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Source: Wildlife Biology, 9(2) : 93-102

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.2003.031>

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Density dependence of reproductive success in grey partridge *Perdix perdix* populations in France: management implications

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Bro, E., Deldalle, B., Massot, M., Reitz, F. & Selmi, S. 2003: Density dependence of reproductive success in grey partridge *Perdix perdix* populations in France: management implications. - Wildl. Biol. 9: 93-102.

The understanding of the demographic and ecological mechanisms of population regulation is central in applied ecology, in particular when it comes to managing harvested populations. We document the density dependence of the reproductive success in French grey partridge *Perdix perdix* populations. We used long-term data collected by the national network monitoring populations with a mere surveillance objective. We investigated a time series spanning 7-14 years for 85 replicate populations by a combined procedure of a regression of reproductive success against density for each population and a meta-analysis of the 85 regression slopes. We avoided two common statistical pitfalls by taking the autocorrelation in time series data into account and by using independent estimates of reproductive success and spring density. The relationship is statistically significant for 10% of the populations, and the meta-analysis of the 85 replicates displays a highly significant pattern (82.3% of the regression slopes being negative). Thus our results both support the existence of a density dependent reproductive success in the grey partridge and moderate the ubiquity of the phenomenon, despite a general trend. We tested whether density dependence occurred through competition or habitat heterogeneity by examining the relationship between the variability of *per capita* reproductive success and pair density. Our results support both alternative hypotheses depending upon the area of concern. In terms of population and habitat management our findings have implications for hunting interests. The best strategy to maximise the hunting quota when reproductive success is depressed with increased density recommends intermediate values of both pair density and reproductive success, which conciliates hunting interests and conservation objectives. To alleviate density dependence, habitat management should supply limited resources that are homogeneously distributed in space when density dependence operates through competition, and should improve habitat quality of the poorest patches when density dependence operates through habitat heterogeneity.

Key words: autoregression, breeding density, density dependence, France, grey partridge, meta-analysis, *Perdix perdix*, reproductive success

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Received 18 April 2002, accepted 9 September 2002

Associate Editor: Jan Lindström

Animal populations fluctuate between thresholds through limiting and regulatory factors. Regulation of population size results from density dependent mechanisms. Indeed, long-term surveys show that populations may experience negative or positive feedbacks at some stages of their life cycle when density increases or decreases (Begon, Harper & Townsend 1996). Such regulatory mechanisms have been reported for a wide spectrum of species; from small and large mammals (e.g. Krebs 1995, Forchhammer & Asferg 2000, Erb, Boyce & Stenseth 2001) to birds such as passerines (e.g. Greenwood & Baillie 1991, Newton, Rothery & Dale 1998), waterfowl (Smith, Diefenbach & Conroy 1992, in Kalchreuter 1996) and galliformes (in Aebischer 1991, Ellison 1991a, Bro, Sarrazin, Clobert & Reitz 2000), invertebrates (e.g. Holyoak & Lawton 1992, Woiwod & Hanski 1992, Bjørnstad, Begon, Stenseth, Falck, Sait & Thompson 1998) and plants (e.g. Begon et al. 1996).

The concept of density dependence is of great importance in applied ecology, in particular in population management of game species (Aebischer 1991, Sutherland 2001), both to satisfy hunting interests (i.e. to provide large shooting bags) and to achieve conservation objectives (i.e. to ensure long-term population viability). Indeed, wise harvesting is rooted in compensatory mechanisms: a decrease in losses (overwinter mortality, emigration) and/or an increase in gains (reproduction, immigration) balance the mortality due to hunting (e.g. Begon et al. 1996, Sinclair & Pech 1996). This concept means that after shooting, the remaining individuals survive better or raise more young than they would have at higher densities. However, in nature, hunting mortality was found to be intermediate between addi-

tive and compensatory (e.g. Dobson, Carper & Hudson 1988, Ellison 1991a), depending upon hunting pressure and species.

