

The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines?

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Summary

1. We model the effect of annual weather conditions on lesser kestrel *Falco naumanni* breeding success in South-western Spain. Models indicate that rainfall is a good predictor of breeding success and has in general a positive effect on reproduction.
2. Rainfall and temperature in spring, during the courtship period, influence colony occupancy rate. Mean minimum temperatures have a positive effect on nest occupation while the relationship between occupation and rainfall is curvilinear with an optimum around 84 mm.
3. Nest success rate is influenced positively by rainfall in winter and negatively by rainfall during the nestling period.
4. The mean number of chicks per successful nest is positively influenced by rainfall during the winter, arrival, courtship, and incubation periods. Rainfall during these periods explains 35% of the variance in this breeding parameter.
5. Nestling body condition is affected positively by rainfall during the courtship and incubation periods.
6. Models that consider the amount of rainfall at each colony in periods defined by the breeding phenology of the lesser kestrel outperform those based on total annual rainfall or on winter NAO-index.
7. Although rainfall in spring has declined significantly since 1966, retrospective predictions of lesser kestrel population growth rate at our colonies indicate that the effect of climate change on breeding success cannot be held responsible for the historical population decline.

Key-words: breeding success, *Falco naumanni*, NAO, predictive models, rainfall.

Journal of Animal Ecology (2003) **72**, 793–810

Introduction

The climate on Earth has warmed by approximately 0.6 °C over the past 100 years (IPCC 2002; Walther *et al.* 2002), and climatic models predict temperature will continue to increase as an effect of increasing concentrations of greenhouse gases (IPCC 2002). Global mean rainfall is also projected to increase, although the pattern is less clear, and while in some regions (i.e. Northern Europe) precipitation will increase others, such as the Mediterranean, will become dryer (as much as –5% per decade, IPCC 2001). Climate change will certainly have serious effects on species distribution by making areas that are currently adequate for one species inadequate in the future (Parmesan *et al.* 1999).

The observed changes in climate during the last decades are consistent with trends predicted by climatic models (IPCC 2002), and it has been shown that temperature increases correlate with changes in the phenology, demography and distribution of different species (Sæther *et al.* 2000; Forchhammer *et al.* 2001; Peñuelas, Filella & Comas 2002; Sanz 2002b). In this scenario of climate change, we need models that relate climatic variables to population demographic parameters if, for instance, we need to manage endangered species.

Numerous studies have shown that local climatic conditions influence survival and reproduction in birds. Many have focused on direct effects of extreme weather during the breeding season, for example: adverse weather precluding breeders of reaching the conditions for starting reproduction (Mearns & Newton 1988; Bradley *et al.* 1997; Steenhof *et al.* 1999), causing mortality of eggs and nestlings (Olsen & Olsen 1989a; Bradley *et al.* 1997) or increasing energy demands of adults or

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nestlings (Kostrzewa & Kostrzewa 1991). Indirect effects of weather on bird reproduction are probably very frequent but tend to be disregarded; for example, weather can influence the abundance of food (Grant *et al.* 2000; Moss, Oswald & Baines 2001), prey activity or accessibility (Wiklund & Stigh 1986; Milsom 1987; Steenhof *et al.* 1999), can reduce the foraging capacity of individuals (Rijnsdorp, Daan & Dijkstra 1981; Olsen & Olsen 1992), or can influence the collateral costs of time devoted to foraging (Erikstad & Spidso 1982; Erikstad & Andersen 1983). Climate can also interact with the effect of predators or parasites (Steen *et al.* 1988; Dufva & Allander 1996; Murray, Keith & Cary 1998), influence reproduction timing (Olsen & Olsen 1989b; Cucco *et al.* 1992; Sanz 2002b) or influence the availability of nesting sites (Wiklund & Stigh 1986; Clarke & Johnson 1994). Most previously mentioned studies have shown significant correlation between meteorological variables and demographic parameters of different species, but rarely have they estimated the magnitude and shape of the effect of weather on demographic parameters of the species. There are hardly any studies (see Sæther *et al.* 2000 for an exception) that have built successfully predictive models of the relation between climate and demography.

To make reliable predictive models we need to know the mechanisms by which meteorological variables translate their effect to demographic parameters. If not, we may extrapolate models to conditions in which they do not apply. As it is not possible to modify climate under controlled experimental conditions to measure its effect on a bird population we have to rely on correlational studies to try to build these models.

We have studied the effect that different meteorological variables, measured along an annual cycle, have on the breeding parameters of a metapopulation of an endangered species, the lesser kestrel *Falco naumanni* (Fleischer), in a Mediterranean climate. This study is timely because the Mediterranean is one of the regions where it is expected that climate and land-use change will have one of the most profound effects on biodiversity in the next 100 years (Sala *et al.* 2000), while being one of the areas in which there are less published data on the influence of recent climate change on birds (Sanz 2002a). The lesser kestrel has suffered an historical decline in western Europe during the 20th century. If climate has an influence on its demography it is possible that recent climate change is in part responsible of population decline.

