

Population trends and spatial synchrony in peripheral populations of the endangered Lesser grey shrike in response to environmental change

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Abstract Regional synchronization in species dynamics as well as particular ecological and demographic characteristics of peripheral populations poses special challenges for conservation purposes, particularly under the current scenario of global climate change. Here, we study the population trend and spatial synchrony of several peripheral populations of the endangered Lesser grey shrike *Lanius minor* at the western limit of its breeding range (southern France and northeast Spain). In an attempt to ascertain the effect of environmental change on the decline of the species we also look for evidence of climate changes in the breeding and wintering area of this shrike and related effects on vegetation by using the normalized difference vegetation index (NDVI). We found that the interannual fluctuations of the peripheral populations in France and Spain are strongly correlated, therefore suggesting that their decline can be under the influence of a common factor. We obtained clear evidence of climatic change (an increased thermal oscillation) in one peripheral population that could have resulted in a decrease of the NDVI index in the area. Our study finds correlational evidence that climatic variables in the breeding area may account for fluctuations in abundances of some populations and that environmental conditions experimented by some population could influence the fate of the neighboring populations. Our results indicate that the studied peripheral populations are spatially synchronized, so that conservation efforts should be applied at a large-scale encompassing all the isolated populations at the western border of the range of the species in the Mediterranean area.

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Introduction

Understanding the spatial distribution of organisms is a crucial issue in population dynamics (Tilman and Kareiva 1997) and has important consequences for more applied sciences such as conservation biology, where strategies for long-term species conservation depend on present and future patterns of abundance (Lawton et al. 1994; Brown et al. 1995; Mehlman 1997; Williams et al. 2003). One major topic in this field is the comprehension of the abundance distribution within the range of a given species and the roles of density-dependent and density-independent processes in determining the variability of population abundances (Hengeveld and Haeck 1982; Brown 1984; Royama 1992; Mehlman 1997; Williams et al. 2003). It is well-known that peripheral populations, frequently relatively small and isolated from central populations (Lawton 1993; Lesica and Allendorf 1995), are likely to experience different regimes of natural selection than central ones, since the relative importance of abiotic and biotic factors on distribution patterns and population limitation are likely to change according to the position within the geographical range (Randall 1982; Hoffmann and Blows 1994; Brown et al. 1995; Williams et al. 2003). There is evidence supporting the fact that environmental changes and abiotic, density-independent factors, like weather, have a higher influence on demographic rates and produce greater fluctuations in peripheral populations than in central ones (Hoffmann and Blows 1994; Brown et al. 1995; Curnutt et al. 1996; Williams et al. 2003), probably because closeness to the edge of range usually indicates poorer environmental conditions for a species (Brown 1984; Brown et al. 1995). Thus, in the present scenario of climate change (Parmesan et al. 1999; Hughes 2000), we would expect peripheral populations of organisms to be under a stronger influence of environmental changes than populations closer to the core of their range.

An additional factor of uttermost importance in the conservation of peripheral populations and/or of rare or endangered species is spatial synchrony in the dynamics of local populations (Kendall et al. 2000). Spatial synchrony refers to coincident changes in the abundance or other time-varying characteristics of geographically disjunct populations (Liebhold et al. 2004). Evidence for widespread spatial synchrony in population fluctuations has been found in a variety of organisms (Paradis et al. 2000; Kendall et al. 2000), and some studies have found that weather is a likely candidate as a synchronizing factor (Paradis et al. 2000; Williams et al. 2003).

Climate per se is a major determinant of geographical distribution for many organisms and recent climate warming has been shown to affect the distribution of different species (Thomas and Lennon 1999; Parmesan et al. 1999; Hughes 2000). However, the potential impact of a change in environmental suitability on abundance within the range of a given species has received relatively little attention (Mehlman 1997; Williams et al. 2003). This is partly because there is generally little comprehensive information on the distribution of abundance within the range of a species and because long-term estimates of densities over wide geographic areas are uncommon (Williams et al. 2003).

