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Synchrony, scale and temporal dynamics of rock partridge (*Alectoris graeca saxatilis*) populations in the Dolomites

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**Summary**

1. Harvesting records of rock partridge (*Alectoris graeca saxatilis*) were examined first to identify the presence of cycles in a species with a southern European distribution and then to 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: subpopulation, population and metapopulation. 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.

**Key-words:** *Alectoris graeca saxatilis*, density dependence, population cycles, rock partridge, spatial synchrony.


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**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, Lindström & Lindén 1995a; Ranta *et al.* 1995b, 1997a,b; Steen, Ims & Sonerud 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, Hall & Bibby 1986; Pollard 1991; Pollard, Van Swaay & Yates 1993; Thomas 1991; Sutcliffe, Thomas & Moss 1996; Sutcliffe *et al.* 1997). To identify synchrony requires temporal data, which can vary. Some of the best time series come from disease incidence data such as measles records from cities (Grenfell, Bolker & Kleczkowski 1995), or hunting statistics such as for snowshoe hares and grouse species (Keith 1963; Krebs, Gilbert & Boutin 1986; Hudson 1992; Sinclair *et al.* 1993; Lindström *et al.* 1995). Populations that show cyclic dynamics have advantages because 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, Below & Hanski 1994; Grenfell et al. 1998) and northern gamebirds (e.g. Ranta et al. 1995a,b; Lindström, Ranta & Linden 1996) but has not been recorded from species with a southern distribution.

This study has been examining the population dynamics of rock partridge Alectoris graeca saxatilis B within the province of Trentino in northern Italy and the extent of populations have been mapped within well-defined environmental boundaries. Temporal abundance data in the form of hunting records from each population were 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 synchronized?
3. Does synchrony vary with scale?

Methods

STUDY AREA AND SPECIES

Trentino (6250 km²) is an autonomous province of north-east Italy. The area is mountainous, with an altitude ranging from 65 to 3750 m a.s.l. and about 50% of the land surface at between 1000 m and 2000 m a.s.l. The mountain areas within the province can be classified into three distinct areas as determined from annual rainfall, altitude, geology and vegetation maps (Boato, Arrighetti & Osti 1988). The western area is a high altitude, alpine area characterized 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 characterized by relatively low altitude and is based on a mix of calcareous and sedimentary rocks; the climate is subcontinental 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 but with 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 spatial levels:

1. Subpopulation: 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 popu-
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. The cyclic fluctuations were classified according to the definitions of Nisbet & Gurney (1982) as either phase-remembering quasi-cycles (sustained autocorrelations), phase-forgetting quasi-cycle (damped autocorrelations) or were non-cyclic. The periods 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 the first 4 lags were examined for the present study, attention was concentrated 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 depen-
dence of each population was further examined using the approach of Royama (1992) and others (e.g. Bjornstad, Falck & Stenseth 1995; Stenseth, Bjornstad & Takashi 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 $a_1$ and $a_2$ 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 because the frequency and time interval between zeros could increase the tendency of a series to exhibit cycles. To avoid the effect of spurious results the proportion of significant autocorrelation functions in time series with less than 10 zeros was compared with 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: subpopulation, population and metapopulation but the autoregressive model was estimated only at the population level.

To determine whether hunting effort made a significant impact on the cyclic pattern observed, the analysis of the metapopulation time series corrected for hunting effort was compared with the series not corrected for hunting effort, for the 20 years during which 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 because the degrees of freedom would be overestimated; in fact out of the 18 metapopulations, only 33 correlations would be independent. In order to avoid this problem the data based simulation method of bootstrapping following the approach of Ranta et al. (1995a,b) was used in the present study. 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-correlation 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 respectively.

To determine spatial patterns of synchrony, $k$-means cluster analysis following Ranta et al. (1995a) was used. Each time series was allocated to a cluster when its addition maximized the $F$ ratio of the one-way ANOVA, maximizing differences between and minimizing differences within the clusters. The analysis was undertaken at both the population and metapopulation level and repeated for four, three and two 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, linear regression analyses were carried out 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 just summer estimates of wetness were examined. Rainfall was selected for these analyses because 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 seven 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’s 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, as correcting for hunting effort did not reduce our ability to detect cycles and as a time series corrected for hunting effort has to be just 20 years the log-transformed bag records were used for the analyses.
POPULATION CYCLES AND SCALE

There was no difference in the relative number of cyclic and noncyclic populations between time series including zeros and time series excluding zeros at each spatial level (for all $\chi^2$, $P > 0.05$). Despite these results, a time series with too many zeros conveyed little information so the time series with more than 15 zeros were ignored. These restrictions resulted in analyses being conducted on 66 subpopulation time series, 57 population series and 18 metapopulation series. Because the subpopulation is an artificial, political subdivision of the larger population level, all data from the subpopulation areas were summed 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 subpopulation, 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 $P > 0.05$ there appears to be a significant similarity between scales ($\chi^2 = 0.75496$, $P = 0.98$). Cycle period at each spatial scale was generally less than 8 years but cycle periods of 10–16 years were also recorded (Fig. 3). It is possible 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 are not of biological significance (Chatfield 1996).