To try to identify possible 'mechanisms' for the correlation between meteorological variables and demography we have decomposed lesser kestrel fertility into different independent components (fraction of females that attempt reproduction, fraction of nests that are successful and chicks fledged per successful nest). As it is possible that we lose predictive ability by decomposing fertility into several components we have also modelled directly the number of chicks fledged per adult female in the population.

As meteorological variables such as rainfall or temperatures at different times of the year are not independent and they tend to show spatial and temporal autocorrelation, it is possible that summary variables (such as annual rainfall, mean temperature) or regional climatic indexes (i.e. the North Atlantic Oscillation Index, NAO) have higher predictive ability of demographic parameters, specially if they are more representative of the conditions influencing the population and have less measurement error than local weather conditions measured in shorter time intervals. The appealing interest of using a single indicator of annual weather conditions to test the hypothesis that climate influences ecological variables has recently extended the use of the NAO-index as a proxy of annual weather conditions in Europe in the ecological literature (Przybylo, Sheldon & Merilä 2000; Ottersen *et al.* 2001; Forchhammer, Post & Stenseth 2002; Sanz 2002b). The aims of this paper are: (1) to quantify the effect of both local and global climatic conditions on the lesser kestrel breeding success, considering which ones have more explanatory power, and (2) by including the effect of these climatic variables in a demographic model of the species, investigate if climate change has had any influence on its historical decline.

Materials and methods

STUDY SPECIES

The lesser kestrel is a small migratory falcon inhabiting open landscapes in the Western Palearctic (Cramp & Simmons 1980) and feeding on large invertebrates, mainly Orthoptera and Coleoptera (Franco & Andrada 1977). It is a colonial species that breeds in old buildings, such as churches or castles within urban areas in western Europe. Our study area holds some of the highest lesser kestrel densities recorded in Europe (Biber 1990). They nest in deep holes in walls (Negro & Hiraldo 1993), sheltered from rain and buffered from temperature changes.

Lesser kestrel breeding success shows a high annual variability and could have an important effect on population dynamics, in particular, in our highly philopatric population (Negro, Hiraldo & Donazar 1997).

The species experienced a marked decline in its Western Palearctic breeding range in the middle of the 20th century (Cramp & Simmons 1980; Biber 1990). Considered previously one of the most abundant raptors in Europe (Bijleveld 1974) the lesser kestrel became extinct in several countries (e.g. Austria, Hungary, Poland) and has practically disappeared in others (e.g. France, Portugal, Bulgaria).

Mediterranean Spain constitutes its stronghold in the Western Palearctic (Biber 1990). None the less, the Spanish population also suffered a precipitous decline, as it dropped from an estimated 20 000–50 000 pairs in the 1970s (Garzón 1977) to 4000–5000 breeding pairs in 1988 (González & Merino 1990).

STUDY AREA

Data were collected in the Guadalquivir river basin (South-western Spain). This is a predominantly flat area (elevation range 20–240 m), cultivated intensively with cereals, sunflowers and olive groves. We use the data from six colonies that have been monitored with constant effort in the period 1988–2000 for a mean of 9 years (Mairena 13, Miguel 13, Victoria 12, Oliva 7, Purificación 7 and Silo 4 years; Fig. 1). All the colonies were located in villages: five in old buildings (four churches and one castle) and one in a cereal silo. Mean colony size was 21 occupied nests (range = 14–35). Mean distance between colonies is 58.7 km (range = 10.2 km–101.2 km). The climate is Mediterranean with rainy winters and dry summers. Annual rainfall is highly variable (the maximum rainfall difference between years at the same colony during the study period was 719 mm) and shows a bimodal distribution with its main peak in winter and a second peak in spring. Mean annual accumulated rainfall averages 595 mm (range = 225–1229 mm).

FIELD PROCEDURES

We started monitoring colonies at the beginning of the breeding season, late March and early April, and

surveyed cavities with a telescope in order to find which ones were occupied by breeding pairs. Around the time of laying we visited all colonies to confirm which nesting sites had been used and record clutch size in each occupied nest. In addition, we made at least one visit at the end of the nestling period to measure and ring chicks. In some big colonies in which all the adequate holes could not be checked, we monitored a fixed proportion of potential nesting sites (always over 70% of the total). We checked the same holes year after year. We noted eggshell remains, non-hatched eggs or dead chicks in each visit to determine which holes had been used by lesser kestrels to nest that season. We also measured chick body mass (accuracy level: 2 g) and length of the 8th primary feather to the nearest 0.5 mm, from which body condition and hatching date were estimated (Negro 1991).