In this paper, we study the pattern of population synchrony of three peripheral populations of the Lesser grey shrike *Lanius minor*, and the relationship between population fluctuations and weather. The Lesser grey shrike is highly endangered throughout Europe, having declined markedly in abundance and range in the last decades (Lefranc and Worfolk 1997). Relict populations of the species in the western limit of its breeding range are known to exist since long (Lefranc 1995). Such peripheral populations, now restricted to very small areas in southern France and northeast Spain, have been reported to decline in the last decades (Lefranc 1995; Giralt and Bota 2003, Giralt 2004). Overall, there is almost no information on which factors may be responsible for the general decline of the species (Lefranc and Worfolk 1997; Krištín et al. 2000). Some authors have pointed out loss of habitat (agricultural intensification) and adverse weather (Lefranc 1995, 1997; Lefranc and Worfolk 1997; Isenmann and Debout 2000) whereas others suggest that adverse circumstances on the wintering grounds or during migration may account for the decline (Herremans 1997a, 1998a). However, no specific work has investigated the causes underlying the decrease of the species. Whereas there is not much information on this shrike (but see Lefranc 1995; Herremans 1997a; Lefranc and Worfolk 1997; Isenmann et al. 2000; Krištín et al. 2000), the distribution of abundance of the species in its westernmost range and changes in the last decade are available, what provides a valuable opportunity for studying population fluctuations and general patterns of changes in abundance in response to environmental changes. Therefore we aim to: (i) evaluate the spatial scale of synchrony in fluctuations of several peripheral populations of this species, (ii) assess the role of climate on the decline of this shrike in an attempt to contribute to the conservation of this particular species. Additionally we aim to illustrate the challenges associated to the conservation of peripheral populations of endangered birds.

Methods

Study species and study area

The Lesser grey shrike is a socially monogamous long-distance migratory passerine whose breeding range is limited to warmer parts of Eurasia, spreading over 6,000 km from west to east (Cramp and Perrins 1993). The westernmost points reached by this species lie in southern France and northeast Spain (Lefranc and Worfolk 1997), at the farthest extreme of its migratory route. This shrike produces a single brood per season, although replacement clutches can be produced after nest failure. Birds arrive on the breeding grounds in Europe during May. In the study area the main egg-laying activity takes place from late May to early June and the main fledging period encompasses from late June to early July (Isenmann and Debout 2000; pers. obs.).

Two main breeding areas existed in Spain until recently (Giralt and Bota 2003). The breeding area in Girona (42° 16' 42.84" N 3°07' 21.66" E, Catalonia) lay in the Natural Park of Aiguamolls de l'Empordá (protected area since 1983) and its periphery, where the species bred for the last time in 2001 (Fig. 1). The breeding area in Lleida (Catalonia) is 220 km southwest from the first one, and consists of two

nuclei 5,5 km apart from each other (Fig. 1). A third, relict nucleus remains in Aragón (35 km west of Lleida).

The breeding population of the study species in France is located in two main breeding areas, Montpellier (43°30' 44.66" N 3°39' 15.26" E, Hérault) (Isenmann et al. 2000) and Aude (43°15' 53.48" N 3°08' 51.78" E, departments of Aude and Hérault, Bara 1995), 60 km from each other and 180 and 120 km from the breeding nucleus in Girona, respectively (Fig. 1). Some isolated pairs (3 in 2002 and 1–2 in 2004) still breed in Vaunage (Gard) (Labouyrie 2003; pers. comm.).

The non-breeding range of the Lesser grey shrike is about one tenth of the size of its breeding range. During the non-breeding season, the world population concentrates in the southern African thornbelt, mainly in the Kalahari basin (Herremans 1997a, 1998a), spreading mostly over Botswana, Namibia and north of South Africa. Birds occupy their final non-breeding destination in January–March and almost all individuals have disappeared from the winter quarters by the end of April (Herremans 1997b).

Abundance data

Data on the past distribution of the species in the Iberian Peninsula have been collected from old and recent literature and personal communications. Long-term data on breeding population come from Girona where the population has been monitored during 1989–1997 (except 1992) by the staff of the Natural Park, and by D.G. from 1998 to 2004. Data on the current distribution of the species in Lleida have been collected on the basis of censuses performed by D.G. during the entire breeding season (15 May–10 July) for the period 2001–2004.

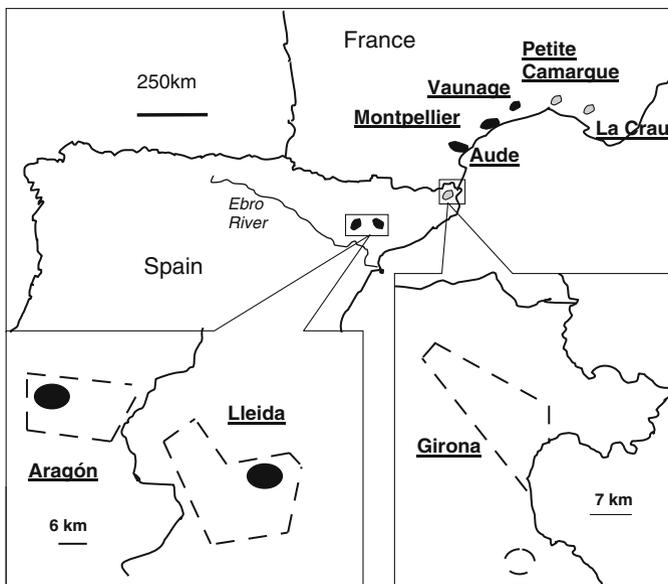


Fig. 1 Contraction of the breeding range of the French and Spanish populations of Lesser grey shrike. Current breeding areas (in black), past breeding locations (shaded areas) and contraction of the range (discontinuous lines) in the study areas are shown

