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The long-term temporal dynamics of four grouse species in the Italian Alps have been investigated in the attempt to reveal if the populations exhibit the tendency to cycle at the southern edge of their European range. Hunting statistics or count data were collected as total number of individuals shot or counted each year from five provinces. For the province of Trento data were available at the level of mountain groups and a more detailed investigation was carried out. The results from Trento were compared with the more general findings from the other four Italian provinces. Time series analysis was performed to investigate the pattern of cycle and autoregressive models were used to describe the density dependence structure. In general, the populations showed a weak or no tendency to regular fluctuations: rock ptarmigan *Lagopus mutus* and black grouse *Tetrao tetrix* populations exhibited the highest tendency to cycle with periods of 5-9 years while capercaillie *Tetrao urogallus* never showed regular fluctuations. Hazel grouse *Bonasa bonasia* cyclic dynamics were restricted to a few populations of Trento. When time series from Trento were corrected for hunting effort the detection of cycle among populations sharply increased but no differences in the strength of second order density dependence or in the period length was observed. A linear first order autoregressive model explained better the intrinsic structure of the majority of populations. We compare the findings with studies conducted on populations of northern Europe and suggest possible reasons for the reduced tendency to cycle in the grouse populations of the Italian Alps.

Key words: grouse, Italian Alps, population cycles, temporal dynamics

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The tendency of grouse populations to exhibit regular fluctuations as well as the period and amplitude of these fluctuations vary geographically within the species' range (Hudson 1992, Lindström 1996). For example, cyclic fluctuations have been recorded in grouse populations of northern Europe but the periods may range within 3-10 years according to the species and location of the populations (Lindström 1994). Within red grouse *Lagopus l. scoticus* populations, the cycle period varies within 4-5 years in north England and 8-9 years in Scotland, while populations located in the dry east side of the country do not exhibit cycles (Hudson, Dobson & Newborn 1985). While experimental studies have demonstrated the importance of parasites in inducing reduction in fecundity as the cause of cycle in red grouse (Hudson, Dobson & Newborn 1998) the causal mechanism of regular fluctuations in most grouse populations remains unknown. The majority of scientists agree that delayed interactions between trophic levels are the principal cause of regular fluctuations although there are still some interesting hypotheses and intrinsic mechanisms that need testing (Royama 1992, Turchin & Taylor 1992, Krebs, Boutin, Boonstra, Sinclair, Smith, Dale, Martin & Turkington 1995, Stenseth, Falck, Björnstad & Krebs 1997, Blasius, Huppert & Stone 1999). There are two main approaches for describing and understanding cyclic dynamics. First, delayed demographic studies coupled with field experimentation and second, comparison between cyclic and noncyclic populations coupled with statistical models.

We have investigated the long-term temporal dynamics of four grouse species in the Italian Alps with two aims: 1) to determine if grouse populations at the southern end of their range exhibit a tendency to cycle and 2) to compare the patterns observed with other published data sets. In this paper we present data from five provinces of Italy to determine if grouse populations at the southern end of their range exhibit cycles.

Material and methods

Hunting statistics

The hunting statistics of rock ptarmigan *Lagopus mutus*, black grouse *Tetrao tetrix*, capercaillie *Tetrao urogallus* and hazel grouse *Bonasa bonasia* were collected from four provinces of the Italian Alps: Trento, Bolzano, Aosta, Sondrio and count data were collected from the Carnic Alps in the province of Udine (Fig. 1). For each province the data were recorded as total number of birds shot or counted each year. For the province of Trento data were collected from 18 main mountain groups. Hunting effort data from Trento were available as the number of hunters and the number of hunter days from 20 (1974-1994) of the 30 years from which data existed. In all the provinces the hunting season was restricted to the autumn months, from mid-September to mid-December, but the hunting policies (i.e. shooting period, hunting restrictions) varied between provinces. Detailed analysis was conducted using the time series from the grouse populations of Trento and the results were compared with the more general findings from populations of the other provinces (details on hunting data and strategies are reported in Cattadori & Hudson 1999, Cattadori, Hudson, Merler & Rizzoli 1999, Cattadori, Merler & Hudson 2000).