A density dependent productivity and a density dependent overwinter survival were found for many species of waterfowl (Kalchreuter 1996) and galliformes (in Ellison 1991a). If we focus on the grey partridge *Perdix perdix*, the issue of density dependence has often been mentioned in studies of population dynamics within two different contexts. First, when identifying the most important demographic parameters for the population status that relate to the decline of the species (Potts 1980, Carroll 1992, Panek 1992, Bro et al. 2000). Secondly, when investigating the best strategy to calculate a hunting plan that optimises the hunting quota (Letty, Reitz & Mettaye 1998). In parallel, density dependence has been reported for recruitment (Potts 1980, Rands 1987), nest losses (Aebischer 1991), brood production rate (Potts 1980, Panek 1997), chick survival rate (Blank, Southwood & Cross 1967, Potts 1980) and overwinter survival rate (Blank et al. 1967, Potts 1980, Aebischer 1991, Panek 1992, Rotella, Ratti, Reese, Taper & Dennis 1996, Tapper, Potts & Brockless 1996). However, some of the analyses used to detect density dependence were likely to raise some statistical (1, 2) and/or ecological (3) concerns:

1. Most studies showed density dependence on a demographic variable such as the overwinter mortality rate (in Aebischer 1991, in Tapper et al. 1996), nest losses (in Aebischer 1991), chick mortality rate (Blank et al. 1967) or reproductive success (Potts 1980, Panek 1992) by using the key-factor analysis or a

derived approach. With these methods, the dependent variable (Y) is calculated more or less directly from density or population size (explanatory variable X) rather than estimating it in the field. This procedure raised criticism from a statistical point of view because Y is partially dependent on X (Lebreton & Clobert 1993).

2. Most analyses did not take the temporal structure of the data into account (Potts 1980, Aebischer 1991, Panek 1992, 1997). Temporal autocorrelation leads to non statistically independent data (e.g. Legendre & Legendre 1984, Royama 1990).
3. Except in some studies (e.g. Potts 1980, N = 8 areas; Rands 1987, N = 17 farms), density dependence was generally tested for in a few populations (Tapper et al. 1996, Panek 1997). Because density dependence is likely to be influenced by environmental conditions (e.g. Morris 1988), it would be interesting to test the relationship over a great number of replicates. This aspect is all the more a concern because density-dependent relationships were sometimes found to vary across areas (e.g. Panek 1992) or over time (Potts 1980), or to be influenced by predator control (Potts 1980).

In this paper, we use data obtained by the 'national survey network of grey partridge populations' (see Reitz 1997) to investigate the occurrence of density dependence. As advised by Lebreton & Clobert (1993), our aim is to look for effects of density at a given stage in the life cycle of the grey partridge. We study the relationship between *per capita* reproductive success and breeding density by using time series analyses (N = 85 areas with 7-14 years of data).

Survey of national network

We analysed data compiled in a network survey of grey partridge populations in north-central France initiated in the late 1970s in 'reference' areas where spring counts and brood surveys (see the 'Field procedures' section below) are conducted every year. The primary objective of this survey is to calculate hunting bag limits. Bags are limited through a quota. Hunting pressure varies between years depending upon both pair density and reproductive output (see the 'Modelling' section). The hunting methods used are drive hunts and walking-up.

We restricted the analyses to areas with no wild red-legged partridges *Alectoris rufa* and with no releases of hand-reared grey partridges to actually examine the population dynamics of the wild grey partridge. We also selected areas with the longest time series (7-14 years).

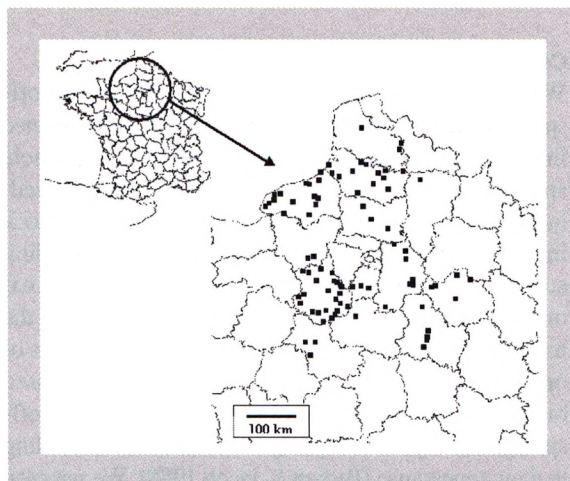


Figure 1. Geographical location of the 85 areas that were part of the national network surveying grey partridge populations in north-central France, and which were included in the analyses. Thin lines delineate Departments (i.e. administrative divisions).