Information about the two main areas in France was collected from Bara (1995), Isenmann et al. (2000), Donck and Bara (2001) and Rufray and Rousseau (2004) and kindly completed by Isenmann, Lefranc and Rufray. Censuses in the population in Aude started in 1992 (Bara 1995). The breeding population in Montpellier was discovered in 1995 (Béchet et al. 1995) and censused from that year onwards.

Abundance data from Spain and France are the result of censuses specifically undertaken to monitor the breeding population of this species. They were performed from territory establishment until fledging. Thus, such information reflects reliable actual counts.

Population trends, fluctuations and spatial synchrony

We studied the occurrence and intensity of population synchrony by correlating the fluctuations in the time series of the French and the Spanish (only Girona) populations (Paradis et al. 2000). We used the software program TRIM (Pannekoek and van Strien 2003), designed to analyze time series of counts with missing observations by using Poisson regressions, that produces estimates of yearly indices and trends.

First, we studied the trend of the French population (Aude and Montpellier) from 1993 to 2004 (two missing data—1993 and 1994—for the population in Montpellier) and of the population in Girona from 1993 to 2002 (although the species bred there for the last time in 2001 we assigned 1 pair to 2002 to allow a better comparison between both populations—see below). For these purposes we used a linear trend model with stepwise selection of change-points. Change-points are moments in time (i.e. years) where the slope parameter changes. This model provides an overall trend as well as selects specific time points (i.e. years) when the slope parameters differ significantly from the ones obtained before and after that time point. Possible violations to the assumption of Poisson distributions due to overdispersion or serial correlation were corrected with the methods implemented in TRIM.

Then, we explored whether the fluctuations of the Spanish (Girona) and French population (Aude and Montpellier) are interrelated by examining the relationship between the annual departures from the long-term trends of each population. For this we first calculated the trend for each population from 1993 to 2002 and the yearly deviations from each linear trend by using the time effects model implemented in TRIM. Since null values are not admitted when using the time effects model we restricted the study period until 2002 (breeding in Girona did not occur from 2002 onwards, see results), and considered one pair to breed in 2002 after checking that the linear trend obtained was similar to the one estimated with the linear trend model run with zero breeding pairs in 2002. In contrast to the linear trend model this one calculates separate parameters for each year and estimates yearly deviations from the linear trend. This model provides the best estimates for deviations of the general trend (van Strien, pers. comm.). Finally, we correlated the yearly deviations from the linear trends found in France and Girona.

Meteorological variables

We used meteorological data from the meteorological stations closest to each breeding population: Mauguio–Montpellier (Montpellier), Béziers (Aude) and Aiguamolls de l'Empordà (Girona), all of them less than 15 km from the respective breeding sites. Weather records consisted in daily rainfall (mm) during

January–July for the period 1989–2001 for Girona and maximum and minimum daily temperatures (°C) during May–June (encompassing most of the breeding period of the study species) for the period 1989–2002 for Aude, Montpellier and Girona. Daily thermal oscillation was calculated as the difference between the latter variables. Mean temperatures were calculated as the average of daily maximum and minimum temperatures.

Rainfall in Botswana and Namibia (October–February) was also gathered from the Tyndall Center for Climate Change Research (data set TYN CY 1.1, Mitchell et al. 2002). Since rainfall varies widely in and around the Kalahari we compared seasonal rainfall (October–February) during the years 1989–2000 with the mean rainfall for those months in the same areas for the larger period 1902–2000 (data set TYN CY 1.1). We got an average of 502.93 mm. We defined a threshold value of 150 mm below and above the long-term mean to classify years of the period 1989–2000 into ‘low’, ‘average’ and ‘high’ rainfall years (thresholds of 352.93 and 652.93 mm, respectively). Similar classifications have been applied in other studies (see, for instance, Wiegand et al. 1999, Tews and Jeltsch 2004).