LESSER KESTREL BREEDING PARAMETERS

We selected three independent variables that add to the colony total breeding output each year: (1) occupancy rate, i.e. the ratio between used and available nesting sites at the colony, and we think it reflects the fraction of females that attempt breeding each year; (2) nest success rate, i.e. the ratio between successful and used nest;

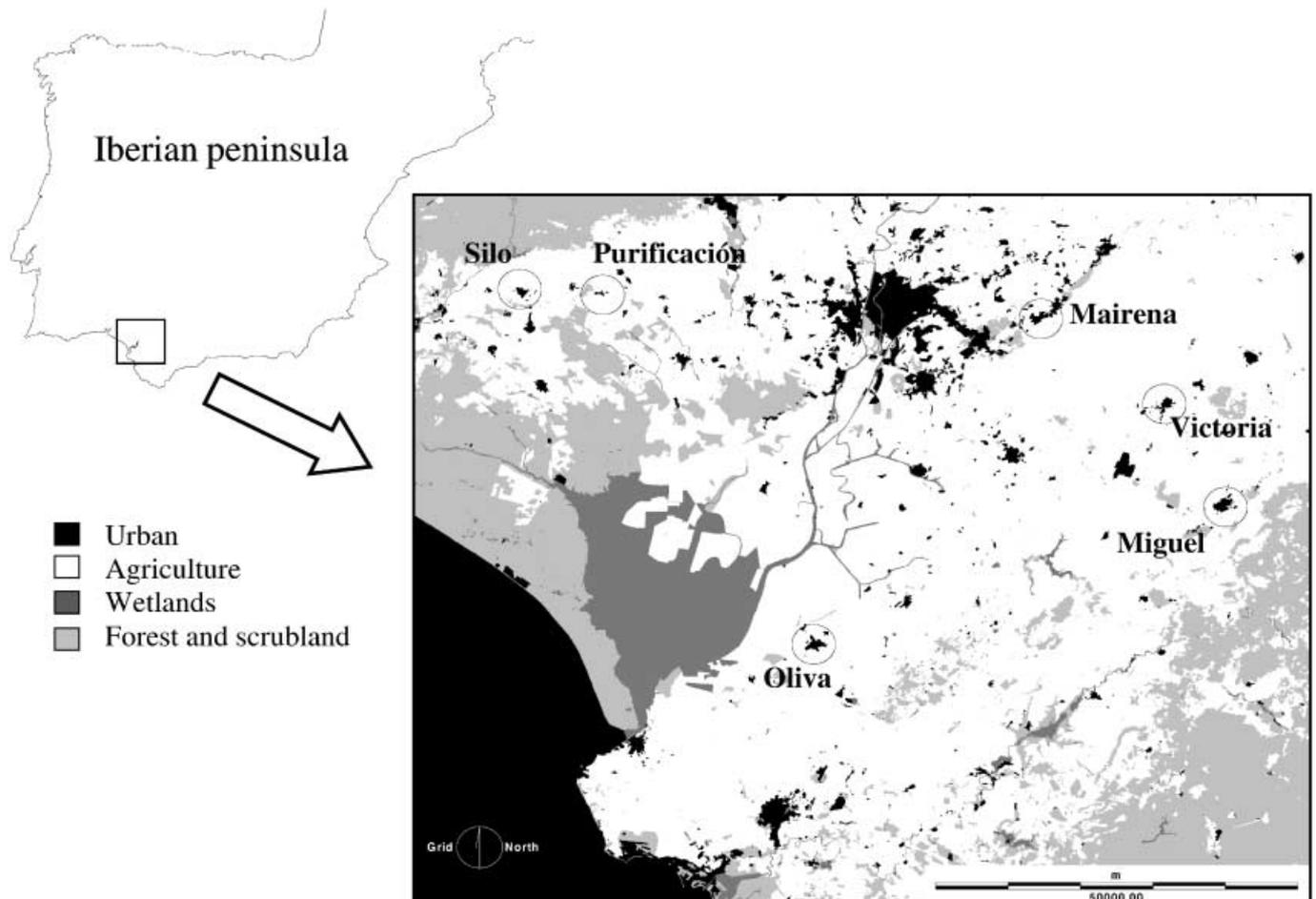


Fig. 1. Location of the six lesser kestrel study colonies and distribution of main land uses in the study area.

and (3) mean number of chicks per successful nest. We consider these variables separately because we think it will be easier to infer possible causal mechanisms. We also built predictive models for the variables: (4) mean number of female chicks per occupied nest and (5) mean number of female chicks per adult female at the colony, because although these variables are not independent from the previous ones, it might be possible to predict them directly with less error than by combining models for other variables. In addition, we analysed the effect of weather on (6) chick body condition at the time of ringing which can be an indicator of survival probability.

We defined as used nest any hole showing attempts of reproduction. Available nests were all holes at the colony that were checked every year and had been used at least once for breeding during the study period. A nest was considered successful when at least one chick fledged. We considered a chick had fledged if it survived until ringing age and was not found dead before fledging in subsequent visits to the colony. Chicks were ringed at a mean age of 21 days (approximately 15 days before fledging, Bustamante & Negro 1994). Mean nestling body condition was calculated from the residuals of a locally weighted regression (LOWESS) between 8th primary feather length and body mass. We used this regression because the relationship between body and feather growth is not linear and data were enough so that a scatterplot smoother such as LOWESS provided a good fit.

METEOROLOGICAL VARIABLES

We used meteorological data from the weather station closest to each colony (often, in the same village). Weather records consisted in daily rainfall (10^{-1} mm), number of rainy days and maximum and minimum daily temperatures (10^{-1} °C). Instead of using calendar months, we estimated meteorological variables for six periods according to the lesser kestrel annual cycle in the study area:

(1) *Premigratory dispersal*. The time between median fledging date in the study area (7 July; Bustamante & Negro 1994) and the date of peak fall migratory crossing over the Gibraltar Straits (30 September; Bernis 1980). Fledglings disperse from the colonies on average 5 days after fledging (Bustamante & Negro 1994). Most birds disperse far with predominantly northern directions (García 2000), and only adults seem to remain in the breeding area.

