertebrate populations (Royama 1992). The pattern of density dependence of each population was further examined using the approach by Royama (1992) and others (e.g. Bjornstad *et al.* 1995, Stenseth *et al.* 1996) by fitting a linear second order autoregressive model to each of the time series and estimating the relative values of the two autoregressive parameters that determine the dynamics: a_1 and a_2.

$$X_t = (1+a_1)X_{t-1} + a_2X_{t-2}$$

where: X_t is the bag data at time *t*, ln(X+1) transformed, and a_1 a_2 are constants that represent the strength of density dependence at the respective time lags.

A number of time series included zeros where no birds had been harvested during that year. A series with zeros could influence the conclusions of the analyses since the frequency and time interval between zeros could increase the tendency of a series to exhibit cycles. To avoid the effect of spurious results we compared the proportion of significant autocorrelation functions in time series with less than 10 zeros, against the proportion of autocorrelations from series with more than 10 zeros. The comparison was repeated at each spatial level.

The time series analysis was repeated at each of the spatial scales: sub-population, population and metapopulation but the autoregressive model was estimated just at the population level.

To determine if hunting effort made a significant impact on the cyclic pattern observed, we compared the analysis of the metapopulation time series corrected with the series not corrected for hunting effort, for the 20 years these data were available.

SPATIAL SYNCHRONY

The level of spatial synchrony in the detrended time series was examined using cross-correlation analysis with bootstrapping (Efron 1982; Efron & Tibshirani 1993). Standard correlation analyses would result in Type I error since the degrees of freedom would be over estimated; in fact out of the 18 metapopulations, only 33 correlations would be independent. To get around this problem we used the data based simulation method of bootstrapping following the approach of Ranta *et al.* (1995a,b). Each bootstrap sample consisted of a re-sampled time series selected at random generating a mean cross-correlation with a standard deviation for each pair of time series. The bootstrap sampling process was repeated 1000 times, and for each pair, the mean and standard deviation of the bootstrap cross-correlations coefficients were estimated at time lag 0. Each pair was tested against the null hypothesis (95% confidence limits) of no significant relationship and two populations were considered synchronous when the cross correlation coefficient was significant and positive. The analysis was repeated at both population and metapopulation level. To evaluate how synchrony declined with distance between populations, the cross correlation coefficients were correlated with distance between the central point of populations and metapopulations respectfully.

To determine spatial patterns of synchrony we used k-means cluster analysis, following Ranta *et al.* (1995a). Each time series was allocated to a cluster when its addition maximised the F ratio of the one-way ANOVA maximising differences between and minimising differences within the clusters. The analysis was undertaken at both the population and metapopulation level and repeated for 4, 3 and 2 clusters. The time series data at metapopulation level were then combined in each group of the selected cluster and analysed to determine cyclic fluctuations and the order of density dependence.

FACTORS ASSOCIATED WITH POPULATION CYCLES

To determine how much of the variation in the second order density dependence could be explained by the ecological effects of wetness, we undertook linear regression analyses using the partial autocorrelation function at lag 2 as the dependent variable against precipitation and days of rainfall measured during the summer months. Winter rainfall consisted principally of snowfall that covered most of the rock partridge habitat so we examined just summer estimates of wetness. We selected rainfall for these analyses since the clear ecological difference between the clusters appeared to be variations in wetness although it is quite possible that this is simply a correlate of some other variables.

Results

HUNTING STATISTICS

There was no evidence of a strong influence of hunting effort on the numbers shot. Number of days of hunting varied little and only 7 of the 18 metapopulation areas exhibited a positive relationship between hunting effort and numbers shot and in all but one case hunting effort accounted for less than 20% of the variation in the number shot. There was no significant difference in the proportion of the time series exhibiting cyclic fluctuations (Fisher exact test P=0·489). There was a tendency for the partial autocorrelation function at lag 2 to be stronger in the uncorrected time series (paired t test t_{17}=-2·093 P=0·052). Nevertheless, since correcting for hunting effort did not reduce our ability to detect cycles and since a time series corrected for hunting effort has to be just 20 years we used the log transformed bag records for the analyses.

POPULATION CYCLES AND SCALE

There was no difference in the relative number of cyclic and non-cyclic populations between time series including zeros and time series excluding zeros at each spatial level (for all X^2, P>0·05). Despite these results, a time series with too many zeros carried little information so we ignored the time series with more than 15 zeros. These restrictions resulted in analyses being conducted on 66 sub-population time series, 57 population series and 18 metapopulation series. Since the sub-population is an artificial, political subdivision of the larger population level, we summed all data from the sub-population areas when constructing the time series for the population and metapopulation time series.

Autocorrelation function analyses identified negative autocorrelations at half cycle periods but rarely any positive autocorrelations (Fig 3). Significant cyclic fluctuations were recorded at each spatial scale but the frequency of cases was less than 40% in each of the spatial levels (30% at sub-population, 26% at population and 38% at metapopulation scales). There was no significant difference in the proportion of the series that were cyclic and not cyclic among the spatial scales, indeed with P>0·95 there appears to be a significant similarity between scales (X_5^2=0·75496, P=0·98). Cycle period at each spatial scale was generally less than 8 years but cycle periods of 10 to 16 years were also recorded (Fig. 3). We suspect that these long cycle periods are an artefact of the length of the time series and a consequence of the harmonic effect in the multiple of the dominant cycle lag and thus not of biological significance (Chatfield 1996).

Partial autocorrelation function analysis exhibited negative density dependence at time lag 2, 3 and 4 in the majority of the time series but the frequency of significant cases was less than 30% at each level (17% at metapopulation, 30% at population and 27% at sub-population level). Analysis of variance on the strength of the density dependence at lag 2 found no significant difference between scales (F_2=0·609, P=0·55). Overall, only 5 of the 18 metapopulations and 11 of the 57 populations exhibited significant autoregressive parameters. The plot of the autoregressive parameters show that most populations exhibited a tendency to damped oscillations (Fig. 4).

SYNCHORNY AND SCALE

Synchrony between populations was identified at both population and metapopulation scale with a greater proportion at the higher metapopulation scale (46%) than the population scale (18%) (X_3^2= 68·6, P< 0·001). However, this increase in synchrony with scale could be a consequence of the larger numbers generated at the metapopulation scale. To examine this effect, we corrected the metapopulation time series by dividing the series by the number of populations within each metapopulation and taking the nearest whole number. The difference with scale still remained between the two spatial levels, even though at a lower level of significance (X_3^2= 9.260, P< 0·002).

The relationship between synchrony and distance showed a large amount of variation in the cross correlation coefficients with respect to distance at both population and metapopulation level (Fig. 5 a, b). There was no clear pattern of a decrease in synchrony with distance; for example, a model describing the decline in correlation with the square root of distance described just 0·51% of variation in the cross correlation coefficients at the metapopulation level and just 0·081% at the population level.

The pattern of clustering between metapopulations was examined using k-means clustering and, not surprisingly, the variance explained increased with the number of clusters examined (Table 1). Nevertheless, examination at each of the clustering levels showed an obvious association between the mountain groups which were located along the dry areas of the province (groups 1, 2, 5, 8, 9 and 11) and the composition of this cluster did not change fundamentally between the 2, 3 and 4 cluster levels (Table 1). Less obvious, but also well defined, was the cluster of mountain groups located in the wetter areas centred around the major groups 3, 4, 6, 7, 12, 14 and 17 and this composition did not change between 3 and 4 clusters. This analyses indicated we are dealing with 2 main population clusters within Trentino (Fig. 6) that reflect the environmental conditions distinguished by Boato *et al.* (1988; Fig. 1). Note that these clusters are not geographically distinct areas and so spatial distribution is not confounding.

Cluster analysis at the population level added more detailed information on the pattern of synchrony among populations but still provided the same general findings observed at the metapopulation level. The cluster within the dry area (that includes the mountain groups 1, 2, 5, 8, 9, and the northern part of the groups 6, 14, 17 and 3) maintained the fundamental composition at the 2, 3 and 4 cluster level.

TIME SERIES ANALYSIS ON CLUSTERS

Time series analysis of the summed data from each of the two clusters (representing the different habitats) exhibited no cyclic pattern in the wet cluster and a tendency (P=0·064) for cycles in the dry cluster (Table 2). The partial autocorrelation function at lag 2 was negative for the cluster in the dry area but not in the wet area, indicating no evidence of second order density dependence in the wet area at this scale. A comparison between cyclic and non-cyclic populations located in the wet and dry areas showed a tendency for the populations to be cyclic in the dry regions (X_3^2=2·89, P=0·089).

RELATIONSHIP BETWEEN WETNESS AND DENSITY DEPENDENCE

To examine how much of the variation in the second order density dependence could be accounted for through regional variation in wetness, linear multiple regression analyses was undertaken on summer precipitation (May, June and July) and number of days of rainfall in each month. Two variables entered the model: quantity of rainfall in June which was negatively associated with the strength of the density dependence, and quantity of rainfall in July which was positively associated. The variables explained 69% of the variance of the model ($F_{3,14}$= 4·283, $P<0·03$) and clearly show that the more cyclic populations tended to be in the drier areas.

Discussion

CYCLES IN ROCK PARTRIDGE

A large number of gamebird species are known to exhibit cyclic fluctuations in abundance in northern latitudes. However, rock partridge populations in the Dolomitic Alps are the first case, we are aware of, where cyclic fluctuations have been recorded from a species with a restricted southern European range. Most of the cases in northern latitudes have concentrated on the abundance of tetranoid species (Hudson 1992, Lindström *et al.* 1995, Lindström 1996) but there is evidence that some partridge species such as *Perdix perdix* probably exhibited cyclic fluctuations in the past (Tapper 1992). The fact that cycles have not been recorded in southern Europe may be due to either a paucity of data or a lack of clear cycles in the data. In this respect it is worth noting that the cyclic fluctuations in rock partridge are not as regular as the gamebirds species seen at more northerly latitudes, the correlograms (e.g. Fig. 3) showed heavily damped, phase forgetting quasi-cycles (Nisbet & Gurney 1982). The application of the second order autoregressive model indicated the tendency for damped oscillations, perhaps a reflection of the downward trend and falling densities in rock partridges (Fig. 4).

While the main factor thought to cause population cycles are density dependent trophic interactions, such effects have yet to be shown and agreed on for any cyclic species. This may be because there are a range of interacting factors (e.g. Krebs *et al.* 1995) or because the critical studies have still to be undertaken. Within the galliform birds, detailed field studies, experiments and mathematical modelling have demonstrated that the parasitic nematode, *Trichostrongylus tenuis (*Eberth.), is sufficient and necessary in causing the cyclic fluctuations of red grouse, *Lagopus lagopus scoticus* (Lath.*),* observed in northern England (Hudson *et al* 1985; Dobson & Hudson 1992; Hudson 1992; Hudson *et al.* 1992; Hudson & Dobson 1997). It is possible that a similar system may operate in rock partridges. Macroparasites that induce a reduction in host fecundity and have a long lived free living stages, may be of significance in destabilising partridge abundance and generating cyclic oscillations (May & Anderson 1978; Dobson & Hudson 1992). The main parasites of rock partridge have been identified (Rizzoli *et al.* 1997) and the intensity of infection of these parasites was found to be greater in cyclic than the non-cyclic populations (Rizzoli *et al.* in ms). Moreover, preliminary unpublished studies with captive birds have found evidence that the parasites may be reducing partridge fecundity. Further experimentation and modelling are required to examine this hypothesis and refute alternative hypotheses.

SCALE AND SYNCHRONY

The proportion of rock partridge exhibiting synchronous fluctuations in abundance was significantly greater when the population data were summed into metapopulation time series representing geographical divisions. This would imply that previous studies that have summed count and other population statistics by political divisions (e.g. snowshoe hare, Sinclair *et al.* 1993; Finnish species, Ranta *et al.* 1995a) may have over-emphasised the significance of spatial synchrony. Sutcliffe *et al.* (1996) examined the role of scale in the population dynamics of butterflies and found less synchrony at the lower than the higher scales. They suggested this was a function of high environmental variability at the small scale that is averaged out at the higher scale at which point synchrony is a function of regionally correlated weather patterns. Our data provides some further evidence to support this observation.

Synchrony in population change is generally thought to be caused either by dispersal or the impact of common stochastic events which will synchronise populations with the same density dependent structure (Moran 1953; Royama 1992; Ranta *et al.* 1995a,b, 1997a). While some populations showed strong synchrony there was no clear decrease in synchrony with distance as would be expected if dispersal was the over-riding mechanism causing cycles. Of course if rock partridge were highly sedentary then there would be no opportunity for dispersal and this could explain the lack of synchrony. Radio-tracking studies on rock partridge have found that annual home ranges can be up to 25km long (average 3.2km) with birds dispersing several kilometres across valleys between mountain groups (Bernard-Laurent 1991a, b). These studies suggest that rock partridge could easily move between local populations and metapopulations, particularly when minimum distances were much smaller than the mid-point distances used in the analysis in Figure 4.

The populations clustered into two distinct groups associated with habitat types, which infers an environmental influence. The lack of spatial synchrony but clustering within habitats could be explained because populations vary in the structure of their density dependence and this is greater between than within habitats. Even small changes in the structure and strength of density dependence will have profound effects on the dynamics of the populations and could account for the patterns we have described here. Indeed these results could be quite significant and indicate that the large-scale synchrony seen in populations with a similar structure in density dependence may be due to stochastic events rather than dispersal. This general explanation requires further empirical and mathematical modelling to elucidate synchronising mechanisms (Hudson & Cattadori in prep.). A contrasting study by Sutcliffe *et al.* (1997) came up with similar findings, they identified strong synchrony between spatially structured populations of butterflies but greater synchrony within than between habitats.

In answer to the three questions posed at the beginning of the paper we can state that the rock partridge with a southern European distribution can exhibit population cycles. Fluctuations in numbers are weakly synchronised between populations but an increase in scale can increase the likelihood of synchrony. Synchrony was greater within than between habitats and these findings will tend to support the role of stochasticity rather than dispersal in causing synchrony.

Acknowledgements

We would like to thank both Chris Thomas and Esa Ranta for their very helpful comments on a previous manuscript. Monica Tonini helped with the efficient archiving of data and Sandrino made comments throughout.

References

Bernard-Laurent, A. (1991a). Migrant rock partridges (*Alectoris graeca saxatilis*) in the southern French Alps. *Journal of Ornithology,* **132**, 220-223.

Bernard-Laurent, A. (1991b). Structure sociale et utilisation de l'espace par la perdix rochassiere (*Alectoris graeca saxatilis* x *Alectoris rufa rufa*): variations saisonnieres et individuelles. *Gibier Faune Sauvage,* **8**, 1-30.

Bernard-Laurent, A. & De Franceschi, P.F. (1994) Statut, évolution et facteurs limitant les populations de perdrix bartavelle (*Alectoris graeca*): sinthèse bibliographique. In: Plans de restauration pour quelques galliformes européens: la gelinotte des bois, le grand tétras, le tétras-lyre et la perdrix bartavelle. *Gibier Faune Sauvage, Game and Wildlife,* **11** (Hors série Tome 1), 267-304.

Bjornstad, 0.N., Falck, W. & Stenseth, N.C. (1995) A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proceedings Royal Society London,* **262**, 127-133.

Boato, S., Arrighetti, A. & Osti, F. (1988) *Parchi e riserve naturali del Trentino.* Temi Trento.

Box, G.E.P. & Jenkins, G.M. (1976) *Time series analysis: Forecasting and control.* S. Francisco: Holden-Day.

Chatfield, C. (1996) *The analysis of time series: An introduction.* Chapman & Hall Ltd., London.

De Franceschi, P.F. (1988) La situazione attuale dei galliformi in Italia. Ricerche recenti o ancora in corso. Problemi di gestione e prospettive per il futuro. *Supplementi Ricerche Biologi della Selvaggina,* **XIX**, 165-180.

Dobson, A.P. & Hudson, P.J. (1992) Regulation and stability of a free living host-parasite system: Trichostrongylus tenuis in red Grouse. II. Population models. *Journal of Animal Ecology,* **61**, 487-498.

Efron, B. (1982) *The Jackknife, the Bootstrap and Other Resampling Plans.* CBMS-NSF Regional Conference Series in Applied Mathematics. Vol. 38, SIAM.

Efron, B. & Tibshirani, R.J. (1993) *An Introduction to Bootstrap.* Chapmam & Hall Ltd., London.

Grenfell, B.T.G., Bolker, B. & Kleczkowski, A. (1995) Seasonality, demography and the dynamics of measels in developed countries. In: *Epidemic Models: their structure and relation to data.* (ed. D. Mollison), pp. 248-268.

Grenfell, B.T.G., Wilson, K., Finkenstädt B.F., Coulson, T.N., Murray, S., Albon, S.D., Pemberton, J.M., Clutton-Brock, T.H. & Crawley M.J. (1998) Noise and determinism in synchronised sheep dynamics. *Nature,* in press.

Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology*, **62**, 656-668.

Heikkilä, J., Below, A. & Hanski, I. (1994) Synchronous dynamics of microtine rodent populations on islands in Lake Inari in northern Fennoscandia: evidence of regulation by mustelid predators. *Oikos*, **70**, 245-252.

Heino, K., Kaitala, V., Ranta, E. & Lindström, J. (1997) Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings Royal Society London,* **264**, 481-486.

Hudson, P. J. (1992). *Grouse in Space and Time*. Game Conservancy Trust. Fordingbridge.

Hudson, P.J., Dobson, A.P. & Newborn, D. (1985) Cyclic and non cyclic populations of red grouse: a role for parasitism? *Ecology and Genetics of Host-Parasite Interactions. (*eds D. Rollinson & R.M. Anderson), pp 78-89. Academic Press, London.

Hudson, P.J., Newborn, D. & Dobson, A.P. (1992) Regulation and stability of a free-living host-parasite system: *Tricostrongylus tenuis* in red grouse I Monitoring and parasite reduction experiments. *Journal of Animal Ecology,* **61**, 477-486.

Hudson, P. J. and Dobson, A.P. (1997) Host parasite processes and demographic consequences. In: *Host parasite evolution: general principles and avian models.* Oxford University Press, Oxford. pp 124-154.

Keith, L.B. (1963) *Wildlife's ten year cycle*. Univ Wisconsin Press. Madison, WI. 1963.

Kendall, M.G. (1984) *Time series.* Oxford University Press, London.

Krebs, C.J. & Myers, J.H. (1974) Population cycles in small mammals. *Advances in Ecological Research,* **8**, 267-399.

Krebs, C.J., Cilbert, B.S. & Boutin, S. (1986) Population biology of snowshoe hares. I. Demography of food-supplemented populations in the Southern Yukon, 1976-1984. *Journal of Animal Ecology*, **55**, 963-982.

Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K. & Turkington, R. (1995) Impact of food and predation on the snowshoe hare cycle. *Science*, **269**, 1112-1115.

Lindström, J., Ranta, E., Kaitala, V. & Linden, H. (1995) The clockwork of Finnish tetraonid populations dynamics. *Oikos*, **74**, 185-194.

Lindström, J. (1996) Modelling grouse population dynamics. PhD thesis, Dept. Ecology and Systematics Division of Population Biology, University of Helsinki, Finland.

Lindström, J., Ranta, E. & Linden, H. (1996) Large scale synchrony in the dynamics of capercaillie, black grouse and hazel grouse populations in Finland. *Oikos,* **76**, 221-227.

May, R.M. & Anderson, R.M. (1978) Regulation and stability of host-parasite population interactions - II Destabilising processes. *Journal of Animal Ecology,* **47**, 248-267.

Meriggi, A., Pandini, W, Sacchi, O., Ziliani, U. & Ferloni M. (1998) Fattori influenzanti la presenza e la dinamica di popolazione della coturnice (*Alectoris graeca saxatilis*) in Trentino. *Report del Centro di Ecologia Alpina,* **n° 15**, Trento.

Monro, D.M. & Branch, J.L. (1976) The chirp discrete Fourier transform of general length. *Applied Statistics*, **26**, 351-361.

Moran, P.A.P. (1952) The statistical analysis of game-bird records. *Journal of Animal Ecology,* **21**, 154-158.

Moran, P.A.P. (1953) The statistical analysis of the Canadian Lynx cycle II Synchronisation meterology. *Australian Journal of Zoology,* **1**, 291-298.

Nisbet, R.M. & Gurney, W.S.C. (1982) *Modelling fluctuating populations.* John Wiley & Sons, Chichester.

Olsen, O.W. (1974) *Animal parasites, their life cycle and ecology.* Dover, New York.

Pollard, E. (1991) Synchrony in population fluctuations: the dominant influence of widespread factors on local butterfly populations. *Oikos,* **60**, 7-10.

Pollard, E., Hall, M.L. & Bibby, T.J. (1986) *Monitoring the abundance of butterflies, 1976-1985.* NCC, Peterbrough. UK.

Pollard, E., Van Swaay, C.A.M. & Yates, T.J. (1993) Changes in butterfly numbers in Britain and The Netherlands, 1990-1991. *Ecological Entomology,* **8**, 93-94.

Priolo, A. & Bocca, M. (1992) Coturnice (*Alectoris graeca*). *Fauna d'Italia XXIX Aves I.* (eds P. Brichetti, P.F. De Franceschi & N. Bacetti), Calderini, Bologna, 766-777.

Ranta, E., Lindström, J. & Lindén, H. (1995a) Synchrony in tetraonid population dynamics. *Journal of Animal Ecology*, **64**, 767-776.

Ranta, E., Kaitala, V., Lindström, J. & Linden, H. (1995b) Synchrony in population dynamics. *Proceedings of Royal Society of London*, **262**, 113-118.

Ranta, E., Kaitala, V., Lindström, J. & Helle, E. (1997a) The Moran effect and synchrony in population dynamics. *Oikos,* **78**, 136-142.

Ranta, E., Lindström, J., Kaitala, V., Kokko, H., Linden, H. & Helle, E. (1997b) Solar activity and hare dynamics: a cross continental comparison. *American Naturalist,* **149**, 765-775.

Rizzoli, A., Manfredi, M.T., Russo, F., Rosà, R., Cattadori, I.M. & Hudson, P.J. (1997) A survey to identify important macroparasites of rock partridge (*Alectoris graeca saxatilis*) from Trentino. *Parasitologia*, **39**, 331-334.

Royama, T. (1992) *Analytical Population Dynamics*. Chapman & Hall Ltd., London.

Sinclair, A.R.E., Gosline, J.M., Holdsworth, G., Krebs, C.J., Boutin, S., Smith, J.N.M., Boonstra, R. & Dale, M. (1993) Can the solar cycle and climate synchronise the snowshoe hare cycle in Canada? *American Naturalist,* **141**, 173-198.

Steen, H., Ims R. & Sonerud, G.A. (1996) Spatial and temporal patterns of small-rodent population dynamics at a regional scale. *Ecology,* **77**, 2365-2372.

Stenseth N.C. Bjørnstad 0.N., Takashi S., (1996) gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proceedings of Royal Society London,* **263**, 1117-1126.

Sutcliffe, O.L., Thomas, C.D. & Moss D. (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal Animal Ecology,* **65**, 85-95.

Sutcliffe, O.L., Thomas, C.D., Yates, T.J. & Greatorex-Davis J.N. (1997) Correlated extinctions, colonizations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia*, **109,** 235-241.

Tapper, S.C. (1992) *Game heritage*. Game Conservancy Trust, Fordingbridge, UK.

Thomas, C.D. (1991) Spatial and temporal variability in a butterfly population. *Oecologia,* **87**, 577-580.

Number of clusters	Variation explained (%)	1	2	5	8	9	11	16	10	13	15	18	3	4	6	7	12	14	17
2	43	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
3	55	1	1	1	1	1	1	2	2	2	2	2	3	3	3	3	3	3	3
4	64	1	1	1	1	1	1	2	2	3	3	3	4	4	4	4	4	4	4

Table 1. Number of clusters, their composition and variation explained at metapopulation level (using 18 mountain groups) as determined by k-means cluster analysis.

Groups	Cycle	Cycle period	Pacf (lag 2)
Dry	TENDENCY*	7.5 years	- 0.227
Wet	No	-	+ 0.148

Table 2. Time series analysis on the two clusters (the composition of each cluster is summed in table 1). * The ACF showed a tendency to cycle (*P*=0.064).

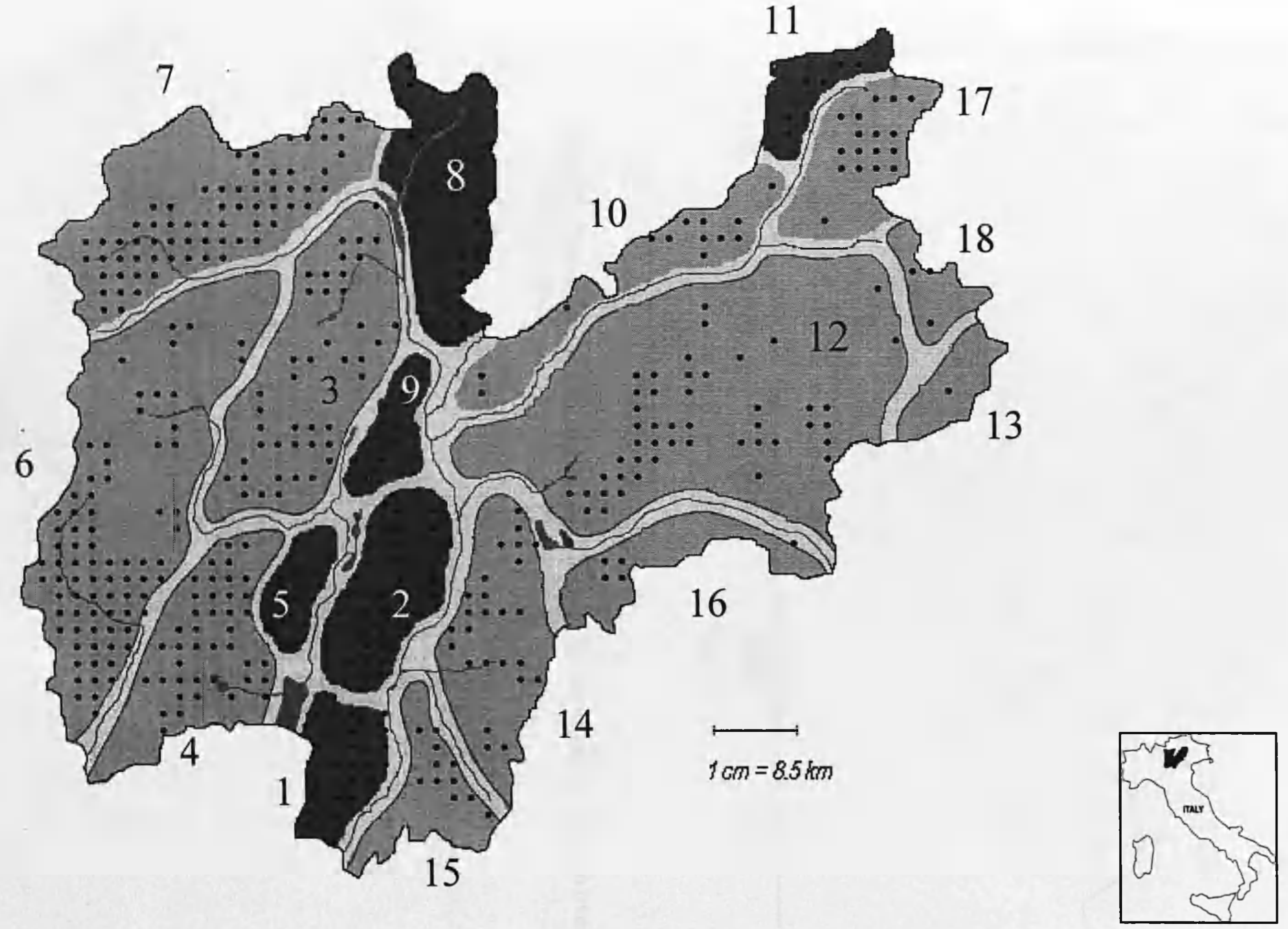


Figure 1. The province of Trentino showing the 18 major mountain groups (metapopulation scale boundaries), the presence of rock partridge within tetrads (2x2 km) following Meriggi *et al.* (1998) and the wet (light) and dry (dark) regions (after Boato *et al.* 1988).

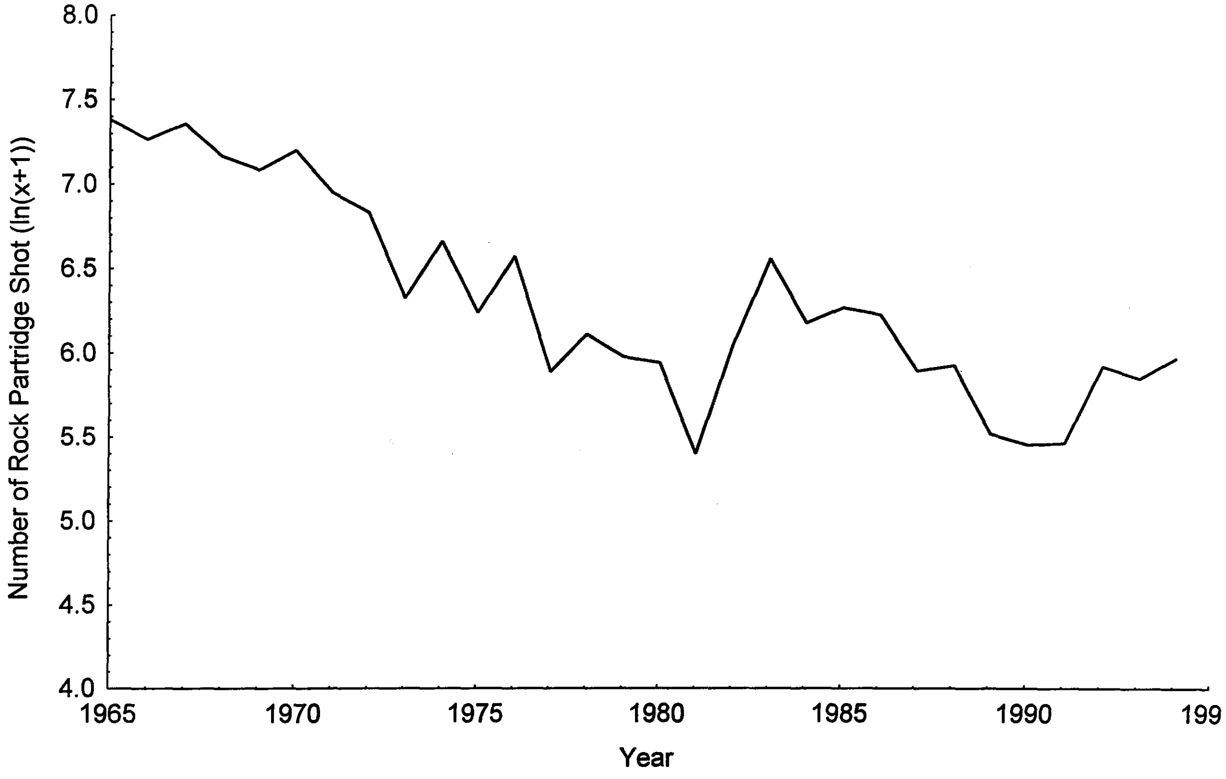


Figure 2. Changes in the total number of rock partridge harvested in Trentino over 30 years from 1965 to 1994.

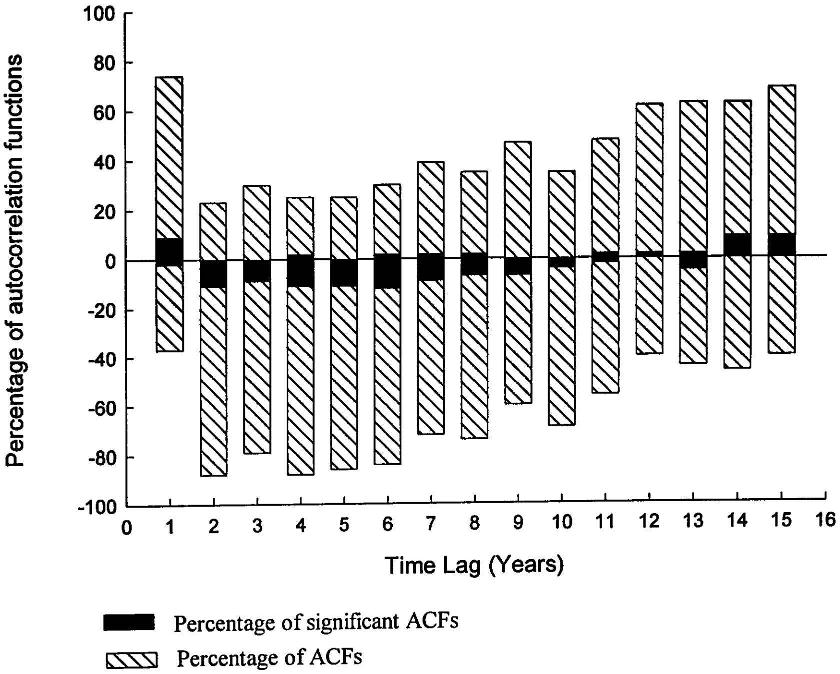


Figure 3. Percentage of autocorrelation functions (shadowed) and percentage of significant autocorrelation functions (dark) at each time lag from each of the 57 rock partridge populations.

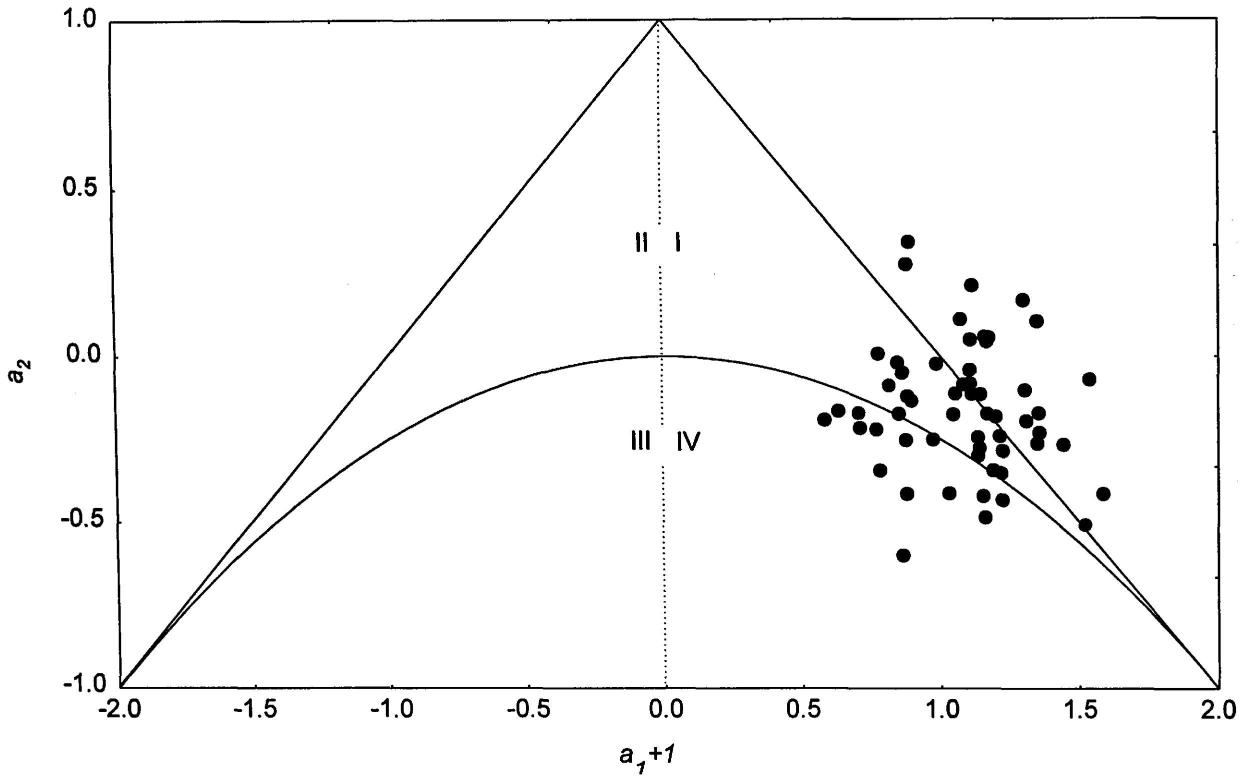


Figure 4. Scatter plot of the linear second order autoregressive parameters $1+a_1$ and a_2 for each of the 57 populations of rock partridge following the approach undertaken by Royama (1992). In the region II, III and IV the populations exhibit damped oscillations, in the region I numbers stabilise to an asymptotic equilibrium (see more details in Royama 1992).