We used data from 85 areas distributed over 13 departments and 25 farming regions (Fig. 1). Areas were located between 47° and 50°N in north-central France (see Fig. 1) and characterised by a temperate climate, a flat to gently undulating topography and a diversity of agricultural landscapes (intensive cereal ecosystems, mixed arable and livestock farming). Their size ranged within 170-15,000 ha.

Methods

Field procedures

Spring counts

To assess the breeding stock, spring counts were carried out in March when birds had paired, and before the crop cover was too high (in particular oil-seed rape and winter cereals). We censused partridges (pairs and single birds) that flushed from the area when fields were 'beaten' by a line of people (Birkan & Jacob 1988). To achieve a census as complete as possible, 20-50 people were needed to count the drive in one area depending upon the size of the units counted (ranging approximately within 80-250 ha).

Spring counts were either reported as the number of pairs and single birds or as the total number of birds. In the former case the number of pairs was calculated as the number of counted pairs plus the number of single birds divided by 2.1; in the latter case as the total number of birds divided by 2.1 (Reitz & Berger 1994). The figure '2.1' was used to take into account an unbalanced sex-ratio (Birkan & Jacob 1988, Reitz & Berger 1994).

Covey surveys

We defined breeding success as the number of offspring per female in summer. This variable was estimated in the field from brood surveys driven over the whole spring area. The summer survey was not a post-breeding census, but a sample count of the grey partridge stock in mid-August after crop harvest to estimate breeding success. Fields were searched by slowly driving a car on lanes and across fields at dawn and dusk when the birds are feeding in cereal stubbles or other patches of open ground. When a covey was detected, we used binoculars to count the number of cocks, hens and offspring. The age of offspring was estimated according to their appearance (Birkan & Jacob 1988). We sampled successful pairs as well as pairs without young (often groups of adults).

A reliable estimate of reproductive success is obtained by sampling at least 30-40% of the females counted in spring (Reitz 1990) - assuming that the number of females was equal to the number of pairs. Given that the spring-to-summer survival rate of breeding females ranged between 0.4 and 0.6 (see Bro, Reitz, Clobert, Migot & Massot 2001), 50-80% of females still alive in summer were sampled.

Statistical analyses

Throughout, the dynamics of the 85 grey partridge populations were considered as independent replicates because areas were sufficiently far away from each other (at least 5-10 km) for individual movements among them to be unlikely (maximum dispersal distances reported were 1.5 km for young females and 4 km for young males; Birkan & Jacob 1988).

All statistical analyses were performed using SAS software (SAS Institute 2000). We tested for density dependence of reproductive success by using a regression of the reproductive success at time t (estimated in August) against density at time t (estimated in March). This simple procedure was statistically correct because density and reproductive success were both estimated in the field and thus independent (see Lebreton & Clobert 1993). Variables were log-transformed to satisfy parametric analysis assumptions (Sokal & Rohlf 1981). The normal distribution assumption was tested for using the Wilk-Sharpino test (proc UNIVARIATE) and homoscedasticity was checked graphically. Because time series were used in regression analysis, the error term was *a priori* non-independent over time (Legendre & Legendre 1984). To properly estimate regressive parameters and compute correct statistical tests, we used the following model with a first-order autoregressive error:

$$Y_{(t)} = \mu + \beta \cdot X_{(t)} + v_{(t)},$$

where $v_{(t)}$ was a function of $v_{(t-1)}$ and included the random error $e_{(t)}$ (proc AUTOREG, maximum-likelihood method); μ and β were constants. Thus the temporal autocorrelation was taken into account. Missing values in the time series were not filled because 1) they were not a problem when using the AUTOREG procedure, and 2) computed values are not independent, consequently we thought that this method was not satisfying.