(2) *Winter*. The period in which most kestrels are in their winter quarters, south of the Sahara desert, although some adults remain for the whole year around the colonies (Negro, de la Riva & Bustamante 1991).

(3) *Arrivals*. Time between first arrivals of migratory individuals to the breeding colonies and the beginning of courtship and pair formation. Median date of first migratory arrivals is 10 February (Negro, Donázar & Hiraldo 1992).

(4) *Courtship*. The time between first courtship feeding (15 April) and median laying date (9 May) (Negro *et al.* 1992). During this period breeding females stay at the colony most of the time and are fed by their mates. The function of this behaviour is to help the female to acquire the optimum condition to lay (Donázar, Negro & Hiraldo 1992).

(5) *Incubation*. Time from median laying date to median hatching date (1 June).

(6) *Nestling period*. Time from median hatching date to median fledging date (7 July). We established the onset of lesser kestrel annual cycle on July 7, because breeding season at that time is just finished and weather from this time onwards could only affect next season breeding parameters.

By using these periods in our models instead of calendar months we reduce the number of potential meteorological predictors, have variables that are better suited to the lesser kestrel breeding cycle and from which it is easier to infer possible causal models.

NORTH ATLANTIC OSCILLATION

The North Atlantic Oscillation (NAO) is a natural large-scale atmospheric fluctuation between the subtropical and the subpolar North Atlantic region (Lamb & Pepler 1987). The winter NAO index is quantified from December to March as the difference of normalized sea level pressure (SLP) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864 (Hurrell & van Loon 1997). The SLP anomalies at each station are normalized by division of each seasonal mean pressure by the long-term mean (1864–1983) standard deviation. Normalization is used to avoid the series being dominated by the greater variability of the northern station. Positive values of the index indicate stronger-than-average westerlies over the middle latitudes and higher temperatures and rainfall over western Europe. Negative values are associated with cold drier winters in northern Europe and wetter winters in southern Europe. This winter NAO index is currently updated at the website: <http://www.cgd.ucar.edu/~jhurrell/nao.html>.

There are good reasons to use this index as indicator of climatic fluctuations and test it as predictor in our models. A major advantage is its extension back to 1864. Moreover, several authors have documented significant relationships between the temporal patterns in this climatic index and variations in biological populations in general (Ottersen *et al.* 2001) and breeding parameters in birds in particular (Przybylo *et al.* 2000; Sanz 2002b).

MODEL SELECTION AND FITTING

We used generalized linear models (GLMs) (McCullagh & Nelder 1989) as a mathematical description of the relationship between the breeding parameters

defined above and weather. GLMs are a class of models of which the linear regression is a particular case. GLMs allow for a greater range of relationships between the response variable and explanatory variables, which include the use of other distribution functions for errors when the normal distribution is not applicable. For response variables such as proportions or percentages a binomial function for the error is adequate, and this was the error function used for the response variables: (1) occupancy rate and (2) nest success rate, using available nests and occupied nests in each colony each year as the binomial denominator, respectively, and a logistic link to constrain predicted values between 0 and 1 (Crawley 1993). This is equivalent to a logistic weighted regression. Normal errors were used for: (3) mean number of chicks per successful nest; (4) mean number of female chicks per occupied nest; (5) mean number of female chicks per female; and (6) nestling body condition. We employed as weights in the models the number of successful nests (for response variable 3), number of occupied nests (for variables 4 and 5) and number of chicks (for variable 6) to compensate for the different sample sizes used to obtain mean values. For models with normal errors we used an identity link.

A set of GLMs was built using S-Plus 2000 (Professional, release 2) statistical package. We modelled the relationship between the response variables that characterized breeding and the following weather explanatory variables for each period in the lesser kestrel phenology: (1) accumulated rainfall; (2) number of rainy days; (3) mean minimum; and (4) mean maximum daily temperatures. As breeding parameters could also be affected indirectly by rainfall in the previous year (e.g. if ecosystem productivity shows a reduced resilience after a period of drought), we also considered as explanatory variable the total amount of rainfall at the same colony the year before. Lesser kestrels are philopatric (57% return to breed to their natal colony, Negro *et al.* 1997). Some start breeding on their first year, and most of them on their second year. Therefore we considered as additional predictors: (i) productivity at the colony the year before (mean number of chicks ringed per successful nest); (ii) productivity at the colony 2 years before; and (iii) and mean productivity of the whole study area of the two previous years. We always tested colony as a factor initially because we expected that differences in the proportion and distribution of land-uses among colonies could affect breeding parameters.