Normalized difference vegetation index (NDVI)

The amount and vigor of vegetation at the land surface was estimated by means of the NDVI. This index, based on satellite images indicating the condition of rainfall-dependent vegetation in time, is strongly correlated with the fraction of photosynthetically active radiation absorbed by vegetation (see Asrar et al. 1984; Prince and Justine 1991; Myneni et al. 1997 for more details about the index and Sanz et al. 2003 for a similar use of the index).

NDVI data corrected by surface topography, land-cover type, presence of clouds and solar zenith angle were provided by Clark Labs in IDRISI format as world monthly images at spatial resolution of 0.1° in a 0–255 scale values. Using IDRISI32 software, we obtained mean NDVI values for the period May–June (at 1-month interval) from 1988 to 2000 for the square areas sized 0.25° occupied by breeding populations in Montpellier (E 3°30′–3°45′ N 43°25′–43°40′), Aude (E 3°–3°15′ N 43°10′–43°25′) and Girona (E 3°–3°15′ N 42°10′–42°25′) and for the period January–March (when most birds occupy their final wintering destination) from 1988 to 2000 for the wintering area (E 18°–28°, S 20°–27°). The selected wintering area matches the Kalahari basin defined by Herremans (1997a, 1998a) as the core area for the Lesser grey shrike.

Statistical analyses

Separate stepwise multiple regressions were performed to determine the effect of climatic variables (thermal oscillation) and NDVI indexes on the population size of each of the three peripheral areas. Thermal oscillations in the three study areas during May–June were the independent variables for the first set of analyses. For the second set we used the mean NDVI index during May–June of each study area as well as the mean NDVI index for January–March in the wintering grounds in Africa. Parametric tests were used where the assumptions for normality were met. In some cases transformations were used to meet the requirements for normality. Otherwise non-parametric tests were used. Statistical analyses were carried out with the

STATISTICA 6.0 package (StatSoft Inc. 2001). Unless otherwise stated means and standard errors are offered and two-tailed tests used.

Results

Contraction of the breeding range

The geographic range of the species at the southwestern limit of its distribution has contracted dramatically. The breeding nucleus in Girona, that held in 1989 around 50% of the estimated breeding population in Spain, contracted progressively until it became extinct in 2002 (Fig. 1). Although the breeding population in Lleida seems relatively stable during the last years (1.4, 2.4, 1.4 and 2.3 breeding pairs/km² for 2001–2004) the breeding range has contracted ca. 50% in last decade due to the progressive disappearance of breeding sites to the south and west of the current breeding area (Fig. 1). As a whole, the contraction of the range in Catalonia (Lleida and Girona) has been estimated at –68% between 1984 and 2002 (Giralt 2004).

The breeding area in Aragón, with ca. 2–7 pairs in the last 3 years, has also contracted during the last decade after disappearance of the easternmost breeding sites (Giralt and Bota 2003; Albero and Rivas, pers. comm.) (Fig. 1).

The French population has also declined in range due to the loss of breeding localities during the 90s in Gard (Petite Camargue) and Bouches du Rhône (La Crau), a stronghold of the species in the 70s (Lefranc 1999; Donck and Bara 2001; Labouyrie 2003) (Fig. 1). More recently, a 50% reduction of the number of pairs in the main nuclei (Aude and Montpellier) since 2002 (Ruf-ray and Rousseau 2004) has contributed to the contraction of the range (Fig. 1).

Population trend and spatial synchrony in peripheral populations

Breeding populations of the Lesser grey shrike have been decimated along the southwestern range of its distribution (Fig. 2).

The decline of the species in France (Montpellier and Aude) fits a linear model (Likelihood ratio = 1.83, df = 10, $P = 0.99$) with a significant decreasing slope of 8.25% per year for the period 1993–2004 (Overall Multiplicative Slope imputed with intercept = 0.917, SE = 0.0069, $P < 0.05$). Particularly marked decreases in the trend occur between 1997–1998, 1999–2000, and 2001–2002 (Tables 1 and 3). During 2002–2004 there was a constant yearly decrease of 75% that has resulted in the lowest ever numbers of the French population (Fig. 2).

The decline of the Spanish population in Girona during the period 1993–2002 also fits a linear model (Likelihood ratio = 0.03, df = 1, $P = 0.85$) with a significant decreasing slope of around 14% per year for the period 1993–2002 (Overall Multiplicative Slope imputed with intercept = 0.856, SE = 0.013, $P < 0.05$) (Fig. 2). Similar to the French population, this tendency is not constant and several significant change-points can be distinguished (Table 2). Sharp decreases occur between 1993–1994, 1995–1996, and 1997–1998 whereas increases occurred between 1994–1995, 1996–1997 and 1998–1999 (Tables 2 and 3). During 1999–2001 there was a constant yearly decrease of 76% that, in fact, led to the extinction of the species in Girona from 2002 onwards (Table 3, Fig. 2).