In a first step, a regression was performed for each area. Then we combined the results of these separate analyses in a file (slope of the regression and standard error (SE), r-square of the model (R^2), length of the time series (N) and the P-value testing whether the slope was null). In a second step we conducted a meta-analysis to test whether the distribution of the slopes was significantly different from zero (proc UNIVARIATE; sign-rank test because the assumptions of parametric tests were violated). The meta-analysis was performed as a global test in which areas were taken as independent replicates, hence it tested the generality of the pattern including the spatial dimension.

We further investigated whether the results of the separate auto-regressions (slope, P-value and R^2) depended upon the temporal variance of density and reproductive success, the length of time series, the area size and the trend of pair density over time. The trend of pair density was given by the slope of a log-linear regression (proc GLM) transformed to '-1' or '+1' when it was statistically negative or positive, respectively, to '0' otherwise. Because the dependent variables (slope, P-value and R^2) did not follow a normal distribution, we performed ANOVAs on ranks (proc NPARIWAY; Kruskal-Wallis test based on χ^2 -approximation). For this purpose, explanatory variables were put into three classes of equal size (proc RANK).

To determine if the decrease in reproductive success occurred through competition or habitat heterogeneity (Rodenhouse, Sherry & Holmes 1997), we examined the variability of the *per capita* reproductive success (C.V. across coveys) against pair density (proc GLM). Under the site-dependent regulation hypothesis (i.e. habitat heterogeneity), we expect an increasing variance between pair reproductive success when density increases, and no relationship under the interference hypothesis (i.e. competition; see Rodenhouse et al. 1997).

Modelling

In France, when a hunting plan is applied for the grey partridge, which is the case for the areas under study,

a quota (i.e. a number of individuals allowed to be hunted/km²) is calculated each year (see Birkan & Jacob 1988). This quota depends upon spring pair density and reproductive success estimated in the field in the current year. It is computed to ensure a constant pair density the following spring assuming that both spring-to-summer and overwinter mortality rates are 0.4. To ensure wise harvesting, hunting mortality is assumed to be fully additive to other overwinter mortality causes. The mortality rates used to calculate the quota actually correspond to field estimates:

- the comparison between the winter counts (at the end of the shooting season) and the following spring counts carried out in several areas from 1984 to 1994 gave apparent overwinter mortality rate estimates of 0.4 (Reitz & Berger 1994).
- the spring-to-summer mortality rate of breeding hens estimated through radio-tracking in 10 areas in France in 1995-1997 varied from 0.4 to 0.6 (Bro et al. 2001).

To investigate how the quota varies with density and its corresponding reproductive success, we simulated the quota as currently applied in France introducing a density-dependent relationship between reproductive success and pair density. For this purpose we constructed the following simple deterministic model parametrised with field data:

$$\text{Quota} = D_{\text{spring}} * S_{s-s} * (2 + RS) - \frac{2 * D_{\text{target}}}{S_w} \quad (1),$$

where the quota is given in number of birds/km², S_w and S_{s-s} are the overwinter and spring-to-summer survival rates, respectively (both set to 0.6), RS the reproductive success (number of young/female in summer), D_{spring} the pair density in spring and D_{target} the target pair density for the next spring in number of pairs/km².