Meteorological variables tend to be correlated. In our data, mean minimum temperature had a positive correlation with rainfall in winter, and mean maximum temperature a negative correlation with rainfall in spring and summer. We built separate GLM models for each set of meteorological predictors: accumulated rainfall, rainy days, mean maximum temperatures and mean minimum temperatures. Starting from a null model, we used the STEP GLM procedure of S-Plus that uses the Akaike information criterion (AIC) to

include a new variable in the model. As the AIC tends to build models with too many predictors (Sakamoto, Ishiguro & Kitigawa 1986) a backward stepwise elimination of variables was applied to the resulting model until all variables were significant with $P < 0.01$ according to an F -test. In GLM it is common to use the deviance, the logarithm of the ratio of two likelihoods (Crawley 1993), to compare models. When errors are normal and an identity link is used deviance is equivalent to variance. To facilitate understanding we use the more habitual term percentage of explained variance when talking about models with normal errors and percentage of explained deviance in the rest.

During the backward stepwise procedure we first eliminated those variables whose effect was biologically implausible (e.g. rainfall or temperatures in the nestling period that influence the occupancy rate). When more than one meteorological predictor could go out of the model, we removed first those for which we had no biological explanation, even when the increase in residual deviance of the model was greater than when we removed other variable first. After obtaining the minimum adequate model with each set of meteorological predictors, we tested if minimum and maximum temperatures could improve the models developed with rainfall and also if rainfall could improve the minimum adequate models obtained with temperatures. At this stage, we also tested if variables from the previous breeding season (total rainfall or kestrel productivity) could improve the minimum adequate models. Final models were explored looking for significant interactions and for nonlinear relationships in the predictors selected. Non-linear relationships were analysed using generalized additive models (GAMs) (Hastie & Tibshirani 1990) that are a further generalization of GLM models. They allow for the use of scatterplot smoothers to model non-linear relationships between response and explanatory variables. In our case, a cubic smoothing spline with 4 degrees of freedom (d.f.) was fitted with the GAM procedure of S-Plus to each predictor and tested for significance by comparing it with its linear equivalent. Significant non-linear relationships were explored and simplified when possible with polynomials to allow for easier interpretation.

Once we selected one or several models for each breeding parameter, we verified the distributional assumptions of the error structure by looking at the residuals, and we checked the robustness of the model by looking at the three more influential points (according to Cook's distance). We tested if all predictors remained significant when these three more influential points were sequentially omitted from the models.

DEMOGRAPHIC MODEL

We used the matrix population model for the lesser kestrel developed by Hiraldo *et al.* (1996) in the same study area using data from 12 colonies intensively colour-ringed and monitored during 6 years (1988–93). The

general formulation for the matrix projection model invariant in time (Lewis 1942; Leslie 1945) takes the form:

$$N_{t+1} = \mathbf{M}N_t \quad \text{eqn 1}$$

where \mathbf{M} is the population projection matrix (Caswell 1989) incorporating data on fertility and survival probabilities of each population age class. N_t is a vector with the abundance of individuals in each of the life-cycle age classes (see Fig. 2). The population of females is divided in two age classes: yearlings and adults (individuals of 2 or more years old). Taking this into consideration the model takes the form:

$$\begin{pmatrix} Y \\ A \end{pmatrix}_{t+1} = \begin{pmatrix} c_0 b s_0 & c b s_0 \\ s & s \end{pmatrix} \times \begin{pmatrix} Y \\ A \end{pmatrix}_t \quad \text{eqn 2}$$

where Y_{t+1} is the number of yearling females at time $t + 1$ (time units are years); A_{t+1} is the number of adult females at time $t + 1$; b is the number of female chicks that fledge per breeding female and year; s_0 is the probability for fledgling females to survive 1 year; c_0 is the proportion of yearlings that attempt breeding; c is the proportion of adults that attempt breeding, and s is the annual survival probability for yearlings and adults.

RETROSPECTIVE PREDICTIONS OF POPULATION GROWTH RATE

We incorporated the effect of annual weather into Hiraldo *et al.*'s (1996) time invariant matrix by predicting with our models estimates of c and b for each colony and year, for a period of 35 years during which lesser kestrel populations have declined (1966–2000). For those demographic parameters for which we had no independent estimates we used the ones provided by Hiraldo *et al.* (1996) (see Appendix I). For each colony and year projection matrix we calculated the growth rate (λ) of the population.

The predictive models developed in this paper for different breeding parameters had to be modified for these retrospective predictions for several reasons: (1) weather data from the meteorological stations were

available only as monthly values for the whole period (1966–2000); (2) although we had fitted linear models for simplicity there are reasons to believe that breeding parameters will not increase or decrease linearly with temperature or rainfall, so we used both models fitted with linear terms and with cubic smoothing splines; and (3) the number of females chicks produced per female in the population can be estimated directly with a model or can be estimated as the product of predictions of different models for occupancy rate, nest success rate and chicks fledged per successful nest.

Four different variations of the models (see Appendix I for details) were explored to estimate for each colony and year the predicted population growth rate (λ) and its temporal trend: Model 1: c (fraction of adult females that attempt breeding) was estimated from the colony occupancy rate model and b (females chicks fledged per breeding female) was estimated from the nest success rate and mean number of chicks fledged per successful nest models. Rainfall and temperatures for the lesser kestrel periods were estimated from monthly data and linear models were refitted. Model 2 is like model 1 but differs in using cubic smoothing splines with 3 d.f. to refit the models using as predictors rainfall in each month included in a lesser kestrel period with a significant influence on the corresponding breeding parameter. Model 3: parameters cb and c_0b from the population matrix were derived from the model for chicks fledged per female in the population. Rainfall for the lesser kestrel periods that were significant were estimated from monthly data and a linear model was refitted. Model 4 is like model 3 but differs in using cubic smoothing splines with 3 d.f. to refit the model using as predictors rainfall in each month included in a lesser kestrel period with a significant influence on the number of chicks per female.