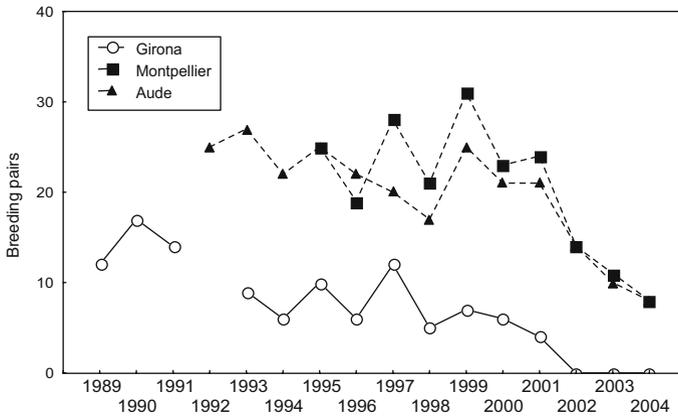


Fig. 2 Population trend of the Lesser grey shrike in Girona (Spain) (open circles) and two French populations (filled symbols) during the period 1989–2004

Table 1 Wald-tests for the significance between time-points of changes in the slope of the population trend of the Lesser grey shrike in France (Montpellier and Aude) during the period 1993–2004

Change-point	Wald-test	df	<i>P</i>
1993	2.80	1	0.09
1994	1.75	1	0.18
1995	2.64	1	0.10
1996	5.05	1	0.02
1997	6.29	1	0.01
1998	14.77	1	0.0001
1999	18.09	1	0.0000
2000	2.92	1	0.08
2001	9.59	1	0.002
2002	1.81	1	0.17

Annual deviations of the Spanish (Girona) and French population (Aude and Montpellier) from their respective long-term trends during 1993–2002 are strongly correlated (Pearson correlation, $r = 0.70$, $P = 0.024$, $n = 10$) (Fig. 3).

NDVI index and climate change in breeding and wintering grounds

The average of the mean temperature for May–June has not changed significantly in the period 1989–2002 in any of the studied locations (Girona, Aude, and Montpellier) (Pearson correlations, $P > 0.10$ and $n = 14$ for all cases). However, the average

Table 2 Wald-tests for the significance between time-points of changes in the slope of the population trend of the Lesser grey shrike in Girona (Spain) during the period 1993–2002

Change-point	Wald-test	df	<i>P</i>
1993	9.19	1	0.002
1994	14.59	1	0.0001
1995	21.38	1	0.0000
1996	26.11	1	0.0000
1997	52.98	1	0.0000
1998	24.20	1	0.0000
1999	11.64	1	0.0006
2001	14.91	1	0.0001

Table 3 Parameter estimates of the trend for each time interval (defined after significant change-points) referred to the French and Spanish population size in the previous interval

French population			Spanish population		
From-up to	Multiplicative slope	Standard error	From-up to	Multiplicative slope	Standard error
1993–1994	0.81	0.099	1993–1994	0.67	0.089
1994–1995	1.07	0.11	1994–1995	1.67	0.21
1995–1996	0.82	0.07	1995–1996	0.60	0.07
1996–1997	1.17	0.10	1996–1997	2.00	0.25
1997–1998	0.79	0.07	1997–1998	0.41	0.05
1998–1999	1.47	0.13	1998–1999	1.45	0.20
1999–2000	0.78	0.06	1999–2001	0.76	0.05
2000–2001	1.02	0.09			
2001–2002	0.62	0.06	2001–2002	0.23	0.06
2002–2004	0.75	0.05	–	–	–

thermal oscillation for the same season (May–June) and period has increased dramatically in Girona ($r = 0.90$, $P < 0.0001$) whereas there is no significant change either in Montpellier ($r = -0.39$, $P = 0.17$) or Aude ($r = -0.16$, $P = 0.58$). Precipitation (total amount during January–July) in Girona has not changed during 1989–2001 ($r = -0.30$, $P = 0.32$).

Climatic changes seem to have influenced the vegetation in Girona, where the mean NDVI index for May–June has decreased significantly during 1989–2000 ($r = -0.62$, $P = 0.033$, $n = 12$). We found non-significant negative correlations in the mean NDVI index for the same season (May–June) and period in the other study areas (Montpellier, $r = -0.16$; Aude, $r = -0.07$, $P > 0.50$ and $n = 12$ for all cases).