To simplify, we did not consider age and sex effects

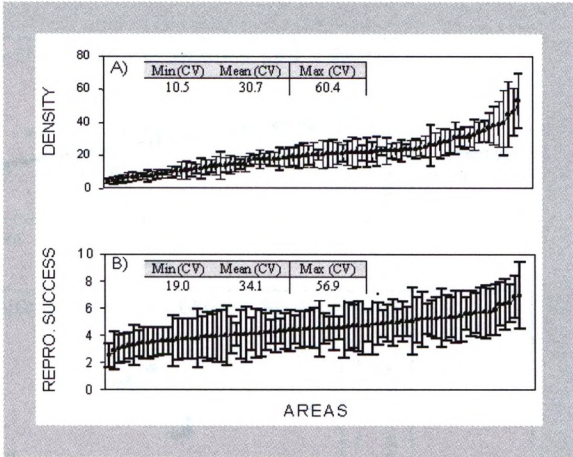


Figure 2. Spatio-temporal variability of spring density (A; number of pairs/km²) and reproductive success (B; number of young/female in summer). The graphs present mean \pm SD over years for each of the 85 areas in increasing order according to their mean density or mean reproductive success. The spatio-temporal variability was computed in two steps: 1) for each area, temporal C.V. = SD over years/mean over years, and 2) mean of temporal C.V. across areas. The tables present descriptive statistics: minimum, mean and maximum values of the coefficient of variation (%).

in survival rates, and we used a balanced sex ratio ('2' in equation 1). In the model, reproductive success was set to the value corresponding to the projection of spring pair density on the density-dependent relationship. The objective of the quota was to maintain constant spring density, so as to set D_{target} to the same value as D_{spring} .

Results

Spatio-temporal variability of spring density and reproductive success

Temporal variability was both moderate and similar for density and reproductive success (mean C.V. of ~30-35%; Fig. 2). Temporal variability of density varied

Table 1. Tests of density dependence of reproductive success and competing hypotheses, competition vs habitat heterogeneity. The results are given for the eight areas where density dependence was evidenced.

| Site/Department | Test of density dependence | | | Test of competing hypotheses | | |
|-----------------------------------|----------------------------|---------|----------------|------------------------------|---------|-------------------------------|
| | Slope \pm S.E. (N) | P-value | R ² | Slope \pm S.E. (N) | P-value | R ² _{adj} |
| GIC Damville sud/Eure | -1.627 \pm 0.536 (9*) | 0.029 | 0.702 | -0.028 \pm 0.006 (7*) | 0.665 | 0.041 |
| GIC du Plateau/Eure | -0.663 \pm 0.174 (7) | 0.019 | 0.792 | 0.043 \pm 0.011 (7) | 0.012 | 0.700 |
| Gallardon/Eure-et-Loir | -0.675 \pm 0.243 (12*) | 0.039 | 0.512 | 0.013 \pm 0.003 (11*) | 0.001 | 0.689 |
| GIC du Plateau Aigre/Eure-et-Loir | -1.406 \pm 0.210 (11*) | < 0.001 | 0.720 | 0.005 \pm 0.003 (10*) | 0.152 | 0.144 |
| Vitry en Artois/Pas-de-Calais | -1.387 \pm 0.313 (9) | 0.004 | 0.768 | 0.037 \pm 0.005 (9) | < 0.001 | 0.862 |
| Jutigny/Seine-et-Marne | -0.170 \pm 0.068 (11) | 0.037 | 0.837 | 0.008 \pm 0.005 (11) | 0.162 | 0.117 |
| Contre/Somme | -1.269 \pm 0.294 (7) | 0.012 | 0.808 | 0.021 \pm 0.015 (7) | 0.223 | 0.135 |
| Ouagne/Yonne | -0.911 \pm 0.088 (8*) | < 0.001 | 0.913 | 0.047 \pm 0.041 (7*) | 0.301 | 0.052 |

* The discrepancy between the number of years in the four analyses is explained by the lack of the detailed data on coveys for certain years for which only the mean value of the reproductive success was available.