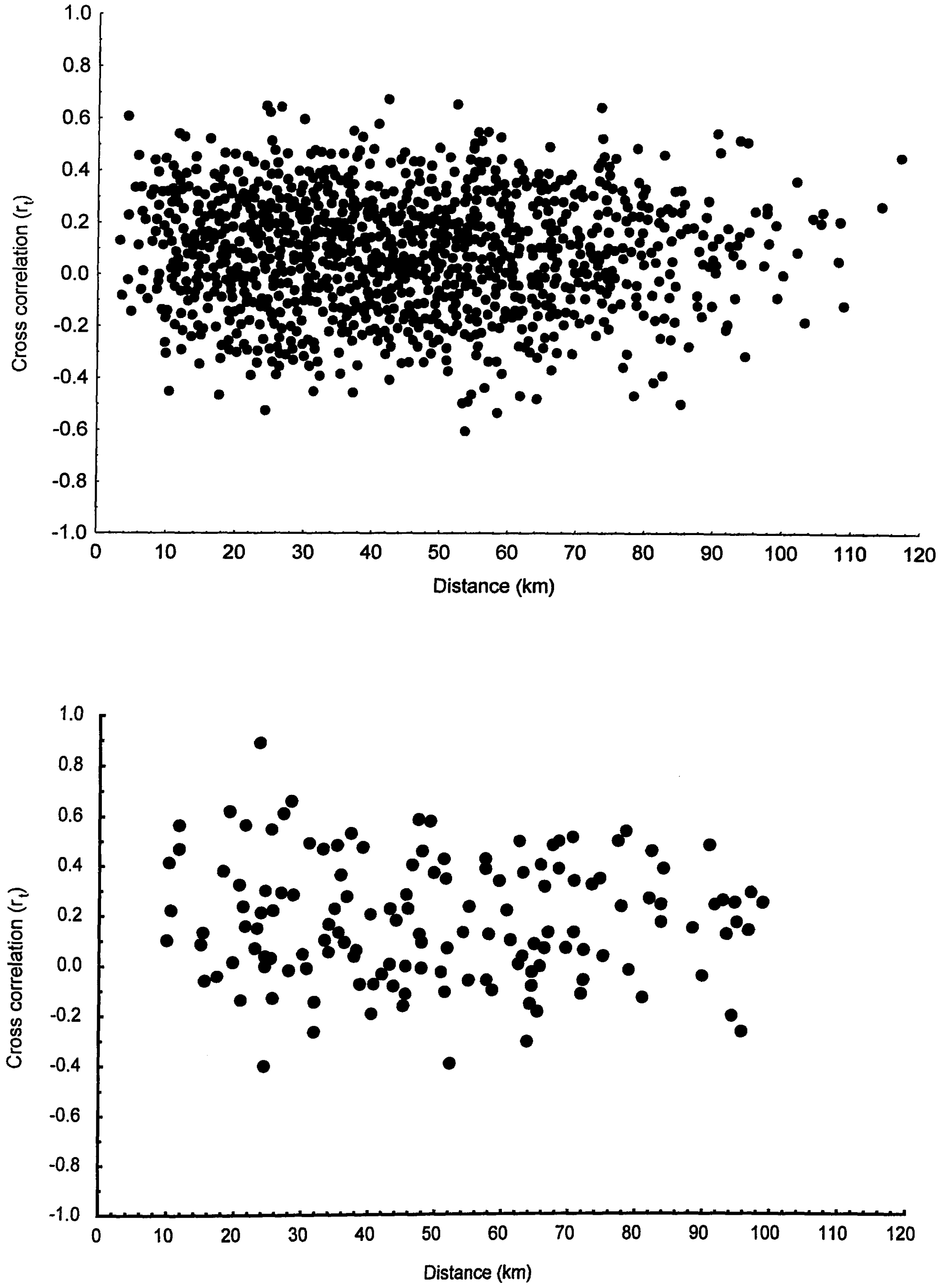


Figure 5. Spatial synchrony in numbers of rock partridge harvested in relation to distance at (a) the population and (b) the metapopulation scale. There was no relationship between synchrony and distance at either scale.

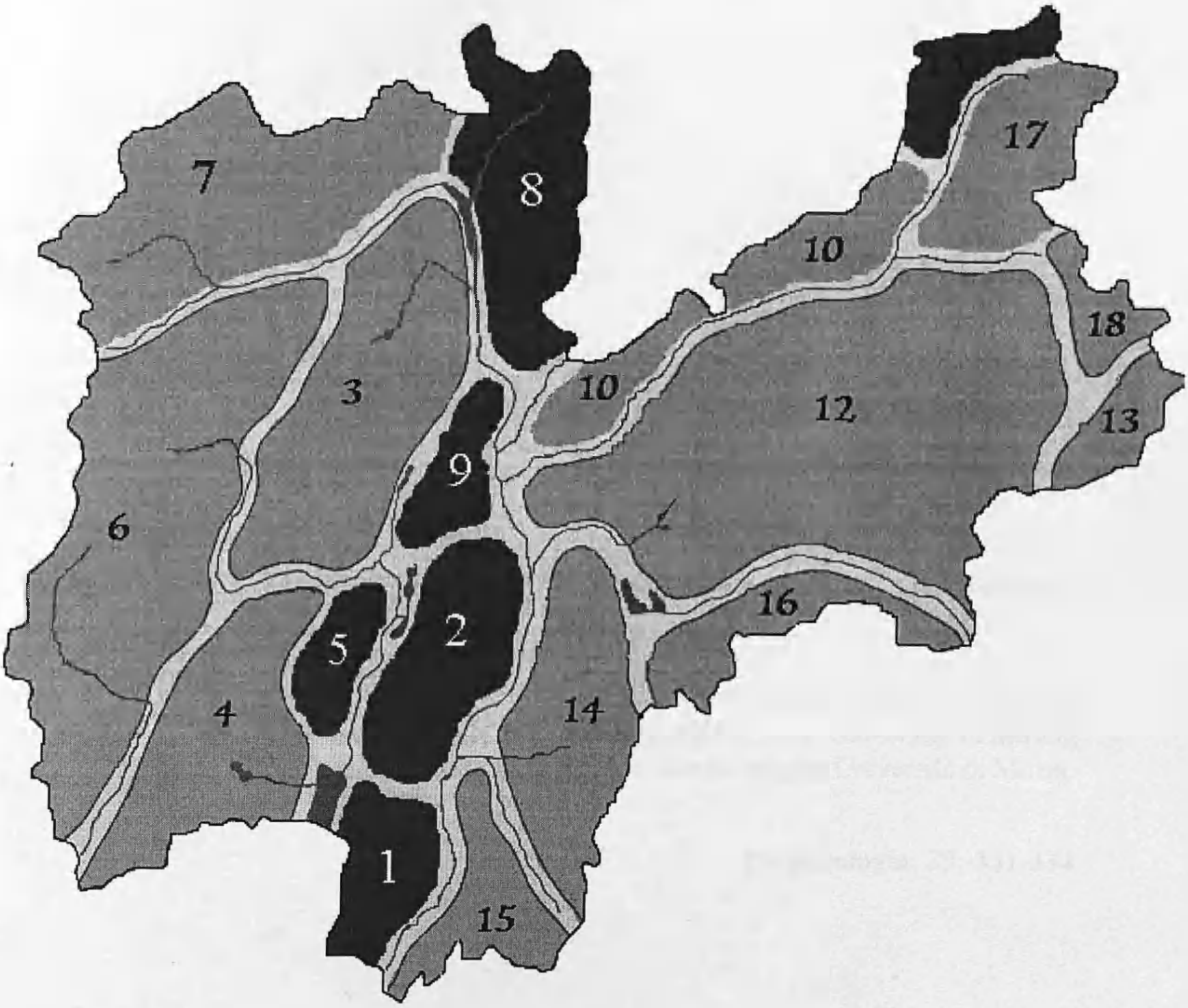


Figure 6. Spatial cluster of rock partridge populations within Trentino, determined from time series data, analysed at the metapopulation level. Note the similarity with the environmental classification in Fig.1.

CHAPTER 6

A Survey to Identify the Important Macroparasites of Rock Partridge (*Alectoris graeca saxatilis*) in Trentino, Italy

A. Rizzoli[1], M.T. Manfredi[3], F. Rosso[2], R. Rosà[2], I.M. Cattadori[1,2], P.J. Hudson[2]

1997

[1]Centro di Ecologia Alpina, Trento, Italy
[2]Institute of Biological Sciences, University of Stirling
[3]Istituto di Patologia Generale Veterinaria e Parassitologia, Università di Milano

Parasitologia, 39: 331-334

A SURVEY TO IDENTIFY THE IMPORTANT MACROPARASITES OF ROCK PARTRIDGE (ALECTORIS GRAECA SAXATILIS) IN TRENTINO, ITALY

Annapaola Rizzoli, Maria T. Manfredi, Fausta Rosso, Roberto Rosà, Isabella M. Cattadori & Peter J. Hudson

ABSTRACT- A preliminary survey of the intestinal helminth community of rock partridge (Alectoris graeca saxatilis) was undertaken in the Italian province of Trentino where the host population exhibits cyclic fluctuations in abundance. 6 helminth species were recorded from 38 rock partridge intestines collected during the hunting season between October and November 1994. Nematoda were the most prevalent (53%) with lower prevalence of Trematoda (11%) and Cestoda (8%). Ascaridia compar (Schrank, 1790) and Heterakis tenuicauda Linstow 1883, were identified as the component species (each with prevalence>10%) in the helminth intestinal community of rock partridge in Trentino. Both of these species exhibit an aggregated distribution.

Introduction

The rock partridge (Alectoris graeca saxatilis) is a species that inhabits the open landscapes of the Alps, Appenines and the northern parts of the Balkan peninsula with an altitudinal range from sea level to 2700 m a.s.l.. Rock partridge populations are decreasing in a large part of the Italian Alps with a clear contraction of its alpine range and a decrease in density (De Franceschi, 1988; Priolo and Bocca, 1992; Bernard-Laurent and De Franceschi, 1994). Densities in Trentino are now estimated at about 2.0 breeding pairs km^{-2} (Cattadori *et al.*, 1995). The principal cause of the decline in distribution has been attributed to habitat changes, in particular the increase in forestry and pasture fields. The decline in density within the remaining habitat has been attributed to over-hunting and diseases (Bernard-Laurent and De Franceschi, 1994).

While parasites have been mentioned by several workers there have been few surveys and no studies have investigated the impact of parasitic diseases on rock partridge populations (Salvini and Colombi, 1982; Meneguz and Rossi, 1988; Belleau, 1993). Since 83 species of microparasites and 28 species of macroparasites could potentially infect galliforms including rock partridge a survey of the potentially important species is required (Schales and Schales, 1994). As part of an extensive study on the status of gamebirds in Trentino and the factors affecting their population dynamics, this study examines the prevalence and pattern of distribution of macroparasites collected from rock partridges.

The population dynamics of rock partridge are interesting since they exhibit population cycles, a characteristic of northern galliform species (Lindstrom, 1996). Time series analyses of hunting records from 210 hunting areas have shown that a number of rock partridge populations exhibit cyclic fluctuation in abundance with a periodicity of 4-7.5 years (Cattadori *et al.*, in ms). The majority of populations exhibit 2nd order negative density-dependence, typical of trophic species interactions, while the tendency to produce cyclic fluctuations is associated with the drier areas of the Trentino province. The mechanisms that could cause this density dependence are currently being investigated but one hypothesis is that dry conditions could favour parasite infection and these result in reduced host fecundity and cyclic changes in numbers (Cattadori *et al.*, in ms.).

May and Anderson (1978) have identified clearly the conditions in a parasite-host system which will destabilise the parasite-host relationship and generate cycles. A random distribution of parasite within the host population, parasite induced reduction in host fecundity and time delays in the parasite life cycle are all important factors that can destabilise the host-parasite interaction and may generate cycles. Such properties, have been investigated in detail for the Trichostrongylus tenuis-red grouse (Lagopus lagopus scoticus) system where the effects of parasites appear both sufficient and necessary in generating cyclic changes in abundance (Hudson *et al.*, 1985, 1992; Hudson and Dobson, 1995).

The objective of this paper is to determine which parasites are prevalent in rock partridge populations that display cyclic fluctuations.

Material and methods

The intestines of rock partridge shot by hunters during November 1994 were collected by hunters within the game districts of Trentino region (Italian Alps). In total, 38 guts were collected from 7 game districts where cyclic fluctuations have been recorded (Cattadori *et al.*, in ms.). Hunters recorded data on the time and location where the sample was taken along with age and sex of the birds. In several instances corpses were available and these were weighed to obtain an estimate of body mass and relative condition. Intestines were preserved at -20°C then separated, scraped and the contents of each portion washed through 200, 75, 38 and 20 μm sieves. Parasites were sorted and preserved in 70% alcohol. Parasites were identified using Travassos (1944), Madsen (1950), Kasimov (1956), Mozgovoj (1968), Skryabin (1970), Skryabin *et al.* (1970), Panin (1984). Cestoda were identified only to genus.

For each species of parasite, prevalence, intensity and abundance were estimated according to Margolis *et al.* (1982). Patterns observed in the helminth community were classified in accordance with Esch *et al.* (1990) and Sousa (1994). Component species (prevalence >10%) and rare species (prevalence <10%) were identified and more detailed analysis conducted only on the component species. Differences with respect to host parameters (age, sex, and body mass) were examinated using Mann-Whitney U test and correlations with the Spearmann rank correlation test. To determine if there were associations between component species, G-test and Fisher exact test were used on two-way tables (Sokal and Rohlf, 1987).

Results

6 helminth species belonging to 3 different taxa were identified. The prevalence, intensity and abundance of infection of each species are listed in Table 1 and the pattern of distribution of each species in Table 2.

Two species were classified as component species, Ascaridia compar (Schrank, 1790 and Heterakis tenuicauda Linstow, 1833, since in both cases prevalence exceeded 10%. The two species were not associated with each other (G-test, Gadj= 0.46, p>0.05) so the presence or absence of A. compar did not influence the presence of H. tenuicauda.

Overall the number of macroparasite species per host ranged from 0 to 4 with a mean of 0.83 parasite species per host. Mean number of parasites per host ranged from 0 to 80 with an arithmetic mean of 7.5.

The pattern of parasite distribution within the rock partridge population was highly aggregated with the variance greater than the mean and this distribution did not conform to the poisson distribution for either A. compar (chi-square = 93.66, p<0.001) or H. tenuicauda (chi-square=64.95 p<0.001). However, the distribution was not significantly different from the negative binomial distribution for A. compar (chi-square= 1.24, p=0.265) and H. tenuicauda (chi-square=1.69, p=0.193) (Fig. 1).

There was no relationship between intensity of parasite infection and host age (Mann Whitney U test, p>0.05) for either species or the combined number of both species, although only 9 individuals were identified as adult and 17 individuals as young. There was no negative relationship between intensity of infection with H. tenuicauda and host body mass (Spearmann rank correlation test R=0.025, p=0.95) or intensity of infection with A. compar and host body mass (Rank Spearmann correlation, R=-0.37, p=0.22). Within this study mean host body mass was 560,4 grams (SD= 89.5, N=25)

Discussion

Among the 6 helminth species recorded in this investigation, A. compar and H. tenuicauda, were the component species in rock partridge collected from Trentino. Both species exhibit a highly aggregated distribution and there is not association between the species. The relatively high prevalence of these species compared to the other helminths species of the intestinal tract has also been observed in rock partridge in the western Alps (Meneguz and Rossi, 1988; Belleau, 1993).

A. compar has been recorded in various galliform gamebirds throughout the world including grouse, ptarmigan, partridge, and pheasants (Vassilev, 1991; Anderson, 1992). H. tenuicauda, occurs in the caeca of galliforms belonging to the genus Alectoris and

Ammoperdix (Madsen, 1950). Their life cycle and impact on host fecundity and body condition have not been clarified for rock partridge.

A. compar may be expected to have a negative effect on body condition, as observed for A. galli (Schrank,1788) in other hosts (Soulsby, 1982). However this study did not find a negative association between body mass and levels of infection of A. compar even if this analysis was an initial investigation and further studies on body condition that correct for body size and age may identify a clearer relationship. Moreover, experimental infections and more detailed analyses may elucidate the relative pathogenicity of A. compar and H. tenuicauda and any synergistic interactions between the species.

Rock partridge exhibit cyclic fluctuation in abundance in some areas of Trentino region and we will investigate the hypothesis that A. compar may be generating cyclic fluctuations in abundance in a similar fashion to that recorded for Trichostrongylus tenuis in red grouse (Hudson *et al.*, 1992, 1995). Parasites with a random distribution within the host population, which reduce body condition and fecundity in the host and have time delays in development are more likely to generate cycles (May and Anderson, 1978). Among the intestinal helminth observed during our initial analyses of samples from 1994, A. compar and H. tenuicauda appear to be the component species in the intestinal helminth community of rock partridge in Trentino region. A compar is more likely to be important since it is known that Ascaridia sp. have an impact on host fecundity and host body mass (Soulsby, 1982). Moreover Ascaridia sp. eggs can remain viable in the environment for long periods of time and such long lived species are more likely to generate cycles (Anderson, 1992). However, the highly aggregated distribution observed in both species would tend to stabilise the parasite host relationship, making cyclic fluctuations in host population less likely.

Acknowledgements

We thank the Forestry and Wildlife Service of the Autonomus Province of Trento, the Presidents, the Game Birds Hunters and Guards of the Trentino Hunters Associations, Sergio Merz and Stefano Maffei for help in data and gut sampling collection.

References

Anderson RC (1992). Nematode parasites of vertebrates. Their development and transmission. C. A. B. International pp 578.

Belleau E (1993). Situation sanitaire de la perdrix bartavelle dans les Alpes françaises. Faune sauvage 175: 31-36.

Belleau E, Leonard P (1991) Le parasitisme digestif chez la perdrix bartavelle (Alectoris graeca saxatilis), le lagopède alpin (Lagopus mutus), le tètras-lyre (Tetrao tetrix), dans le département des Haute-Alpes. Gibier Faune Sauvage 8:161-173.

Bernard-Laurent A, De Franceschi P (1994). Statut, évolution et facteurs limitant les populations de perdrix bartavelle (Alectoris graeca): synthése bibliografique. Gibier Faune Sauvage, Game Wildl. 11: 267-307.

Cattadori I, Pandini V, Cistoldi E, Meriggi A (1995). A model of habitat suitability for rock partridge (Alectoris greaca saxatilis) in the Trentino Alps: preliminary results. Gibier Faune Sauvage, in press.

Cattadori I, Hudson P, Merler S, Rizzoli AP (1997). Scale and temporal dynamics of rock partridge (Alectoris graeca saxatilis) populations in the Dolomites (Trentino, Italy). In ms.

De Franceschi P (1988). La situazione attuale dei galliformi in Italia. Ricerche recenti o ancora in corso. Problemi di gestione e prospettive per il futuro. In: Atti I Conv. Naz. Biol. Selvaggina. Suppl. Ric. Biol. Selvaggina (M Spagnesi, S Toso; Eds) 19, 165-180 pp.

Esch GW, Bush AO, Aho JM (1990). Parasite Communities: Patterns and Processes.: Chapman and Hall, London. pp. 335.

Hudson PJ, Dobson AP, Newborne D (1985). Cyclic and non-cyclic population of red grouse: a role for parasitism? In: Ecology and genetics of host-parasite interaction (D Rollison, RM Anderson, Eds) Academic Press, London: 77-90.

Hudson PJ, Newborn D, Dobson AP (1992). Regulation and stability of a free-living host parasite system - Trichostrongylus tenuis in red grouse 1. Monitoring and parasite reduction experiment. J Anim Ecol 61: 477-486.

Hudson PJ, Dobson AP (1995). Macroparasites: observed patterns in naturally fluctuating animal populations. In: Ecology of Infectious Diseases in Natural Populations (BT Grenfell, AP Dobson, Eds) Cambridge University Press: 144-176.

Kasimov GB (1956). Helminth fauna of domestic and gamebirds of the order Galliformes. Moscow, Izdatelstvo Academii Nauk SSSR pp.554 [in russian].

Lindstrom, J., (1996). Modelling grouse population dynamics. Phd thesis, University of Helsinki, Finland.

Madsen H (1950). Studies on species of Heterakis (Nematodes) in birds. Danish Review of Game Biology 1: 3-43.

Margolis L, Esch J, Holmes JC, Kuris AM, Schad GA (1982). The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). J Parasitol 68: 131-133.

May RM, Anderson RM (1978). Regulation and stability of host-parasites population interactions. II. Destabilising processes. J Animal Ecol 47: 249-267.

Meneguz PG, Rossi L (1988). Indagine parassitologica sulla fauna minore di montagna oggetto di prelievo venatorio: risultati preliminari.In: Atti del I Convegno Nazionale dei Biologi della Selvaggina, Suppl. Ric. Biol. Selvaggina (M Spagnesi, S Toso, Eds), 14, 639-640 pp.

Mozgovoj AA (1968). Ascaridata of Animals and Man and the diseases caused by them. Israel Program for Scietnific Translations, Jerusalem pp.390.

Panin VY (1984). Dicrocoelid Trematodes of the World Fauna. Alma Ata pp. 111.

Priolo A, Bocca M (1992). Coturnice (Alectoris graeca). In: Fauna d'Italia XXIX Aves I (P Brichetti, P De Franceschi, N Bacetti, Eds), Calderini, Bologna, pp. 766-777.

Salvini GP, Colombi GC (1982). La coturnice. Studi sulle popolazioni di coturnice sulle Alpi. Unione Nazionale Cacciatori Zona Alpi. UTVI, Vicenza

Schales C, Schales K (1994). Galliformes. In: Avian medicine. Principles and application (BW Ritchie, GJ Harrison, LR Harrison Eds.), Wingers Publishing Inc., Florida, 1218-1236 pp.

Skryabin KI (1970). Trematodes of animals and man. Vol XXIII Moscow pp.595.

Skryabin KI, Shikhobalova NP, Orlov IV (1970). Trichocephalidae and Capillariidae of Animals and Man and the Diseases caused by them. Israel Program for Scientific Translations, Jerusalem pp.599.

Sokal R, Rohlf FJ (1987). Introduction to Biostatistics. Second edition: W. H. Freeman and Company - New York pp.301

Soulsby EJL (1982). Helminths, arthropods and protozoa of domesticated animals. Baillière Tindall- London pp.809.

Sousa WP (1994). Pattern and processes in communities of helminth parasites. TREE 9:52-57.

Travassos L (1944). Revisão da famiglia Dicrocoelidae Odhner 1910. Monografias do Instituto Oswaldo Cruz 2:1-357.

Vassilev I (1987). On the development of Ascaridia compar (Schrank, 1790) in the host. Khelmintologiya 23: 30-35.

Vassilev I (1991). To the ecology of Ascaridia compar (Schrank, 1790) Travassos, 1913. Khelminthologiya 29:3-21.

Helminth species	**Prevalence** %	**Intensity** range	$\bar{x}$ ± **S.E.**	**Abundance** $\bar{x}$ ± **S.E.**
Ascaridia compar Schrank, 1790	36.84	1-27	8.78 ± 2.62	3.23 ± 1.17
Heterakis tenuicauda Linstow 1883	26.3	1-80	14.7 ± 7.48	3.86 ± 2.17
Aonchotheca caudinflata Molin 1858	5.26	1-3	2 ± 1	0.10 ± 0.08
Cestoda	7.89	n.d.	n.d.	n.d.
Postharmostomum commutatum Diesing 1858	5.26	1-20	10.5 ± 9.5	0.55 ± 0.52
Platynosomum alectoris Noeller et Enigk 1933	5.26	4-7	5.5 ± 1.5	0.28 ± 0.21

Table 1. Prevalence, intensity and abundance of intestinal helminths identified from 38 rock partridge, collected from Trentino in 1994. Intensity is classified as the arithmetic mean of all infected individuals and abundance as the arithmetic mean of all individuals sampled; n.d.= not done.

Helminth species	**Variance to mean ratio** v/m	**Standardized variance** v/m^2	**k** of the negative binomial
Ascaridia compar	16.15	4.98	0.148
Heterakis tenuicauda	46.45	12.03	0.078

Table 2. The pattern of aggregation of the two component helminth species in rock partridge from Trentino region. Parameters presented include the variance to mean ratio, the variance to mean ^{2}, and *k* of the negative binomial. The high variance to mean ratio and the low value of *k* indicate a highly aggregated distribution.

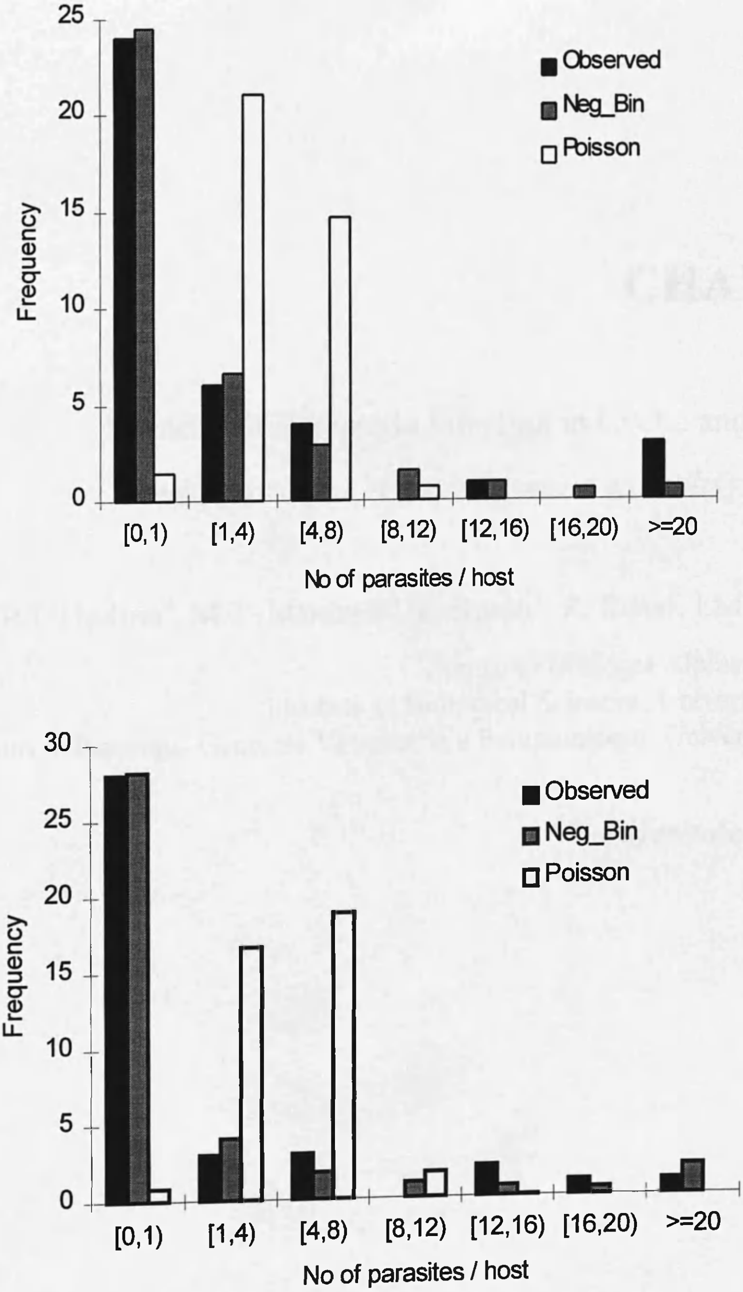


Figure 1. Observed parasite frequency distributions compared with expected distribution based on Poisson and negative binomial distributions, estimated by maximum likelihood techniques. (a) *Ascaridia compar*; Poisson goodness of fit to observed frequency distribution: Chi_squared=419.2, P=0.0; Negative binomial fit: Chi_squared=0.31, P=0.57. (b) *Heterakis tenuicauda*; Poisson goodness of fit to observed frequency distribution: Chi_squared=960.54, P=0.0; Negative binomial fit: Chi_squared=0.11, P=0.74.

CHAPTER 7

Intensity of Nematode Infection in Cyclic and non Cyclic Rock Partridge (*Alectoris graeca saxatilis*) Populations

A. Rizzoli[1], P.J. Hudson[2], M.T. Manfredi[3], F. Rosso[1], R. Rosà[1], I.M. Cattadori[1,2]

[1]Centro di Ecologia Alpina, Trento, Italy
[2]Institute of Biological Sciences, University of Stirling
[3]Istituto di Patologia Generale Veterinaria e Parassitologia, Università di Milano

Parasitologia, in press

INTENSITY OF NEMATODE INFECTIONS IN CYCLIC AND NON CYCLIC ROCK PARTRIDGE (ALECTORIS GRAECA SAXATILIS) POPULATIONS

Annapaola Rizzoli, Maria T. Manfredi, Fausta Rosso, Roberto Rosà, Isabella M. Cattadori & Peter J. Hudson

ABSTRACT- Populations of rock partridge (Alectoris graeca saxatilis), in the Trentino province of Italy, exhibit cyclic fluctuations in abundance associated with relatively dry habitat. One of the hypothesis to explain these cycles is that survival of some free living parasitic stages and rates of infection are greater in these areas leading to higher parasite burden. This hypothesis was examined by investigating the intensity of parasite infection in cyclic and non cyclic rock partridge populations. Analyses of 87 intestine samples collected from shot rock partridges during 1994 and 1995 identified 8 species of helminths parasites: Ascaridia compar (P=33.33%; I= 9.28± 1.78), Heterakis tenuicauda (P=19.54%; I=10.29±4.58), Heterakis gallinarum (P=1.15%; I=1.0 ± 0.0), Heterakis altaica (P=1.15%; I=17±0.0), Aonchoteca caudinflata (P=6.89; I=2.17± 0.65), Postharmostomum commutatum (P=5.75; I=7.0±3.48), Brachylaema fuscata (P=1.15; I=7.0± 0.0), Platynosomum alectoris (P=2.29; I=5.5± 1.5). Cestoda, recorded with a prevalence of 5.75, were not identified to species level. A. compar and H. tenuicauda were prevalent in the rock partridge populations and there was no positive association between these species. Intensity of infection in both species was not influenced by host age, sex or year of study but levels of infection with A. compar burdens were significantly greater in cyclic populations than in non cyclic populations and there was a tendency for H. tenuicauda to be greater in cyclic populations. There was no negative relationship between intensity of infection with A.compar or H. tenuicauda and host body mass. These data provide some support for the hypothesis that these parasite may play a role in generating rock partridge population cycles.

Introduction

A number of northern game birds exhibit cyclic fluctuations in density and the patterns and mechanisms that cause these fluctuations have been investigated in detail (Hudson et al., 1992, 1998; Hudson, 1992; Lindström, 1996). The integration of empirical data into a series of mathematical models have shown that parasitic worms can destabilize host numbers and generate cyclic fluctuations when the parasite induced reduction in host fecundity is large relative to the impact on host survival (May and Anderson, 1978; Dobson and Hudson, 1992). The dynamics of both host and parasite is dependent on the tension between these and other parameters including the pattern of parasite distribution within the host population and the presence of time lags in the parasite life cycle. Essentially, cyclic fluctuations are more likely when the parasite has long lived free living stages with a random rather than an aggregated distribution (May and Anderson, 1978) .

The rock partridge (Alectoris graeca saxatilis) is a game bird inhabiting Alpine prairie and meadows, whose population are decreasing in density and distribution in most of its alpine range (Bernard-Laurent and De Franceschi, 1994; Cattadori et al., 1995). Detailed time series analyses of hunting records found that within Trentino province (46°31'N, 10°27'E and 46°31'N, 11°58'E in the north; 45°27'N, 10°27'E and 45°27'N, 11°58'E in the south) populations within the dry parts of the province, with mean annual rainfall <1000 mm (Boato et al., 1998), exhibit significant 2nd order density dependence and were more likely to oscillate than populations in the relatively wetter parts of the province (Cattadori et al., in press).

The mechanism that could generate such cycles is not known but one of the parsimonious hypothesis should incorporate the relative importance of parasitism and the effect of dryness on the population dynamics of the host and its parasites (Rizzoli et al., 1997). Ascaridia compar (Schrank, 1970) and Heterakis tenuicauda Linstow,1883, were identified as component species of the rock partridge helminth community in a preliminary survey on the macroparasites of rock partridge in Trentino province (Rizzoli et al., 1997). These helminth species are commonly recorded in wild galliformes (Vassilev, 1991; Anderson, 1992) but their pathogenicity in the wild hosts have yet to be clarified, even though we expect a negative impact on host fitness as observed in domestic galliformes (Soulsby, 1982).

This paper examines the prediction that levels of infection of these nematode species should be greater in cyclic than non cyclic populations of rock partridge in Trentino province.

Materials and methods

A total of 87 samples of guts of rock partridge were collected from hunters during the months of October to December. 36 were collected in 1994 and 51 in 1995. When hunters shot a partridge they removed the guts, placed them in a plastic bag with details of location and the date when the sample was taken. Samples were later stored frozen. Hunters sexed and aged the bird as either young of the year or breeding adult according to plumage and male spur characteristics. The sample consisted of 18 adult bird (> 1 year), 8 female (mean weight = 651 g) and 10 male (mean weight = 640 g); 41 young birds (<1 year), 26 female (mean weight = 497 g) and 15 male (mean weight = 434 g); 28 individuals whose age and sex were not determined. 43 samples were collected from cyclic rock partridge populations and the remainders from non cyclic populations, as identified by Cattadori et al. (in press). The intestines were separated, scraped and the contents of each portion washed through 200, 75, 38 and 20 μm sieves. Parasites were sorted and preserved in 70% alcohol. Nematodes were cleared using lactophenol; cestodes and trematodes were stained with carmine aluminum acetate then mounted in Canada balsam. The helminths were identified to species according to Travassos (1944), Madsen (1950), Kasimov (1956), Mozgovoj (1968), Skryabin (1970), Skryabin et al. (1970) and Panin (1984). Cestoda were identified only to genus. Prevalence, intensity and abundance of each species were determined according to Margolis et al. (1982). Further statistical analysis were carried on only with the component species (each with prevalence > 10%) (Esch et al., 1990).