Partial autocorrelation function analysis exhibited negative density dependence at time lags 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 subpopulation 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 five 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).

SYNCHRONY AND SCALE

Synchrony between populations was identified at both population and metapopulation scales, with a greater proportion at the higher metapopulation scale (46%) than at the population scale (18%) ($\chi^2 = 68.6$, $P < 0.001$). However, this increase in synchrony with scale could be a consequence of the larger numbers generated at the metapopulation scale. To examine this effect, the metapopulation time series was corrected 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, although at a lower level of significance ($\chi^2 = 9.260$, $P < 0.002$).

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. 5a,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 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
Fig. 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 regions II, III and IV the populations exhibit damped oscillations, in region I numbers stabilize to an asymptotic equilibrium (see more details in Royama 1992).

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

<table>
<thead>
<tr>
<th>Number of clusters</th>
<th>Variation explained (%)</th>
<th>1</th>
<th>2</th>
<th>5</th>
<th>8</th>
<th>9</th>
<th>11</th>
<th>16</th>
<th>10</th>
<th>13</th>
<th>15</th>
<th>18</th>
<th>3</th>
<th>4</th>
<th>6</th>
<th>7</th>
<th>12</th>
<th>14</th>
<th>17</th>
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</thead>
<tbody>
<tr>
<td>2</td>
<td>43</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
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</tr>
<tr>
<td>3</td>
<td>55</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
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<td>3</td>
</tr>
<tr>
<td>4</td>
<td>64</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
</tbody>
</table>

(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 analysis indicated that within Trentino there are two main population clusters (Fig. 6) which 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 (which 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 \((\chi^2 = 2.89, P = 0.089)\).

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Fig. 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.
Table 2. Time series analysis on the two clusters (the composition of each cluster is summed in Table 1)

<table>
<thead>
<tr>
<th>Groups</th>
<th>Cycle</th>
<th>Cycle period</th>
<th>PACF (lag 2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry</td>
<td>Tendency*</td>
<td>7.5 years</td>
<td>-0.227</td>
</tr>
<tr>
<td>Wet</td>
<td>No</td>
<td>-</td>
<td>+0.148</td>
</tr>
</tbody>
</table>

PACF, autocorrelation function.  
* The ACF showed a tendency to cycle (P = 0.064).

RELATIONSHIP BETWEEN WETNESS AND DENSITY DEPENDENCE

To examine how much of the variation in the second-order density dependence could be accounted for by regional variation in wetness, linear multiple regression analysis was undertaken on summer precipitation (May, June and July) and the 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_{2,14} = 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 game-bird species are known to exhibit cyclic fluctuations in abundance in northern latitudes. However, rock partridge populations in the Dolomitic Alps represent 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 a result either of 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 populations are not as regular as those in the game-birds 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 factors 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, Dobson & Newborn 1985; Dobson & Hudson 1992, Hudson 1992; Hudson, Newborn & Dobson 1992; Dobson & Hudson 1997). It is possible that a similar system may operate in rock partridges. Macroparasites that induce a reduction in host fecundity and have long-lived free living stages, may be of significance in destabilizing 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 noncyclic populations (A. Rizzoli et al., in press). 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 overemphasized 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. The data presented here provide some further evidence to support this observation.

Synchrony in population change is generally thought to be caused either by dispersal or by the impact of common stochastic events which will synchronize 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 overriding mechanism causing cycles. Of course if rock partridge were highly sedentary then there would be no opportunity for dis-
persal and this could explain the lack of synchrony. Radio-tracking studies on rock partridge have found that annual home ranges can be up to 25 km long (average 3.2 km), 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 Fig. 4.

The populations clustered into two distinct groups associated with habitat types, which implies 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 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 a result of stochastic events rather than dispersal. This general explanation requires further empirical and mathematical modelling to elucidate synchronizing mechanisms (P.J. Hudson & I.M. Cattadori, unpublished). 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 synchronized 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.

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References


De Franceschi, P.F. (1988) La situazione attuale dei gal···


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