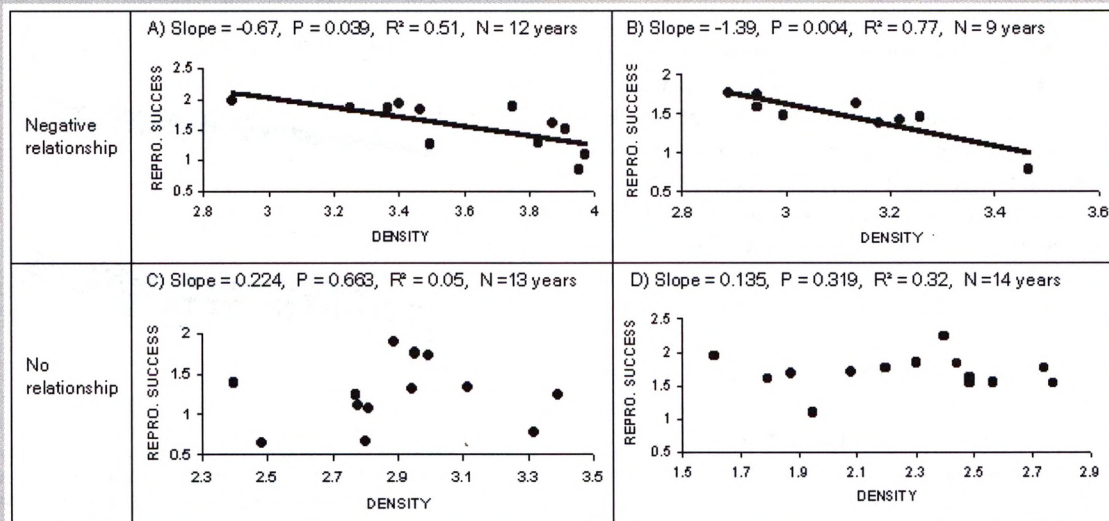


Figure 3. Regression of reproductive success (log-transformed number of young/female in summer) against density (log-transformed number of pairs/km²) for the four areas Gallardon, Eure-et-Loir (A), Vitry-en-Artois, Pas-de-Calais (B), GIC du Petit Caux, Seine-maritime (C) and Sognolles-en-Montois, Seine-et-Marne (D) used to describe the different patterns observed and to present a sample of the available data.

greatly across areas (see Fig. 2) - in correlation with the mean density over the time series ($\rho = 0.814$). Temporal variability of reproductive success was more homogeneous across areas (see Fig. 2).

Density dependence of reproductive success

We observed eight significant (negative) relationships (9.4%) at $\alpha = 0.05$ with R^2 ranging from 0.5 to 0.9 (Table 1, Fig. 3). Due to the high number of tests (i.e. 85), four relationships were expected to be significant by chance. Seven other relationships had a P-value lower than 0.10. Despite this low prevalence of significant rela-

tionships, the meta-analysis of the 85 slopes indicated a highly significant negative pattern (sign rank test < -100 , $P < 0.001$) because most slopes were negative (82.3%; Fig. 4).

The slope and the R^2 of the separate regressions did not depend upon the length of the time series, the temporal variability of density and reproductive success, the trend of pair density and area size ($P > 0.05$ for all tests).

Ecological mechanism: interference vs site-dependent regulation

We tested whether the density dependence of reproductive success corresponded to the predictions of the interference vs site-dependent regulation hypotheses for the eight areas where density dependence was evidenced. For this purpose, we tested whether the variability of *per capita* reproductive success increased when density increased. The first hypothesis predicts no relationship, whereas the second predicts a positive relationship. We found a significant positive relationship for three areas and no relationship for the other five areas (see Table 1).

Effect of density dependence of reproductive success on the shooting quota

The shooting quota increased with pair density when reproductive success was not related to pair density, whereas under density dependence it increased with density up to a given threshold of pair density beyond

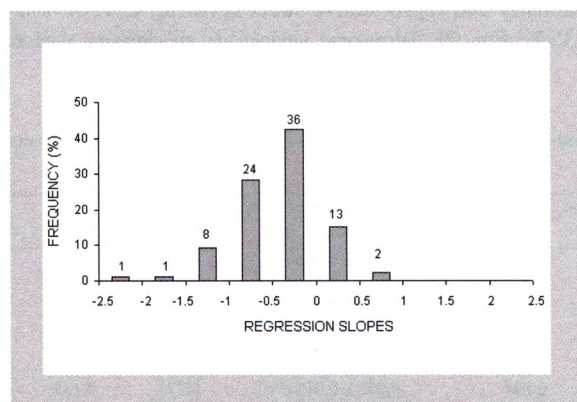


Figure 4. Frequency distribution (in %) of regression slopes for reproductive success against spring density in the 85 areas.