Overall, the NDVI index recorded during 1989–2000 for each area correlates with the one in the other areas (Pearson correlations, $P < 0.01$ in all cases).

An analysis of rainfall in the wintering grounds (October–February) during the period 1989–2000 suggests that it has not changed significantly ($r = 0.10$, $P = 0.76$, $n = 12$). A comparison of precipitations during October–February for each of the years in that period with the average precipitation (502.93 mm) and the threshold values (352.93 and 652.93 mm) (see Methods) for the longer series 1902–2000 suggests that only two seasons in the period 1989–2000 (1991/1992—273.1 mm—and 1994/1995—311.4 mm) can be classified as dry whereas the remaining seasons have average precipitations. Accordingly, the mean NDVI index for January–March does not show any trend along 1988–2000 ($r = 0.11$, $P = 0.72$, $n = 13$).

Population declines and climatic variables

Variation in the number of breeding pairs in Girona during the period 1989–2002 (except 1992) can be explained by climatic variables (i.e. thermal oscillation during May–June) in the local area. A multiple regression analysis provided a significant model (Table 4) where only thermal oscillation in Girona proved significant ($\beta = -0.92$, $P = 0.0007$), suggesting that the larger the thermal oscillation, the less birds in Girona (Table 4). Repeating the analysis with the NDVI values for the breeding locations and the wintering grounds (period 1989–2000) as independent variables yields a significant model (Table 4) where only the NDVI in Aude is excluded. The strongest effect was found for the NDVI in Girona

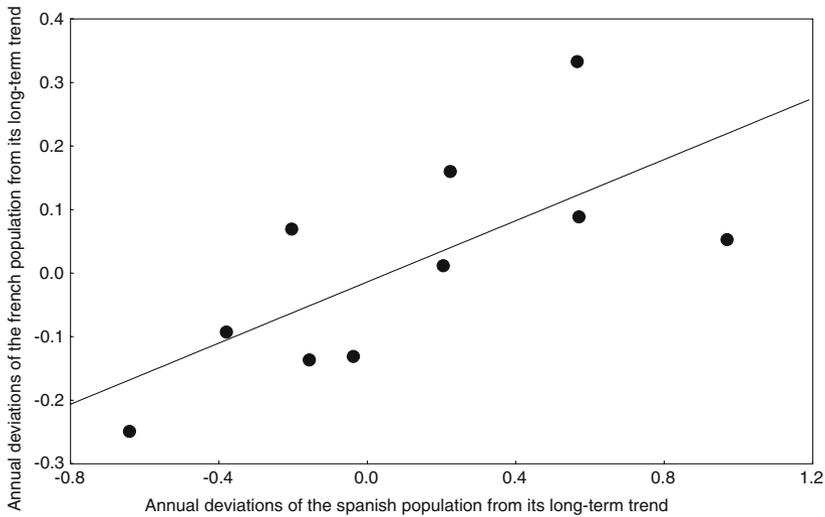


Fig. 3 Correlation between the annual deviations from the long-term trend calculated separately for the breeding populations of Lesser grey shrike in Girona (Spain) and France (Montpellier and Aude) from 1993 to 2002

($\beta = 1.44, P = 0.006$), the other significant variables being the NDVI in Montpellier ($\beta = -1.22, P = 0.009$) and in the wintering grounds ($\beta = -0.78, P = 0.01$) (Table 4).

The fluctuations in the number of breeding pairs in Aude during the period 1992–2002 can be explained by a marginally significant model ($P = 0.056$, Table 4) where

Table 4 Results of stepwise multiple regression analyses with number of breeding Lesser grey shrike pairs in three peripheral populations (Girona, Aude and Montpellier) as dependent variables and (i) climatic variables (mean thermal oscillation during May–June), (ii) vegetation variables (mean NDVI index during May–June for the breeding locations and mean NDVI index during January–March for the wintering area) in each of these locations as independent ones. β coefficients, P values and statistics of each model are shown