Once we had the predictions of λ from each model we tested if there was a temporal trend in λ by fitting a GLM model with colony, year (as a continuous variable) and the interaction colony \times year, and testing the significance of each term by backwards elimination from the full model.

Results

OCCUPANCY RATE

The best minimum adequate model (Table 1) indicated differences among colonies, a linear increase in occupancy rate with mean minimum temperature during the courtship period and a curvilinear relationship with rainfall during the same period. This curvilinear relationship could be modelled adequately with a second degree polynomial that indicated a maximum occupancy rate when accumulated rainfall during the courtship period (15 April–9 May) was around 84 mm – the first derivative of the polynomial (Fig. 3). There were no significant interactions between rainfall and temperature, rainfall and colony or temperature and

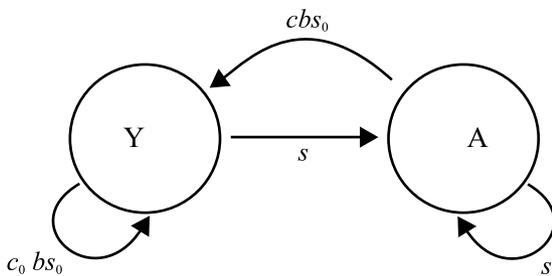


Fig. 2. Life-cycle graph for the lesser kestrel demographic model: Y = yearlings; A = adults (≥ 2 years old); b = female fledglings per reproductive female; c_0 = proportion of yearling females attempting breeding; c = proportion of adult females attempting breeding; s_0 = juvenile survival (i.e. during the first year of life); s = adult and yearlings annual survival.

Table 1. Best model for occupancy rate

Explanatory variables	Parameter estimate	SE ¹	<i>F</i>	Δ d.f.	<i>P</i>	% total deviance	
Colony	Intercept	-2.478	0.570	11.45	-5	< 0.0001	44.60
	Mairena	aliased	aliased				
	Miguel	0.169	0.195				
	Oliva	0.630	0.237				
	Purificación	1.126	0.245				
	Silo	2.122	0.451				
	Victoria	0.730	0.199				
Courtship rainfall	X	1.18 e-3	3.86 e-4	5.10	-2	0.0098	7.95
	X ²	-6.99 e-7	2.35 e-7				
Courtship mean minimum temperature	1.30 e-2	4.74 e-3	7.50	-1	0.0086	6.84	

Null model deviance 295.03 with 55 d.f. Residual deviance 122.76 with 47 d.f. ¹SE corrected for overdispersion.