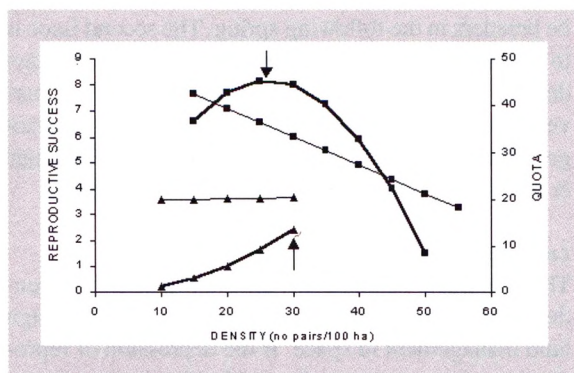


Figure 5. Effect of density dependence of reproductive success (expressed as the number of young birds/female in summer; thin line) on the hunting quota (expressed as the number of birds/100 ha; thick line) by comparing areas with (■ 'Gallardon') and without (▲ 'Sognolles-en-Montois') density dependence. Arrows indicate the range of density maximising the quota in the two situations.

which it decreased because the increase in density did not compensate any more for the decrease in reproductive success (Fig. 5). This pattern was found in the eight areas where the density dependence of reproductive success was evidenced.

Discussion

Our findings both support the existence of a density-dependent reproductive success in grey partridge populations in France and moderate the extent of the phenomenon. On the one hand, the phenomenon has clearly been evidenced in some areas. On the other hand, despite a significant global pattern (we observed a negative trend between reproductive success and pair density in more than 80% of the areas), the relationship was statistically significant only in a few sites. These results may be considered to be reliable and valuable both because the data are extending over more or less one decade and rely on 85 replicate populations surveyed throughout the whole French range of the species in its wild state (see Reitz 2003).

Having established that in some areas reproductive success may be density dependent, our next objective was to test the predictions of two hypotheses of density-dependent mechanisms: interference and site-dependent regulation (Rodenhouse et al. 1997). The first one suggests that reduction of the reproductive success with increased density results from competition for limited resources (e.g. food and nesting site). The second one suggests that the preemptive use of good habitat patches relegates subordinate pairs to lower-quality patches

where they experience a lower reproductive success (habitat heterogeneity). Our indirect evidence both supports the two alternative mechanisms depending upon areas. These contrasting results may reflect differences in habitat characteristics or saturation among areas. In Poland, Panek (1997) thoroughly investigated the ecological mechanism of a decrease in breeding performance when pair density increased by examining habitat occupancy by pairs. His results identified the habitat-heterogeneity mechanism. He also found that patch quality was correlated with the abundance of suitable nesting cover. Both mechanisms were reported for birds (e.g. Dhondt, Kempeanaers & Adriansen 1992, Fernandez, Azkona & Doñazar 1998, in Rodenhouse et al. 1997, Krüger & Lindström 2001) depending upon their ecological requirements and their social behaviour.

Our data did not allow us to identify the demographic mechanism leading to density dependence of the reproductive success in grey partridge. Density dependence of fecundity seems to be common in birds (e.g. Dhondt et al. 1992, Kalchreuter 1996). In waterfowl, Kalchreuter (1996) also reported that at low density, a larger proportion of the population breeds successfully, and offspring survival is better than at high density.