Location	Thermal oscillation			Vegetation variables (NDVI)			
	β coeff.	P	Model	β coeff.	P	Model	
<i>Girona</i>							
Girona	-0.92	<0.001	$F_{3,9} = 8.5,$	Girona	1.44	<0.01	$F_{3,7} = 6.3,$
Montpellier	-0.38	0.17	$P < 0.01,$	Montpellier	-1.22	<0.01	$P = 0.02,$
Aude	0.25	0.33	$R^2 = 0.74$	Wintering area	-0.78	0.01	$R^2 = 0.73$
<i>Aude</i>							
Girona	-0.71	<0.05	$F_{2,8} = 4.2,$	Wintering area	-0.42	0.25	$F_{1,7} = 1.5,$
Montpellier	0.29	0.28	$P = 0.056,$				$P = 0.25,$
Montpellier			$R^2 = 0.51$				$R^2 = 0.17$
<i>Montpellier</i>							
Montpellier	-0.39	0.33	$F_{1,6} = 1.1,$	No variable entered			
			$P = 0.33,$				
			$R^2 = 0.15$				

only thermal oscillation in Girona had a significant effect ($\beta = -0.71$, $P = 0.021$). Remarkably, thermal fluctuations in Aude did not enter the model. Variations in the breeding population in Aude during 1992–2000 could not be explained by the NDVI indexes in the breeding and wintering areas (non-significant model, Table 4).

Finally, we did not find any significant model explaining variation in the breeding population in Montpellier either with thermal oscillation (period 1995–2002, Table 4) or with NDVI indexes (period 1995–2000, no variable entered the model).

Discussion

Both the breeding range and the abundance of the Lesser grey shrike at the southwestern limit of its distribution have drastically decreased in the last decades. The French population has been decimated in a few years with a yearly decline of 8.25% during 1993–2004. A stronger yearly decline of 14% during 1993–2002 in the population in Girona resulted in the extirpation of the species from the northeast portion of its range in Spain. The extinction of the species in this protected area in 2002 seems durable and this may very well be the fate for the French population in the near future (Rufay and Rousseau 2004).

Several reasons have been argued to explain the decline of the Lesser grey shrike, most of them pointing out at large-scale processes (like agricultural intensification or climatic changes) acting on the breeding areas (Lefranc and Worfolk 1997; Isenmann and Debout 2000) or on the winter quarters (Herremans 1998a). However, to our knowledge, no specific study has been done in this regard. Our results show correlated fluctuations of the French and the Spanish population in the last decade (suggesting that their decline can be under the influence of a common factor) together with concomitant climate changes, what suggests that climate may play a role in the decline of the species (see Schaub et al. 2005). We found clear evidence of climatic change in our study area in Girona (a drastic increase in thermal oscillation during May–June) in the last years, what agrees with other studies performed in the area (Piñol et al. 1998; Peñuelas et al. 2002; Gordo et al. 2005). Specifically, Piñol et al. (1998) described an increase in temperature in northeastern Spain resulting from increased maximum but not minimum temperatures (1910–1994 period) or from the increase of both maximum and minimum temperatures (1968–1994 period). Such changes may have probably resulted in the observed decrease of the NDVI index in the area, which suggests less vigorous and abundant vegetation. For the two other study areas in France we found no significant trends either in climatic variables or vegetation index during the studied period (May–June). However, there is strong evidence supporting climate change in those areas too. Spring temperature (March–May) rose significantly at Montpellier during the period 1984–1992 (Chuine et al. 1998) and in this same area the flowering date occurred at progressively earlier dates during this period (Osborne et al. 2000).

Climatic conditions can directly influence survival and reproduction in birds (Ringsby et al. 2002 and references therein). Moreover, the peripheral location of these breeding populations could enhance the negative effect of climate change since density-independent factors, like weather, have a high influence on demographic rates in border areas (Hoffmann and Blows 1994; Mehlman 1997; Williams et al. 2003). Thus, it could be that shrikes at the border of the range are more sensitive to

these changes than populations at the core of the area. In line with this, the only comparative data available come from a Slovak population, connected to the main breeding area, which keeps a stable and dense population since years (Krištín 1995; Krištín et al. 2000).

A non-mutually exclusive explanation is that climate changes may have altered the availability/quality of basic resources (like habitat quality or food abundance) that are known to largely influence the size of peripheral populations (McArdle et al. 1990; Williams et al. 2003). In fact, we found a positive relation between the breeding population in Girona and the NDVI index that, in turn, decreases with time. Alterations in northeast Spain in the last decades (like increased aridity—Piñol et al. 1998—or altered life cycles of plants and insects—Peñuelas et al. 2002) due to climatic changes may have resulted in a decrease of food availability and/or in a decoupling between bird physiology and their food supply (Crick et al. 1997; Visser et al. 1998; Sanz et al. 2003) that could influence the reproduction of this predator specialized on large phytophagous insects (Krištín 1995).

Alternatively, human-related activities could account for the decline of the species via habitat modification. Widespread agricultural intensification has been occurring in western Europe since the sixties. However, the protected area in Girona and its periphery has not experienced appreciable changes in the last decade (Romero and Martí, pers. comm.) and the breeding areas in France have not seemingly suffered substantial alteration so as to produce the observed drastic decline of the breeding population (Rufay and Rousseau 2004; Lefranc, pers. comm.).