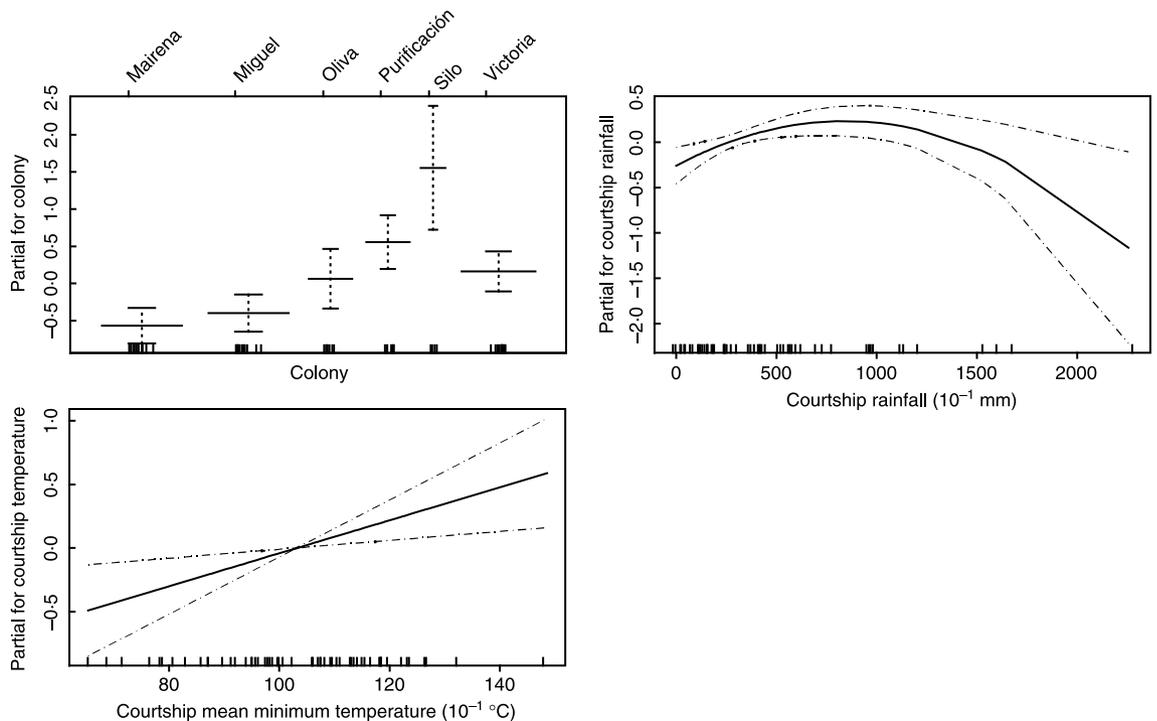


Fig. 3. Mean partial effect of each predictor in the best model for occupancy rate. Broken lines indicate the SE of the mean. A second-degree polynomial is fitted to courtship rainfall. The rugplot on the *x*-axes indicates the density of data points.

colony. The model explained 58% of the deviance in occupancy rate.

NEST SUCCESS RATE

Initially the best parametric minimum adequate model explained 28% of the deviance. Rainfall during winter had a linear positive effect on nest success rate ($F_{1,54} = 11.45$, $P = 0.0013$), while rainfall during the nestling period had a linear negative effect ($F_{1,54} = 10.83$, $P = 0.0018$). There were no significant interactions. This model could be improved significantly by fitting a cubic smoothing spline (4 d.f.) to rainfall in the nestling period ($\chi^2 = 18.83$, d.f. = 3, $P = 0.0003$). The smoothing

spline suggested that the negative effect of rainfall in the nestling period remained constant for rainfall in excess of 20 mm. We tested a parametric model in which we fitted a slope only in the interval 0–20 mm for rainfall in the nestling period (Fig. 4). This final model explained 36% of the deviance and did not differ significantly from the one with a smoothing spline (Table 2).

MEAN NUMBER OF CHICKS PER SUCCESSFUL NEST

The best model explained 72% of the variance (Table 3). There were significant differences among colonies.

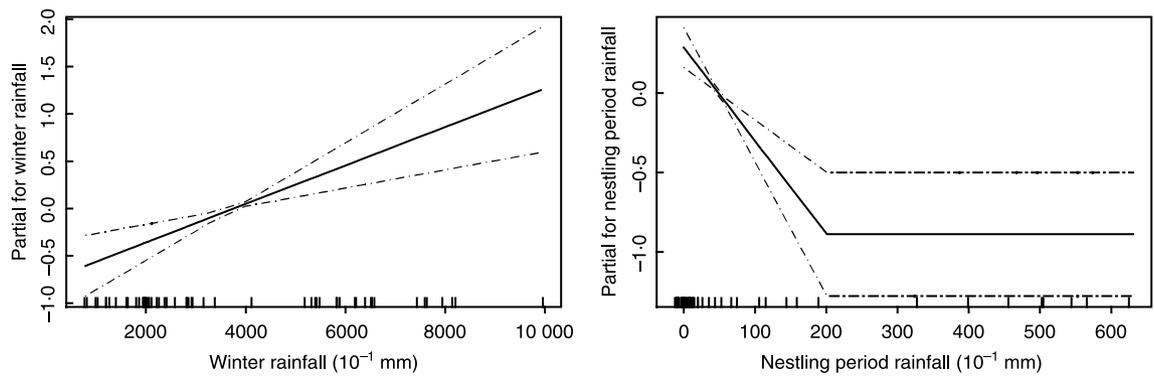


Fig. 4. Mean partial effect of each predictor in the best model for nest success rate. Broken lines indicate the SE of the mean. The rugplot on the x-axes indicates the density of data points.

Table 2. Best model for nest success rate

Explanatory variables	Parameter estimate	SE ¹	<i>F</i>	Δ d.f.	<i>P</i>	% total deviance
	Intercept	1.26 e-2	2.81 e-1			
Winter rainfall	2.03 e-4	5.37 e-5	16.35	-1	0.0002	15.94
Nesting period rainfall ²	-5.88 e-3	1.29 e-3	20.22	-1	< 0.0001	19.74

Null model deviance 184.67 with 55 d.f. Residual deviance 118.78 with 53 d.f. ¹SE corrected for overdispersion. ²Slope for rainfall < 20 mm. The effect of rainfall over 20 mm is considered constant and added to the intercept.

Table 3. Best model for mean number of chicks per successful nest

Explanatory variables	Parameter estimate	SE ¹	<i>F</i>	Δ d.f.	<i>P</i>	% total deviance	
	Intercept	1.342	0.169				
	Mairena	aliased	aliased				
	Miguel	-0.133	0.140				
Colony	Oliva	-0.333	0.175	10.25	-5	< 0.0001	36.53
	Purificación	0.159	0.142				
	Silo	1.235	0.207				
	Victoria	0.296	0.138				
Winter rainfall	8.76 e-5	2.25 e-5	15.16	-1	0.0003	10.80	
Arrival rainfall	3.79 e-4	9.24 e-5	16.84	-1	0.0002	12.00	
Courtship rainfall	3.93 e-4	1.13 e-4	12.02	-1	0.0012	8.56	
Incubation rainfall	4.48 e-4	1.84 e-4	5.93	-1	0.0189	4.22	

Null model deviance 351.47 with 55 d.f. Residual deviance 98.02 with 46 d.f.