Our results showed that despite a general negative trend density dependence was only evidenced in few sites. The explanations may be statistical as well as ecological. From a statistical point of view, because some relationships were significant, the power of our test did not seem to hinder the detection of density dependence. Moreover, the detection of density dependence was not correlated with the length of the time series (contrarily to Holyoak & Lawton 1992, Woiwod & Hanski 1992), the magnitude of the variations of reproductive success and density over years, nor with the trend of pair density over time. From an ecological point of view, because density dependence involves competition (Begon et al. 1996), predation (Sinclair & Pech 1996) or habitat heterogeneity (Rodenhouse et al. 1997), its occurrence depends upon environmental conditions and thus is likely to vary in space and over time. In particular, hunting and land management for hunting purposes may reduce or remove the phenomenon, for instance by providing resources (such as nesting cover or food; Reitz 2001) that otherwise could be limiting in a mosaic spatial design, or by preventing habitat saturation through population exploitation. Furthermore a density-dependent pattern may have been hidden by weather conditions which have a great influence on the grey partridge reproductive success (Reitz 1988), partly in a density-independent way (e.g. cold and rain).

Management implications

Hunting quota

Knowledge of density dependence is a key element when deciding on a hunting strategy (Aebischer 1991, Sutherland 2001) or to justify hunting of declining species (Ellison 1991b). The grey partridge is a vulnerable species (Potts 1997, Aebischer & Kavanagh 1997), and thus hunting should all the more be based on scientific grounds to ensure the long-term viability of the populations (i.e. conservation objectives) together with satisfying hunting interests (i.e. sustainable harvesting). For this purpose, rules to limit the shooting bag have progressively been undertaken in France. Currently, a shooting limit is set in half of the hunting territories (Reitz 2003) whereas until the mid-1980s there were no limitations at all. Bag limits mainly result from a quota (hunting plan) calculated in accordance with the breeding density and reproductive success (Birkan & Jacob 1988), both estimated in the field.

The principle of the quota is wise harvesting since it preserves the principal (i.e. breeding density) and hunts the interests (i.e. productivity - see the Methods section). Hence land management often aims to improve reproductive success (for instance by planting set-asides to provide nesting sites and insect-rich cover or artificial feeding; Reitz 2001) to lead to a high shooting bag. When density dependence occurs, our model showed that the best strategy is to improve pair density together with reproductive success. This option conciliates conservation objectives, as it favours population viability through relatively high levels of pair density, and shooting interests, as it maximises the shooting bag. On the contrary, our results do not support the strategy that maximises pair density unless under an intensive land management scheme that lessens the phenomenon of density dependence - but it only exists on a few sites in France.

Using the presented equation to calculate the hunting quota simplifies and makes it easier for the administrators to manage the populations and takes into account that several questions remain open or have not yet been sufficiently documented, despite extensive research programmes on grey partridge population dynamics. So the prudent option has been to consider hunting mortality as additive. A better adjustment of the hunting bag to population dynamics would need further research, and this work is only step one. We should now focus our efforts on two issues in population regulation that are crucial for management. The first issue is to find out whether, and to what extent, overwinter mortality compensates or does not compensate for hunting mortality. Hunters do not fulfill the quota to preserve birds for the next year; they hope that the birds they do not shoot will

be breeders in the following spring. The second issue is to investigate the demographic mechanisms at low-density levels. Despite compensation mechanisms, harvesting in combination with Allee effects might endanger some populations (Myers, Barrowman, Hutchings & Rosenberg 1995, Stephens & Sutherland 1999).

Land management

The ecological mechanisms generating density dependence have implications on how to correctly design land management in space. If the depression of reproductive success operates through habitat heterogeneity, land management should be designed to improve specifically poor habitat patches, while still preserving good patches. A prior diagnosis should be made before any management measures are undertaken. However, if density dependence operates through competitive interference, habitat management should aim to provide the limiting resource. More research is now needed to identify the environmental factors responsible for the two mechanisms operating in the field.

Acknowledgements - we acknowledge all the field technicians of the 'Fédérations Départementales de Chasseurs' and the 'Office National de la Chasse' who have been collecting the data for many years. We thank Ph. Landry (ONCFS) for his help in mapping the study areas. F. Sarrazin and J. Clobert (University Paris VI) provided criticism on the first draft of the work. Two anonymous referees provided constructive comments that helped very much in the revision of the manuscript. We gratefully acknowledge one referee and E. Taran for their editorial comments that gave clarity to our paper and improved our faulty English.

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