The parasite frequency distributions in a number of different hosts was compared with the expected distribution based on the negative binomial distribution, estimated using maximum likelihood techniques. To determine differences in parasite abundance in relation to host sex, host age, year of study, cyclic or non cyclic behaviour of the population, ANOVA and MANOVA were used. Data were transformed to natural logarithms (x+1). Relationships between intensity of infection and host body mass were analyzed using the Spearman rank correlation test.

Results

Prevalence of infection of all the helminth species from 87 rock partridge was 60,2%. Two nematode species were dominant within the sample, A. compar and H. tenuicauda. Other species were recorded but at low prevalence and included the nematodes Heterakis gallinarum (Schrank,1788) and Heterakis altaica Spaul, 1929 present in 1 individual each. Aonchotheca caudinflata (Molin, 1858) was present in 6 individuals and the trematodes Postharmostomum commutatum (Diesign, 1958), Platynosomum alectoris Noeller et Enigk, 1933 and Brachylaema fuscata (Rudolphi, 1819) were present in 5, 2 and 1 individuals respectively. Cestoda were recorded in 6 individuals but were not classified to species level (Tab.1).

There was no association between the presence of Ascaridia compar and Heterakis tenuicauda (chi squared with Yates' correction = 0.01; P=0.93). In the analysis that follows we consider both species separately and then combined.

A. compar was found in 33.33% of the partridges analysed and exhibited a highly aggregated distribution with the variance larger than the mean and a distribution that conformed to the negative binomial (sample size=87, variance to mean ratio=15.96, k=0.13) (Figure 1a). This distribution was significantly different from the Poisson distribution (chi square=199.14, P<0.001). In cyclic population (sample size=43, variance to mean ratio=13.57, k =0.2) (Fig. 1 b) parasite distribution was also aggregated as it was in non cyclic population (sample size=44, variance to mean ratio=19.91, k=0.08) (Fig. 1c). Intensity of infection (mean=3.09, SE=0.75) (Tab. 2), transformed to natural logarithms (x+1) was not influenced by age ($F_{1,54}$=0.079, P=0.778) or year of study ($F_{1,85}$=0.26, P=0.61) but there was a tendency for parasite burdens to be greater in females ($F_{1,52}$=3.03, P=0.08). Cyclic populations had significantly greater parasite burden (mean=3.95, SE=1.12) than non cyclic populations (mean = 2.25, SE=1.01, $F_{1,51}$= 4.54, P=0.038) (Figure 1a and 1b; Tab. 2). There was no negative relationship between intensity of infection with A.compar and host body mass (Spearman rank correlation, R=-0.31, P=0.12).

H. tenuicauda was found in 19.54% of the partridges analyzed and exhibited an aggregated distribution that conformed to the negative binomial (sample size=87, variance to mean ratio=49.28, k=0.08) (Figure 2a). In both cyclic population (sample size=43, variance to mean ratio=42.81, k=0.13) (Fig 2b) and non cyclic populations this parasite had an aggregated distribution (sample size=44, variance to mean ratio=59.84, k=0.03) (Fig. 2c). Like A. compar the intensity of infection (mean=3.07, SE=1.32) was not influenced by age ($F_{1,56}$=0.13, P=0.72), sex ($F_{1,53}$=0.67, P=0.41) or year of study ($F_{1,85}$=0.92, P=0.34). Similar to A. compar there was a tendency, but not significant at the 5% level of probability, for there to be a greater intensity of parasite burdens in cyclic populations (mean=3.67; SE=1.91, $F_{1,85}$=2.8, P=0.098) (Tab 2). There was no negative relationship between intensity of infection with H. tenuicauda and host body mass (Spearman rank correlation, R= 0.27, P= 0.32).

Using the transformed data from both A. compar and H. tenuicauda as the dependent variables in a MANOVA there was a significantly greater nematode burden in the cyclic populations (Wilks $\text{lambda}_{2,84}$=0.906, P=0.016). These data show that nematode burdens in rock partridge were greater in cyclic (mean=7.63, SE=2.26) than non cyclic populations (mean=4.72, SE=2.03).

Discussion

The data presented in this paper provide evidence that the intensity of infection of rock partridge with nematodes is greater in population exhibiting cyclic than non-cycling fluctuations in Trentino. However this is just one aspect of the hypothesis that these parasites may cause these cyclic fluctuations since the expected dynamics of the host will also be influenced by the impact of the parasite on the individual host, the survival of the free-living stages and the pattern of distribution of the parasites within the host population. Indeed, random rather than aggregated distributions will tend to destabilize parasite-host dynamics (May and Anderson, 1978; Dobson and Hudson 1992) and the final dynamics will be influenced by the tension between these different parameters. In this respect it is interesting to note that both species have a highly aggregated distribution (Figure 1 and 2). Previous research has demonstrated through experimentation, long term monitoring and mathematical modeling that the parasitic nematode Trichostrongylus tenuis (Mehlin, 1846) can cause population cycles in red grouse (Hudson et al., 1985, 1992, 1998; Hudson, 1992; Dobson and Hudson, 1992). Like the findings from this study, greater parasite burdens were found in cyclic populations but the important component generating the cyclic change in numbers is the parasite induced reduction in host fecundity. The pathogenicity of A. compar in relation to worm burden and its impact on host fecundity is now under investigation with captive rock partridges.

There are a number of similarities between the rock partridge-A. compar and the red grouse-T.tenuis system. Both species inhabit open prairie habitat in the sub montane habitat and show similarities in life history and behavior. One interesting difference is that survival of free living stages of T. tenuis depend on wet conditions and cyclic populations are only found in wet, peatland areas (Hudson et al., 1985) while A. compar and H. tenuicauda may require relatively dry conditions for prolonged survival.

Acknowledgements

We thank the Forestry and Wildlife Service of the Autonomous Province of Trento, the Presidents, the Game Birds Hunters and Guards of the Trentino Hunters Associations, Sergio Merz and Stefano Maffei for help in data and gut sampling collection.

References

Anderson, R.C. (1992). Nematode parasites of vertebrates. Their development and transmission. C. A. B. International, 578 pp.

Bernard-Laurent A., De Franceschi P. (1994). Statut, évolution et facteurs limitant les populations de perdrix bartavelle (Alectoris graeca): synthése bibliografique. Gibier Faune Sauvage, Game and Wildlife 11: 267-307.

Boato S., Arrighetti A., Osti F. (1988). Parchi e riserve naturali del Trentino. - Ed Temi, Trento.

Cattadori I., Pandini V., Cistoldi E., Meriggi A.(1995). A model of habitat suitability for rock partridge (Alectoris graeca saxatilis) in the Trentino Alps. Proceeding Perdix VII, International Symposium on Partridges, Quails and Pheasants. Durdan France. Gibier Faune Sauvage, in press.

Cattadori, I.M., Hudson, P.J., Merler, S., Rizzoli A. (in press). Synchrony, scale and temporal dynamics of rock partridge (Alectoris graeca saxatilis) populations in the dolomites. J. An. Ecol., in press.

Dobson, A. P., Hudson P.J. (1992). Regulation and stability of a free-living host parasite system - Trichostrongylus tenuis in Red Grouse. II: population models. J. An. Ecol. 61, 487-498.

Esch G.W., Bush A.O., Aho J.M. (1990). Parasite Communities: Patterns and Processes. Chapman and Hall, London. pp. 335.

Hudson P.J., Dobson A.P., Newborne D. (1985). Cyclic and non cyclic population of red grouse: a role for parasitism? In: Ecology and genetics of host-parasite interaction (Rollison D and Anderson R.M. Eds.), Academic Press, London, pp. 77-90.

Hudson P.J., Newborn D., Dobson A.P. (1992). Regulation and stability of a free-living host parasite system - Trichostrongylus tenuis in red grouse 1. Monitoring and parasite reduction experiment. J. Anim. Ecol. 61: 477-486.

Hudson, P.J. (1992). Grouse in Space and Time. Game Conservancy Trust, Fordingbridge, Hants, pp. 244.

Hudson PJ, Dobson AP, Newborn D (1998). Prevention of population cycles by parasite removal. Science 282: 2256-2258

Kasimov, GB (1956). Helminth fauna of domestic and gamebirds of the order Galliformes. Izdatelstvo Academii Nauk SSSR, Moscow, pp. 554.

Lindström, J (1996). Modelling grouse population dynamics. Phd thesis, University of Helsinki, Finland, pp. 142.

Madsen, H. (1950). Studies on species of Heterakis (Nematodes) in birds. Danish Review of Game Biology 1: 3-43.

Margolis L., Esch G.W., Holmes J.C., Kurtis A.M., Schad G.A (1982). The use of ecological terms in parasitology. J. Parasitol. 68:131-133

May R.M., Anderson R.M. (1978). Regulation and stability of host-parasites population interactions. II. Destabilising processes. J. Anim. Ecol. 47: 249-267.

Mozgovoj AA. (1968). Ascaridata of Animals and Man and the diseases caused by them. Israel Program for Scientific Translations, Jerusalem, pp. 390.

Panin V.Y. (1984). Dicrocoelid Trematodes of the World Fauna. Alma Ata, pp.111.

Rizzoli A., Manfredi M.T., Rosso F., Rosà R., Cattadori I.M., Hudson P.J., (1997). A survey to identify the important macroparasites of rock partridge (Alectoris graeca saxatilis) in Trentino, Italy. Parassitologia 39: 331-334.

Skryabin K.I. (1970). Trematodes of animals and man. Vol XXIII, Moscow, pp.595.

Skryabin K.I., Shikhobalova N.P., Orlov I.V. (1970). Trichocephalidae and Capillariidae of Animals and Man and the Diseases caused by them. Israel Program for Scientific Translations, Jerusalem, pp 599.

Travassos L. (1944). Revisão da famiglia Dicrocoelidae Odhner 1910. Monografias do Instituto Oswaldo Cruz 2:1-357.

Helminth species	**Prevalence** **%**	**Range** **min-max**	**Intensity** $\bar{x}$ **± S.E.**	**Abundance** $\bar{x}$ **± S.E.**
Ascaridia compar Schrank, 1790	33.33	0-33	9.28 ±1.78	3.09±0.75
Heterakis tenuicauda Linstow 1883	19.54	0-80	10.29 ± 4.58	3.07±1.32
Heterakis gallinarum Schrank, 1788	1.15	0-1	1.0±0.0	0.01±0.01
Heterakis altaica Spaul,1929	1.15	0-17	17.0±0.0	0.19±0.19
Aonchotheca caudinflata Molin 1858	6.89	0-5	2.17±0.65	0.15±0.07
Cestoda	5.75	n.d.	n.d.	n.d.
Postharmostomum commutatum Diesing 1858	5.75	0-20	7.0±3.48	0.4±0.25
Brachylaema fuscata Rudolphi, 1819	1.15	0-7	7.0±0.0	0.08±0.08
Platynosomum alectoris Noeller et Enigk 1933	2.29	0-7	5.5±1.5	0.13±0.09

Table 1. Prevalence, intensity and abundance of the intestinal helminths species identified from 87 rock partridges collected in Trentino during 1994 e 1995.

	All sample (Sample size=87)			**Cyclic population (Sample size=43)**			**Non Cyclic population (Sample size=44)**		
	mean ± SE	**Variance/ mean**	**k**	**mean ± SE**	**Variance/ mean**	**k**	**mean ± SE**	**Variance/ mean**	**k**
Ascaridia compar	3.09 ± 0.75	15.96	0.13	3.95 ± 1.12	13.57	0.2	2.25 ± 1.01	19.91	0.08
Heterakis tenuicauda	3.07 ± 1.32	49.28	0.08	3.67 ± 1.91	42.81	0.13	2.48 ± 1.84	59.84	0.03
Both species	6.16 ± 1.52	32.56	0.21	7.63 ± 2.26	28.87	0.33	4.72 ± 2.03	38.43	0.12

Table 2: Mean parasite burden and aggregation indices (variance to mean ratio and k of the negative binomial) of Ascaridia compar and Heterakis tenuicauda in rock partridge, considering the whole population, the cyclic population and the non cyclic population.

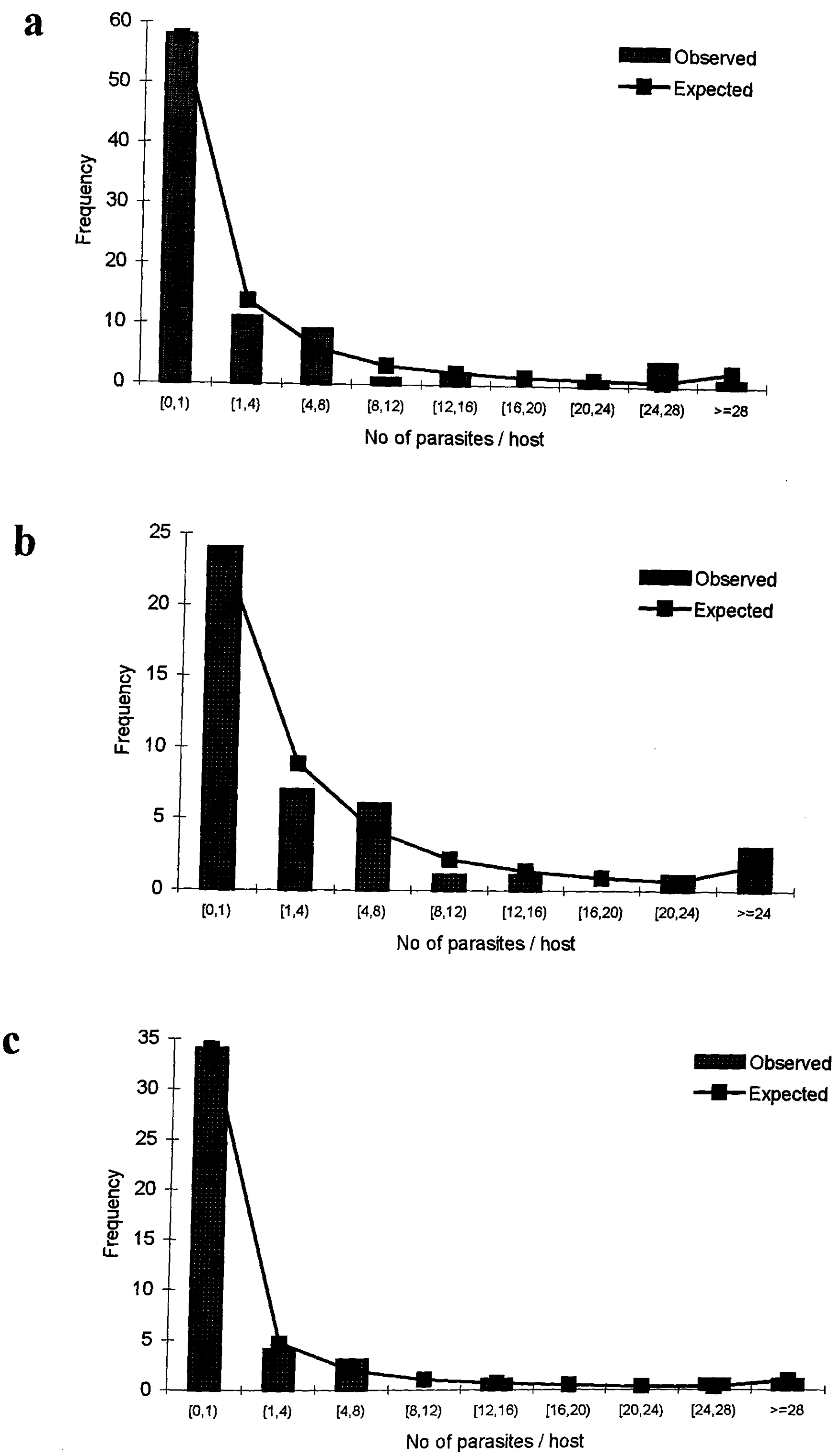


Figure 1. Observed parasite frequency distributions of Ascaridia compar in rock partridge compared with expected distribution based on the negative binomial distribution, estimated by maximum likelihood techniques. (a) All samples (Sample size=87, variance to mean ratio=15.96, k=0.13); Negative binomial fit: chi-squared=3.05, DF=3, P=0.38. (b) Cyclic population (Sample size=43, variance to mean ratio=13.57, k =0.2); Negative binomial fit: chi-squared=2.04, DF=1, P=0.15. (c) Non cyclic population (Sample size=44, variance to mean ratio=19.91, k=0.08); Negative binomial fit: chi-squared=0.76, DF=1, P=0.38.

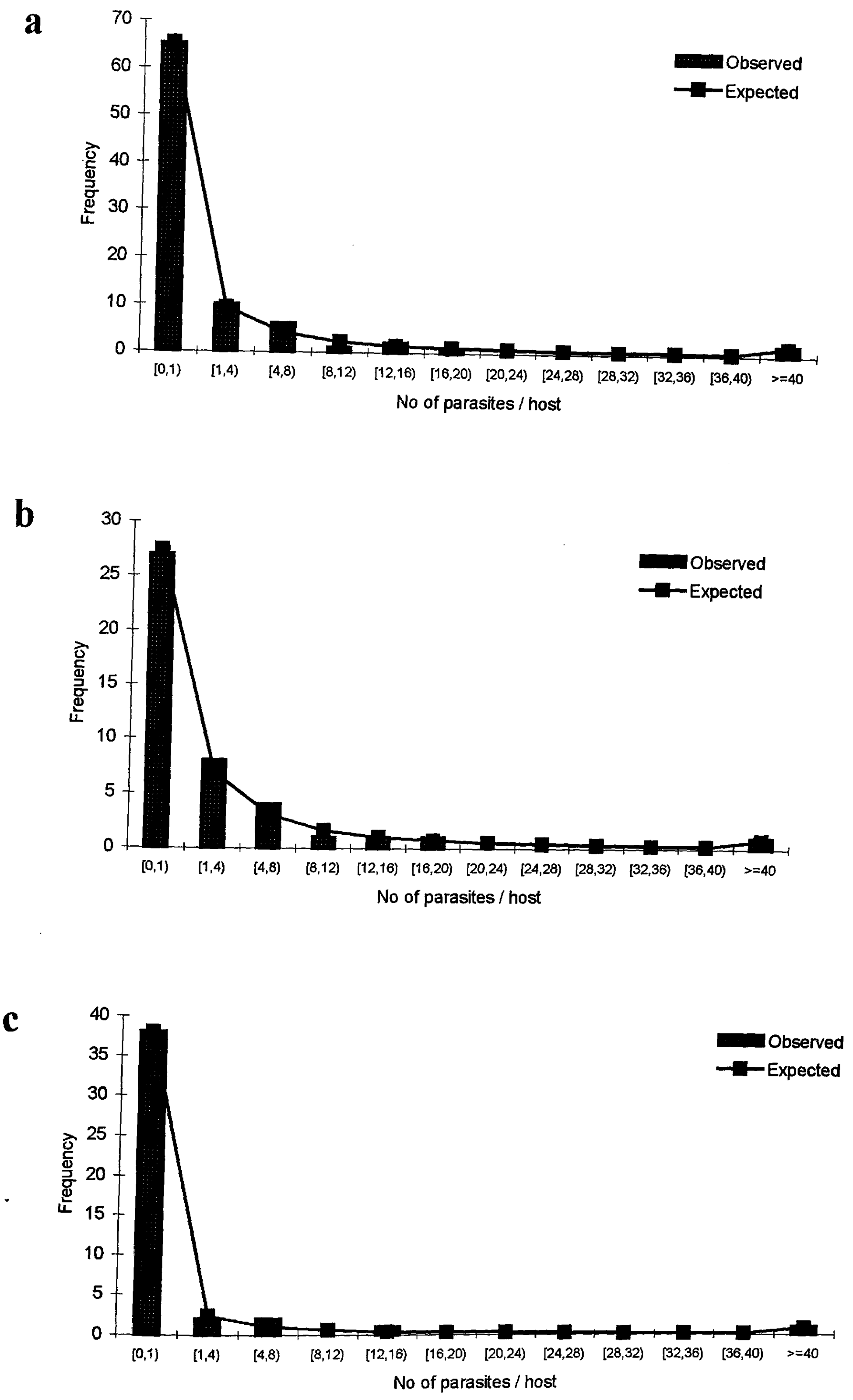


Figure 2. Observed parasite frequency distributions of Heterakis tenuicauda in rock partridge compared with expected distribution based on the negative binomial distribution, estimated by maximum likelihood techniques. (a) All samples (Sample size=87, variance to mean ratio=49.28, k=0.08); Negative binomial fit: chi-squared=3.12, DF=2, P=0.21. (b) Cyclic population (Sample size=43, variance to mean ratio=42.81, k=0.13); Negative binomial fit: chi-squared=1.16, DF=1, P=0.28. (c) Non cyclic population (Sample size=44, variance to mean ratio=59.84, k=0.03); Negative binomial fit: chi-squared=2.13, DF=1, P=0.14.

CHAPTER 8

Temporal Dynamics of Grouse Populations at the Southern Edge of their Distribution: the Dolomitic Alps

I.M. Cattadori[1,2] & P.J. Hudson[1] 1999

[1]Institute of Biological Sciences, University of Stirling
[2]Centro di Ecologia Alpina, Trento, Italy

Ecography 22, in press

TEMPORAL DYNAMICS OF GROUSE POPULATIONS AT THE SOUTHERN EDGE OF THEIR DISTRIBUTION

Isabella M. Cattadori & Peter J. Hudson

Studies of grouse conducted at northern latitudes have shown that tetraonids frequently exhibit cyclic fluctuations in abundance but little is known about the dynamics of grouse species at the southerly edge of their range. Hunting statistics from four species of grouse based on 30 years of data collected from 210 hunting areas were examined from the Dolomitic Alps in the province of Trentino. These data were summed to represent 18 time series from discrete mountain groups. Analyses identified cycles of approximately 5 years in the minority of rock ptarmigan *Lagopus mutus* and hazel grouse *Bonasa bonasia* populations. These cycles only showed significant negative autocorrelation at half the cycle period and were classified as phase-forgetting quasi-cycles. Cycles were not found in time series of black grouse *Tetrao tetrix* or capercaillie *Tetrao urogallus*. Correcting time series for hunting effort or hunting restrictions tended to increase the proportion of populations that exhibited cycles but no difference in the strength of second order density dependence. A linear first order density dependent autoregressive model described the dynamics of most of the populations with the exception of a proportion of rock ptarmigan and black grouse populations where a non linear first order model provided the best fit. We compare the findings with studies conducted in Finland and suggest possible reasons for the reduced tendency to cycle in the populations of southern Europe.

A number of studies have examined the temporal dynamics of grouse species and identified the presence of cyclic fluctuations in abundance (Siivonen 1952, Hörnfeldt 1978, Keith and Rusch 1986, Lindén 1989, Hudson et al. 1992a, Lindström et al. 1995). The tendency of the populations to exhibit cycles as well as the period and amplitude appears to vary geographically within the species' distribution. For example, in willow ptarmigan (*Lagopus lagopus*) 9 year cycles have been recorded in Arctic Canada (Mossop 1988), 10 year cycles in Siberia (Andreev 1988) and 4 year cycles in Norway (Myrberget 1984). In Britain, the red grouse subspecies (*Lagopus l. scoticus*) exhibit a cycle period that ranges from 4 years in northern England to 12 years in northern Scotland and yet populations on the dry east side of the country exhibit no periodic fluctuations (Potts et al. 1984, Hudson et al. 1985, Hudson 1992). Detailed field experiments, coupled with monitoring and modelling of red grouse dynamics have shown that the cause of the cycles in English populations is parasite induced reduction in breeding production (Hudson et al. 1985, Dobson and Hudson 1992, Hudson et al. 1992a, b, Hudson and Dobson 1997, Hudson et al. 1998). Changes in the life expectancy of free living parasitic stages or the propensity of the parasite to exhibit arrested development can account for the geographical differences in cycle periods (Dobson and Hudson 1992).

While the mechanism that generates the cyclic pattern in red grouse populations in England has been demonstrated, the factors that operate in most other cyclic species, including the other tetraonids have not been identified. Generally speaking, delayed density-dependent interactions between trophic levels are considered the principal mechanism (Moran 1953a, Keith 1963, Krebs et al. 1986, Royama 1992, Turchin and Taylor 1992, Bjørnstad et al. 1995, Lindström et al. 1995, Lindström 1996, Stenseth et al. 1996).

The majority of studies on tetraonid populations have been conducted at northern latitudes where cyclic fluctuations are observed. Surprisingly little has been recorded from the same species at the southern extreme of their ranges, particularly the European species whose distributions reach southwards through the Alps to the Dinaric Alps. In this paper we investigate the temporal dynamics of some of the most southerly populations of Rock ptarmigan (*Lagopus mutus*), Black grouse (*Tetrao tetrix*), Capercaillie (*Tetrao urogallus*), and Hazel grouse (*Bonasa bonasia)* in the Dolomitic Alps of Trentino, Italy. The analysis is based on hunting statistics collected from 210 hunting areas over a period of 30 years. Our aim is to answer three main questions: (i) Do southerly grouse populations exhibit cyclic fluctuations in abundance? (ii) What is the influence of hunting effort or hunting restrictions on the temporal patterns of harvesting? (iii) What autoregressive models explain the dynamics of alpine grouse populations and are these comparable with previous studies on grouse?

Material and Methods

Study area and species

A large proportion of the Dolomitic Alps is found in the Autonomous Province of Trentino in northern Italy. Altitudes range from 65 m to 3750 m and about 50% of the total province is between 1000 m and 2000 m. The mountains within the region fall into 18 discrete mountain groups separated by valleys with vineyards, orchards and other agricultural or industrial activities (Fig. 1a). The grouse populations inhabit most of the mountain groups and exhibit a clear altitudinal distribution along an ecological habitat gradient ranging from deciduous woodland at the base of the mountains to the rocky mountain plateaux (Fig. 1b).

Rock ptarmigan are restricted to the high rocky mountain plateaux (mean range: 2000-2400 m). Black grouse have a broad altitudinal range (mean range: 1400-1900 m) and are found in the coniferous woodland habitat and up into scrub patches and the lower slopes of the alpine prairies. Capercaillie inhabit the mature conifer woodland with small stands of deciduous trees and small clearings at a lower altitude (mean range: 1100-1500 m). Hazel grouse inhabit the medium low altitudes (mean range: 700-1200 m), mostly in a mosaic of old and young stands of deciduous trees with a mixture of conifers and small clearings.

Hunting statistics

Numbers of grouse shot each year between 1965 and 1994 were obtained from the 210 administrative hunting areas of Trentino province. Bag data from each of the hunting areas were summed to provide a figure for the total number of animals shot each year, from each of the 18 mountain groups.

Each species of grouse has been subjected to specific hunting restrictions within the past 30 years. Both sexes of rock ptarmigan are hunted but numbers shot have been restricted since 1989 (Fig. 2a). Numbers of black grouse harvested has been restricted to males with a maximum number since 1974 (Fig. 2b). When the number of black grouse shot are plotted against time, and compared with counts from other populations in the east alpine area (De Franceschi 1994c), it is apparent that the bag data in 1974 and 1975 were influenced by the restrictions. These two years of data were ignored in the analyses and abundance estimated by interpolating the average value between neighbouring points in the time series. Hunting of capercaillie has been restricted to males, numbers harvested were limited after 1973 and hunting was stopped after 1989 (Fig. 2c). As with black grouse, restrictions had a clear affect on the number shot in 1974 and 1975 (De Franceschi 1994b) and we interpolated the bag data for these two years. Interpolation was also done in 1971 when the harvest of capercaillie was suspended. Hazel grouse were hunted up until 1987 and then hunting stopped; during the hunting period both sexes could be shot and no restrictions were imposed (Fig. 2d).

While restrictions included a maximum limit, this maximum was never reached in any one hunting season (Anon. 1991). In some years and in some hunting areas a small number of male, black grouse and capercaillie were hunted on leks in April and May but these data were not included in these analyses.

The hunting season is restricted to the autumn months from September to December but the Provincial Department of Wildlife sets the number of days available for harvesting each year and this varied between 32 and 44 days for all species. Provincial Hunting Associations of Trentino monitor and control the numbers of animals harvested and provide hunting licences to local people with no limit on the number of licences produced each year. The number of hunters was recorded through the hunting licences scheme from 1994 to 1974, and we defined hunting effort as the number of hunter days (number of hunters*days of hunting available).

To determine whether the temporal patterns of grouse observed in Trentino are representative of the north-eastern alpine populations, we also analysed three time series that had been collected by other workers. First, a time series of late summer annual counts data (adults and young) undertaken between 1955 and 1993 in an area of the Carnic Alps (East of the Dolomites) by De Franceschi and co-workers (1988, 1994a, b, c). Second, a hunting time series from 1953 to 1992 in Alto Adige, a neighbouring province to the north of Trentino (Artuso 1994). Third, a hunting time series collected in Trentino province from 1886 to 1912 (Ramponi 1928). The bag records were available for each species and in each year as simply the total number harvested in the whole area. Since two of the time series sets overlap with the 30 year Trentino hunting time series we compared the pattern of fluctuations between areas.

Time series analysis

Not all the species inhabited every mountain group and in some areas the data were sparse with either missing values or zeros. Time series with more than five missing values or with more than five zeros were ignored. In those time series with less than five missing values any missing data points were interpolated from the neighbouring data values. Each time series was transformed to natural logarithms [$\ln(X_t+1)$] before the analyses. Previous workers have noted that the addition of an arbitrary number to the data may bias the results (McArdle et al. 1990) so we compared the time series analysis results from a time series $\ln(X_t)$ transformed with a $\ln(X_t+1)$ transformation. A total of 54 time series for the 4 species were used together with the 3 additional time series from the other alpine areas.

Most of the time series exhibited a downward trend that was removed by fitting a third order polynomial model ($X_t = b_0 + b_1 t + b_2 t^2 + b_3 t^3$) and the residuals used for the subsequent analysis. Autocorrelation function analysis (Kendall 1984) was undertaken on each time series to determine if the populations exhibited a tendency to cycle and the cycle period determined using spectral analyses with the fast fourier transform algorithm (Monro and Branch 1976, Chatfield 1996). The strength of density dependence was estimated using partial autocorrelation function analysis (Box and Jenkins 1976, Royama 1992).

We undertook autocorrelation function analysis, spectral analysis and partial autocorrelation function analysis on six types of data:

1. Time series for each species, from each of the 18 Trentino mountain groups (30 years in most cases).
2. Time series corrected for hunting effort (20 years in most cases).
3. Time series during the period when hunting effort statistics were available (20 years in most cases), to compare with the corrected time series and so evaluate the effect of hunting effort.
4. Sub sets of the time series on capercaillie and black grouse, before (9-10 years) and after (17-20 years) hunting restrictions.
5. The total bag statistics for each species from Trentino compared with the time series obtained from the Carnic Alps and the Alto Adige series of the same length (about 30 years).
6. The full-length time series from Alto Adige, Carnic Alps and the early Trentino time series (from 26 to 40 years).

Autoregressive models

Autoregressive models were fitted to the time series following the approach of Royama (1992). The pattern of direct and delayed density dependent relationships was first examined by plotting population growth rate [$R_t = X_{t+1} - X_t$, where $X_t = \ln(X_t+1)$] against X_t and X_{t-1} and X_{t-2}. While linear models have been used to represent the density dependence of several populations (Moran 1953a, Bjørnstad et al. 1995, Stenseth et al. 1996, Grenfell et al. 1998), non linear 2nd order functions have provided parsimonious models for grouse populations in Finland (Lindström 1996). We considered both models, a linear autoregressive model:

$$X_t = (1+a_1)X_{t-1} + \ldots\ldots a_n X_{t-n}$$

and a non linear autoregressive model:

$$X_t = X_{t-1} + 1 - \exp(-a_1 X_{t-1} + \ldots\ldots - a_n X_{t-n})$$

where: X_t is the $\ln(X_t+1)$ transformed bag data at time t, and the constants a_1 and a_n are the direct and delayed autoregressive parameters, respectively. To determine which model provided the best fit to the data we used Akaike's information criterion (AIC) following the approach used by Bjørnstad et al. (1995) and Stenseth et al.(1996). Four alternative orders of complexity were considered for each model: n=1, 2, 3 and 4. To estimate the confidence limits of the non-linear model and compare the linear and non-linear equation, we linearized the non-linear model following the approach taken by Lindström (1996). The model with the smallest AIC value was selected to describe the structural dynamics for each population.

Results

There was no significant difference in the frequency of significant autocorrelation or partial autocorrelation functions between the $\ln(X_t)$ and the $\ln(X_t+1)$ transformations at lag 2, 3 and 4 for all the species (for all, Fisher exact test: $p>0.05$). Since the $\ln(X_t+1)$ transformation did not change the results and the zeros provide information we used this transformation for all time series.

Rock ptarmigan

Bag time series analysis; the 30 year rock ptarmigan times series showed a weak tendency to produce cyclic fluctuations in abundance (Table 1 and Fig. 3) with significant negative autocorrelation at approximately half the cycle period but no positive autocorrelation at full cycle period. This pattern has been defined as phase-forgetting quasi-cycles by Nisbet and Gurney (1982) to distinguish them from the mathematically perfect phase-remembering cycles. Significant periodic fluctuations occurred in 20% of the populations and the period length ranged from 3 to 6 years. Partial autocorrelation function analysis identified negative coefficients at lag 2, 3 and 4 in most of the cases but this was significant in only 30% of the time series.

Hunting effort; there was no consistent difference in the frequency of significant autocorrelation functions between the shortened time series corrected for hunting effort with the series not corrected for hunting effort (Fisher exact test: $p=1.000$). While negative partial autocorrelation functions at lag 2, 3 and 4 were observed in most populations, only 20% of both these shortened time series showed a significant relationship. No consistent differences were observed in the strength of the 2nd order PACF coefficients (Wilcoxon matched pairs sign test: Z=0.255, p=0.800, Table 1) between the two data sets. Correcting time series for hunting effort therefore had no influence on the overall pattern of the time series.

Black grouse

Bag time series analysis; no tendency to cycle was observed in the full-length time series and while a number exhibited a negative PACF at lag 2, 3 and 4 none were significant (Table 1 and Fig. 3). A clear and significant first order density-dependence was detected in 44% of the cases.

Hunting effort; the shortened time series did exhibit significant population cycles although there were no consistent differences in the proportion of the series exhibiting regular fluctuations between corrected and not corrected time series (Fisher exact test: p=0.461, Table 1). The dominant periods of the cycles were either 4 or 7 years in both data sets. Significant PACFs at lag 2, 3 and 4 were observed (39% corrected and 22% not corrected) but no consistent differences in the strength of the PACFs at time lag 2 were detected in the two time series (Wilcoxon matched pairs sign test: Z=0.936, p=0.350).

Hunting restrictions; these shortened time series did exhibit cycles but there was no significant difference between the frequency of regular fluctuations before and after the application of restrictions (28% before and 33% after restrictions, Fisher exact test: p=0.539). Nevertheless there was a consistent difference in the strength of PACFs at lag 2 with a stronger density dependence imposed before restrictions (Wilcoxon matched pairs sign test: Z=3.332, p=0.001). Time series before restrictions were only 10 years in length and it would be unwise to draw any firm conclusions from this result.

Capercaillie

Bag time series analysis; using the full time series, none of the capercaillie time series exhibited cyclic fluctuations (Table 1 and Fig. 3). Significant PACFs at lag 1 were recorded in most of the populations (70%) but no significant density dependence was detected at lags of 2 or more years.