Factors like drought or habitat changes on the wintering grounds could also account for the decline of the species (Herremans 1997a, 1998a). We did not find any significant trend in precipitation in the main wintering area, what agrees with previous findings (see Herremans 1998b and references therein). Whereas we did not detect differences in NDVI index either, qualitative changes in vegetation cover types in the Kalahari basin due to human and natural causes do have occurred (Ringrose et al. 2002), including an increasing prevalence of thorn trees and widespread bush encroachment. The Lesser grey shrike prefers in the wintering grounds open habitat with limited presence of trees, scattered low bushes and low grass cover that favors prey visibility (Herremans 1997a, 1998a). We found that increases in NDVI in Africa influenced negatively the breeding population in Girona. Thus, it is likely that human factors and/or a series of years with average precipitations could deteriorate the structural qualities of the habitat for the Lesser grey shrike (e.g. bush encroachment caused by overgrazing, increase of grass cover) and thus reduce food availability either directly or indirectly by reducing prey visibility (Herremans 1998a, b).

Our results have two remarkable aspects. One is the spatial synchrony of the studied populations, which can be caused by similar extrinsic effects operating on different populations (Kendall et al. 2000; Williams et al. 2003; Liebhold et al. 2004). Weather has been frequently reported as a likely synchronizing factor (Paradis et al. 2000; Williams et al. 2003). For the population in Girona we detected a strong relationship between climatic variables and fluctuations in population abundances. The lack of correlation for other populations can be due to inaccuracies of our climatic data (e.g. the period when temperature or any other environmental variable influences habitat quality could be different to the one here considered), to the interaction between climate and local factors (Ringsby et al. 2002) or to the limited sample size. However, both our results and evidence from other studies (Chuine et al. 1998, Osborne et al. 2000) suggest that the studied populations are under

similar changing environmental conditions and, therefore, common climatic conditions could be one factor accounting for the observed population declines.

A second relevant aspect arising from our study is that the circumstances experimented by one population could influence the fate of neighboring populations. Variations in the population size of Aude are correlated with environmental variables in Girona. Similarly, the NDVI in Montpellier correlated negatively with the population size in Girona. The migration pattern of the species implies that birds have to pass through the breeding areas in France to reach the ones in Spain. It is therefore likely that these populations are closely interconnected, so that individuals produced in a population recruit into neighboring populations in the next breeding season. It could well be that some birds born in Spain could decide to breed in France the next year (philopatry in juveniles of this species is known to be low, Krištín et al. in press). On the other side, favorable conditions in, let's say, Montpellier, could influence birds' decision to stay there rather than continue on migration to Girona. Curnutt et al. (1996) showed that source-sink dynamics can explain variability at the periphery of a species range where population size is governed largely by migration rather than by reproduction and survival (Curnutt et al. 1996). The role of each of the studied populations in this dynamic remains to be investigated.

Conservation implications

Species with synchronous populations are thought to confront greater risk of extinction because density crashes can occur simultaneously in all populations (Heino et al. 1997; Palmqvist and Lundberg 1998). Faced to the widespread extinction of this species in the southwestern border of its range, it is crucial to identify the causes of the decline and the ecological mechanisms involved and to establish conservation measurements. Whereas the occurrence of a major factor accounting for the decline of this shrike would make its conservation easier, this is unlikely given its migratory nature and the variety of environmental conditions they have to face at different locations throughout the year (Schaub et al. 2005). Our study adds to the preservation of this species by identifying some issues of practical importance to conservation biology. The parallel fluctuations of the French and Spanish (Girona) populations suggest common causes for the decline of the species in this area. Our results suggest that climatic change, acting directly or indirectly on the different populations and probably moderated by local conditions (Osborne et al. 2000; Ringsby et al. 2002) can be one of such causes. However, the correlational nature of this study limits our ability to determine causal factors. More effort is needed to identify other possible factors and the exact mechanisms by which climate may influence population dynamics of this species so that mitigation activities can be implemented.

Although climate change can be observed globally, the magnitude of changes and their effects on organisms is likely to vary considerably within a given region (Osborne et al. 2000). It is therefore crucial to preserve those populations/areas where the study species seems to be stable (e.g. Lleida). However, conservation actions could prove useless if applied separately for some population given that the fates of these populations seem to be interconnected. In line with this more information is needed about the degree of interconnection among peripheral populations and be-

tween these and more central ones, and whether the spatial synchrony here reported occurs at a larger spatial scale.

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