Time series analysis

Time series were transformed to natural logarithms [$\log(n_t+1)$ where n_t is bag or count data at time t]. The 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 subsequent analysis. Autocorrelation function analysis (Kendall 1984) was undertaken on each time series to determine if the populations exhibited a tendency to cycle. The autocorrelation coefficients were plotted with respect to time lag and when they exhibited negative coefficients larger than two standard errors of the white noise (Bartlett's band) we considered the series to show a tendency to oscillate. We classified the cyclic fluctuations following Nisbet & Gurney (1982) as phase-remembering quasi-cycles (sustained autocorrelations with significant negative autocorrelations at the full cycle period), phase-forgetting quasi-cycle (damped autocorrelations with signifi-

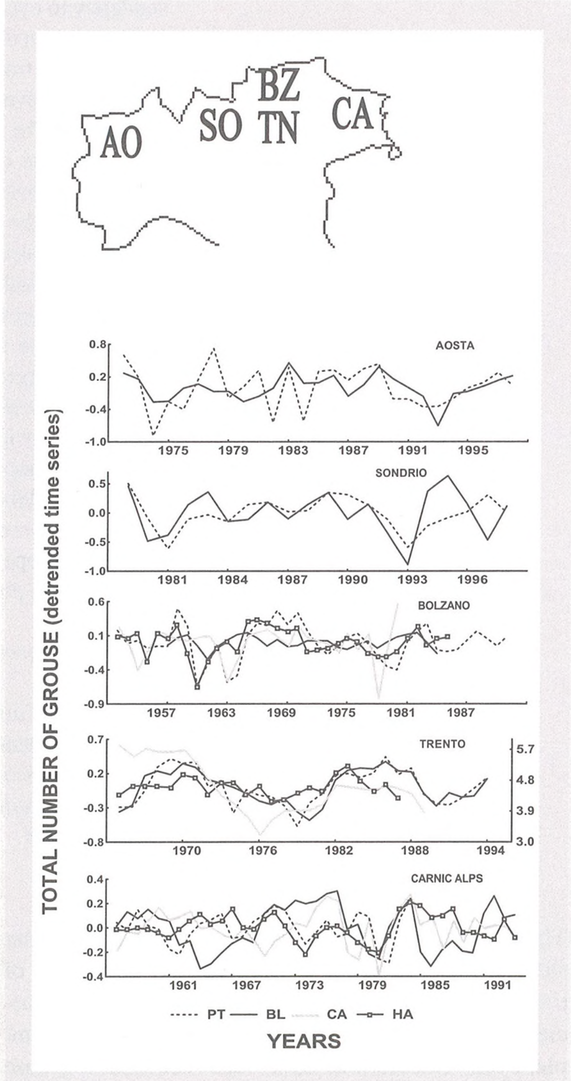

Figure 1. Location of the five provinces in the Italian Alps in which the grouse populations were studied. The total number of grouse in each province is given for rock ptarmigan (PT), black grouse (BL), capercaillie (CA) and hazel grouse (HA) based on hunting statistics for the provinces of Trento (TN), Bolzano (BZ), Sondrio (SO) and Aosta (AO) and count data for the Carnic Alps (CA). Data are log(n+1) transformed and the time series detrended. For Trento, capercaillie data are reported on the right axe.

cant negative autocorrelations at half the cycle period) or non-cyclic. The period of the cycle was determined using spectral analyses with the fast Fourier transform algorithm (Chatfield 1996). The period values were plotted against time and we selected the period which exhibited the highest spectral value. To investigate the mechanism of regulation in the long-term dynamics, the density dependent structure of each population was examined (Royama 1992). The strength of density dependence was estimated using partial autocorrelation function analysis where the partial autocorrelation coefficients were plotted against time and the significance of the first five time lags was investigated. The time series exhibited an intrinsic regulation when a negative partial autocorrelation coefficient was larger than two standard errors of the white noise. The structural pattern of the time series was determined fitting an autoregressive model following the approach taken by Royama (1992). We used a linear autoregressive model:

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

and a non-linear autoregressive model linearised following Lindström (1996):

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

where X_t is the detrended data at time t, and the constants a_1 and a_n are the direct and delayed autoregressive parameters, respectively. In the autoregressive function the population abundance at time t is related with the abundance the year before t-1 (first order or direct density dependence) and the previous years t-n (n^{th} order or delayed density dependence). To determine the model that provided the best fit to the data, i.e. the order of the process that the populations' fluctuations obey, we used Akaike's information criterion (AICm). Four alternative orders of complexity were considered for each model: N = 1, 2, 3 and 4 (Cattadori & Hudson 1999).

Results

Trento

None of the four grouse species showed a tendency to cycle when the total number of birds shot from the whole province was used. The analysis was repeated selecting the time series from the 18 mountain groups and cycles of approximately five years were identified in the minority of rock ptarmigan and hazel grouse populations (20 and 25%, respectively). These cycles only showed significant negative autocorrelation at half the cycle period, a pattern described as damped oscillations (Nisbet & Gurney 1982). Cycles were not found in time series of black grouse and capercaillie. When the time series were corrected for hunting effort (i.e. bags divided by number of hunters*days of hunting available) and compared with the non-corrected times series, referred to the same shorted period (1974-1994), the proportion of populations that exhibited cycles sharply increased but there were no consistent differences between the

Table 1. Time series analysis carried out on hunting statistics or counts of gamebirds from five Italian provinces. The first five time lags are investigated. We reported the length of the time series, the autocorrelation function (ACF), the period length and the partial autocorrelation function (PACF). *The cyclic pattern of populations from the 18 mountain groups was considered. ** Data published in Artuso 1994. ***Data published in De Franceschi 1994a, b, c.

Province	Data sets	N (years)	ACF (significant time lag)	Period length	PACF (significant time lag)
Trento*	Rock ptarmigan	30	2, 3 (20%)	5 & 11	2, 3
	Black grouse	30	-	-	0, 1
	Capercaillie	25	-	-	0, 1
	Hazel grouse	23	3, 4 (25%)	3 & 6	3, 4
Bolzano**	Rock ptarmigan	40	-	-	1
	Black grouse	27	3	5.5	2
	Capercaillie	28	-	-	0
	Hazel grouse	33	-	-	1
Carnic Alps***	Rock ptarmigan	29	2	7	2
	Black grouse	39	-	-	1
	Capercaillie	39	-	-	0
	Hazel grouse	39	-	-	1
Aosta	Rock ptarmigan	27	4	9	4
	Black grouse	27	4 tendency	6.5	0
Sondrio (SO)[1]	Rock ptarmigan	20	-	-	0
(SO)[1]	Black grouse	20	2	4	2
(BO)[2]	Rock ptarmigan	20	-	-	0
(BO)[2]	Black grouse	20	2	4	2

[1] The subarea of Sondrio

[2] The subarea of Bormio

two data sets for all the species (Fisher exact test: P > 0.05) except for capercaillie (Fisher exact test: P < 0.01). Similar results were recorded in the strength of the second order partial autocorrelation coefficients between the time series corrected and non-corrected (for all: Wilcoxon matched pairs sign test P > 0.05, Table 1). This result suggests that the intrinsic structure of the population did not significantly change under the effect of the hunting effort.

Bolzano

Hunting statistics from Bolzano did not exhibit the tendency to cyclic dynamics in any of the four species except for black grouse that showed regular fluctuations with a period of six years and a significant second order negative partial autocorrelation function (see Table 1).

Carnic Alps

The time series of rock ptarmigan counts from the Carnic Alps was the only series that exhibited a significant tendency to cycle with a period of seven years and a significant second order negative partial autocorrelation function (see Table 1).

Aosta

Two grouse species, rock ptarmigan and black grouse inhabit the province. The hunting time series of rock ptarmigan showed a clear cyclic pattern with a period of nine years and a significant second order negative partial autocorrelation function, while black grouse exhibited a tendency, though not significant, to regular fluctuations with a six years period (see Table 1).