Hunting effort; using the shortened time series, significantly more of the time series corrected for hunting effort exhibited cycles than the uncorrected series (Fisher exact test:

p=0.001, Table 1). The dominant cycle period length was 3 to 5 years for the uncorrected series while it was not possible to perform the analysis on the corrected series. Negative partial autocorrelation functions at lag 2 or more were recorded in most of the populations with 40% in the corrected, and 50% in the uncorrected cyclic time series. There was no consistent difference between the strength of PACF at lag 2 (Wilcoxon matched pairs test: Z=1.274, p=0.203).

Hunting restrictions; there were a significantly greater proportion of cyclic series after than before the restrictions were imposed (Fisher exact test: p=0.001) but there was no consistent differences in the strength of the 2nd order density dependence (Wilcoxon matched pairs sign test: Z=0.561, p=0.575).

Hazel Grouse

Bag time series analysis; just 25% of hazel grouse time series exhibited cycles of either 5 or 11 years in period (Table 1 and Fig. 3). The longer period of 11 years was probably a consequence of the harmonic effect of the 23 year time series and we do not consider this biologically significant (Chatfield 1996). As with the rock ptarmigan, the hazel grouse only exhibited significant negative autocorrelation at half the cycle period, defined as phase-forgetting quasi cycles. Partial autocorrelation function analysis identified negative values at lag 2, 3 and 4 in most of the cases but only 19% of the cases were significant.

Hunting effort; analysis on bag data corrected and not corrected for hunting effort showed a tendency for a greater proportion of the corrected time series to exhibit cyclic fluctuations although this was not significant at the 5% level (Fisher exact test: p=0.067). The dominant period length was 5 years in both data sets. Negative PACFs at lag 2, 3 and 4 were identified in most of the time series with 37% of corrected and 25% of not corrected series significant. The strength of the 2nd order partial autocorrelation coefficient was not consistently different between corrected and uncorrected series (Wilcoxon matched pairs sign test: Z=1.603, p=0.109, Table 1).

Time series analysis of additional data sets

Neither the full length count time series from the Carnic Alps nor the bag time series from Alto Adige exhibited a significant tendency to cycle with the exception of rock ptarmigan in the Carnic Alps and black grouse in Alto Adige. Both of these series showed a significant 2^{nd} order negative PACF (Table 2 and Fig. 4). The hunting time series from Trentino in the 1886-1912 period did not exhibit cyclic dynamics in any species except for rock ptarmigan that showed a tendency to cycle with a period of 9 years (Table 2).

The shortened time series with the same temporal range as the Trentino data (1965-1994) exhibited a weak tendency to cycle in rock ptarmigan and black grouse in the Carnic Alps count series and also in hazel grouse hunting series from Alto Adige. None of the summed time series (i.e. all 18 mountain groups) using the hunting statistics in Trentino showed cycles.

Synchrony within species between the three areas was observed only for black grouse and hazel grouse populations between the Carnic Alps and Alto Adige (Bootstrap random cross correlation at time lag 0 -95% confidence limits- $r=0.61$ and 0.63, respectively) but not in the other species or with Trentino.

Autoregressive models

Correlations between R_t and X_t and partial correlations between R_t and X_{t-1} (corrected for X_t) and between R_t and X_{t-2} (corrected for X_t and X_{t-1}) clearly revealed a significant negative relation between R_t and X_t in the majority of populations (for $p<0.05$: rock ptarmigan 80%, black grouse 67%, capercaillie 40% and hazel grouse 50%). Significant relationships with both X_{t-1} and X_{t-2} were recorded in only 4 cases.

In general, linear models provided a better explanation of the density dependent structure of the time series than a non-linear model. First order processes best explained the majority of capercaillie (90%) and hazel grouse (81%) time series. Linear, first order model still explained the dynamics of most black grouse (61%) and rock ptarmigan (50%) time series although non linear first order models better described a proportion of the time series (39% and 40%, respectively). Second or higher order models were recorded in only one case (rock ptarmigan, 2^{nd} not linear model).

Discussion

Tetraonid populations at the southern edge of their European distribution exhibited a weak tendency to cycle. The minority of hazel grouse and ptarmigan populations produced significant cyclic fluctuations but autocorrelation functions were only significant at half the cycle period and not at the full period, a pattern defined as phase-forgetting quasi-cycles (Nisbet and Gurney 1982). Black grouse did not exhibit cycles in Trentino but regular fluctuations were recorded in the time series of the total number hunted in Alto Adige, while for capercaillie no significant cycles were observed in any of the time series. There was evidence of weak delayed density dependence in all the species, since the majority exhibited negative 2nd order partial autocorrelation functions but these were not significant in most of cases. In contrast, analyses of 21 years of count data of grouse species in Finland identified population cycles in the majority of black grouse, capercaillie and hazel grouse time series with significant 2nd order partial autocorrelation (Lindén 1989, Lindström et al. 1995, Lindström 1996). Similarly, other studies on tetraonids have identified the presence of cycles (Siivonen 1952, Hörnfeldt 1978, Keith and Rusch 1986, Hudson et al. 1985, Hudson 1992). Thus, we conclude that the tendency to cycle is weaker in tetraonids at the southern end of their European distribution than further north.

One limitation with this conclusion is that we used hunting statistics in the analyses and we may expect that hunting effort or restrictions on hunting will influence the pattern. In this respect we undertook comparative analyses of time series corrected and not corrected for hunting effort and analysis of time series before and after the introduction of hunting restrictions. Overall, there was some weak evidence to suppose that correcting for hunting effort could increase the tendency for the series to cycle although this was only significant with the capercaillie, a species that was effectively not cyclic in this part of its range. Despite this tendency, no evidence of a change in the strength of the second order density dependence was observed from partial autocorrelation function analyses for any species suggesting that the structural pattern remained fundamentally the same. Hunting restrictions also increased the tendency to cycle in capercaillie, but again, not the density dependence at a time lag of 2 years. We suspect that hunting restrictions had no real impact since the period of hunting with restrictions was relatively short and the earlier hunting time series with no restrictions for the whole of Trentino showed a similar pattern. As such, hunting strategies probably reduced the tendency of the time series to exhibit cycles but this was insufficient to influence our conclusions.

A second limitation with the use of hunting statistics is that they may not provide a true linear reflection of density. We know for some grouse species such as red grouse, that there is a reasonable linear relationship between actual density and numbers harvested (Picozzi 1968, Hudson 1992). We also know that hunters tend to stop hunting when stocks fall below a critical density and therefore bag records under estimate low densities (Hudson 1992, Hudson et al. 1998). However, hunting traditions and strategies vary between countries (Lindén 1981b) and obtaining country and species specific relationships was outside the scope of this study. Even so, like many previous studies that have used hunting time series, we were not specifically interested in comparing population density but in the pattern of fluctuations in relative numbers (Elton and Nicholson 1942, Krebs et al. 1986, Hudson 1992, Royama 1992, Sinclair et al. 1993).

A third limitation with the use of hunting statistics is that they are frequently collected from areas that tend to reflect political boundaries rather than biological divisions between populations and this aggregation of data could have influenced the patterns observed. By summing data within the 18 discrete mountain groups of Trentino we have avoided this problem to some extent since the mountain groups are separated by poor grouse habitat and should be biologically distinct units. In fact some of our previous studies on rock partridge (*Alectoris graeca saxatilis*) in this province indicate that these mountain groups provide a reasonable scale at which to compare such data (Cattadori et al. *in press*). Previous studies, including that by Lindström et al. (1995, 1996), aggregated data within political boundaries and this may have influenced conclusions.

A comparison of the pattern of cycles with the detailed studies of Lindström and colleagues (1995, 1996) provides a good opportunity to identify geographical variations in cycle pattern. Cycle period in the three species studied by both ourselves and Lindström et al. (1995) identified a 6 years period length in all cases and so we may expect the structure of the density dependence to be somewhat similar. In contrast, the analysis of the autoregressive models showed that grouse populations in the Dolomites tended to exhibit first order density dependent processes. The absence of a clear delayed density dependent process similar to that observed for the Finnish populations could explain quantitatively the reduced tendency of the Italian populations to cycle. Of course the actual mechanisms may be different in the two areas and simply be operating at the same time scale.

Time series analyses shows that ptarmigan and hazel grouse exhibit phase forgetting quasi-cycles, which by definition would fade out unless subjected to stochastic perturbations (Johnson et al. 1986, Potts et al. 1984, Townsend et al. 1990, Royama 1992, Kaitala et al. 1996a). The generation of oscillations and the production of a correlogram similar to that observed in grouse species at northern latitudes depends on the strength of the delayed density dependence, the reproductive rate of the population and the frequency and strength of the stochastic factors. Reproductive outputs of black grouse in Italy (e.g. De Franceschi 1994c) appear to be much lower than those recorded in Finland (Lindén 1981a) and this would imply that the populations were unable to oscillate with the same amplitude. However, little is known about the relative stochasticity in the different populations. There is greater seasonality at higher latitude and this may also play a role in destabilising the system. While all these hypotheses are open to further investigation the most important task for future research is to investigate if the reduced reproductive output in Italy could account for the variations observed.

In summary, analyses of hunting bag records of grouse species from the southern edge of their range provides evidence to suppose tetraonid populations may still exhibit cyclic fluctuations but these are weaker than those observed at higher latitudes. Hunting restrictions and hunting efforts may reduce the tendency to cycle but probably do not alter the pattern of the cycles to any great extent. Further work will attempt to identify some of the mechanisms involved and examine the geographical variation in extrinsic factors that influence cycle patterns.

ACKNOWLEDGEMENTS

We are very grateful to the Hunting Association of Trentino that provided the basic hunting statistics on galliform birds. Stefano Merler kindly provided statistical advice. We would

like to thank Jan Lindström and Arto Lindén for the constructive comments on the manuscript. This paper is dedicated to Paolo F. De Franceschi in recognition of his great contribution to Alpine gamebird studies in Italy.

REFERENCES

Anon. 1991. Censimento Tetraonidi, Gallo cedrone e Forcello. - Provincia Autonoma di Trento, Servizio Foreste, Caccia e Pesca. Ufficio Caccia e Pesca.

Andreev, A. 1988. The ten year cycle of the willow grouse of Lower Kolyma. - Oecologia 76: 261-267.

Artuso, I. 1994. Progetto Alpe - F.I.d.C., U.C.Z.A.

Bjørnstad, Ø. N., Falck, W., and Stenseth, N. C. 1995. A geographic gradient in small rodent density fluctuations: a statistical modelling approach. - Proc. R. Soc. Lond. B 262: 127-133.

Box, G. E. P. and Jenkins, G. M. 1976. Time series analysis: Forecasting and control. - S. Francisco: Holden-Day.

Cattadori, I. M., Hudson, P. J., Merler, S. and Rizzoli A. Synchrony, scale and temporal dynamics of rock partridge (*Alectoris graeca saxatilis*) populations in the Dolomites. - J. Anim. Ecol. *In press.*

Chatfield, C. 1996. The analysis of time series: An introduction. - Chapman and Hall Ltd.

De Franceschi, P. F. 1988. La situazione attuale dei galliformi in Italia. Ricerche recenti o ancora in corso. Problemi di gestione e prospective per il futuro. - In: Spagnesi, M. and Toso, S. (eds.), Atti I Conv. Naz. Biol. Selvaggina. - Suppl. Ric. Biol. Selvaggina, XIX: 165-180.

De Franceschi, P. F. 1994a. Status, geographical distribution and limiting factors of hazel grouse (*Bonasa bonasia*) in Italy. - Gibier Faune Sauvage, Game and Wildl. Vol. 11 (Hors série Tome 2): 141-160.

De Franceschi, P. F. 1994b. Status, geographical distribution and limiting factors of capercaillie (*Tetrao urogallus*) in Italy. - Gibier Faune Sauvage, Game and Wildl. Vol. 11 (Hors série Tome 2): 161-184.

De Franceschi, P. F. 1994c. Status, geographical distribution and limiting factors of black grouse (*Tetrao tetrix*) in Italy. - Gibier Faune Sauvage, Game and Wildl. Vol. 11 (Hors série Tome 2): 185-206.

Dobson, A. P. and Hudson, P. J. 1992. Regulation and stability of a free living host-parasite system: *Trichostrongylus tenuis* in red Grouse. II. Population models. - J. Anim. Ecol. 61: 487-498.

Elton, C. and Nicholson, M. 1942. The ten-year cycle in numbers of the Lynx in Canada. - J. Exp. Biology 11: 215-244.

Grenfell, B. T. G., Wilson, K., Finkenstädt, B. F., Coulson, T. N., Murray, S., Albon, S. D., Pemberton, J. M., Clutton-Brock, T. H. and Crawley, M. J. 1998. Noise and determinism in synchronised sheep dynamics. - Nature 394: 674-677.

Heino, K., Kaitala, V., Ranta, E. and Lindström, J. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. - Proc. R. Soc. Lond. B 264: 481-486.

Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls and tularemia in Northern Sweden. - Oecologia 32: 141-152.

Hudson, P. J. 1986. Red grouse, the biology and management of a wild gamebird - The Game Conservancy Trust, Fordingbridge.

Hudson, P. J. 1992. Grouse in Space and Time. - The Game Conservancy Trust. Fordingbridge.

Hudson, P. J., Dobson, A. P. and Newborn, D. 1985. Cyclic and non cyclic populations of red grouse: a role for parasitism? - In: Rollinson, D. and Anderson, R. M. (eds.), Ecology and Genetics of Host-Parasite Interactions. Academic Press, pp 77-89.

Hudson, P. J., Newborn, D. and Dobson, A. P. 1992a. Regulation and stability of free-living host-parasite system: *Tricostrongylus tenuis* in red grouse. I Monitoring and parasite reduction experiments. - J. Anim. Ecol. 61: 477-486.

Hudson, P. J., Dobson, A. P. and Newborn, D. 1992b. Do parasites make prey vulnerable to predation? Red grouse and parasites. - J. Anim. Ecol. 61: 681-692.

Hudson, P. J. and Dobson, A. P. 1997. Host parasite processes and demographic consequences. - In: Clayton D. H. and Moore J. (eds.), Host-Parasite Evolution: General Principles and Avian Models. Oxford University Press, pp. 128-154.

Hudson, P. J., Dobson, A. P. and Newborn, D. 1998. Prevention of population Cycles by Parasite Removal. – Science: 282, *in press*.

Johnson, D. F. Botsford, L. W. Methot, R. D. Jr. and Wainwright, T. C. 1986. Wind stress and cycles in dungenees crab (*Cancer magister*) catch off California, Oregon, and Washington. - Can. J. Fish Aquat. Sci. 43: 838-845.

Kaitala, V., Ranta, E. and Lindström, J. 1996a. Cyclic population dynamics and random perturbations. - J. Anim. Ecol. 65: 249-251.

Keith, L. B. 1963. Wildlife's ten years cycle. - University of Wisconsin Press, Madison.

Keith, L. B. and Rush, D. H. 1986. Predation's role in the cyclic fluctuations of ruffed grouse. - Proc. XIX Int. Orn. Congr. Vol. 1: 699-732.

Kendall, M. G. 1984. Time series. - Oxford University Press.

Krebs, C. J., Cilbert, B. S. and Boutin, S. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the Southern Yukon, 1976-1984. - J. Anim. Ecol. 55: 963-982.

Lindén, H. 1981a. Estimation of juvenile mortality in the capercaillie, *Tetrao urogallus,* and the black grouse, *Tetrao tetrix,* from indirect evidence. - Finnish Game Res. 39: 35-51.

Lindén, H. 1981b. Hunting and tetraonid populations in Finland. - Finnish Game Res. 39: 69-78.

Lindén, H. 1989. Characteristics of tetraonid cycles in Finland. - Finnish Game Res. 46: 34-42.

Lindström, J. 1996. Modelling grouse population dynamics. – Dr. Phil. thesis, Dept. Ecology and Systematics Division of Population Biology, University of Helsinki, Finland.

Lindström, J., Ranta, E. Kaitala, V. and Lindén, H. 1995. The clockwork of Finnish tetraonid population dynamics. - Oikos 74: 185-194.

McArdle, B. H., Gaston, K. J. and Lawton, J. H. 1990. Variation in the size of animal populations: patterns, problems and artefacts. - J. Anim. Ecol. 59: 439-454.

Monro, D. M. and Branch, J. L. 1976. The chirp discrete Fourier transform of general length. - Appl. Statistics 26: 351-361.

Moran, P. A. P. 1953b. The statistical analysis of the Canadian Lynx cycle II Synchronisation meteorology. Australian Journal of Zoology, 1: 291-298.

Mossop, D. H. 1988. Survival strategies of willow ptarmigan. - In: Bergerud, A. T. and Gratson M. W. (eds.), Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis, pp. 330-378.

Myrberget, S. 1984. Population dynamics of Willow Grouse *Lagopus lagopus* on an island in northern Norway. - Fauna norv. Ser. C, Cinclus 7: 95-105.

Nisbet, R. M. and Gurney, W. S. C. 1982. Modelling fluctuating populations. - John Wiley and Sons.

Picozzi, N. 1968. Grouse bags in relation to the management and geology of heather moors. - J. Appl. Ecol. 5: 483-488.

Potts, G. R., Tapper S. C. and Hudson, P. J. 1984. Population fluctuation in red grouse: analysis and bag records and simulation model. - J. Anim. Ecol. 53: 21-36.

Ramponi, S. 1928. I Tetraonidi. - Biblioteca Venatoria vol II, Monauni Trento.

Royama, T. 1992. Analytical Population Dynamics. - Chapman and Hall Ltd.

Siivonen, L. 1952. On the reflection of short-term fluctuation in numbers in the reproduction of tetraonids. - Finnish Game Res. 9: 1-43.

Sinclair, A. R. E., Gosline, J. M., Holdsworth, G., Krebs, C. J., Boutin, S., Smith J. N. M., Boonstra, R. and Dale, M. 1993. Can the solar cycle and climate synchronise the snowshoe hare cycle in Canada? - Am. Nat. 141: 173-198.

Stenseth, N. C., Bjørnstad, Ø. N. and Saitoh, T. 1996. A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. - Proc. R. Soc. Lond. B 263: 1117-1126.

Turchin, P. and Taylor, A. D. 1992. Complex dynamics in ecological time series. - Ecology 73: 289-305.

Townsend, C. R. Sutherland, W. J. and Perrow, M. R. 1990. A modelling investigation of population cycles in the fish *Rutilus rutilus*.- J. Anim. Ecol. 59: 469-485.

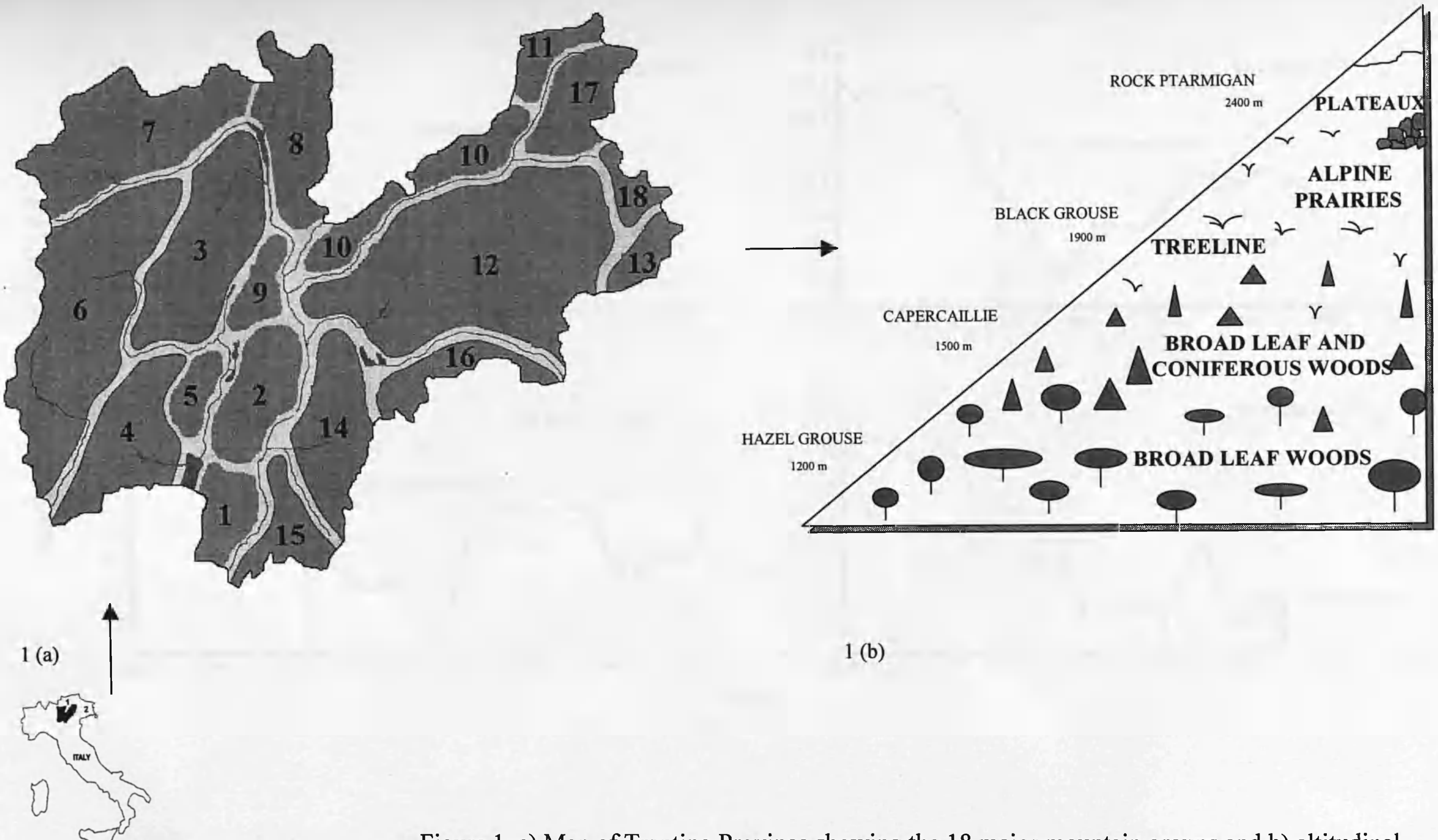
Species		**Complete time series (30 years)**			**Time series corrected for effort (20 years)**			**Time series not corrected for effort (20 years)**		
	N	Cyclic (%)	Period dominant	PACF at lag 2 (mean)	Cyclic (%)	Period dominant	PACF at lag 2 (mean)	Cyclic (%)	Period dominant	PACF at lag 2 (mean)
Rock ptarmigan	10	20	5-11		30	5-6		30	3-5	
Black grouse	18	no cycle	-	-0.094	39	2-7	-0.143	33	2, 4, 7	-0,160
Capercaillie	10	no cycle	-	-0.123	30	*	-0.379	60	3, 4, 5	-0.412
Hazel grouse	16	25	3, 6	-0.094	38	3-5	-0.385	25	3-5	-0.357

* not possible to perform the analysis

Table 1. Time series analysis on the complete hunting time series (30 years), and on shortened time series corrected and not corrected for hunting effort (20 years).

Data sets		**N (years)**	**Cycle (ACF)**	**Period length**	**PACF**
Trentino in 1886-1912*	Rock ptarmigan	26	5	9	5
	Black grouse	26	0	9	0
	Capercaillie	26	1	13	1
	Hazel grouse	26	5	13	0
Alto Adige**	Rock ptarmigan	40	0	20	1
	Black grouse	27	3	5.5	2
	Capercaillie	28	0	4.4	0
	Hazel grouse	33	0	17	1
Carnic Alps***	Rock ptarmigan	29	2	7	2
	Black grouse	39	0	19	1
	Capercaillie	39	0	7.5	0
	Hazel grouse	39	0	19	1

Table 2. Time series analysis carried out on data sets available from other long term studies (* Ramponi 1928, **Artuso 1994, ***De Franceschi 1988, 1994a, b, c)



1 (a)

1 (b)

Figure 1. a) Map of Trentino Province showing the 18 major mountain groups and b) altitudinal distribution of the 4 grouse species with respect to habitat and mean altitudinal range. Points 1 and 2 in the map of Italy show the locations of Alto Adige province and Carnic Alps, respectively.

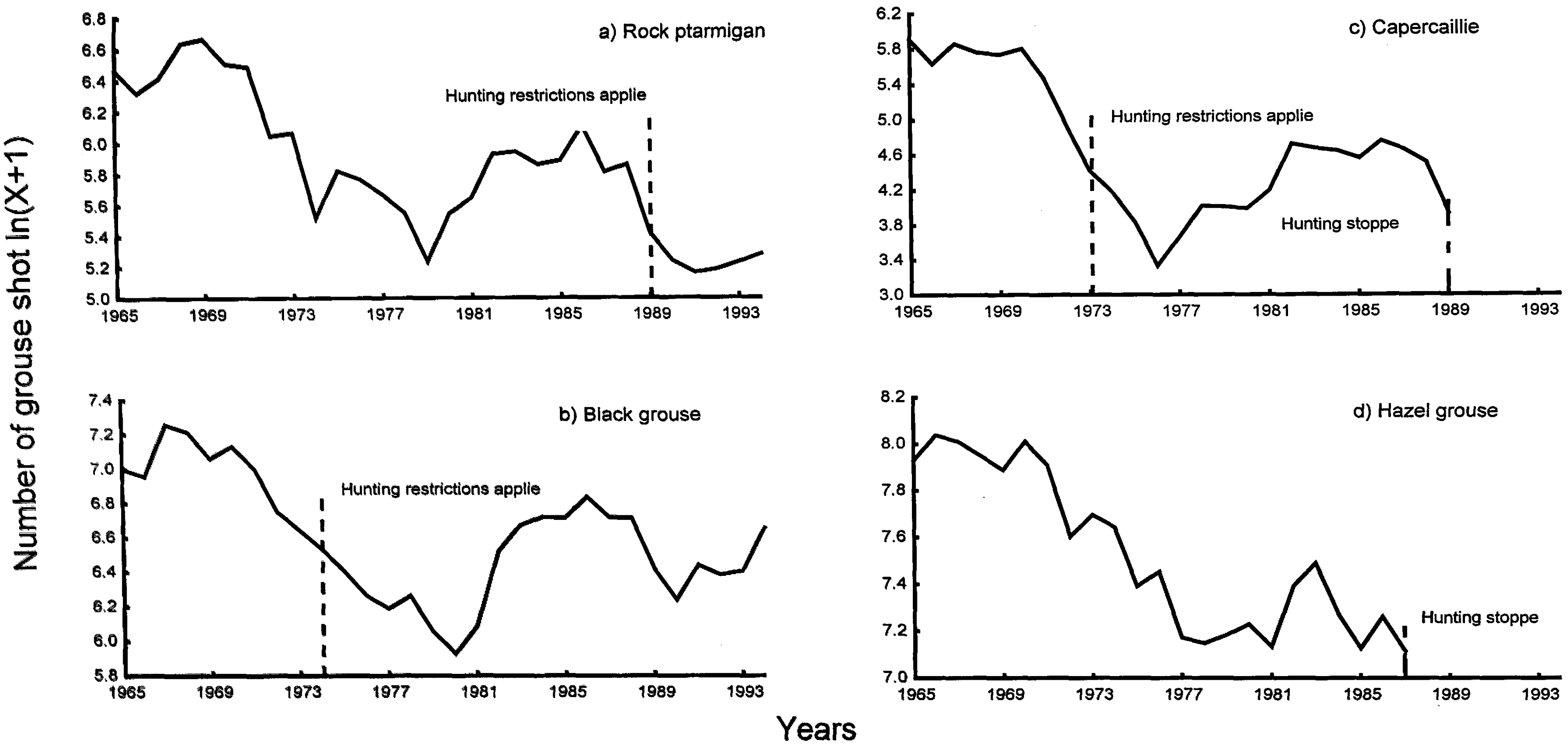


Figure 2. Total number of tetraonids shot in Trentino, a) Rock ptarmigan, b) Black grouse (males), c) Capercaillie (males), and d) Hazel grouse.

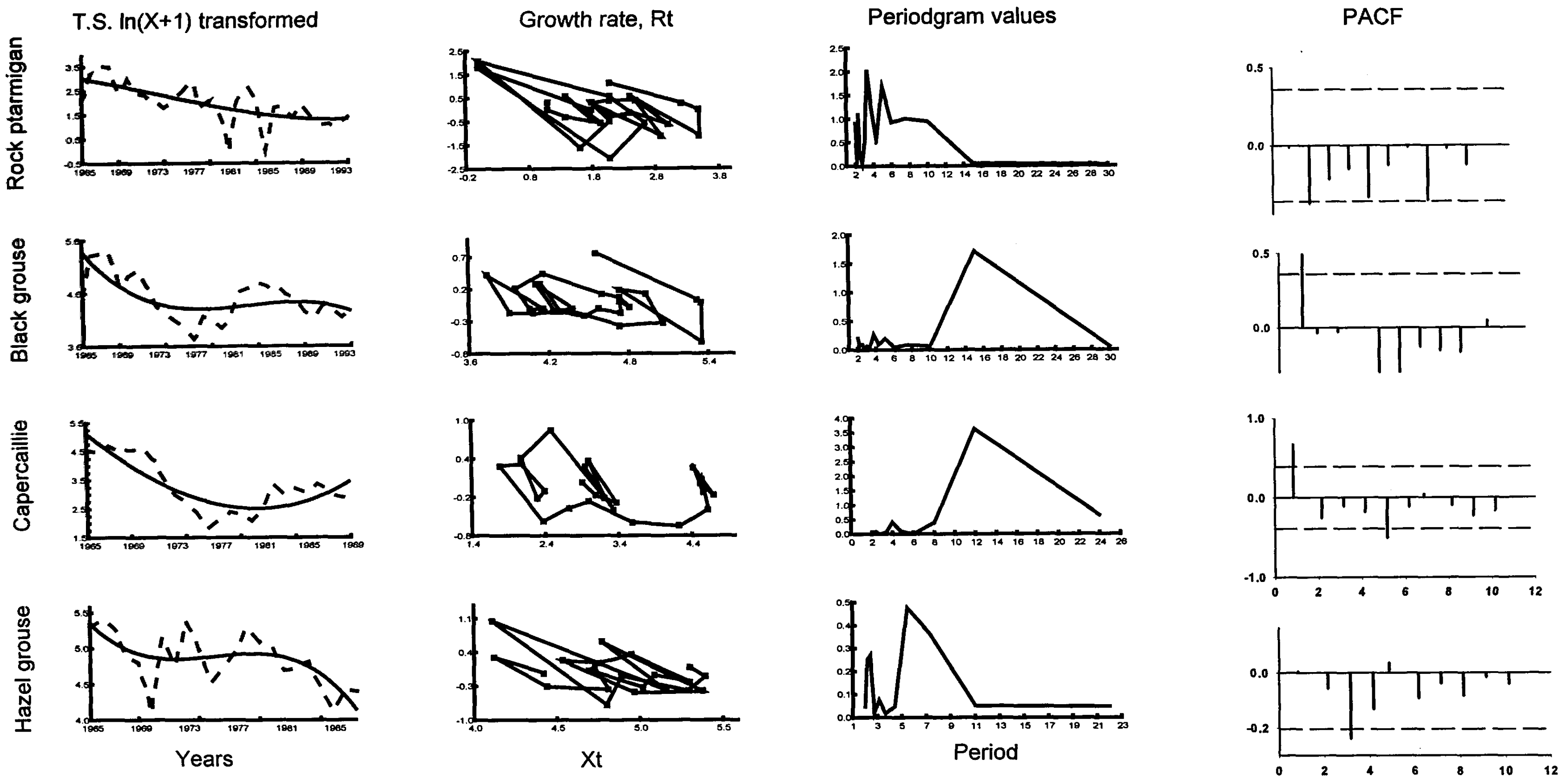


Figure 3. Examples of time series analysis of one population from each species showing: ln(X+1) transformed time series and interpolation of the 3rd order polynomial equation; growth rate, R_t, as function of population abundance, X_t; spectral analysis and partial autocorrelation function analysis, respectively.

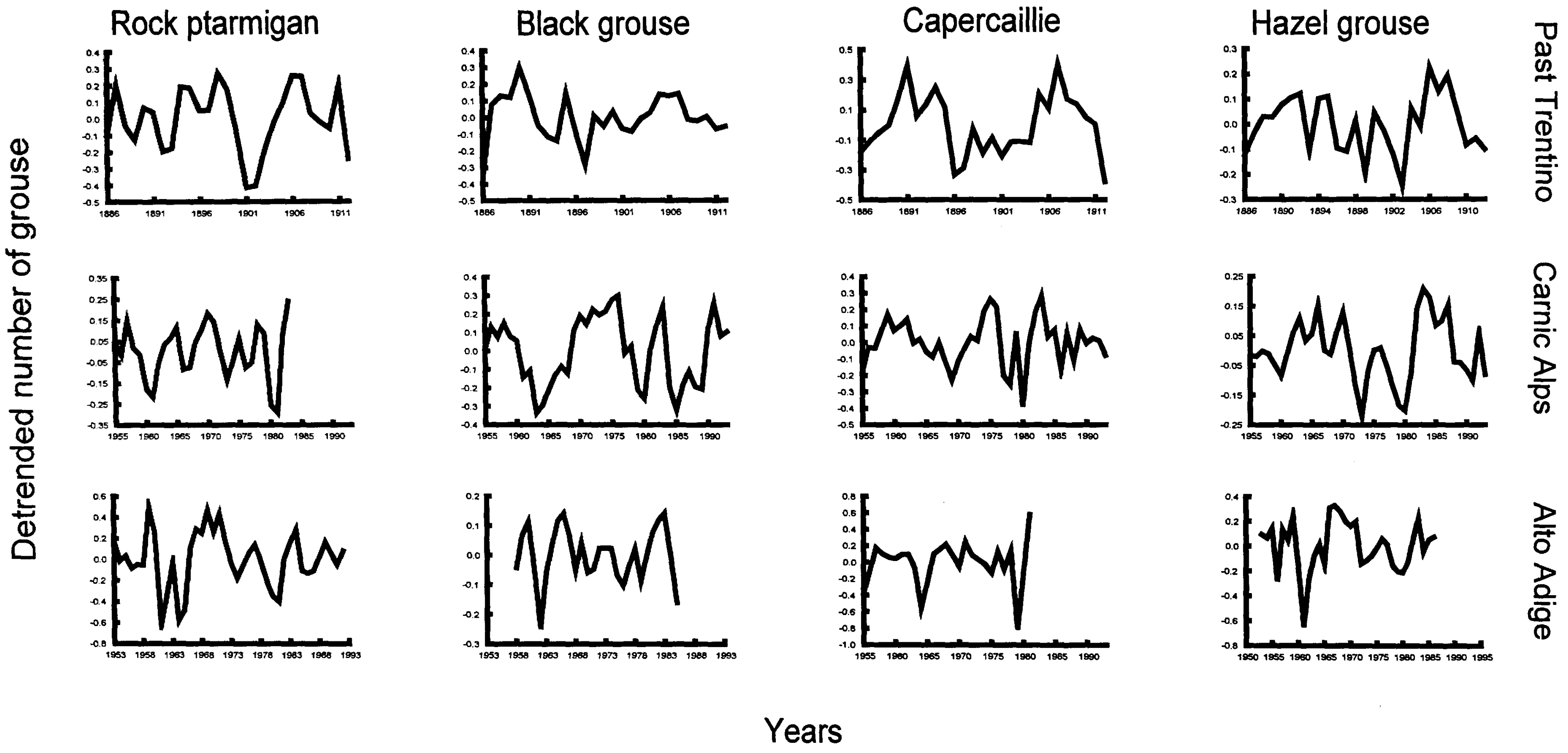


Figure 4. Total number of each grouse species harvested in Trentino (1886-1912 , Ramponi 1928); Carnic Alps (1955-1993, De Franceschi 1988, 1994a, b, c) and Alto Adige (1953-1992, Artuso 1994). Series detrended.

CHAPTER 9

Mechanisms of Synchrony in Spatially Structured Gamebird Populations

I.M. Cattadori[1,2], S. Merler[2] & P.J. Hudson[1]

[1]Institute of Biological Sciences, University of Stirling
[2]Centro di Ecologia Alpina, Trento, Italy

Journal of Animal Ecology, under review

MECHANISMS OF SYNCHRONY IN SPATIALLY STRUCTURED GAMEBIRD POPULATIONS

Isabella M. Cattadori, Stefano Merler & Peter J. Hudson

Summary

1. Hunting records of five gamebird species from the Italian, Dolomitic Alps were used to examine the relative importance of dispersal and common stochastic events in causing synchrony between spatially structured populations.
2. Cross correlation analysis of detrended time series was used to describe the spatial pattern of fluctuations in abundance while standardised time series was used to describe both fluctuations and the general trend in abundance. There were large variations in synchrony both within and between species and only weak negative relationships with distance.
3. Species in neighbouring habitats were more likely to be in synchrony than species separated by several habitats. Species with similar density dependence structure were more likely to be in synchrony.
4. To estimate the relative importance of dispersal and environmental stochasticity we modelled the spatial dynamics of each species using two different approaches. First, we estimated the intensity of environmental stochasticity from climatic records during the breeding season and then modelled the dispersal rate and distance for each species. Second, we used estimating functions and bootstrapping of time series data to calculate the relative importance of dispersal and stochastic effects for each species. The two models showed similar results for rock ptarmigan, black grouse and rock partridge while contrasting patterns were observed for capercaillie and hazel grouse.
5. The results suggest that environmental stochasticity plays the dominant role in most species although there will also be some dispersal between populations.

INTRODUCTION

A central objective of population ecology is to understand how populations are spatially structured. An informative way of looking at this is to describe how species abundance varies temporally and spatially and then to identify the mechanisms that can cause synchrony. A pattern common to many taxa is a decrease in synchrony with distance between populations (e.g. Marcström et al. 1990, Steen, Yoccoz & Ims 1990, Thomas 1991, Pollard Van Swaay & Yates 1993, Hanski & Woiwod 1993, Sutcliffe Thomas & Moss 1996, Ranta, Lindström & Lindén 1995a, Ranta et al. 1995b, 1997a, b, Ranta, Kaitala & Lindström 1997c, Ranta, Kaitala & Lundberg 1998, Stenseth, Bjørnstad & Takashi 1996, Heino et al. 1997). Two principal mechanisms have been identified as the possible causes of this synchrony. First, dispersal between spatially structured populations (Maynard Smith 1974) and second, the correlated effect of density independent factors that synchronise populations with the same density dependent structure, an effect referred to as the Moran effect (Moran 1953b, Hanski 1991, Royama 1992, Ranta et al. 1997a, Hudson & Cattadori 1999, Cattadori et al. 1999). The relative importance of each mechanism seems likely to depend to some extent on scale. At the local scale, dispersal between populations may well dominate whereas at higher scales where distances exceed dispersal distances, synchrony is more likely to be caused by correlated stochastic factors (Moran 1953b, Pollard 1991, Hanski & Woiwod 1993, Sutcliffe *et al.* 1996, Ranta *et al.* 1995a, b, 1997a, 1998). Distinguishing between the two mechanisms is an important problem in population biology since it has repercussions on the persistence of local populations and the risk of global extinction (Heino et al. 1997, Heino 1998, Palmqvist & Lundberg 1998).

The only clear way to distinguish between the two processes is by experimentally preventing dispersal or decoupling the environmental density independent factors. Such experiments on natural populations are logistically difficult. Nevertheless, a recent study on populations of sheep in the St Kilda archipelago was able to dismiss the possible role of dispersal since sheep populations were separated by several kilometres of lethal Atlantic ocean (Grenfell et al. 1998). Analyses of population data with modelling demonstrated the important role of climatic perturbations in driving the synchronous fluctuations of these closed populations and also identified that non-linear density dependence can have a desynchronising effect. Of course, dispersal and the Moran effect are not mutually exclusive and it seems likely that both may operate at the local scale. Thus, the parsimonious hypothesis is that large-scale synchrony can only really be caused by the Moran effect but local synchrony may be caused by a combination of one or both factors (Hudson & Cattadori 1999). Ranta and colleagues (1995a,b) used a simulation model to examine the relative effects of the two mechanisms and concluded that both can independently drive synchrony but that superimposing the Moran effect on dispersal sharply improved the cross correlations.

Without question, the best approach for identifying the mechanisms that influence synchrony is an experimental manipulation. However, such an approach is logistically limited in the majority of natural populations and, since the question is so important to the conservation of threatened species, the only solution is to apply statistical techniques that can indicate the relative importance of the mechanisms. We examine this issue by looking at spatial synchrony within and between closely related species inhabiting the same area. We postulate that synchrony between closely related species, particularly those inhabiting similar habitats is probably caused by correlated environmental factors. By investigating the patterns of synchrony within and between species and by applying simple models we argue that we should be able to obtain an estimate of the relative importance of dispersal and common environmental stochasticity.

The alpine gamebirds provide a suitable data set to examine problems of spatial synchrony. All the species are restricted to discrete mountain groups and exhibit a distinct altitudinal distribution with the woodland grouse on the lower altitudes and the open habitat species on the mountain plateaux. The data set is based on long term hunting statistics that provide a reasonable estimate of changes in abundance (Cattadori *et al.* 1999, Cattadori & Hudson 1999). Population data on gamebirds are particularly useful since they are collected in autumn and exhibit large scale fluctuations in abundance that are driven principally by changes in productivity and particularly the mortality of chicks during the first few weeks of life. While a number of workers have highlighted the importance of climatic conditions in influencing survival of gamebird chicks it is apparent that other factors such as the availability of invertebrate food and the condition of the female will also play a role

(Hudson 1986, Potts 1986, Potts & Aebischer 1994). Even so, harsh weather conditions are likely to have either a direct or indirect negative effect on the survival of chicks and we can expect these stochastic effects to be the principal synchronising force in gamebirds. The climatic data for Trentino is aggregated into different macroclimatic areas and this distribution avoids some of the confounding interactions between correlated weather and distance (Boato Arrighetti & Osti 1988, Gafta 1994, Cattadori *et al.* 1999).

In this paper we specifically address three questions:

1. Do close related galliform species exposed to common stochastic events exhibit similar patterns of synchrony?
2. How does synchrony vary between species relative to habitat differences?
3. Are dispersal or common stochastic events the cause of the spatial patterns of synchrony observed in galliforms?

We reproduce the spatial patterns of synchrony using two spatially explicit models. First, we applied the Ricker model assuming *a priori* the stochastic effect of a climatic variable and then estimate the dispersal rate and range of each species using the modifications applied by Ranta et al. (1995a,b). Second, we estimated both the dispersal and the effect of environmental perturbations using estimating functions method (Godambe 1991, Lele, Taper & Gage 1998).

Materials & Methods

STUDY AREA

Trentino (6250 km^2) is an autonomous province situated in the Dolomitic Alps in north-east Italy. Altitude ranges from 65 m to 3750 m a.s.l. and the mountains fall into 18 discrete mountain groups separated by obvious valleys with fruit growing and vineyards (Fig. 1a). The climate within each mountain group is dominated by two rainfall patterns. First, the annual precipitation that divides the province into three distinct areas: an eastern and a western wet zone where the rain exceed 1000 mm per annum, and a central dry zone with less than 1000 mm of rain per annum (Boato *et al.* 1988). Second, the seasonal distribution of the precipitation which divides the southern, pre-alpine, sub-continental area with an equinoctial peak in rainfall, from a northern area with continental conditions and a summer peak in rainfall (Gafta 1994). The combination of these two patterns determine the macro-climates of the province that varies both from west to east and from south to north.

CLIMATIC FACTORS

We postulated that severe weather conditions during the period of brood rearing were likely to be the main density independent feature determining synchrony in these data for three reasons. First, the data describe the variance in hunting statistics from one year to the next and it is well known that year to year variance in these data are influenced principally by chick survival (Potts 1990, Bergerud 1985, Hudson 1992, Potts & Aebischer 1994). Second, harsh weather conditions are likely to be the main density independent factor reducing chick survival. During the first few weeks of life, chick growth rate is high and it is in this period that chicks become independent of the brooding behaviour of the parents and are vulnerable to exposure during wet, cold periods. Third, previous works on gamebirds in the Alps have highlighted the significance of summer rainfall when accounting for year to year variation in chick survival (Zbinden 1987, Klaus, Seibt & Boock 1991, De Franceschi 1994a).

Climate data were collected from 1965 to 1994 from 31 meteorological stations distributed throughout the province and located at different altitudes (from 70 m to 2125 m). The stations were assigned to the mountain groups in which they resided and a monthly mean estimated for each climatic variable and for each mountain group. Data were not corrected for altitude since we were not concerned with the mean but the variation of the variables between years, in particular the occasional extreme years that would synchronise populations. Following previous studies on gamebirds, we postulated that two climatic variables were likely to have a significant influence on chick survival: cold periods and summer rainfall storms (De Franceschi 1994a, Potts 1986, Zbinden 1987, Hudson 1992, Meriggi *et al.* 1990). Cold weather was measured as the average of the monthly minimum temperature, and rainfall storms as the total monthly millimetres of rainfall per days of rain. Not surprisingly, the two variables were inversely correlated ($P<0.01$) and so we used mean monthly rainfall per day as the climatic variable. Climatic and population temporal variability were estimated using the coefficient of variation (Sokal & Roklf 1981).

SPECIES AND HUNTING STATISTICS

The Dolomites are inhabited by five species of gamebird, which exhibit an altitudinal pattern of distribution associated with a change in habitat type (Fig. 1b). Hazel grouse (*Bonasa bonasia*) inhabit the lower and medium altitude woodland (700-1200 m average range) and are associated with a mosaic of deciduous trees and conifers in different aged stands. Capercaillie (*Tetrao urogallus*) (1100-1500 m average range) inhabit the mature, well structured coniferous forests at higher altitude while black grouse (*Tetrao tetrix*) (1400-1900 m average range) are more widespread and can overlap with both capercaillie and the open landscape rock partridge. Above the timberline, the habitat opens out into typical rocky alpine prairies and meadows inhabited by rock partridge (*Alectoris graeca saxatilis*) (800-1900 m average range). The rock ptarmigan (*Lagopus mutus*) (2000-2400 m average range) are restricted to the high mountain plateaux in boulder screes.

Hunting statistics were obtained for each species from the 210 administrative hunting areas of the province between 1965 to 1994. Time series were summed within each of the 18 main mountain groups of Trentino (Cattadori & Hudson 1999). Shooting of hazel grouse ceased in 1987, capercaillie in 1989. A restriction on the number of animals shot per season was imposed except for hazel grouse, although the maximum limits were never reached (Anon. 1991). Further details on hunting strategy and interpretation of bag records are presented elsewhere (Cattadori *et al.* 1999, Cattadori & Hudson 1999).

TIME SERIES ANALYSIS

Each time series was log transformed [ln(x+1)]. Time series with more than five missing values or more than five zeros were ignored. In time series with less than five missing data, the points were interpolated averaging the neighbouring data values. Since most of the time series exhibited a downward trend, this trend was removed by fitting a third order polynomial model ($x_t = b_0+b_1t+b_2t^2+b_3t^3$) and the residuals used for time series analysis.

We restricted our analysis to 54 time series: 18 black grouse, 16 hazel grouse, 14 rock partridge 10 rock ptarmigan and 10 capercaillie (Fig. 2).

The order and strength of direct and delayed density dependence was estimated using partial autocorrelation function analysis (Box & Jenkins 1976, Royama 1992) with the lags greater than 2 standard errors of the white noise (Bartlett's bar).

SPATIAL SYNCHRONY

The degree of spatial synchrony within each species was evaluated using cross correlation analysis at time lag 0 and confidence limits (95%) that were estimated by bootstrapping the data with 1000 random resamples (Efron 1982, Efron & Tibshirani 1993, Ranta et al. 1995a,b). Cross correlation was undertaken first using detrended time series, to investigate the strength of stochastic fluctuations in abundance of populations, and second using standardised time series, to examine both the strength of fluctuations and the general population decline. The pattern of spatial synchrony was determined using the spatial correlogram that relates the cross correlations between populations with the Euclidean distance between the central points of each population.

Synchrony between species used the same techniques as estimating synchrony within species. We estimated the relative "habitat distance" between the species within the mountain groups as the number of intervening habitats ranging from 1, the distance between neighbouring species, to 4 the distance between hazel grouse in the deciduous woodland and rock ptarmigan on the mountain plateaux (Fig. 1b). Synchrony between species was repeated both for detrended series and standardised series.

MODELLING THE DYNAMICS OF SPATIALLY STRUCTURED POPULATIONS

To assess the relative importance of dispersal and common stochastic effects we applied two approaches. First, we assumed that specific climatic factors had an impact on chick production and using these data we estimated dispersal rate and range using the Ricker model. Second, we estimated both the dispersal and the impact of environmental perturbations without any general assumptions but using estimating functions method and bootstrapping on the time series, a powerful generalisation of the maximum likelihood estimation (Godambe 1991, Lele et al. 1998).

Estimating dispersal assuming the pattern of stochasticity

We applied the basic Ricker model:

$$x_{i(t+1)} = x_{it} \exp r_{it} (1 - x_{it})$$

where x_{it} is the population size at time t in the ith patch and r_{it} is the fecundity parameter at time t in the ith patch. Following the approach of Ranta *et al.* (1995a, b, 1997a) and Heino *et al.* (1997) the model was modified to include dispersal between mountain groups thus:

$$x_{it}* = x_{it}(1 - m) + \frac{\sum_{j \neq i} m x_{jt} \exp(-cd_{ij})}{\sum_{k \neq i} \exp(-cd_{jk})}$$

where: i, j and k are patch indices, d_{ij} is the Euclidean distance between patch i and patch j, and c is an inverse parameter of dispersal distance (c>0), such that when c approaches zero the probability that an individual will cover long or short distances is the same between the patches. In Ranta's model, m was defined as the constant fraction of dispersing individuals from each patch (0<m<1), in our model we consider this fraction density dependent since this is more relevant to gamebird populations (e.g. Hudson 1992):

$$m = \frac{M x_{it}}{1 + x_{it}}$$

where M represents the fraction of migrants from an infinite population. Environmental stochasticity was considered at two levels: the local level of each mountain group, u_{it}, and the regional level of all 18 populations, z_t. Local noise was modelled as:

$$r_{it} = r(1 + u_{it})$$

where u_{it} is assumed to be an independently and identically distributed (i.i.d.) random variable uniformly distributed $[-u_i, u_i]$ and r the maximum reproductive rate. Regional noise influenced population abundance at time t ($x_{it}{\sim}z_t x_{it}$) and was the combination of the intensity z_t of occurrence with a probability p ($0 \leq p < 1$). When the intensity deviates from 0 in year t the intensity is assumed to have a uniform distribution $[\bar{x}_Z - \sigma_Z, \bar{x}_Z + \sigma_Z]$. The lower z_t the stronger is the Moran effect (Ranta *et al.* 1995a, b, 1997a).

The fraction of migrants, *m*, and the range of dispersal, *c*, were estimated by fitting the model to the detrended time series of each species and minimising the mean squared error. For each time series, 1000 simulations were carried out and a smoothed version of the mean squared error was obtained. Parameters *M* and *c* were then calculated at the point that minimised the smoothed model error and provided the best model of the observed pattern for each species.

For each species, we defined the parameters as follow:

r	maximum reproductive rate taken as the maximum clutch size for each species in the Alps (Brichetti, De Franceschi & Bacetti 1992),
d	Euclidean distance between the 18 mountain groups of the province of Trentino,
u_{it}	variance of local noise, that is, variance in the July rainfall per days of rain from each of the 18 patches (u_{it} = 0·034-0·085),
p	equal to $1/P$ where P is the period of monthly July rainfall per day of rain from all the province (p= 0·02),
$\bar{x}_Z$	regional mean stochastic events: mean monthly July rainfall per days of rain from the whole province ($\bar{x}_Z$= 0·359),
σ^2_Z	variance of regional noise; the variance in the monthly July rainfall per day of rain from all the province (σ^2_Z= 0·05).

Estimating dispersal and stochasticity without a priori *stochasticity assumption*

Again, we used the Ricker model applied to the time series and the spatial structure of grouse populations in Trentino and then following the approach by Lele et al. (1998) the model was modified as follow:

$$x_{i(t+1)} = x_{it} \exp(r_{it} + bx_t + \varepsilon_t)$$

where r_t is an intrinsic fecundity parameter and b_t is the impact of intra-specific competition on growth rate, both these parameters were assumed to be spatially homogeneous. ε_{it} represents the environmental noise at time t in the ith patch and for each patch it combines the effect of the local and the regional stochasticity. The environmental noise was assumed to be temporally independent but spatially correlated and decreasing exponentially with distance, so the stochasticity in patch i was defined as:

$$\mathrm{cov}(\varepsilon_i, \varepsilon_j, \rho, \sigma^2) = \sigma^2 \rho^{\|s_i - s_j\|}$$

where σ^2 is the variance of the perturbation, ρ a parameter with range (0-1) such that the spatial covariance decreases exponentially with distance and $\|s_i - s_j\|$ is the absolute distance between patch i and patch j and corresponds to the Euclidean distance between the 18 mountain groups. The model was modified to include dispersal between mountain groups:

$$x_{it}^* = x_{it} - \sum_{j \neq i} k(s_j, s_i) x_{it} + \sum_{j \neq i} k(s_j, s_i) x_{it}$$

where $k(s_i, s_j)$ is the proportion of individuals that migrate from patch i to patch j, and $k(s_j, s_j)$ is the proportion of individuals that immigrated into i from j. We did not consider any species-specific pattern of dispersal and assumed that dispersal depends only on the distance between the patches. The half exponential model was used (Skellam 1951):

$$k(s_j, s_i) = \frac{d^{\|s_j - s_i\|}}{\sum_i d^{\|s_j - s_i\|}}$$

where d is the dispersal parameter with values between [0,1).

The parameters r, b, σ^2, ρ and d were estimated from the time series using the estimating function method (for details Godambe 1991, Lele et al. 1998). The general approach of this technique consists in equating a set of linear functions with the parameters to estimate to zero and solving the equations selecting the value of the vector that satisfies the set of equations simultaneously and minimising the mean square error. For each species the estimated parameters were used to generate time series and then using bootstrap random procedures to determine the distribution of the parameters and the cross correlation coefficients. We implemented 100 replicates for each pair of time series making no assumptions about the pattern of distribution of the environmental noise.

Results

SPATIAL SYNCHRONY WITHIN SPECIES

There were differences between species in the temporal variability of population abundance (detrended time series: Kruskal-Wallis ANOVA by ranks test: $P < 0{\cdot}001$). Hazel grouse, that live at the base of the mountain where seasonal variation in climatic conditions is relatively low exhibited relatively low levels of variation ($CV = 29{\cdot}73 \pm 10{\cdot}694$) while rock ptarmigan, that inhabit the mountain plateaux with large seasonal variation in climate exhibited the highest variation ($CV = 55{\cdot}41 \pm 22{\cdot}228$, Fig 2). Rock partridge, capercaillie and black grouse exhibited intermediate levels of variation ($CV = 49{\cdot}78 \pm 35{\cdot}191$; $48{\cdot}12 \pm 28{\cdot}662$; $39{\cdot}08 \pm 15{\cdot}772$, respectively).

With the exception of Capercaillie, all species exhibited large variation in synchrony with cross correlation coefficients between populations being significantly positive, negative or not significant. This was true for both detrended (i.e. year to year variations) and standardised time series (i.e. trend plus year to year variations; Table 1). Capercaillie exhibited less variation and higher positive synchrony between populations. Cross-correlations were consistently higher in standardised than detrended time series for all the species (Wilcoxon matched paired sign test for all: $P < 0{\cdot}01$) with the exception of rock ptarmigan (Wilcoxon matched paired sign test: $P < 0{\cdot}40$; Table 1). This suggested that both population trend and population variability were spatially correlated, probably as a consequence of spatially correlated habitat loss.

Generally there was a weak negative relationship between synchrony and distance for both data sets although different spatial patterns were observed between species (Fig. 3). Almost 90% of capercaillie populations were in synchrony (Table 1) and the correlation remained high even between populations more than 60 kilometres apart (Fig. 3). The other four species showed larger variation, with all exhibiting both strong positive correlations and weak negative correlations at distances less than 20 km. For black grouse and hazel grouse detrended series, a significant negative relationship was observed in synchrony with distance ($r = -0{\cdot}20$, $n = 153$, $P < 0{\cdot}05$; $r = -0{\cdot}39$, $n = 120$, $P < 0{\cdot}001$, respectively).

RELATIVE IMPORTANCE OF SYNCHRONISING MECHANISMS

Estimating dispersal assuming the pattern of environmental stochasticity

The mean rainfall per day in July was used to estimate the local and regional environmental stochasticity and then the dispersal rate and dispersal range, were estimated from the Ricker model to generate time series that minimised the mean squared error (Table 2). A relatively high proportion of rock ptarmigan tended to disperse ($m = 0{\cdot}23$) with movements over long distances ($c = 0{\cdot}75$). Capercaillie and black grouse exhibited a high dispersal rate ($m = 0{\cdot}32$ and $0{\cdot}18$, respectively) but the range of the movements was restricted to local populations (for both the species $c = 3{\cdot}0$). Rock partridge and hazel grouse showed similar dispersal patterns with a tendency to be more sedentary (for both the species: $m = 0{\cdot}08$) and if dispersing to move preferably to the neighbouring patches ($c = 4{\cdot}0$). When density is assumed very high ($x >> 0$) the estimated proportion of individuals that disperse under a density dependence effect, M, included 70% of capercaillie, 50% of rock ptarmigan, 40% of black grouse, and just 20% of rock partridge and hazel grouse. A comparison of the spatial pattern of synchrony on distance produced by the model compared with the observed data sets is reasonable for most species with the exception of hazel grouse (Fig. 4a).

Estimating dispersal and environmental stochasticity without a priori *stochasticity assumptions*

Using estimating functions method and the Ricker model with bootstrapping we estimated both dispersal rate and the effect of environmental perturbations for all species (Table 3 and Fig. 4b). As with the previous model, the rate of dispersal was high in rock ptarmigan and black grouse ($d = 0{\cdot}39 \pm 0{\cdot}065$ and $0{\cdot}29 \pm 0{\cdot}057$, respectively) while the rock partridge remained relatively sedentary ($d = 0{\cdot}00 \pm 0{\cdot}089$). In contrast to the previous model hazel grouse exhibited a high rate of dispersal ($d = 0{\cdot}38 \pm 0{\cdot}116$) and capercaillie showed a tendency for low dispersal rate ($d = 0{\cdot}00 \pm 0{\cdot}040$).

According to the statistical model, more than 50% of rock partridge, black grouse, capercaillie and hazel grouse populations fluctuate in synchrony because of common environmental events but in rock ptarmigan this was just 20% of the populations. In general the stochastic perturbations had a relatively low impact on the variation of abundance of all the species, and among them the effect was strongest in hazel grouse populations ($\sigma^2 = 0{\cdot}074$) and weakest in black grouse ($\sigma^2 = 0{\cdot}014$).

SPATIAL SYNCHRONY BETWEEN SPECIES

Cross correlation analysis between species within mountain groups showed a significant negative relationship with the number of intermediate habitats between the species for the detrended series but not for the standardised series (Spearman rank correlation on bootstrapped data, $r = -0{\cdot}27$, $n = 102$, $P < 0{\cdot}01$; Fig. 5).

DENSITY DEPENDENCE AND SYNCHRONY BETWEEN SPECIES

The order of density dependence within each population was determined from the detrended series. Significant, density dependence regulation was identified in just 46% of the gamebird populations and this was dominated by first order density dependence (32.5%) while delayed structures were relatively scarce (2nd order = 3%, 3rd order = 4.5%

and 4th order = 6%) (Table 4). Neighbouring species with similar structural order showed a tendency to fluctuate in synchrony (Table 4: $X^2 = 3{\cdot}41$ with Yates correction, $P = 0{\cdot}065$)

Discussion

In general, statistical analysis of the spatial dynamics of gamebird populations in the Italian Dolomites implied that common, environmental stochastic factors are the principal cause of regional patterns in synchrony between populations. Specifically, we posed three questions about the spatial patterns of synchrony and we shall examine each of these in turn.

DO CLOSELY RELATED SPECIES EXPOSED TO COMMON STOCHASTIC EVENTS EXHIBIT SIMILAR PATTERNS OF SYNCHRONY?

Unlike many previous studies on spatial dynamics in animal populations (Hanski & Woiwod 1993, Ranta et al. 1995a, b, 1997a, b Lindström 1996, Sutcliffe et al. 1996, Heino et al. 1997) the galliform birds in the Italian Dolomites do not exhibit a strong negative relationship between synchrony and distance. In this study species either showed no clear relationship with distance or a weak negative relationship with large variations in the degree of synchrony between neighbouring populations. Capercaillie was somewhat of an exception in that they showed strong synchrony with no decrease in the correlations with distance. Previous modelling studies have shown that when dispersal is the dominant cause of synchrony a strong negative relationship between synchrony and distance can be expected but this may not occur when stochastic events are the main cause (Ranta et al 1995b, 1997, 1998, Lindström 1996). In this respect our data imply that stochastic events are the main cause of synchrony although we may also observe a weak negative relationship when the correlation of climatic conditions decreases with distance. This pattern will confound the analysis of spatial data. One of the strengths of this data set is that the climatic data from the Dolomites falls into 11 distinct macroclimatic regions (Gafta 1994) so this confounding effect is avoided and there is only a weak relationship between climatic variables and distance. For example July rainfall, the variable we postulated would be an important synchronising climatic factor, exhibits large variations in synchrony between neighbouring areas with only a weak decrease in the correlation with distance (Fig. 6). In this respect, the spatial patterns observed in the gamebirds of Trentino imply that common stochastic events are probably the main driving force that determines the spatial pattern of synchrony although in reality the relative importance of dispersal play a role in some species, as discussed below.

In contrast to this study, work in Finland on the same woodland species of grouse, recorded large-scale synchrony in the cyclic grouse populations and a clear decrease in synchrony with distance (Ranta et al. 1995a, b, Lindström 1996). The patterns and modelling indicated a principal role of dispersal but with an additional impact of common environmental events. The Finish data differ from these data in two important respects. First, the habitats are relatively homogenous over large areas and second, the environmental data are highly synchronised over large regional scales (Heino 1994, Lindström 1996). In this respect dispersal may be easier in Finland and it may be difficult to disentangle the confounding effects of climate and dispersal.

ARE CLOSE RELATED SPECIES IN SIMILAR HABITATS IN SYNCHRONY?

The finding that species with similar density dependence structure and inhabiting neighbouring habitats exhibit stronger synchrony than species separated by several habitats provides further support for the hypothesis that common environmental factors influence the pattern of synchrony observed since clearly dispersal between species is not possible. However, an alternative hypothesis to account for this observation is that common natural enemies could cause the synchrony. For example year to year variations in predation pressure from a shared predator may synchronise species (Ydenberg 1987, Ims & Steen 1990, Steen et al. 1990, Heikkilä, Below & Hanski 1994). This explanation can not be specifically refuted for the galliform birds of Trentino although the circumstantial evidence supporting the role of common stochastic factors appears to dominate.

IS DISPERSAL OR STOCHASTIC EVENTS THE CAUSE OF SYNCHRONY?

The modelling of the spatial population dynamics provides positive evidence of the dominating role of environmental stochastic events in determining the spatial patterns of synchrony. Estimating function method demonstrated that common environmental perturbations explained more than 50% of the synchronous pattern for rock partridge, black grouse, capercaillie and hazel grouse populations. The rock ptarmigan was the exception, where common stochastic events were less important. One explanation is that ptarmigan inhabit the high mountain plateaux where they are more exposed to the very localised thunderstorms and hailstorms. Since these tend to be highly localised there may be little spatial correlation in severe weather conditions. An alternative explanation is that heavy snow or winter sports may push the birds from the high tops so they mix with birds from other mountain areas and this could lead to increased dispersal.

In the first model, we selected rainfall per day in July, *a priori,* as the environmental synchronising factor, following the findings of previous workers. For rock ptarmigan, rock partridge and black grouse this assumption provided outputs of a reasonable comparison with the observed patterns but a poor fit for capercaillie and hazel grouse. While the pattern of synchrony in capercaillie provides a reasonable comparison to that observed, the model predicts high dispersal rates of individuals over short distances (Table 1). This seems unlikely in capercaillie since all the hunting data is from males and females are the dispersing sex. The situation for hazel grouse is not so clear although these birds probably breed earlier. A general explanation for both species is that July rainfall may not be the only environmental factor involved. In this respect it is worth noting that the second model provided a more acceptable fit to the observed patterns. Indeed we suspect that without good data on the precise combination of environmental factors that influence chick mortality then the best approach for identifying the importance of stochastic events is to use the estimating functions method, a method that has not previously been applied to questions of synchrony. Respect the previous modelling this method estimates the parameters and their approximate confidence intervals using a simple computational approach. Moreover the essential step suggested by Lele et al. (1998) is that we assumed environmental perturbations to be site-specific that is, they represented the heterogeneity of the habitat but were spatially correlated and decreasing with distance so that the Moran effect was assumed to be affected by the distance between the populations.

In summary these data provide evidence that common environmental factors are probably the main cause of synchrony between populations although the relative importance of dispersal will vary between species. To demonstrate this experimentally would be logistically very difficult and to obtain detailed data of individuals from individual populations would be expensive. These results have important implications for the management of wild animal populations since if common stochastic events are the main cause of synchrony then if a local populations goes extinct the habitat may not be recolonised for a relatively long time interval determined by distance to neighbouring populations.

Acknowledgements

We would like to thank the Hunting Association of Trentino that provided the hunting statistics. The Centro di Ecologia Alpina finantially supported this work.

References

Anon. (1991) Censimento Tetraonidi, Gallo cedrone e Forcello. Provincia Autonoma di Trento, Servizio Foreste, Caccia e Pesca. Ufficio Caccia e Pesca.

Boato, S., Arrighetti, A. & Osti, F. (1988) Parchi e riserve naturali del Trentino. Temi Trento.

Box, G.E.P. & Jenkins, G.M. (1976) Time series analysis: Forecasting and control. S. Francisco: Holden-Day.

Berengud, A.T., Mossop, D.H. & Myrberget, S. (1985) A critique of the mechanics of annual changes in ptarmigan numbers. *Canadian Journal of Zoology*, **63**, 2240-2248.

Brichetti, P., De Franceschi, P.F. & Bacetti, N. (1992) Fauna D'Italia vol. II Zanichelli, Bologna.

Cattadori, I.M., Hudson, P.J., Merler, S. & Rizzoli, A. Synchrony, scale and temporal dynamics of rock partridge (*Alectoris graeca saxatilis*) populations in the dolomites. *Journal of Animal Ecology*, in press.

Cattadori, I.M. & Hudson, P.J. Temporal dynamics of grouse populations at the southern edge of their distribution: The Dolomitic Alps. *Ecography*, in press.

De Franceschi, P.F. (1994a) Black grouse *Tetrao tetrix* population on Mount Baldo (Verona, Italy), 1985-90. Atti 6^ Convegno Italiano di Ornitologia, Museo Regionale di Scienze Naturali, Torino.

Efron, B. (1982) The Jackknife, the Bootstrap and Other Resampling Plans. CBMS-NSF Regional Conference Series in Applied Mathematics. Vol. 38, SIAM.

Efron, B. & Tibshirani, R.J. (1993) An Introduction to Bootstrap. Chapmam & Hall Ltd., London.

Gafta, D. (1994) Tipologia, sinecologia e sincorologia delle abetine nelle Alpi del Trentino. Braun-Blanquetia, *Review of Geobotanical Monographs*, vol. **12**.

Grenfell, B.T.G., Wilson, K., Finkenstädt, B.F., Coulson, T.N., Murray, S., Albon, S.D., Pemberton, J.M., Clutton-Brock, T.H. and Crawley, M.J. (1998) Noise and determinism in synchronised sheep dynamics. *Nature*, **394**, 674-677.

Godambe, V.P. (1991) Estimating functions. Oxford University Press.

Hanski, I. (1991) Single-species metapopulation dynamics: concepts, models and observations. *Metapopulation Dynamics* (eds M. Gilpin & I. Hanki), Academic Press, London.

Hanski, I. & Woiwod, I.P. (1993) Spatial synchrony in the dynamics of moth and aphid populations. *Journal of Animal Ecology*, **62**, 656-668.

Heikkilä, J., Below, A. & Hanski, I. (1994) Synchronous dynamics of microtine rodent populations on islands in Lake Inari in northern Fennoscandia: evidence of regulation by mustelid predators. *Oikos*, **70**, 245-252.

Heino, R. (1994) Climate in Finland during the period of meteorological observations. *Finnish Meteorological Institute Contribution*, n. **12**.

Heino, M., Kaitala, V., Ranta, E. & Lindström, J. (1997) Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings Royal Society London*, **264**, 481-486.

Heino, M. (1998) Noise colour, synchrony and extinctions in spatially structured populations. *Oikos*, **83**, 386-375.

Hudson, P.J. (1992) Grouse in Space and Time. Game Conservancy Trust. Fordingbridge.

Hudson, P.J. (1986) Red grouse, the biology and management of a wild gamebird. The Game Conservancy Trust, Fordingbridge.

Hudson, P.J. & Cattadori, I.M. (1999) The Moran effect: a cause of population synchrony. *TREE*, **1**, 1-2.

Klaus S., Seibt, E. & Boock W. (1991) Zur Ökologie des Birkhuhns (*Tetrao tetrix*) im mittleren Thüringer Wald. Acta ornithoecologica. **2**, 211-229.

Ims, R.A. & Steen, H. (1990) Geographical synchrony in microtine population cycles: a theoretical evaluation of the role of the nomadic avian predators. *Oikos*, **57**, 381-387.

Lele, S., Taper, M.L. & Gage, S. (1998) A spatial analysis of population dynamics in space and time using estimating functions. *Ecology*, **79**, 1489-1502.

Lindström, J. (1996) Modelling grouse population dynamics. Dr. Phil. thesis, Dept. Ecology and Systematics Division of Population Biology, University of Helsinki, Finland.

Marcström, V., Höglund N., & Krebs, C. (1990) Periodic fluctuations in small mammals at bota, Sweden from 1961 to 1988. *Journal of Animal Ecology*, **59**, 753-761.

Maynard Smith, J. (1974) Models in ecology. Cambridge University Press, Cambridge.

Meriggi, A., Montagna, D., Zacchetti D., Matteucci C. & Toso S. (1990) Population dynamics of the Gray partridge in relation to agriculture and weather in northern Italy. In: K.E. Church, R.E. Warner & S.J. Brady (eds.) Kansas Dep. Wildl. Parks Emporia: 241-256.

Moran, P.A.P. (1953b) The statistical analysis of the Canadian Lynx cycle II Synchronisation meteorology. *Australian Journal of Zoology*, **1**, 291-298.

Palmqvist, E. & Lundberg, P. (1998) Population extinctions in correlated environments. *Oikos*, **83**, 359-367.