Sondrio

Bag records from Sondrio were collected from the subareas of Sondrio and Bormio. Black grouse exhibited a 4-year cycle and a significant second order negative partial autocorrelation function in both districts (see Table 1). In contrast, rock ptarmigan did not exhibit cycles or significant second order negative partial autocorrelation functions.

Autoregressive models

Linear models explained better the density dependent structure of the time series than a non-linear model in all the provinces. First order linear processes described better the majority of time series for all species: capercaillie 85%, hazel grouse 79%, black grouse 56% and rock ptarmigan 41%. Second order linear autoregressive models explained the remaining proportion for capercaillie and hazel grouse, and part of black grouse (16%) and rock ptarmigan populations (17% second and 12% third order). Non-linear first order models were significant in 28% of black grouse and 30% of rock ptarmigan populations. These results suggest that direct and linear processes seem the common intrinsic mechanism in the majority of cases while delayed processes seem less frequent.

Discussion

This study is one of the few detailed analyses describing the cyclic pattern of grouse populations at the southern range of their European distribution (Cattadori & Hudson 1999). However, time series only exhibited a weak tendency to produce regular fluctuations. A minority of rock ptarmigan and black grouse produced significant cycles with periods of 4-9 years; hazel grouse showed regular fluctuations of three and six years in some populations of Trento, while capercaillie did not exhibit cyclic dynamics.

Populations showed negative but not significant second order partial autocorrelation functions in most cases. Since generation of cycles depends on the strength of the delayed density dependence, a weak intrinsic structure may fail to detect a cyclic pattern when there is little stochastic influence or the population dynamics are heavily influenced by stochastic factors. Since the populations are clearly unstable we suspect that a weak second order density dependent structure coupled with relatively high stochasticity explained the patterns observed. On top of this we identified that the majority of populations exhibited a significant first order density dependent structure but since the populations exhibited large variability this is unlikely to have been a very strong mechanism of regulation.

The weak tendency to cycle could be a characteristic of the Alpine grouse populations. Indeed, a further investigation of the total number of grouse shot in Trento between 1886 and 1912 revealed that only rock ptarmigan cycled with periods of nine years. Furthermore, total hunting statistics of rock ptarmigan and black grouse during the period 1963-1995 in the Swiss canton of Tessin (Zbinden & Salvioni 1997) showed a pattern similar to the Italian populations despite different hunting strategies. In particular, rock ptarmigan exhibited cyclic fluctuations with a period of eight years and no significant second order partial autocorrelation functions, and black grouse showed a tendency to significant 6-year cycles with no significant second order partial autocorrelation functions.

In contrast, other studies on tetraonids at the northern latitudes have identified cyclic dynamics in the majority of grouse species with significant second order partial autocorrelation functions using both hunting statistics and count data (Hörnfeldt 1978, Hudson et al. 1985, Hudson 1992, Keith & Rush 1986, Lindén 1989, Lindström, Ranta, Kaitala & Lindén 1995, Lindström 1996). Moreover, the modelling of the intrinsic structure of these populations suggested that a second order density dependent autoregressive process seems the parsimonious function to describe the mechanism of regulation at the northern latitudes.

While the use of hunting statistics instead of count data is a limitation to the conclusions of this study, similar results were observed from each of the Italian provinces. These similarities suggest that despite the differences in hunting practises among the provinces or the scale of the investigation, we have captured the important temporal patterns of the Italian grouse population. Analysis of hunting effort of bag statistics from Trento suggests that there can be an increase in the tendency to cycle after correcting for hunting effort but there were no consistent differences in the frequency of cycle (Cattadori & Hudson 1999). Moreover, no evidence of a significant change in the strength of the second order density dependence was observed from partial autocorrelation coefficients, suggesting that the structural pattern remained fundamentally the same when we corrected the time series for hunting effort.

In conclusion, this study indicates a weak tendency for grouse populations at the southern edge of their range to exhibit cycles. Further work is needed to identify the mechanisms that cause these regular fluctuations.

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