Pollard, E. (1991) Synchrony in population fluctuations: the dominant influence of widespread factors on local butterfly populations. *Oikos*, **60**, 7-10.

Pollard, E., Van Swaay, C.A.M. & Yates, T.J. (1993) Changes in butterfly numbers in Britain and The Netherlands, 1990-1991. *Ecological Entomology*, **8**, 93-94.

Potts, R.G. (1986) The Partridge. Pesticides, Predation and Conservation. Collins

Potts, R.G. (1990) Cause and decline in Partridge Populations and Effect of the Insecticide Dimethoate on the Chick Mortality. In: T.J. Lumeij & Y.R. Hoogeveen (eds.) The future of Wild Galliformes in the Netherlands. Gegevens Koninklijke Bibliotheek, *The Hague*, 62-71.

Potts, R.G. & Aebisher, N.J. (1994) Population dynamics of the Grey partridge *Perdix perdix* 1793-1993: monitoring, modelling and management. *Ibis*, **137**, s29-s37.

Ranta, E., Lindström, J. & Lindén, H. (1995a) Synchrony in tetraonid population dynamics. *Journal of Animal Ecology*, **64**, 767-776.

Ranta, E., Kaitala, V., Lindström, J. & Lindén, H. (1995b) Synchrony in population dynamics. *Proceedings of Royal Society of London*, **262**, 113-118.

Ranta, E., Kaitala, V., Lindström, J. & Helle, E. (1997a) The Moran effect and synchrony in population dynamics. *Oikos*, **78**, 136-142.

Ranta, E., Lindström, J., Kaitala, V., Kokko, H., Lindén, H. & Helle, E. (1997b) Solar activity and hare dynamics: a cross continental comparison. *American Naturalist*, **149**, 765-775.

Ranta, E., Kaitala, V., Lindström, J. (1997c) Dynamics of Canadian lynx in space and time. *Ecography*, **20**, 454-460.

Ranta, E., Kaitala, V. & Lundberg, P. (1998) Population variability in space and time: the dynamics of synchronous population fluctuations. *Oikos*, **83**, 367-382.

Royama, T. (1992) Analytical Population Dynamics. Chapman & Hall Ltd., London.

Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika*, **38**, 196-218.

Sokal, R.R. Rohlf, F.J. (1981) Biometry 2nd ed. W.H. Freeman and Company , New York.

Steen, H., Yoccoz N.G. & Ims R.A. (1990) Predators and small rodent cycles: an analysis of a 79-year time series of small rodent population fluctuations. *Oikos*, **59**, 115-120.

Stenseth, N.C., Bjørnstad, 0.N., Takashi, S. (1996) gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proceedings of Royal Society of London*, **263**, 1117-1126.

Sutcliffe, O.L., Thomas, C.D. & Moss D. (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal Animal Ecology*, **65**, 85-95.

Thomas, C.D. (1991) Spatial and temporal variability in a butterfly population. *Oecologia*, **87**, 577-580.

Zbinden, N. (1987) Zum Aufzuchterfolg des Birkhuhns *Tetrao tetrix* im Tessin. *Ornithologische Beobachter*, **84**,49-61.

Ydenberg, R.C. (1987) Nomadic predators and geographical synchrony in microtine population cycles. *Oikos*, **50**, 270-272.

Species	**Mean cross correlation: detrended series (95% conf interval)**	**Percentage of significant positive cross-correlations in detrended series**	**Mean cross correlation: standardised series (95% conf. Interval)**	**Percentage of significant positive cross-correlations in standardised series**	***P***
Rock ptarmigan	0.21 (0.13-0.29)	35	0.20 (0.12-0.28)	27	n.s.
Rock partridge	0.23 (0.18-0.28)	53	0.51 (0.46-0.55)	79	*
Black grouse	0.33 (0.28-0.37)	48	0.38 (0.35-0.42)	54	*
Capercaillie	0.62 (0.58-0.67)	89	0.70 (0.65-0.76)	95	*
Hazel grouse	0.18 (0.12-0.24)	28	0.38 (0.33-0.44)	54	*

* Wilcoxon matched paired sign test between detrended and standardized cross correlations for each species: $P < 0{\cdot}01$).

Table 1. Synchrony within each species and comparison in the proportion of positive and significant cross-correlation between detrended and standardized time series (Wilcoxon matched paired sign test for all: * $P < 0{\cdot}01$).

Species	Minimum squared error (M.S.E.)	Maximum growth rate (*r*)	Local stochasticity (min-max)	Regional stochasticity (x_Z, σ^2_Z, p)	Dispersal Distance (*c*)*	Dispersal Rate (*m*)*
Rock ptarmigan	0.061	10	0.034-0.085	0.359, 0.05, 0.2	0.75	0.23
Rock partridge	0.039	14	0.034-0.085	0.359, 0.05, 0.2	4.00	0.08
Black grouse	0.034	12	0.034-0.085	0.359, 0.05, 0.2	3.00	0.18
Capercaillie	0.039	10	0.034-0.085	0.359, 0.05, 0.2	3.00	0.32
Hazel grouse	0.053	10	0.034-0.085	0.359, 0.05, 0.2	4.00	0.08

*Parameters estimated from minimum squared error.

Table 2. Mean population parameters for each species estimated using Ricker model with the stochastic perturbation *a priori* measured.

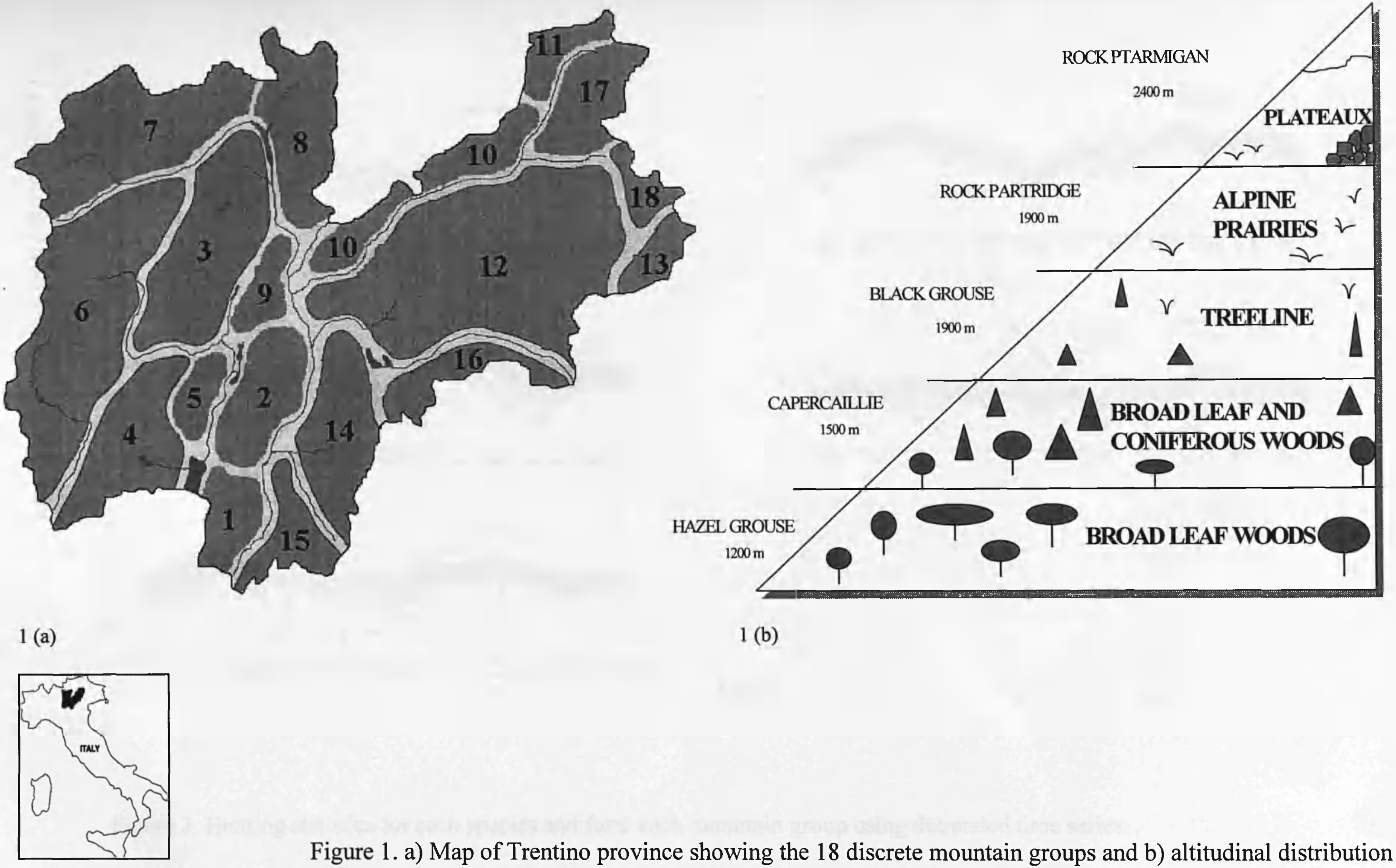
Species	Growth rate (*r*)	Intra-specific competition (*b*)	Dispersal rate (*d*)	Variance in the perturbation (σ^2)	Correlation in the perturbations (ρ)
Rock ptarmigan	0.44 (±0.120)	-0.49 (±0.132)	0.39 (±0.065)	0.032 (7.7E-4)	0.19 (±0.037)
Rock partridge	0.79 (±0.073)	-1.10 (±0.102)	0.00 (±0.089)	0.041 (3.7E-4)	0.57 (±0.012)
Black grouse	0.37 (±0.076)	-0.44 (±0.092)	0.29 (±0.057)	0.014 (3.1E-4)	0.54 (±0.012)
Capercaillie	0.62 (±0.112)	-0.71 (±0.129)	0.00 (±0.040)	0.032 (8.0E-4)	0.53 (±0.022)
Hazel grouse	0.76 (±0.110)	-1.04 (±0.149)	0.38 (±0.116)	0.074 (7.3E-4)	0.61 (±0.011)

Table 3. Mean population parameters for each species estimated using Estimating Function method.

Mountain groups	Rock ptarmigan	Rock partridge	Black grouse	Capercaillie	Hazel grouse
1		0	0		0
2		0	1		0
3	1	1*	1*	1	4*
4	2	1*	1	1*	0*
5		0	0		0
6	0	1	1	1*	0*
7	0*	1	1	0*	0
8		4	1	1	1
9		0	0		0
10	0	2	0	1*	0*
11	0		0		
12	0	0	1*	1*	0*
13			0		4
14		0	0*	1	0*
15		3	0	0	3
16	3		1	0	0
17	1	0	0		
18	4		0		0

*Populations not in synchrony, although they may be in synchrony with a third population.

Table 4. Order of density dependence in each population estimated using PACF analysis on detrended time series. Zero means no significant density dependence identified. Populations within the same mountain group that exhibited significant positive synchrony (random bootstrap cross correlation on detrended series, $P < 0{\cdot}05$) are shown with similar shaded patterns.


1 (a)

1 (b)

Figure 1. a) Map of Trentino province showing the 18 discrete mountain groups and b) altitudinal distribution of the 5 grouse species with respect to habitat and mean altitudinal range in Trentino.

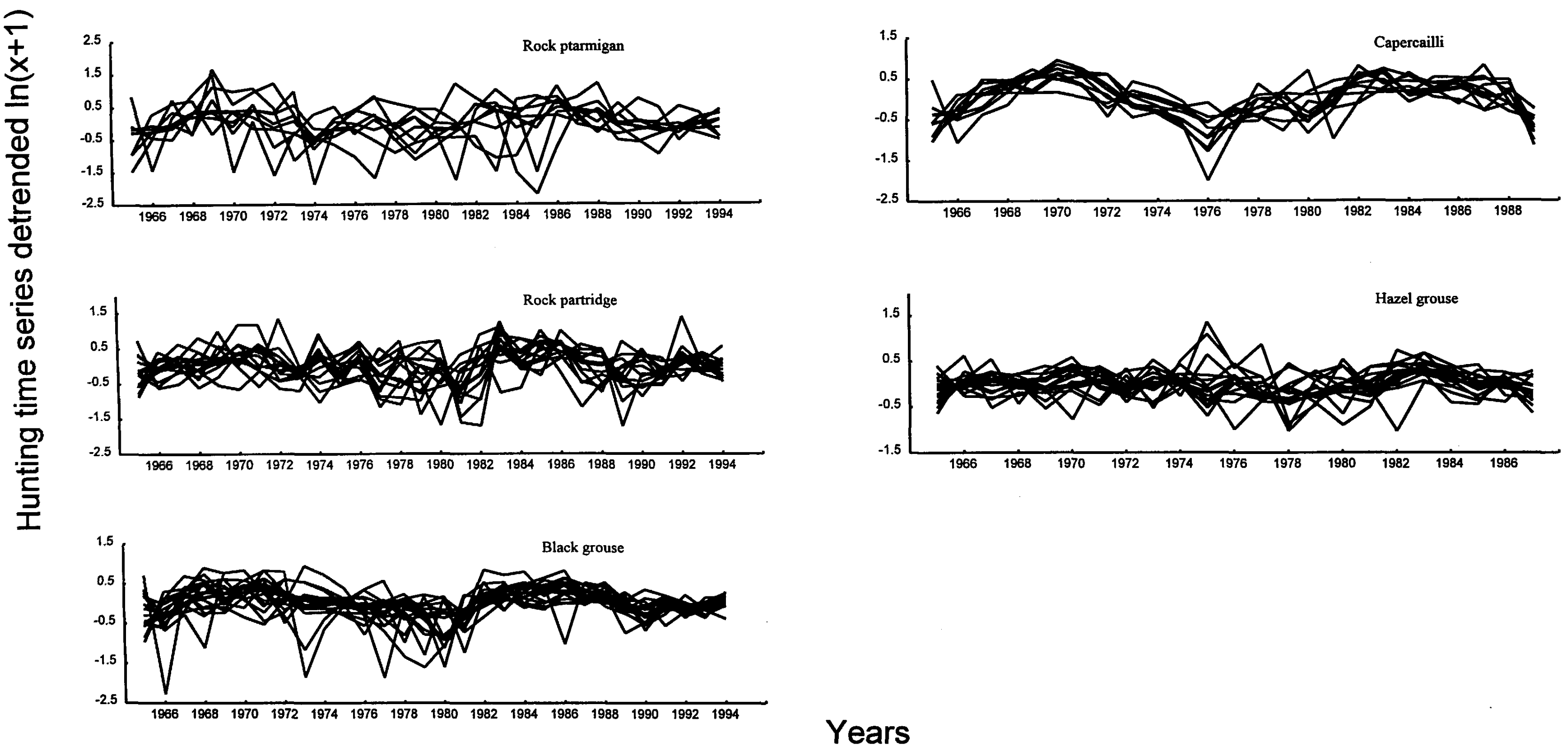


Figure 2. Hunting statistics for each species and form each mountain group using detrended time series.

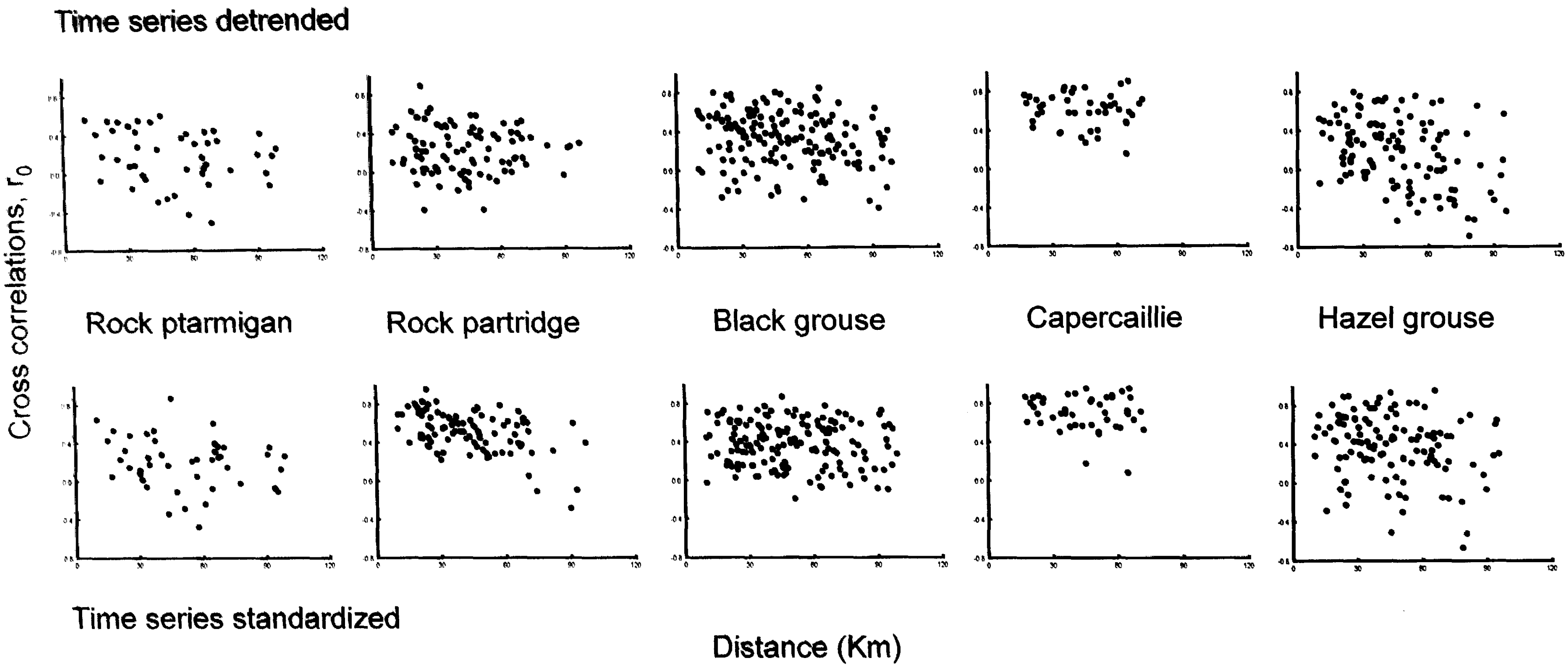
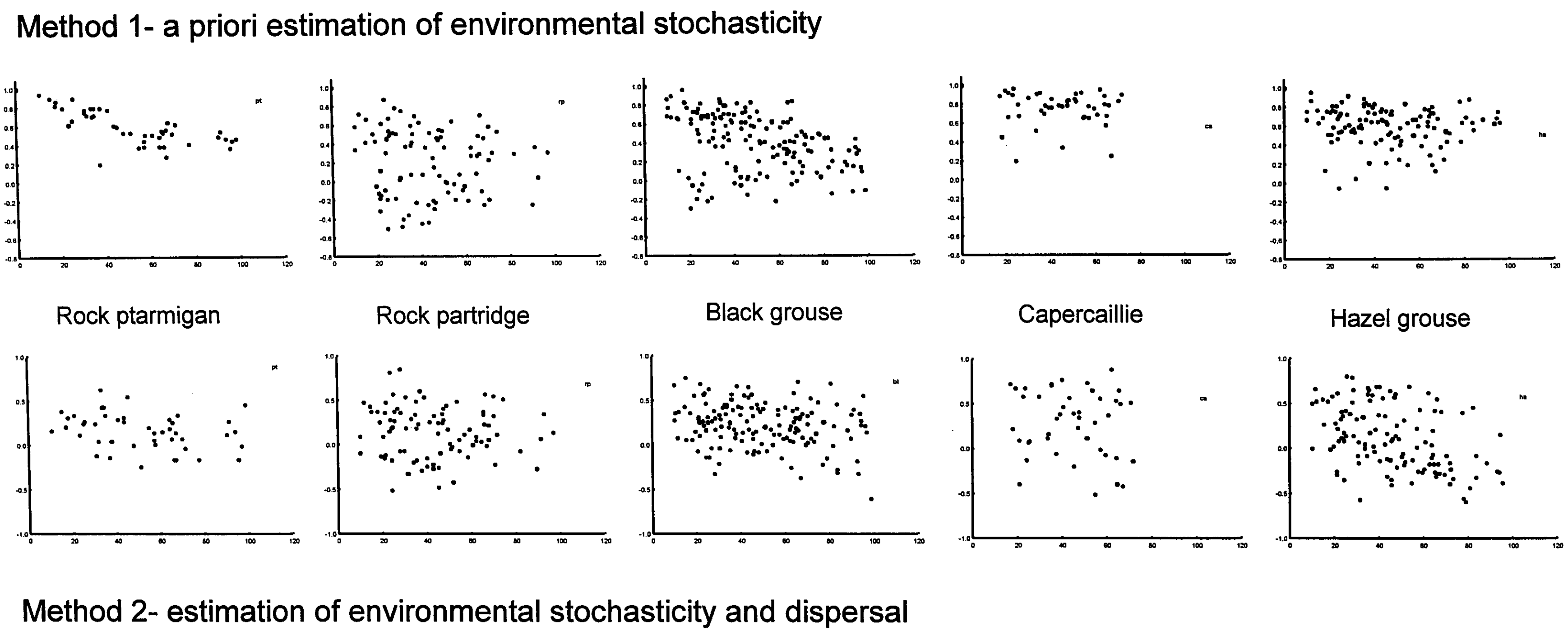


Figure 3. Spatial synchrony in numbers harvested in relation to distance for each species using: a) detrended series, and b) standardised series.



Method 1- a priori estimation of environmental stochasticity

Rock ptarmigan

Rock partridge

Black grouse

Capercaillie

Hazel grouse

Method 2- estimation of environmental stochasticity and dispersal

Figure 4. a) Spatial synchrony in numbers harvested in relation to distance for each species using: method 1) Ricker model with the stochastic perturbation fixed and estimation of rate and range of dispersal and, method 2) using Estimating functions.

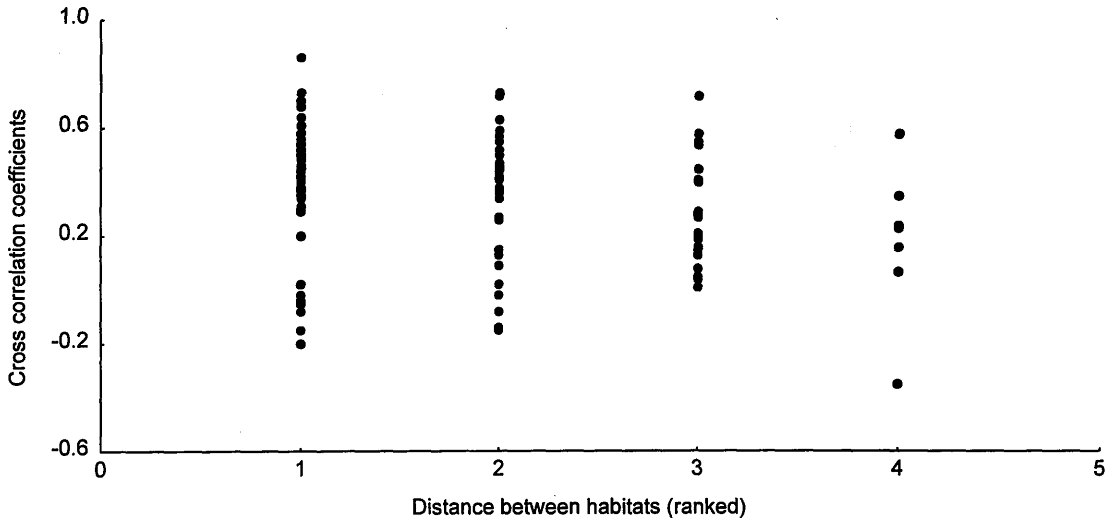


Figure 5. Correlogram of synchrony on distance between species within mountain groups. Ranked habitats and detrended series have been used.

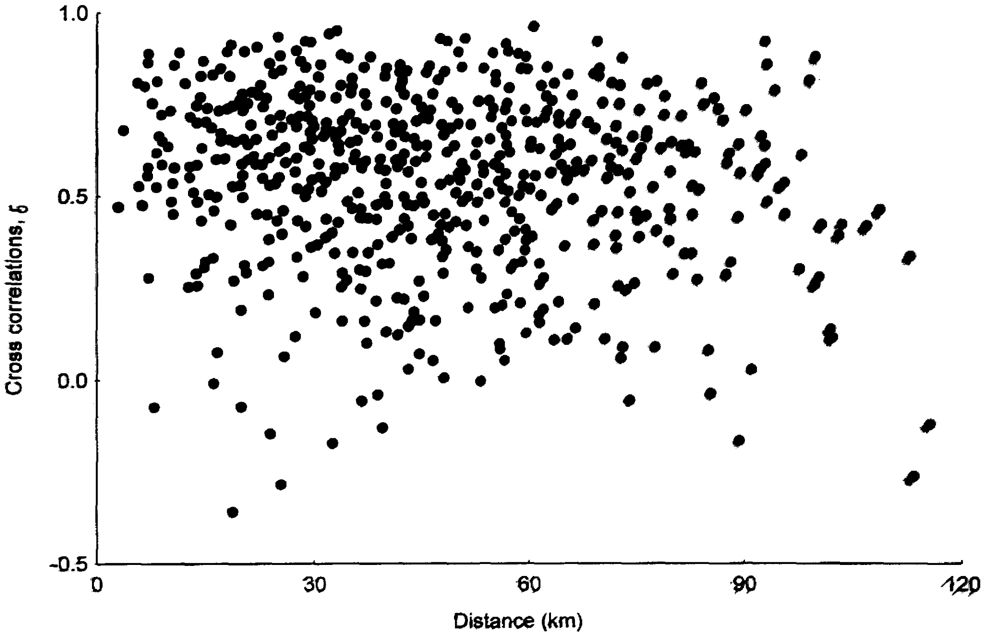


Figure 6. Spatial synchrony of rainfall (mm) in relation to distance between the climatic stations in Trentino.

CHAPTER 10

A Population Viability Analysis of the Grey Partridge (*Perdix Perdix*) in Europe

G. De Leo[1], S. Focardi[2], M. Gatto[1] & I.M. Cattadori[3,4]

[1]Dipartimento di Elettronica e Informazione, Politecnico di Milano
[2]Istituto Nazionale per la Fauna Selvatica, Bologna, Italy
[3]Institute of Biological Sciences, University of Stirling and
[4]Centro di Ecologia Alpina, Trento, Italy

Journal of Applied Ecology, under review

A POPULATION VIABILITY ANALYSIS OF THE GREY PARTRIDGE (*PERDIX PERDIX*) IN EUROPE

Giulio A. De Leo, Stefano Focardi, Marino Gatto, Isabella M. Cattadori

Summary

1. A population viability analysis of the grey partridge (*Perdix perdix*) in Europe has been performed by means of stochastic demographic models that explicitly account for variability in the vital rates and dispersal of the juveniles. The models are built by utilising many of the available data collected in several European sites.
2. Statistical and demographic analyses have shown that the data can be separated into two main sets: the British populations from 1930-1960 and the "declining" continental populations from 1970 to present. The goal is to assess: (i) the relative importance of the basic vital rates characterising partridge life cycle, (ii) their dependence upon partridge density, (iii) the probability of extinction under various conditions, and (iv) the possibility of developing conservative hunting strategies.
3. Density dependence for the spring-to-summer rate of increase and autumn-winter survival is found for both UK and continental populations. Overwinter losses in UK positively correlate with the young-to-adult ratio thus suggesting an important role of dispersal.
4. The results of the two separate stochastic models confirm that the UK populations prior to 1960 were intrinsically much more resilient than the continental populations in recent decades. Even very small harvesting cannot be tolerated by the present continental populations and this may indicate that the persistence of hunting activity, although with a limited effort, has contributed to the extinction of many sub-populations and is critically threatening the remaining ones.
5. It is shown that the introduction of stochasticity is fundamental for assessing the real extinction risk for partridge populations under different management scenarios: in fact, the deterministic model for continental populations would lead to unreliable results, because it would predict a stable positive equilibrium. On the contrary, the stochastic model shows that extinction is very likely to occur.

Introduction

The grey partridge (*Perdix perdix* L.1758) is a typical game bird of open arable landscapes; this species has probably a ponto-pannonic origin and spread into Europe following the diffusion of agriculture (Toso & Cattadori 1993). After World War II, the European populations underwent an impressive decline, as clearly documented by Potts' (1986) seminal book. The British populations exhibited a dramatic fall of density at a rate which reached 7% per year (Blank, Southwood & Cross 1967, Potts & Aebischer 1989), but the decline was even more remarkable in continental countries. For instance, in Italy, at the beginning of the 1980s, the species disappeared from most of its previous range and only 14 self-sustaining populations, inhabiting protected areas, were still recorded (Matteucci & Toso 1985). The attempt to hinder partridge decline by extensive restocking was apparently insufficient to reconstruct viable populations (Prigioni *et al.* 1977; Birkan 1977a; Birkan & Damange 1977; Mazzoni della Stella 1990, Dowell 1991) and, nowadays, no self-sustaining population is left.

The decline of this important quarry species in UK motivated the Game Conservancy to promote a long-term study, from 1968 till present, to determine the causes of its decline. This study was carried out in a partridge range of Sussex where the spring density has declined from 21 to 4 pairs/km^2 in the period 1968-1993 (Potts 1977, 1980, 1986; Potts & Aebischer 1989, 1991, 1994). British studies showed that the most important cause for decline was likely the reduction of chick survival due to the strong increase in the use of agro-chemicals (Potts 1990; Sotherton, Robertson & Dowell 1992). Moreover, reproduction was hampered by a lower availability of hedges (Rands 1986; Aebischer, Blake & Boatman 1994) and the reduction in predator control by gamekeepers (Tapper, Potts & Brockless 1996). By using a simulation model to analyse the dynamics of the Sussex population, it was shown that the effect of agro-chemicals on partridge density leads to a quasi-extinction demography in absence of predation control (Potts 1986; Potts & Aebischer 1994).

Although the importance of modern agricultural techniques in determining the decline is clearly assessed, recent French and Italian studies suggest that partridge populations may remain viable in modern agricultural landscapes (Reitz 1992; Matteucci &

Toso 1985; Cattadori & Zacchetti 1991). On the other hand, hilly areas in northern and central Italy, once characterised by high population densities (cf. Potts, 1986 pp. 18-19) are now unable to maintain viable populations even under strictly protected conditions and despite the traditional agricultural landscape has been preserved (Zacchetti, Montagna & Matteucci 1988; Montagna & Meriggi 1991; Mazzoni della Stella & Burrini 1993).

Potts' (1986, Tab. 10.4) analysis of world data shows that there are significant differences between British and continental populations both for chick mortality and overwinter losses. Chick mortality in eastern Europe is lower than in UK and western Europe, while overwinter losses are lower in UK. Chlewski & Panek (1988) showed that in Poland overwinter losses are usually more important than chick mortality and that agro-chemicals might not affect chick mortality as much as in UK.

The important issue of density dependence has also been examined by some authors. Panek (1992) pointed out that Polish populations are mainly regulated by density dependent brood production, especially when pair density is high. Moreover, a relationship between overwinter losses and population density in autumn was demonstrated in some case studies of continental Europe (Panek 1992; Potts & Aebischer 1989 — for Russia). However, given the methods used to census partridge populations, the interpretation of overwinter losses is difficult, as these are determined by two different processes: mortality (due to predation and/or weather conditions) and dispersal of young birds outside the study area, following the breakup of coveys in January-March. Despite its importance, spring dispersal has been scarcely documented. Jenkins (1961) was the first author to distinguish between losses due to death and those due to emigration using tagged birds. Potts (1986) and Reynolds *et al.* (1991) measured the dispersal rates of British populations while Weigand (1980) and Church, Harris & Stiehl (1980) gave results for American populations. A recent study by Aufradet (1995) provides an estimate of dispersal in continental Europe.

The available evidence shows that both the spatial and temporal variability of demographic parameters and related processes is quite large. For instance, Middleton (1934) recorded in 34 British estates a young/adults ratio ranging between 1.1 and 5.6 in just one season. The study by Panek (1992) also showed that there is high between-area variability in Poland. The very large temporal variability which characterises partridge populations was documented by Potts & Aebischer (1994) who reported bag data from

1793 to present. Despite this variability, the attempts to model the population dynamics of grey partridge have been up to now based on deterministic models (Potts 1980, 1986, Panek 1992, Potts & Aebischer 1994). These models can describe the population trends of specific areas, but cannot account for parameter variability and the effect of random events on extinction probability.

The aim of this study is to perform a population viability analysis of the grey partridge in Europe by means of stochastic demographic models that explicitly account for variability in the vital rates and dispersal of the juveniles. In fact, only a better understanding of partridge population dynamics may help devise more efficient management strategies than the ones adopted in the seventies. The models are built on the basis of the data collected in several European sites (UK included) other than Sussex. Statistical and demographic analyses have been performed separately on two main groups: the "traditional" British populations from 1930-1960 and the "declining" continental populations from 1970 on. Accordingly, we have developed two separate stochastic models which are then used to assess: (i) the relative importance of the basic vital rates characterising partridge life cycle, (ii) their dependence upon partridge density, (iii) the probability of extinction under various conditions, and (iv) the possibility of developing conservative hunting strategies. All the model parameters and their variances have been estimated from our datasets and hence closely reproduce the form of density dependence and the level of dispersal and environmental stochasticity observed in the field. As a consequence, the resulting demographic models are able to realistically mimic the dynamics of the two groups of partridge populations both in their natural habitat and under different management scenarios. The results of our analysis are then compared with those of the Sussex study.

Materials and methods

PARTRIDGE LIFE CYCLE AND AVAILABLE 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, the highest clutch size in any bird species. Hatching occurs from the beginning of

June and, in case of failure, further clutches may be laid in summer. Nestlings are subject to the highest mortality during the first three weeks of life, while hen mortality peaks during incubation. By the end of September, juveniles can no longer be distinguished from older birds during field counts. Young and adult birds form coveys in late summer. These will break up only in February-March when young birds may disperse. Hunting mainly occurs in October and November.

The present study is based on an extensive survey of published European data. Only censuses based on periods of at least three years have been considered. For UK we have used the following studies: Middleton (1934, 1936, 1937), Jenkins (1961), Blank & Ash (1959), Blank Southwood & Cross (1967), Potts (1973). In the case of continental Europe we have used Panek (1992) and Chlewski & Panek (1998) for Poland; Birkan,Olivier & Aubineau (1975), Birkan (1985), Birkan (1977b), Serre & Reitz (1989) and Reitz (1992) for France; Montagna & Meriggi (1991) and Mazzoni della Stella & Burrini (1993) for Italy. In a few cases (Middleton 1934, 1936, 1937; Blank & Ash 1959; Blank Southwood & Cross, 1967) the data series for one study area has been reconstructed by using information from different papers. From now on, we will use N^p, N^s, N^a, and N^w to indicate grey partridge density in spring (February-March), summer (late August), autumn (October-November after hunting) and winter (December-January), respectively. h will indicate the harvest per unit area (we assume $N^s - h = N^a$), and ρ the ratio of young to old birds in summer, when the two age classes are still distinguishable.

Data on partridge density are usually available at least in spring and autumn and, despite some methodological differences, the census techniques to estimate the above parameters are rather similar among the different studies. Two rather homogenous subsets can be clearly identified in the available data: the first one comprises the UK censuses performed between 1933 and 1968, when partridge populations were still characterised by high density. The second subset consists of continental data from France, Poland and Italy in the 1965-1993 period and mostly refers to declining populations. To our knowledge, no published data are available on continental populations before 1965. The reason for this partition into UK and continental datasets is twofold. First, habitats corresponding to the two datasets are different, hilly in UK, mainly flat in the continent. Second, partridge density in continental populations is significantly lower than that in UK in the first half of this century (Table 1). Moreover, continental populations are more variable in size and have larger coefficients of variation than in UK: according to Wright and Hubbel (1983), this is itself an indication that continental populations are more prone to extinction that UK populations.

Published works report a wealth of other data on the partridge life cycle, such as the density of pairs in March, the density of broods in July-August, the average brood size, the average number of chicks per pair, the chick mortality. Unfortunately, this information is so scattered and sampling methodologies are often so varied that these data cannot be compared. Therefore, we have not been able to use them in the present study either to test differences between the two datasets (UK and the Continent) or to build the demographic models.

Demographic parameters

The following demographic parameters have been computed from the data reported in the various censuses:

- $R = N^s / N^p$	population growth rate between spring and summer counts (reproduction and mortality during spring included)
- $M^h = (N^s - N^a)/ N^s$	hunting mortality
- $M^a = (N^a - N^w)/ N^a$	autumn mortality
- $M^w = (N^w - N^p_{t+1})/N^w$	winter mortality, migration included (N^p_{t+1} is the spring density in the following year)
- $M^{aw} = (N^a - N^p_{t+1})/N^a$	autumn-winter mortality
- $S^i = 1 - M^i$	fraction of individuals surviving during season i ($i = h, a, w, aw$)

All the means of the demographic parameters in UK and the continent have been tested for significant differences.

Model Structure and Statistical methodology

Although the Sussex study pointed out five different sources of mortality ("killing factors") along the annual life cycle, the lack of a homogeneous dataset led us to utilise a demographic model based on fewer periods. UK data have allowed us to distinguish 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. As for the continental populations, the available data were insufficient to estimate winter survival, and thus a single autumn-winter period has been considered.

The occurrence of two phenomena needs to be tested on available data to build 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_t^p in year t to that in the following year N_{t+1}^p as follows:

<u>UK</u>

$N_t^s = R_t\ N_t^p$	spring-summer survival and recruitment
$N_t^a = N_t^s - h_t$	late summer - early autumn hunting
$N_t^w = S_t^a N_t^a$	autumn survival
$N_{t+1}^p = S_t^w N_t^w$	winter survival

<u>Continent</u>

$N_t^s = R_t\ N_t^p$	spring-summer survival and recruitment
$N_t^a = N_t^s - h_t$	late summer - early autumn hunting
$N_{t+1}^p = S_t^{aw} N_t^a$	autumn-winter survival

where R_t and S_t^a are possibly functions of partridge density in spring and autumn respectively, while S_t^w and S_t^{aw} might be functions also of the young to old partridge ratio.

There is a further problem to be taken into account for a complete specification of the model. Obviously, when the spring-to-summer growth rate R is higher, the ratio ρ is also higher. It is therefore reasonable to assume that ρ_t is an increasing function of R_t. To sum up, the population growth rate during spring-summer and the autumn-winter and winter-spring survivals are modelled as follows:

$$R_t = \Phi(N_t^p)\,\varepsilon_t^p \qquad (1.1)$$

$$\rho_t = \Delta(R_t)\, \varepsilon_t^{\rho} \qquad (1.2)$$

$$S_t^a = \Psi(N_t^a)\, \varepsilon_t^a \qquad (1.3)$$

$$S_t^w = \Gamma^w(N_t^w, \rho_t)\, \varepsilon_t^w \qquad (1.4)$$

$$\mathrm{S}_t^{aw} = \Gamma^{aw}(\mathrm{N}_t^a, \rho_t)\, \varepsilon_t^{aw} \qquad (1.5)$$

where Φ, Δ, 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 are implicitly assuming 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 some distribution function. A lognormal distribution with unitary median and variance to be estimated from available data is the natural choice and is more appropriate than a normal one because the latter may imply negative values for R, ρ and the S's. The use of a multiplicative lognormal noise in population ecology has been assessed on the basis of both empirical observations (Allen 1973) and theoretical arguments (Walters & Hilborn 1976) and is considered a standard assumption when testing for density dependence (see Dennis & Taper 1994, for a comprehensive review of the issue). Note that the model implicitly assumes no compensation between hunting related mortalities and autumn-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 need to be tested against data by means of a correlation analysis.

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

$$\alpha\, exp(-\beta N), \quad \alpha>0, \quad \beta\geq 0 \qquad (2.1)$$

which was first introduced by Ricker (1954) and has been 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. 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 value of β not significantly different from zero implies density independence.

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

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

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

The choice of the functional relationship Δ between ρ and R requires a more careful argumentation. In fact, given that $R = F\, S_Y + S_A$, 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

$$\rho = F\, S_Y / S_A\, .$$

It is reasonable to assume 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

$$\Delta(R) = \frac{a(R-b)}{(1+a)b + R - b} \qquad (2.4)$$

with $a = kF$.

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

$$ln\, R = -\beta_\Phi N^P + ln\, \alpha_\Phi + ln\, \varepsilon^P \qquad (3.1)$$

$$ln\, \rho = ln\, \frac{a(R-b)}{(1+a)b + R - b} + ln\, \varepsilon^\rho \qquad (3.2)$$

$$ln\, S^a = -\beta_\Psi N^a + ln\, \alpha_\Psi + ln\, \varepsilon^a \qquad (3.3)$$

$$ln\, S^w = -\beta_\Gamma N^w - \beta_\rho\, \rho + ln\, \alpha_\Gamma + ln\, \varepsilon^w \qquad (3.4)$$

$$ln\, S^{aw} = -\beta_\Gamma N^a - \beta_\rho\, \rho + ln\, \alpha_\Gamma + ln\, \varepsilon^w \qquad (3.4)$$

All these relationships have been tested against available data. Normality assumption 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:

$$y = f(x) + \mathrm{Norm}(0,\sigma(x))$$

where Norm(0,σ) is a random number drawn from a normal distribution with null mean and standard deviation equal to σ. $\sigma(x)$ can be computed as follows (Hines and Montgomery 1980):

$$\sigma(x) \; = SEE \sqrt{1 + \frac{1}{n} + \frac{(x - E(X))^2}{\sum_i (x_i - E(X))^2}}$$

where *SEE* is the Standard Error of Estimate, n is is the number of observations (available data points), x_i is the *i-th* value of the independent variable (i=1,2,..n), and $E(X)$ is the expected value of X.

POPULATION VIABILITY ANALYSIS

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 $N_{t+1}^P > N_t^P$, the one below the line by a decreasing population, as $N_{t+1}^P < N_t^P$. The deterministic model (ε's set to one) 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). 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.

Then, the stochastic demographic models have been used to assess extinction probability (Burgman et al. 1993). We have run 1000 Monte-Carlo simulations lasting 100 *yr* each (Mace and Lande 1991) 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 effects and demographic stochasticity, which are not accounted for by our model, the population viability analysis 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 certain extinction) to all effects. When the density is below the threshold, the models here derived are no longer appropriate to describe properly the dynamics of the population. As populations in the continent are typically restricted over preserved areas of 2-5 km^2, 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 extinction threshold would be highly debatable, we have computed the likelihood of extinction corresponding to different quasi-extinction thresholds.

Results

PRELIMINARY STATISTICAL ANALYSIS

A *t*-test on the means of the demographic parameters resulting from the UK and continental cases has been performed to check whether there are significant differences (Table 2). Autumn mortality M^a in the continental populations in recent decades is significantly larger than that in UK population of the first half of the century, while hunting mortality and spring-to-summer recruitment R are slightly but significantly smaller. On the other hand, differences between ρ and M^{aw} in the two datasets are not significant.

As for the autumn-winter period, we tested whether there is compensation between hunting and natural mortality. Unfortunately, data were insufficient to run the test for continental populations, hence compensation has been tested for UK populations only. This analysis shows that natural mortality M^a is not correlated to hunting mortality M^h (r=0.075, p>>0.05). Also, there is a positive correlation between the overall autumn mortality — computed as $(N^s - N^w)/N^s$ — and hunting mortality M^h (r=0.76, p<<0.01): this means that larger overall losses are to be expected at higher exploitation rate. Thus we can conclude that there is no compensation between hunting activity and other sources of mortality.

Some form of compensation between autumn and winter mortality cannot be ruled out in UK, but the correlation is weak (r=–0.465) and non-significant (p=0.08).

ESTIMATION OF MODEL PARAMETERS

Regressions for R, ρ, S^a, S^{aw} and S^w given by eqs. (3) have been performed separately on UK and continental datasets to (*i*) test whether these regressions are indeed significant, (*ii*) derive R, ρ, and the S's accordingly, and finally (*iii*) estimate the variance of the random factors ε^p, ε^a, ε^ρ, and ε^w that will be used in the stochastic models. Results are reported in Table 3. The most interesting findings are summarised in Fig. 1. Population growth rate R decreases as density increases both in UK (Fig. 1a) and continental populations (Fig. 1b). Moreover, for any density N^p, R was systematically greater in UK in the first half of the century than in the continent in recent decades. On the contrary, the regressions R – lnρ and N^a– $ln\, S^a$ are significant only when tested on the UK dataset. As for UK, winter survival S^w depends on ρ only (Fig. 1c), while in the continental case S^{aw} depends only on N^a and not on ρ. Tests on residuals show that the normality assumption is indeed valid.

The resulting stochastic models for the two datasets and parameter assignment values are reported in the Appendix .

POPULATION VIABILITY ANALYSIS

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. 2. Dispersion around the deterministic values is pictorially rendered by a shaded region comprised between the 5th and 95th percentile boundaries.

For the UK populations in the first half of the century there was a non-trivial stable equilibrium at N^p= 93.9 *ind. Km*$^{-2}$ (Fig. 2a). In the deterministic case, 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 had a negligible probability of ending up in the declining region when N_t^p<40 *ind.* km^{-2}, while chances would increased at larger densities.

The graphic representation of the model for the continental populations in recent decades is reported in Fig. 2b. The deterministic model has a non-trivial equilibrium at a density considerably lower than in UK, namely N^p= 52 *ind.* km^{-2}. Compared to the UK case, a smaller fraction of the autumn population (28%) could be sustainably harvested every year to maximise the yield (19.3 *ind.* Km^{-2}) if there were no random fluctuations. Even though the equilibrium point of the deterministic model is stable, environmental stochasticity may produce a great impact on partridge demography: as shown in the figure, 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, vs. 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 even at low density values.

Not surprisingly, UK populations before 1968 and continental populations after 1965 were characterised by quite different extinction probabilities, as shown in Fig. 3. This figure reports the interval extinction risk for different harvesting rates, namely the probability that partridge density fall 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 it was in the first half of the century before the use of herbicides and with predation control, was practically negligible even if threshold density were assumed to be as high as 25 birds per 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 figure corresponding to the same extinction probability in UK is remarkably larger, namely 39 *ind.* km^{-2}.

The same Fig. 3 shows that the effect of harvesting is obviously quite different for UK and Continental populations. The UK population in the first half of the century, before the use of herbicides, could have endured substantial harvesting rates. Even when the harvest rate is set so as to maximise the deterministic yield (i.e., 47%), extinction probability does not exceed 5% even for thresholds as high as 13 *ind.* km^{-2}. On the contrary, the effect of hunting the fragile continental populations may be dramatic: a 30% harvesting rate (which is slightly more than that required to maximise the autumn catch in the deterministic case) would extinguish the population in 100 years with probability 1 for a threshold of 8 *ind.* km^{-2}, while a catch as small as 10% of the total population implies a 5% likelihood of pushing the population below 3.2 *ind.* km^{-2}.

Fig. 4 reports the probability of extinction as a function of time in the continental case for three different thresholds - 2, 5 and 10 *ind.* km^{-2}, respectively - and two harvesting policies - a prudent hunting rate, i.e., 15% (Fig. 4a), and an intensive hunting rate, i.e., 30% (Fig. 4b). The extinction probability rises quite quickly with time for high threshold densities (i.e., 10 *ind.* km^{-2}), but an intensive catch would seriously threatens the viability of the population also for a quasi-extinction threshold as low as 2 *ind.* km^{-2} (Fig. 4b). As the probability of a 90% decline (from 52 to 5 *ind.* km^{-2}) exceeds 30% over 50 years when one third of the autumn population is harvested (Fig. 4b, 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 *yr* (Fig. 4a).

For those simulations for which the continental population declines below a given quasi-extinction threshold, it may be useful to compute the first-passage-time, i.e., the first year the population drops below that threshold. Fig. 5 reports the mean time and the standard deviation of the first-passage-time along with the corresponding probability of decline under that threshold. By increasing the harvesting rate from 0 to 30% the mean time needed 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).

Discussion

Our results confirm the traditional viewpoint that the UK populations prior to 1960 were intrinsically much more resilient than the continental populations in recent decades. Year to year variation of partridge density in UK between 1933 and 1968 as predicted by the stochastic model was substantially smaller than in the continent in the recent decades, namely 20% in the average vs. 50%. As reported by Wright and Hubbel (1983), populations characterised by smaller year-to-year variation in size are intrinsically less prone to extinction. Accordingly, given the demography prevailing at that time, the UK population had an almost negligible probability of dropping below 10 *ind.* km^{-2} and a harvest rate as high as 50% was still sustainable. On the contrary, even very small harvesting cannot be tolerated by the present continental populations and this may indicate that the persistence of hunting activity, although with a limited effort, has 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 a greatly fragmented population, is dramatically high even under 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.

The present analysis shows that the different components of autumn-winter survival are not only density dependent, as suggested by Potts (1980) for Sussex, but may be a function of the proportion of juveniles in the population. Overwinter survival, in particular, significantly decreased in UK with the young to adult ratio, which suggests that dispersal may play an important role when hunting reserves are small and spaced out so that dispersing youngs are lost to unsuitable habitats. Quantitative data about dispersal are unfortunately rather scant (see Aufradet 1995 for continental populations and Jenkins 1961, Potts 1986, Reynolds et al. 1991 for UK populations). This prevented an explicit incorporation of dispersal in our demographic model, but our results point out that it might be worthwhile to devote a greater effort to studying the phenomenon.

As for the spring-to-summer rate of increase *R*, we have found out that it is density dependent both in UK and in the continent. Available data unfortunately has not allowed a systematic estimation of the single components of *R* - reproductive success, chicken mortality, and adult mortality during spring -for both groups. For the continent only, we have been able to identify which factors are responsible for density dependence: the number of chicks per pair decreases with N_p as well as adult survival during spring-summer, while chicken mortality is density independent at least in the range of densities experienced by the continental populations. As for UK, it was not possible to detect which components were responsible for density dependence, but it is remarkable that our findings for the continent are in agreement with those of Potts (1980): he found that chick survival rate is density independent in the Sussex population, while brood production rate (the proportion of paired hens in spring that successfully hatch chicks) is density dependent. Our results are consistent also with recent findings by Rotella *et al.* (1996) in U.S. who observed density dependence in both spring-to-summer recruitment and autumn-winter mortality.

The comparison of UK and continental demographies does not evidence a single main bottleneck for the continental populations. A concurrent deterioration of reproduction and survival during spring-summer and survival during autumn-winter is fundamental for explaining the extinction dynamics of continental partridge. In fact, we have found that, if the continental stochastic population model is altered by replacing one *or* the other demographic parameter with the corresponding UK parameter (along with its density dependences), the viability of continental populations is in any case dramatically increased. Our simulations show that in this case continental populations can safely reach densities similar to those recorded in UK before the decline initiated. These results are quite obvious for the spring-summer period: in fact R was systematically greater (about double) in UK for any spring density than that for continental population in recent decades, as shown in Figs. 1a and 1b. Less obvious is the effect of replacing the continental survival with the UK survival during autumn-winter. In fact, the overall average mortality M^{aw} in the continent was slightly greater than in the UK populations before 1965, though the difference was not significant (Table 2). Therefore the resulting increase of viability of the continental populations is in a way paradoxical. However, as shown in Table 3, this comparison is unfair, because M^{aw} is density dependent in the continent, while it was not in UK, and densities in the continent are much lower than attained in UK before the sixties. It is only through the proper use of the population viability model that one can perform a correct assessment.

Our analysis has something to suggest also with regard to the decline of UK population in the recent decades, even if the UK data we consider mainly come from studies prior to the start of this decline. Potts and Aebischer (1994) reported that a 33% reduction of chicken survival as a consequence of herbicide use and lack of nest predation control is sufficient to explain such a decline. Further simulations with our UK model actually show that even a 50% reduction of R would have decreased the population at the deterministic equilibrium from 93.9 to 69.2 *ind. km*$^{-2}$, while the probability that the population dropped below a threshold as high as 20 *ind. km*$^{-2}$ would have been still negligible. We are thus inclined to believe that herbicide use and lack of nest predation control are undoubtedly important causes of population decline in UK, but alone are insufficient to fully explain this pattern. In fact, all the rest being equal, the density dependent feedbacks operating during autumn and winter should have been sufficient for the population to compensate, at least partially, the increase of chick mortality. We thus argue whether other mechanisms could have played a synergistic role in explaining the reduction of UK population. In particular, an increasingly fragmented landscape might have enhanced the importance of migration in determining overwinter losses and thus triggered the decline. As a matter of fact, recent advances on bird conservation in Europe (Tucker & Heath 1994) clearly point out that modification in the agricultural landscape is one of the most relevant cause of declining bird numbers in Europe since this habitat holds nearly 60% of the species exhibiting decreasing population trends. Almost 40 threatened species are particularly linked to lowland farmlands, among which we find the red-legged partridge (*Alectoris rufa*), the quail (*Coturnix coturnix*), the dove (*Streptopelia turtur*), the skylark (*Alauda arvensis*) and the swallow (*Hirundo rustica*).

Of course our analysis is no free of limitations. In particular, we are conscious that pulling together data coming from different populations sampled in different areas and in different years could give rise to confounding effects, but we are more worried about the risk that a heterogeneous data set could possibly hide some patterns rather than generating fake ones. Yet, we pooled the data in two sets for at least two reasons. First, the available data exhibit some degree of homogeneity: the continental populations used in our analysis come from flat landscape, while the UK populations were located in hilly areas. Moreover, all continental data refer to populations sampled after 1965, with no predation control and possibly subject to the detrimental effects of herbicides; on the contrary, the UK data set refers to population sampled before 1968, with predation control and no use of herbicides. Second, some variability in partridge density of different populations polled together can be anyway informative of how the basic demographic rates respond to different density conditions. Eventually each single population should certainly be analysed by its own, but our picture is anyway significant of a general condition reflecting partridge decline in all Europe. It should be understood why there remain some cases of self-sustaining populations in continental Europe (Potts, *personal communication*), if only data were accessible. Further field studies would be of great value if they allowed for a quantitative estimation of the basic vital rates to assess the demographic consequences of the use of herbicides, changes in landscape, etc., as Potts and Aebischer (1994) have already stressed. The choice of considering only two data sets was constrained by the availability of reliable data: indeed, we have tried to perform the analysis on single, isolated populations, but the paucity of data prevented us from obtaining significant and reliable estimates of demographic rates for the *full* life-cycle.

Despite these reservations, we are confident that our approach, which fully implement a PVA calibrated rigorously on field observations, allows us to analysis thoughtfully the reasons of the grey partridge decline and to investigate the impact of different harvesting scenarios. As stressed by Potts and Aebischer (1994), the use of demographic models, such as those presented in this study, substantially improve the understanding of the crucial role of density dependent factors and how they interact among themselves and with density independent factors. As shown in the present study, 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 (1994), less than 2% of scientific papers relating to gamebird research makes use of models that are at all realistic. The PVA performed in this study represents a further improvement with respect to the deterministic models that were used in previous studies (Potts 1986, Panek 1992, Potts & Aebischer 1994). 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. On the contrary, the stochastic model shows that extinction is very likely to occur. In addition, the model is an instrument that can be used by wildlife managers to assess the likelihood of success of various policies, such as restocking, habitat restoration and shooting plans. In fact, one can 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. Although peculiar to grey partridge, our analysis can be easily modified to understand the decline of other bird species and thus contribute to formulating programs of habitat conservation at both local and regional level.

Acknowledgements

Giulio De Leo is grateful to Andy Dobson for his valuable suggestions on the first draft of this work. The study was partially supported by Progetto MRST 40% "Fondamenti della Conservazione della Natura". The authors are also very thankful to Dot. Potts and to an anonymous referee for their help in improving the paper.

REFERENCES

Aebischer, N.J., Blake, K. A. & Boatman, N.D. (1994) Field margins as Habitats for Game. *BCPC Monograph* (ed N.D. Boatman), **58**, 95-104. Framham: BCPC Publications.

Akçakaya, H.R. (1992) Population viability analysis and risk assessment. In: *Wildlife 2001: Populations*.(eds D. R. McCullough & R.H. Barrett) pp. 148-157.

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. (1995) Behaviour and fate of single grey partridge (*Perdix perdix*) in a French population (Seine and Marne region). (in press) *Proceeding PERDIX VII. Durham, Paris. Gibier Faune Sauvage.*

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-dècembre et d'adultes en mars. *Bulletin de l'Office Nationale de la Chasse*, num. spec. 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). *Proceedings of the XII International Congress of Game Biologists* pp. 63-69.

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. *Bulletin de l'Office Nationale de la Chasse*, num. spec. 47-83.

Birkan, M.G. (1977b) Analiyse de tableaux de chasse de Perdix. Structure e dynamique de population. *Ecologie du Petit Gibier et Aménagement des Chasses* (eds P. Pesson & M. G. Birkan), pp. 55-77, Gauthier-Villars, Paris.

Birkan, M.G. (1985) Dynamique de population et relation avec l'occupation du milieu par la Perdix grise (*Perdix perdix*) *Proceedings of the XVII Congress International Congress of Game Biologists* (ed S.A. De Crombrugge), pp. 927-934.

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. *Journal of Animal Ecology,* **36**, 549-556.

Burgman, M.A., Ferson S. & Akçakaya, H.R. (1993). Risk Assessment in Conservation Biology. Chapman & Hall, London.

Cattadori, I.M. & Zacchetti, D. (1991) Dinamica e Biologia riproduttiva di una popolazione di starne (*Perdix perdix*) in un sistema ad agricoltura intensiva della pianura padana orientale. *Supplemento Ricerche Biologi della Selvaggina,* **19**, 609-612.

Chlewski, A. & Panek, M. (1986) Population dynamics of partridge on hunting grounds of Czempin, Poland. *Proceedings of the Common Partridge (Perdix perdix L) International Symposium* (ed Z. Pielowski), pp. 143-156. Polish Hunting Association, Warsaw.

Church, K.E., Harris, H.J. & Stiehl, R.B. (1980) Habitat utilization by Gray Partridge (*Perdix perdix* L.). *Proceeding of Perdix II Gray partridge Workshop* (eds S.R. Peterson & L.Jr. Nelson), pp. 9-20. The Forest, Wildlife and Range Experiment Station, University of Idaho.

Dennis, B. & Taper, M.L. (1994) Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs*, **64**, 205-224.

Dowell, S.D. (1991) Problems and pitfalls of gamebird reintroduction and restocking: an overview. *Gibier Faune Sauvage,* **9**, 773-780.

Ginzburg, L.R., Slobodkin, L.B., Johnson, K., & Bindman, A.G. (1982) Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis*, **21**, 171-181.

Hines, W.W. & Montgomery, D.C. (1980) Probability and Statistics in Engineering and Management Science. J. Wiley & Sons, New York.

Jenkins, D. (1961) Population control in protected partridges (*Perdix perdix*). *Journal of Animal Ecology,* **30**, 235-258.

Mace, G.M. & Lande, R. (1991) Assessing extiction threaths: towards a reevaluation of IUCN threated species categories. *Conservation Biology,* **5**, 148-157.

Matteucci, C. & Toso, S. (1985) Note sulla distribuzione e lo status della starna, *Perdix perdix* in Italia. *Atti Seminario Biologia Galliformi, Problemi di gestione venatoria e conservazione* (eds F. Dessì Fulgheri, & T. Mingozzi,) pp. 29-34. Dipartimento di Ecologia dell'Università della Calabria, Arcavacata, Italia.

Mazzoni della Stella, R. (1990) La reintroduzione della starna in un ambiente tipico della provincia di Siena. *Amministrazione Provinciale di Siena, Servizio Risorse Faunistiche*, pp. 36.

Mazzoni della Stella, R. & Burrini, L. (1993) L'ultima popolazione di starna della provincia di Siena. *La Provincia di Siena*, **1**, 1-4.

Middleton, A.D. (1934) The population of partridges (*Perdix perdix*) in 1933 and 1934 in Great Britain. *Journal of Animal Ecology*, **4**, 137-145.

Middleton, A.D. (1936) The population of partridges (*Perdix perdix*) in Great Britain during 1935. *Journal of Animal Ecology*, **5**, 252-261.

Middleton, A.D. (1937) The population of partridges (*Perdix perdix*) in Great Britain during 1936. *Journal of Animal Ecology*, **6**, 318-321.

Montagna, D. & Meriggi, A. (1991) Population dynamics of grey partridge (*Perdix perdix*) in northern Italy. *Bulletin of Zoology*, **58**, 151-155.

Panek, M. (1992) Mechanisms determining population levels and density regulation in polish grey partridges (*Perdix perdix*). *Proceeding of the First International symposium on Partridges, Quails and Francolins* (eds M. Birkan, R.G. Potts, N.J. Aebischer, & S.D. Dowell), *Gibier Faune Sauvage*, **9**, 325-335.

Potts, G.R. (1973) The Grey Partridge: Problems of Quantifying the Ecological Effects of Herbicides. *Proceedings of the XI International Congress of Game Biologist* (eds I. Kjerner, & P. Bjurholm) pp. 405-413. National Swedish Environment Protection Board.

Potts, G.R. (1977) Population dynamic of the Grey Partridge: Overall Effects of Herbicides and Insecticides on Chick Survival Rates. pp. 203-211. *Proceedings of the XIII International Congress of Game Biologists* (ed. T.J. Peterle), Atlanta Georgia 1977.

Potts, G.R. (1980) The effects of modern agriculture, nests predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Advances in Ecological Research*, **11**, 1-79.

Potts, G.R. (1986) The Partridge: Herbicides, predation and conservation. London, Collins, 274 pp.

Potts, G.R., Aebischer, N.J. (1989) Control of population size in birds: the grey partridge as a case of study. *Towards a more Exact Ecology* (eds P.J. Brubb & J.B. Whittaker) pp. 141-161. Blackwell Scientific Publications, Oxford.

Potts, G.R. (1990) Causes of Decline of Partridge Populations and Effect of Insecticide Dimethoate on Chick Mortality. (eds J.T. Lumeij & Y.R. Hoogeveen) *The Hague*, 62-71.

Potts, G.R. & Aebischer, N.J. (1991) Modelling the population dynamics of the Grey Partridge: Conservation and management. In: *Bird Population Studies* (eds C.M. Perrins, J.D. Lebreton & G.J.M. Hirons) pp. 373-390.

Potts, G.R. & Aebischer, N.J. (1994) Population Dynamics of the Grey Partridge *Perdix* 1793-1993: monitoring, modelling and management. *Ibis*, **137**, 29-37.

Prigioni, C., Meriggi, A., Fasola, M., Bogliani, G. & Barbieri F. (1977) Ripopolamento di starne (*Perdix perdix* L.) in provincia di Pavia: primi dati sull'inanellamento. *Atti del VII Simposio Nazionale sulla Conservazioni della Natura* (ed Cacucci) Bari, 77-85.

Rands, M.R.W. (1986) Effect of hedgerow characteristics on partridge breeding densities. *Journal of Applied Ecology*, **23**, 479-487.

Reitz, F. (1992) Adult survival and reproductive success in abundant populations of grey partridge (*Perdix perdix*) in north-central France. *Proceeding First International symposium on Partridges, Quails and Francolins* (eds M. Birkan, G.R. Potts, N.J. Aebischer & S.D. Dowell), *Gibier Faune Sauvage*, **9**, 313-324.

Reynolds, J., Dowell, S., Brockless, M., Blake, K. & Boatman, N. (1991) Tracking partridge predation. *The Game Conservancy Review of 1994*, **23**, 60-62.

Ricker, W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**, 559-623.

Rotella, J.J., Ratti, J.T., Reese, K.P., Taper, M.L. & Dennis, B. (1996) Long-term population analysis of gray partridges in Eastern Washington. *Journal of Wildlife Management*, **60**, 817-825.

Seal, U.S. & Lacy, R.C. (1990) Florida Panther Viability Analysis and Species Survival Plan. Captive Breeding Specialist Group, Species Survival Commission IUCN. 264 pp.

Serre, D. & Reitz, F. (1989) Démographie de la Perdix grise en Beauce. Etude de deux cas tres différents. *Bulletin de l'Office Nationale de la Chasse*, **139**, 5-9.

Sotherton, N.W., Robertson, P.A. & Dowell, S.D. (1992) Manipulation pesticide use to increase the production of wild game birds in Britain. *Quail III National quail* *symposium* (eds K.E. Church & T.V. Dailey) pp. 92-101. Pratt, Kansas, Kansas Department of Wildlife and Parks.

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 partdridges *Perdix perdix. Journal of applied Ecology,* **33**, 965-978.

Toso, S. & Cattadori, I. M. (1993) La starna (*Peridx perdix* L) in Italia: analisi dell'origine e della presenza storica di una specie influenzata dalle attività antropiche. *Atti del VII Convegno dell'Associazione A. Ghigi per la Biologia e la Conservazione dei Vertebrati* (eds M. Spagnesi & E. Randi), *Supplemento Ricerche Biologia della Selvaggina,* **XXI**, 175-186.

Tucker, G.M. & Heath, M.F. (1994) *Birds in Europe. Their conservation status.* Birdlife International, Cambridge UK (Birdlife Conservation Series No 3).

Walters, C.J. & Hilborn, R. (1976) Adaptative control of Fishing Systems. *Journal of the Fisheries Research Board of Canada*, **33**, 145-159.

Weigand, J.P. (1980) Ecology of the Hungarian Partridge in North-Central Montana. *Wildlife Monographs*, **74,** 1-106.

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. *Atti del I Convegno Italiano dei Biologi della Selvaggina* (eds M. Spagnesi & S. Toso), *Supplemento Ricerche Biologi della Selvaggina,* **XIV**, 197-205.

Appendix

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) $N_t^s = R_t N_t^p$ where $R_t = exp\{1.797 - 0.0118\, N_t^p + \mathrm{Norm}(0, \sigma_p)\}$

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

ii) $N_t^a = N_t^s - h_t$

iii) $N_t^w = S_t^a N_t^a$ where $S_t^a = exp\{-0.003\, N_t^a + 0.25 + \mathrm{Norm}(0,$
$\sigma_a)\}$

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

iv) $N_{t+1}^p = S_t^w N_t^w$ where $S_t^w = exp\,(0.175\, \rho_t + 0.179 + \mathrm{Norm}(0,$
$\sigma_w))$,

$$\sigma_w = 0.199\sqrt{1 + \frac{1}{10}},$$

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

$\sigma_\rho)\}$,

and $$\sigma_\rho = 0.125\sqrt{1 + \frac{1}{22}} \; .$$

As for continental populations we have:

i) $N_t^s = R_t N_t^p$ where $R_t = exp\{1.172 - 0.00734\, N_t^p + \mathrm{Norm}(0, \sigma_p)\}$

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

ii) $N_t^a = N_t^s - h_t$

iii) $N_{t+1}^p = S_t^{aw} N_t^a$ where $S_t^{aw} = exp\{-0.0021\, N_t^a + 0.55 + \mathrm{Norm}(0, \sigma_a)\}$

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

	CONTINENTAL DATA SET after 1965		**UK data set before 1968**	
	Mean ± St. Dev.	# obs.	Mean ± St. Dev.	# obs.
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

Table 1. Mean partridge densities and standard deviations in the two datasets. Continental densities are always significantly lower than in UK ($p<0.01$). UK dataset refers to populations of the first half of the century before the use of pesticides and with predation control. On the contrary, the continental population of the last decades have been subject to little predation control and, possibly, to the detrimental effects of pesticides on chick survival.

	CONTINENT after 1965		**UK before 1968**		
	Mean ± St. Dev.	# obs.	Mean ± St. Dev.	# obs.	Difference between UK & Continent
ρ	3.14 ± 159	41	2.73 ± 1.32	34	n.s.
R	2.82 ± 1.45	56	3.56 ± 1.34	28	*
M^h	14.76 ± 21.28	51	25.29 ± 20.51	21	*
M^a	80.87 ± 27.56	5	11.15 ± 14.18	16	**
M^w	-	-	39.40 ± 12.33	15	-
M^{aw}	58.38 ± 21.27	49	50.77 ± 14.27	18	n.s.

n.s.: $p>0.05$, *: $0.01<p\leq0.05$, **: $p\leq0.001$

Table 2. Means and standard deviations of the main demographic parameters of UK and continental partridge populations. A *t*-test has been used to assess the significance of the difference between the means of the two datasets.

REGRESSION	CONTINENT after 1965	UK before 1968
$\ln R$ vs. N^p	$-0.00735 \pm .0026$ ** (d.f.=49)	-0.0118 ± 0.002 ** (d.f.=26)
$\ln S^a$ vs. N^a	n.s.	-0.003 ± 0.0011 ** (d.f.=19)
$\ln S^{aw}$ vs. N^a	-0.002 ± 0.001 * (d.f.=55)	n.s.
$\ln S^w$ vs. N^w	no data available	n.s.
$\ln S^w$ vs. ρ	no data available	-0.175 ± 0.056 * (d.f.=8)
$\ln \rho$ vs. R (†)	n.s.	$a = 33.42 \pm 16.30$ * $b = 0.885 \pm 0.036$ ** (d.f.=20)

n.s.: $p>0.05$; *: $0.01<p\leq 0.05$, **: $p\leq 0.01$; †: non-linear regression

Table 3. Results of regression between the main demographics parameters and partridge densities or young-to-adult ratio in the two datasets.

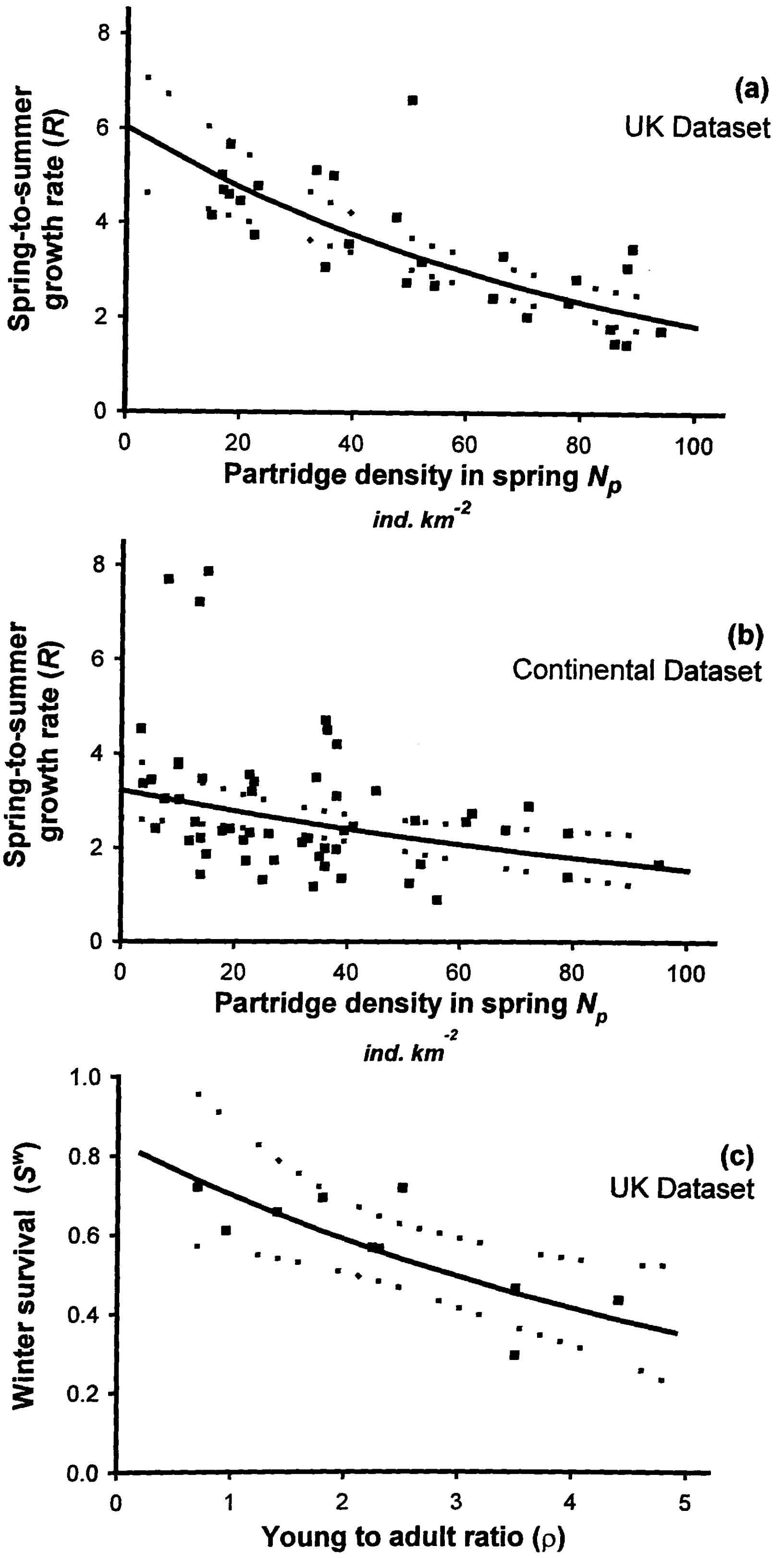


Figure 1 (a) Spring-to-summer rate of increase as a function of partridge density in spring for UK populations; (b) Same for continental population; (c) Relationship between winter survival and young-to-adult ratio in UK. Black squares represent field data, while the olid line is the result of regression (see also Table 3). The dotted lines show the 95% confidence intervals for the regression.

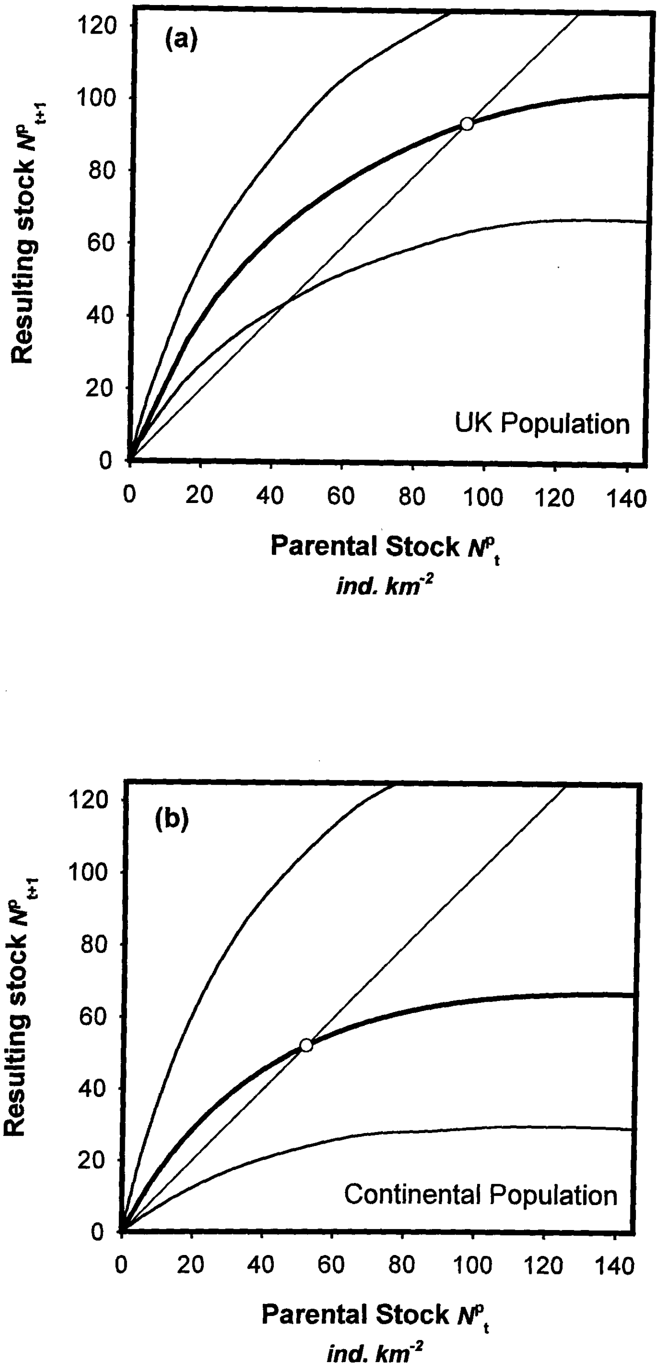


Figure 2. The relationship between the partridge spring populations in two subsequent years for UK (a) and continental Europe (b). The solid line represents the deterministic model and gives N^p_{t+1} as a function of N^p_t. The shaded region is bounded below by the 5th percentile and above by the 95th percentile 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 $N^p_{t+1} > N^p_t$, the lower one by a decreasing population, as $N^p_{t+1} < N^p_t$. Circles indicate stable equilibria for the deterministic model.

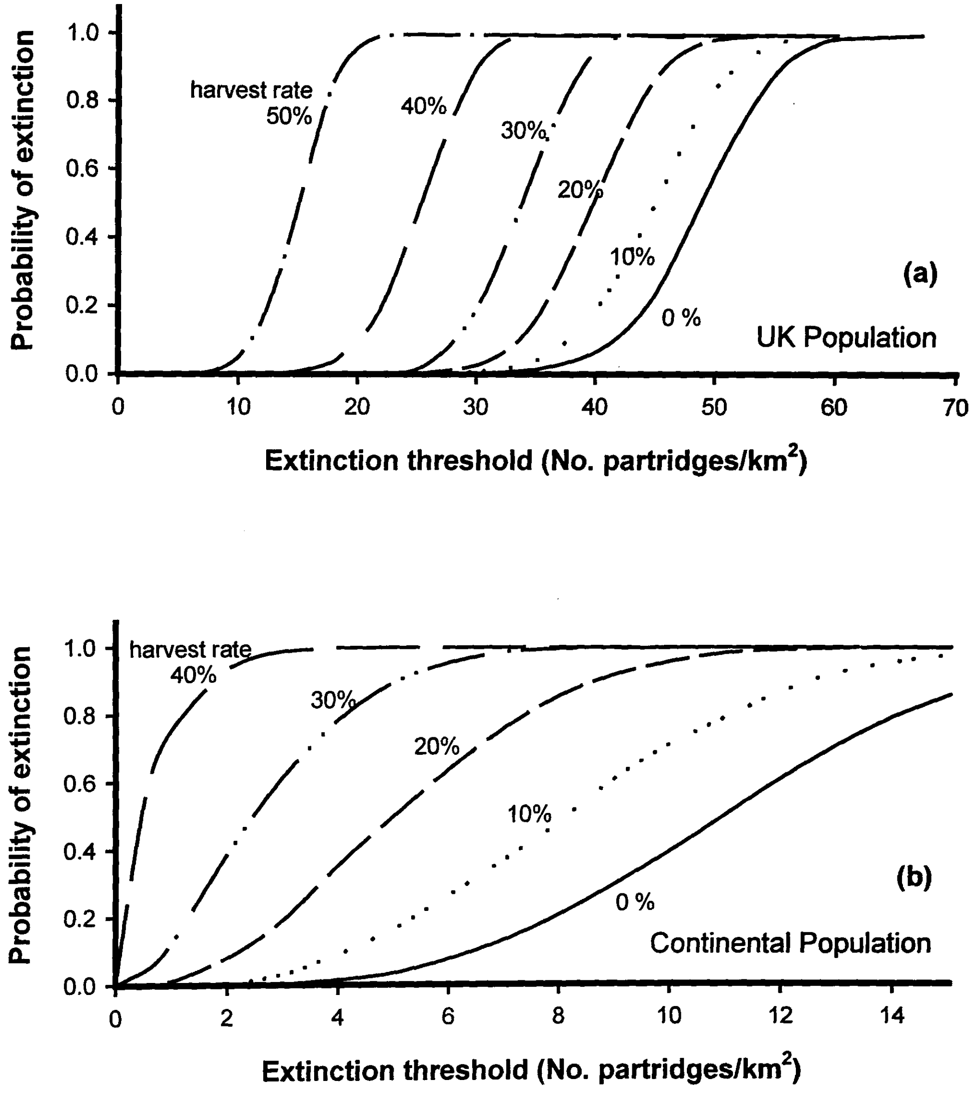


Figure 3. Interval extinction risks, for a protected population and 5 levels of harvesting rate, evaluated as a function of quasi extinction threshold for the UK (a) and Continental populations (b). Probabilities have been estimated from 1000 replicates of a 100 *yr* simulation.

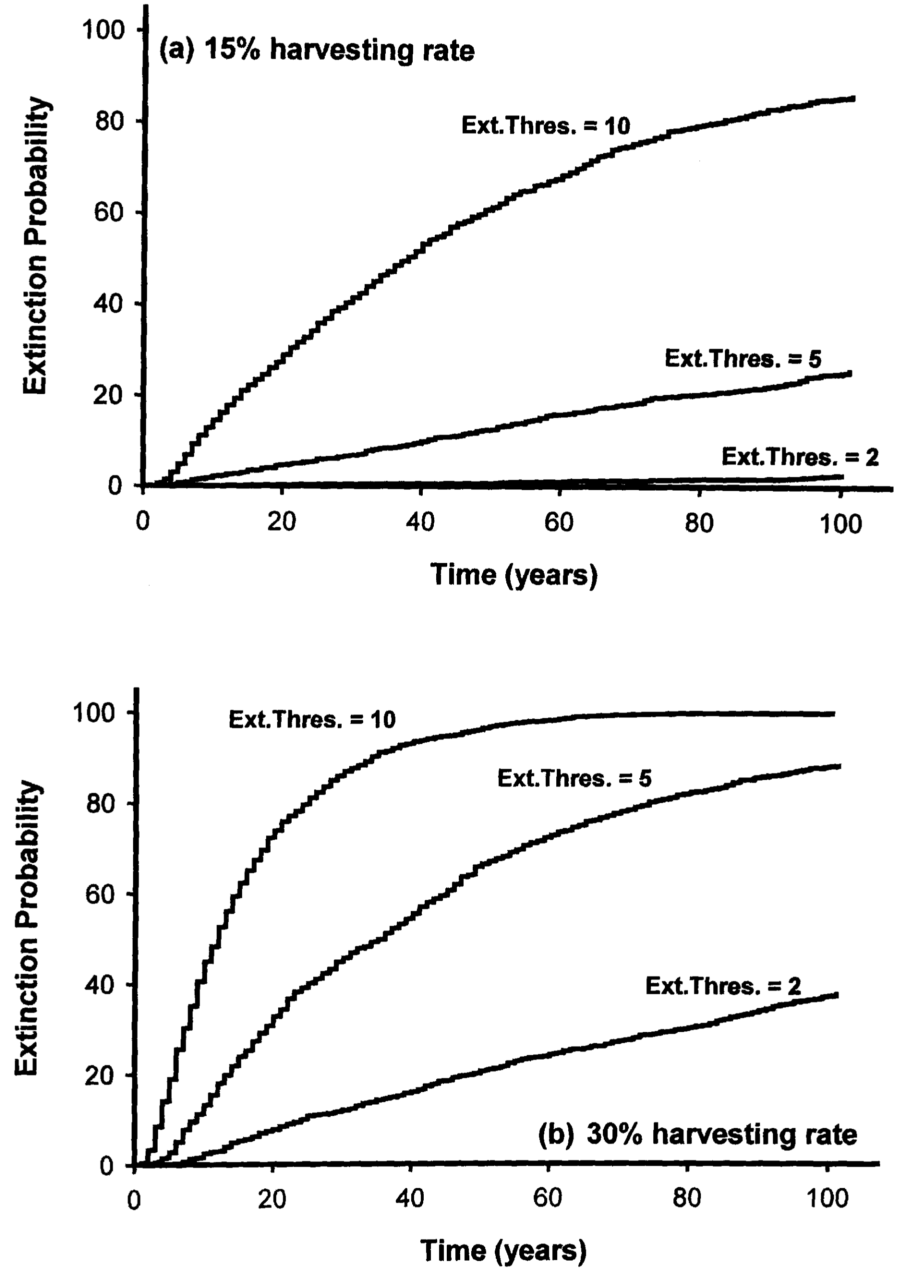


Figure 4. Likelihood of extinction for the continental populations as a function of time elapsed from the beginning of the simulation, for three threshold densities and a 15% (a) and 30% (b) harvesting rate. Probabilities have been estimated from 1000 replicates of 100 *yr* runs of the stochastic model.

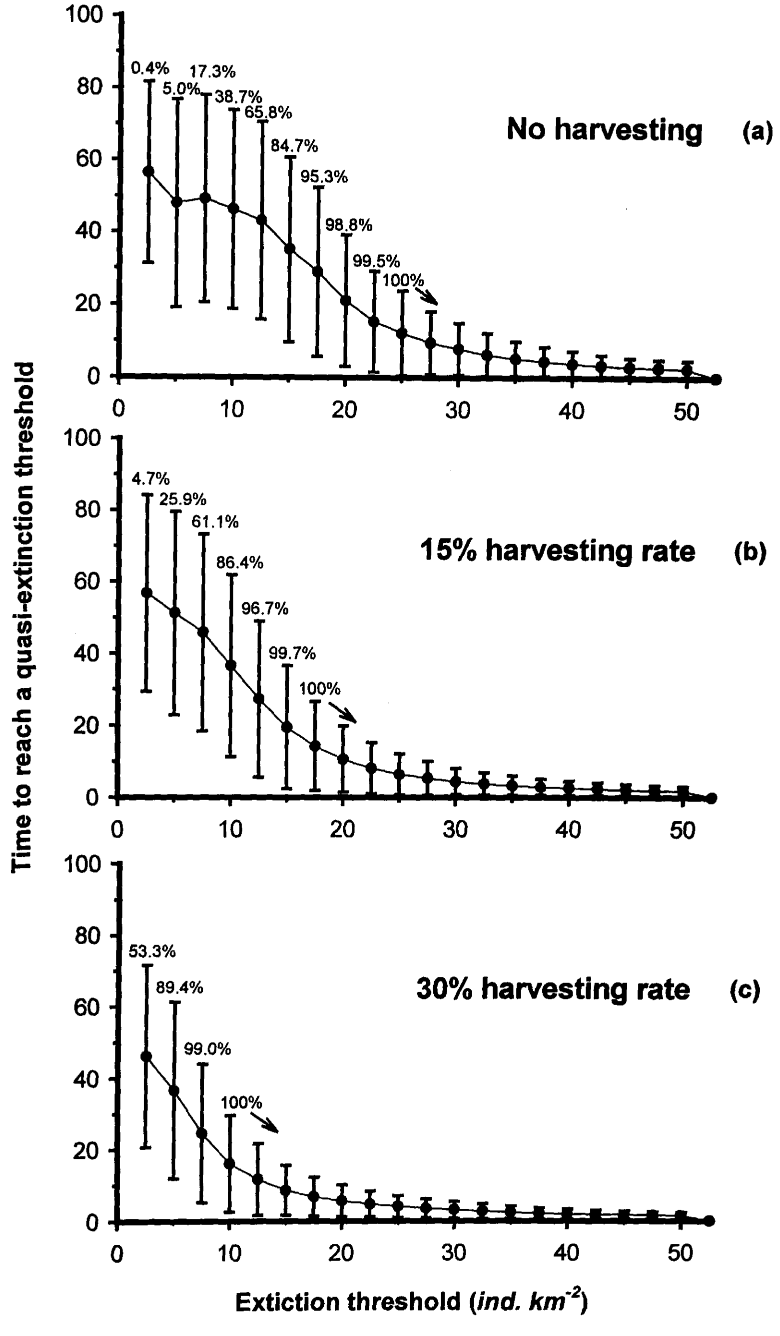


Figure 5. Average time (computed from 1000 replicates of a 100 *yr* simulation) to fall below a quasi-extinction threshold density for three different harvesting rates in the continental populations. Standard deviations are represented by error bars, while the percentages reported above the bar are the probabilities of dropping below each threshold.

GENERAL DISCUSSION

In conservation biology it may be obvious but a better understanding of population dynamics is fundamental if we are to design and improve the management and conservation of natural populations. The fact that most species are not continuously distributed in space but are aggregated in discrete populations that reflect the distribution and structure of habitats, has greatly modified the traditional approach to the study of population dynamics. Areas of unsuitable or poor quality habitat spatially separate populations, while dispersal potentially connects the populations, reducing the risk of local extinction. Even low dispersal rates permit fragmented populations to persist in a stochastic environment (Stacey & Martin in Hanki & Gilpin 1997, Fahrig & Merriam 1985, Hanski 1991). Common stochastic events increase the populations probability of extinction when bad or catastrophic events occur (Foley in Hanski & Gilpin 1997).

The galliform species of Trentino have provided a good source of information to investigate fundamental questions of population dynamics. The general approach used throughout this study was based on an integration of temporal and spatial data assuming that the populations of each species can be classified as a metapopulation, according to the broader definition used by Hanski & Simberloff and Harrison & Taylor (in Hanski & Gilpin 1997). This spatial pattern was mainly caused by the fragmented structure of the Dolomites, where the landscape can be divided into 18 main mountain groups. The assemblage of mountain groups represents a "population of 18 discrete populations" spatially separated by unsuitable habitat in the valleys, which includes orchards, vineyards and other agricultural habitats not used by the mountain gamebirds investigated in this study. Dispersal of individuals between the mountain groups links these populations together. However, at a lower scale of each mountain group, discrete populations inhabit different areas and their long-term persistence is regulated through a balance of intrinsic density-dependent processes and environmental stochastic events. Hence, the galliform birds of Trentino exhibit a spatial structure, which can vary with scale, where variation in temporal dynamics can be investigated.

The general pattern that emerges from the long-term hunting records of the galliform birds in Trentino is that there is a weak tendency to cycle in the grouse species at the southern edge of their European distribution (Chapter 8). Moreover, the presence of cycles in rock partridge is the first case where cyclic fluctuations have been recorded in a vertebrate species with a restricted southern European range (Chapter 5). Hazel grouse and rock ptarmigan produced significant cyclic fluctuations in a relatively small number of populations, while capercaillie and black grouse never showed regular oscillations. Rock partridge exhibited a higher tendency to cycle and populations in the drier habitat exhibited a higher tendency to regular fluctuations. These cycles only showed significant negative autocorrelation at half the cycle period and the common pattern was damped oscillations with time, suggesting that regular fluctuations would fade out unless stochastic effects continue to stimulate the populations to oscillate (Johnson et al. 1986, Townsend et al. 1990, Potts et al. 1984, Royama 1992, Kaitala et al. 1996a,b, Lindström 1996a, b).

Although the tendency to cycle was generally low in the species of Trentino, we were still interested in investigating the potential mechanism that could cause the regular fluctuations in these populations at the southern European latitudes. In fact, this pattern contrasts with the more regular cyclic behaviour of the grouse populations observed at the northern latitudes where distinct periods between 4 to 10 years have been recorded and where significant delayed density dependence has been observed (Siivonen 1952, Hörnfeldt 1978, Keith & Rusch 1986, Hudson et al. 1985, Lindén 1989, Hudson 1992, Lindström et al. 1995, Lindström 1996a,b). In general, delayed density-dependent interactions between trophic levels or stochastic environmental perturbations, occurring with regular frequency and moderate to high strength, are considered the principal mechanism causing the regular fluctuations in animal populations (Moran 1953a, Keith 1963, Krebs et al. 1986, Royama 1992, Turchin & Taylor 1992, Bjørnstad et al. 1995, Lindström et al. 1995, Lindström 1996a,b, Stenseth et al. 1996). The galliform species of Trentino exhibited a weak delayed density dependent structure with the majority showing a negative but not significant second order partial autocorrelation. Moreover, the modelling of the long-term population dynamics was captured using a linear, first-order density dependent autoregressive model, suggesting that the intrinsic tendency of the populations to cycle is relatively low and that the majority of the populations are regulated by a single year delayed processes. The reproductive rate of the Italian galliform birds was generally low (e.g. De Franceschi 1992a, b, c and d, Chapter 4) and since the tendency to oscillate is related to the product of the intrinsic growth rate of the population and the time lag in the intrinsic structure of regulation, we can expect these populations to exhibit damped oscillations.

Damped oscillations have been observed both in the galliforms in Trentino and the grouse species at the northern latitude suggesting that the cyclic behaviour must be sustained by density independent factors that stimulate the more regular fluctuations observed. The importance of stochastic perturbations in sustaining cycle has been examined by Lindström and colleagues (1996). They found that simulating the dynamics of the grouse populations in Finland with a AR(2) model with an added perturbation effect, either correlated or uncorrelated, produced a high probability of sustained oscillations similar to those observed. However, as they noted, it is difficult to identify the agent causing these perturbations and they need not be the same in every population (Lindström 1996a,b). The mechanism that generates the cyclic fluctuations in the galliform populations in Trentino is still not known.

We investigated the possible role of parasites in destabilizing numbers of rock partridge in Trentino (Chapters 6, 7). Within the galliform birds, Hudson and co-workers (Hudson et al. 1985, 1992; Dobson & Hudson 1992; Hudson 1992; Hudson & Dobson 1997, 1998) have demonstrated that the impact of the parasitic nematode, *Trichostrongylus tenuis* is sufficient to cause the cyclic fluctuations of red grouse, *Lagopus lagopus scoticus*, in northern England. Macroparasites induce a reduction in host fecundity and have a long-lived free living stages that may destabilise the abundance and generate cyclic oscillations (May & Anderson 1978; Dobson & Hudson 1992). The analysis of guts helminths in rock partridge showed that the intensity of infection of *Ascaridia compar* was greater in cyclic than non-cyclic populations and preliminary unpublished studies with captive birds have found evidence that the parasites may be reducing partridge fecundity (Rizzoli et al. unpublished). These results imply that parasites could have an important role in the dynamics of rock partridge (Chapter 5, 4) but further experiments need to be carried out to test the hypothesis that parasite could cause cycles in rock partridge populations. It is possible that shared parasites could also cause the cycles in the grouse populations of Trentino.

Galliform populations in Trentino exhibit an interesting variation in synchronous fluctuations between populations both within and between species (Chapters 5, 9). The tendency to produce synchronous fluctuations was generally high between species but highly variable within species. Indeed, this high variability allowed us to examine in more detail the potential mechanisms that generate the synchrony or the lack of synchrony in spatially structure populations Since we were able to factor out confounding variables such as distance. Populations within the same habitat were more likely to be in synchrony than populations in different habitats and species in neighbouring habitats were more in synchrony than species separated by several habitats. The strength of synchrony was higher when the populations or the species exhibited a similar density dependent structure. In the majority of cases, the common pattern of synchrony within species was a large variation in synchrony and a weak negative relationship with distance. The modelling of this mechanism indicated the important role of environmental stochasticity in regulating the spatial dynamics of the populations (Chapter 9). At the regional level, wide spread common environmental events were probably the mechanism responsible for the synchronous fluctuation in abundance in the majority of the species although dispersal was more important in some specie such as rock ptarmigan, black grouse and hazel grouse. A detailed analysis of the pattern of synchrony in rock partridge found an increase in synchrony from the population to the metapopulation scale but a general large variation in synchrony on distance was at both spatial levels (Chapter 5). This result suggests that the heterogeneity of the local stochastic effects was averaged out at the regional scale, while the general demographic pattern of the populations was transferred from a fine scale to a more broad scale without changing the basic information.

Environmental stochasticity proved to be important for both the small and large populations of galliform birds in Trentino at both local and regional scale. Identifying and measuring the effect of environmental stochasticity on population dynamics is empirically difficult. We may be able to investigate the effect of an environmental variable or group of environmental variables on the demography of a population or relate environmental variations to the distribution of a species. However, the *a priori* selection of the environmental variable or even the quantitative description of its characteristics leads to a range of general assumptions, which will influence the final results. To avoid any affect *a* *priori* assumptions could have on the general conclusion we used estimating functions model with bootstrapping. This approach estimated, for each species, the strength and the pattern of stochastic events from the long-term dynamics of spatially structured populations (Chapter 9). The originality of this new approach centres on three principal points. First, with this model we can explicitly estimate habitat heterogeneity. Second, we can account for the covariation between the environmental perturbations of each patch when it occurs. Third, using a the statistical methodology of estimating functions it is possible to estimate the confidence intervals of the parameters without any *a priori* assumption on the distribution of the demographic and stochastic variables. This method partly resolves the extensive effort that has been done to model and estimate the environmental stochasticity and its effect on population dynamics (May 1973a, Nibset & Gurney 1982, Dennis et al. 1991). Moreover, this approach takes into account the geographical distribution of the populations and relates their pattern to the spatial structure of the environmental events. The conclusion that environmental perturbations were the major cause of synchronous fluctuations in the populations clearly implies that the demographic models that include the stochastic environmental components provides a better representation of the population dynamics of the galliform birds in Trentino.

At the scale of the mountain group, dispersal appared to have an important role in connecting the fragmented populations of rock ptarmigan and synchronizing their fluctuations. The synchronous effect of dispersal was moderate for black grouse and hazel grouse, and almost absent in capercaillie and rock partridge where populations were generally influenced by the synchronous effects of environmental events (Chapter 9). In this respect, capercaillie and rock partridge could be considered the most threatened species in Trentino. In fact, the majority of the populations are spatially isolated and with low densities such that a correlated catastrophic event or bad and frequent environmental perturbations could strongly increase the probability of local extinction. Rock ptarmigan could be considered the third most threatened species in Trentino. Indeed, while there is a moderate tendency to dispersal the majority of the populations are small and isolated on the mountain plateaux and it is possible that the decrease in abundance observed in these recent years will reduce dispersal increasing the isolation of the populations. Black grouse and hazel grouse seem to be the species less at risk to extinction. The populations showed strong synchronous fluctuations but also a moderate tendency to dispersal, however, the persistence of many populations is actually threatened by the fragmentation of the habitat and the constant decline since the sixties (Chapter 8).

This work has emphasised the importance of spatial processes in animal populations and the necessity to take into account the heterogeneity of the habitat and the fragmentation of populations when the temporal processes are investigated. The interest in spatial processes is quite recent and many of these studies have arisen form the emergence of the metapopulation concept (Chapters 1, 2). The number of studies that identified synchrony in animal populations has increased exponentially in the last decade and the detection of the mechanism that causes synchrony is an important aspect of population biology since it has repercussions on the probability of persistence of local populations and the risk of global extinction (Heino et al. 1997, Heino 1998, Palmqvist & Lundberg 1998). The metapopulation theory has therefore stimulated important insights for conservation should now and inspire new experimental approaches. Within the more broad definition of the metapopulation concept there is a danger that workers will apply the metapopulation approach even when it does not necessarily occur. In fact, there is the tendency to combine data from areas that reflect political boundaries rather than biological divisions between populations, and this could lead to a misunderstanding.

This study has described and investigated some of the more general patterns that characterised the population dynamics of galliform birds in Trentino. However there are many other aspects that need to be analysed both in the species of Trentino and, at a larger scale, at the southern European latitudes. Little is known about the long-term temporal dynamics and the spatial pattern of tetraonids in other parts of Europe. Further investigations could clarify if the weak tendency to cycle is a characteristic of the populations at the southern latitudes. In parallel, we need to determine the role of parasites in destabilizing partridge numbers. The study of galliform birds in Trentino has emphasised the importance of environmental stochasticity on population dynamics and a future study could examine the spatial structure of the populations in relation to different management procedures of the habitat. Comparative studies to investigate the role of stochastic events in causing synchronous fluctations in populations could be carried out in different Alpine regions and on different species. The use of estimating function models on different metapopulations of other regions could test the validity of this new technique. Finally the use of this method on other species changing the definition of the parameters in relation to the spatial and demographic structure of the populations will permit to improve the flexibility of the model and the possibility to use this approach in more general and different situations.

In summary this work provided some information to tentatively conclude that stochastic environmental factors are important in influencing spatial synchrony and temporal dynamics of gamebirds populations in the Italian Dolomites.

REFERENCES

Bjornstad 0.N., Falck W. & Stenseth N.C. 1995. A geographic gradient in small rodent density fluctuations: a statistical modelling approach. Proc. R. Soc. Lond. B 262: 127-133.

De Franceschi P.F. 1992a. Francolino di monte (*Bonasa bonasia*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 697-708.

De Franceschi P.F. 1992b. Pernice Bianca (*Lagopus lagopus*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 708-721.

De Franceschi P.F. 1992c. Gallo Forcello (*Tetrao tetrix*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 721-739.

De Franceschi P.F. 1992d. Gallo Cedrone (*Tetrao urogallus*). In: Brichetti P., De Franceschi P.F. & Bacetti N. (eds), Fauna d'Italia XXIX Aves I. Calderini, Bologna, 740-756.

Dennis B., Munholland P.L. & Scott J.M. 1991. Estimation of growth and extinction parameters for endangered species. Ecol. Monogr. 61: 115-143.

Dobson A. P. & Hudson P. J. 1992. Regulation and stability of a free living host-parasite system: *Trichostrongylus tenuis* in red Grouse. II. Population models. J. Anim. Ecol. 61: 487-498.

Fahrig L. & Merriam G. 1985. Habitat patch connectivity and population survival. Ecology 66: 1762-1768.

Foley P. 1997. Extinction Models for Local Populations. In: Hanski I.A. & Gilpin M.E. (eds). Metapopulation Biology. Ecology, Genetics and Evolutions, Academic Press.

Hanski I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Metapopulation Dynamics (eds M. Gilpin & I. Hanki), Academic Press, London.

Hanski I. & Simberloff D. 1997. The Metapopulation approach, its History, Conceptual Domain, and Application to Conservation. In: Hanski I.A. & Gilpin M.E. (eds), Metapopulation Biology. Ecology, Genetics and Evolutions. Academic Press.

Harrison S. & Taylor A.D. 1997. Empirical Evidence for Metapopulation Dynamics. In: Hanski I.A. & Gilpin M.E. (eds), Metapopulation Biology. Ecology, Genetics and Evolutions. Academic Press.

Heino K., Kaitala V., Ranta E. & Lindström J. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. Proc. R. Soc. Lond. B 264: 481-486.

Heino M. 1998. Noise colour, synchrony and estinctions in spatially structured populations. Oikos 83: 386-375.

Hörnfeldt B. 1978. Synchronous population fluctuations in voles, small game, owls and tularemia in Northern Sweden. Oecologia 32: 141-152.

Hudson P.J., Dobson A.P. & Newborn D. 1985. Cyclic and non cyclic populations of red grouse: a role for parasitism? Ecology and Genetics of Host-Parasite Interactions. (eds D. Rollinson & R.M. Anderson). Academic Press, London.

Hudson P. J. 1992. Grouse in Space and Time. The Game Conservancy Trust. Fordingbridge.

Hudson P.J., Newborn D. & Dobson A.P. 1992. Regulation and stability of a free-living host-parasite system: *Tricostrongylus tenuis* in red grouse I Monitoring and parasite reduction experiments. J. Anim. Ecol. 61: 477-486.

Hudson P. J., Dobson A. P. & Newborn D. 1998. Prevention of population Cycles by Parasite Removal. Science: 282, 2256-2258.

Kaitala V., Ranta E. & Lindström J. 1996a. Cyclic population dynamics and random perturbations. J. Anim. Ecol. 65: 249-251.

Kaitala V., Ranta E. & Lindström J. 1996b. External perturbations and cyclic dynamics in stable populations Ann. Zool. Fennici. 33 in press.

Keith L. B. 1963. Wildlife's ten years cycle. University of Wisconsin Press, Madison.

Keith L. B. & Rush D. H. 1986. Predation's role in the cyclic fluctuations of ruffed grouse. Proc. XIX Int. Orn. Congr. Vol. 1: 699-732.

Krebs C. J., Cilbert B. S. & Boutin S. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the Southern Yukon, 1976-1984. J. Anim. Ecol. 55: 963-982.

Johnson D. F. Botsford L. W. Methot R. D. Jr. & Wainwright T. C. 1986. Wind stress and cycles in dungenees crab (*Cancer magister*) catch off California, Oregon, and Washington. - Can. J. Fish Aquat. Sci. 43: 838-845.

Lindén H. 1989. Characteristics of tetraonid cycles in Finland. Finnish Game Res. 46: 34-42.

Lindström J., Ranta E., Kaitala V. & Lindén H. 1995. The clockwork of Finnish tetraonid populations dynamics. Oikos 74: 185-194.

Lindström J., Ranta E. & Lindén H. 1996a. Large scale synchrony in the dynamics of capercaillie, black grouse and hazel grouse populations in Finland. Oikos 76: 221-227.

Lindström J. 1996b. Modelling grouse population dynamics. PhD thesis, Dept. Ecology and Systematics Division of Population Biology, University of Helsinki, Finland.

Lindstrom J. 1996c. Weather and grouse population dynamics. Wildlife Biology 2: 93-100.

May R.M. 1973a. Stability and Complexity in Model Ecosystems. Princeton University Press.

Moran P.A.P. 1953a. The statistical analysis of the Canadian Lynx cycle. II Synchronisation and meteorology. Austr. J. Zool. 1: 291-298.

Nisbet R.M. & Gurney W.S.C. 1982. Modelling fluctuating populations. John Wiley & Sons, Chichester.

Palmqvist E. & Lundberg P. 1998. Population extinctions in correlated environments. Oikos 83: 359-367.

Potts G.R., Tapper S.C. & Hudson P.J. 1984. Population fluctuations in r grouse: analysis of bag records and simulation model. J. Anim. Ecol. 53: 21-36.

Royama T. 1992. Analytical Population Dynamics. Chapman and Hall Ltd.

Siivonen L. 1952. On the reflection of short-term fluctuation in numbers in the reproduction of tetraonids. Finnish Game Res. 9: 1-43.

Stacey P.B. & Martin K. 1997. Metapopulation structure and population rescue in the white-tailed ptarmigan. In: Hanski I.A. & Gilpin M.E. (eds), Metapopulation Biology. Ecology, Genetics and Evolutions. Academic Press.

Stenseth N.C. Bjørnstad 0.N. & Takashi S. 1996. Gadient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. Proc. R. Soc. Lond. B 263: 1117-1126.

Townsend C. R. Sutherland W. J. & Perrow M. R. 1990. A modelling investigation of population cycles in the fish *Rutilus rutilus*. J. Anim. Ecol. 59: 469-485.

Turchin P. & Taylor A. D. 1992. Complex dynamics in ecological time series. Ecology 73: 289-305.