Rainfall during winter, arrival, courtship and incubation had linear positive effects on the mean number of chicks per successful nest. Rainfall during incubation was only marginally significant according to our $P < 0.01$ limit. The best model indicates that although most of the rain comes in winter, rainfall in spring is responsible for two thirds of the positive effect of rainfall on chicks per successful nest. No significant interactions were found among the variables included in the model. A GAM model with cubic smoothing splines did not improve significantly the best parametric model.

successful nest. We assume that half of the chicks fledged are females, because the observed nestling sex ratio in the area does not differ from 1 : 1 (Negro & Hiraldo 1992). The best model explained 66.61% of the variance, indicated significant differences among colonies, and a positive effect of rainfall during the periods of winter, arrival and courtship (Table 4). If the mean number of female chicks per occupied nest is predicted with a combined model using the best model for nest success rate and mean number of chicks per successful nest, the explained variance is 4% higher (70.30%).

MEAN NUMBER OF FEMALE CHICKS PER OCCUPIED NEST

This variable is not independent from previous variables: nest success rate and mean number of chicks per

MEAN NUMBER OF FEMALE CHICKS PER ADULT FEMALE

To calculate this parameter it is necessary to estimate first which fraction of the population of adult females

Table 4. Best model for mean number of female chicks per occupied nest

Explanatory variables		Parameter estimate	SE ¹	F	Δd.f.	P	% total deviance
Colony	Intercept	0.460	0.100	7.52	-5	< 0.0001	32.62
	Mairena	aliased	aliased				
	Miguel	-0.142	0.086				
	Oliva	-0.112	0.114				
	Purificación	0.113	0.093				
	Silo	0.677	0.139				
	Victoria	0.178	0.089				
Winter rainfall		6.41 e-5	1.45 e-5	19.52	-1	< 0.0001	16.92
Arrival rainfall		1.36 e-4	5.66 e-5	5.77	-1	0.0203	5.00
Courtship rainfall		2.77 e-4	7.57 e-5	13.43	-1	0.0006	11.65

Null model deviance 149.21 with 55 d.f. Residual deviance 50.43 with 47 d.f.

Table 5. Best model for mean number of female chicks per female

Explanatory variables		Parameter estimate	SE ¹	F	Δd.f.	P	% total deviance
Colony	Intercept	6.24 e-1	6.62 e-2	10.34	-5	< 0.0001	41.37
	Mairena	aliased	aliased				
	Miguel	-2.78 e-1	6.12 e-2				
	Oliva	-8.00 e-2	9.44 e-2				
	Purificación	1.31 e-1	7.78 e-2				
	Silo	6.17 e-1	1.50 e-1				
	Victoria	3.21 e-2	7.21 e-2				
Winter rainfall ¹		9.10 e-5	2.32 e-5	15.40	-1	0.0003	12.31
Courtship rainfall	X	6.33 e-4	1.44 e-4	10.93	-2	0.0001	17.47
	X ²	-2.68 e-7	7.90 e-8				

Null model deviance 277.84 with 55 d.f. Residual deviance 80.14 with 47 d.f. ¹Slope for rainfall < 400 mm. The effect of rainfall over 400 mm is considered constant and added to the intercept.

breeds each year. If all adult females at a colony laid eggs the mean number of female chick per adult female would not be different from the mean number of female chicks per occupied nest. Observations at the colony suggest that not all adult females present in early spring lay eggs (Hiraldo *et al.* 1996; personal observation). We assume that the fraction of the adult female population at a colony laying eggs is variable between years and it is reflected in the occupancy rate. We have estimated it as the observed occupancy rate divided by the maximum occupancy rate observed at each colony in the years of the study period (1988–2000), because colonies differ in quality of available nesting sites.

The best model for mean number of female chicks per female (Table 5 and 71.34% explained variance) indicated significant differences among colonies, a positive effect of rainfall in winter up to 400 mm (the effect is constant for rainfall > 400 mm) and a curvilinear relationship with rainfall during the courtship period: 15 April–9 May (Fig. 5). This curvilinear relationship could be modelled adequately with a second degree polynomial that indicated a maximum positive effect of rainfall during the courtship period when it was around 120 mm.

NESTLING BODY CONDITION

The best model explained up to 58% of the variance (Table 6). The model indicated that there were differences among colonies and that rainfall during courtship and incubation (spring) had both positive linear effects.

MODELS WITH OTHER PREDICTORS

Models with other explanatory variables were also explored. The number of days with rain gave models very similar to those with accumulated rainfall, but days with rain explained less variance than accumulated rainfall. Relations with temperature in most cases could be attributed to the correlation between temperature and rainfall, and once rainfall was in the model temperature was no longer significant. We also tested if mean hatching date had an effect on mean number of chicks per successful nest or in nestling body condition, because it is known that hatching date within a year shows a negative correlation with breeding success in some raptors such as the sparrowhawk *Accipiter nisus* (Newton 1986) or the Eurasian kestrel *Falco tinnunculus* (Village 1990), but this variable did

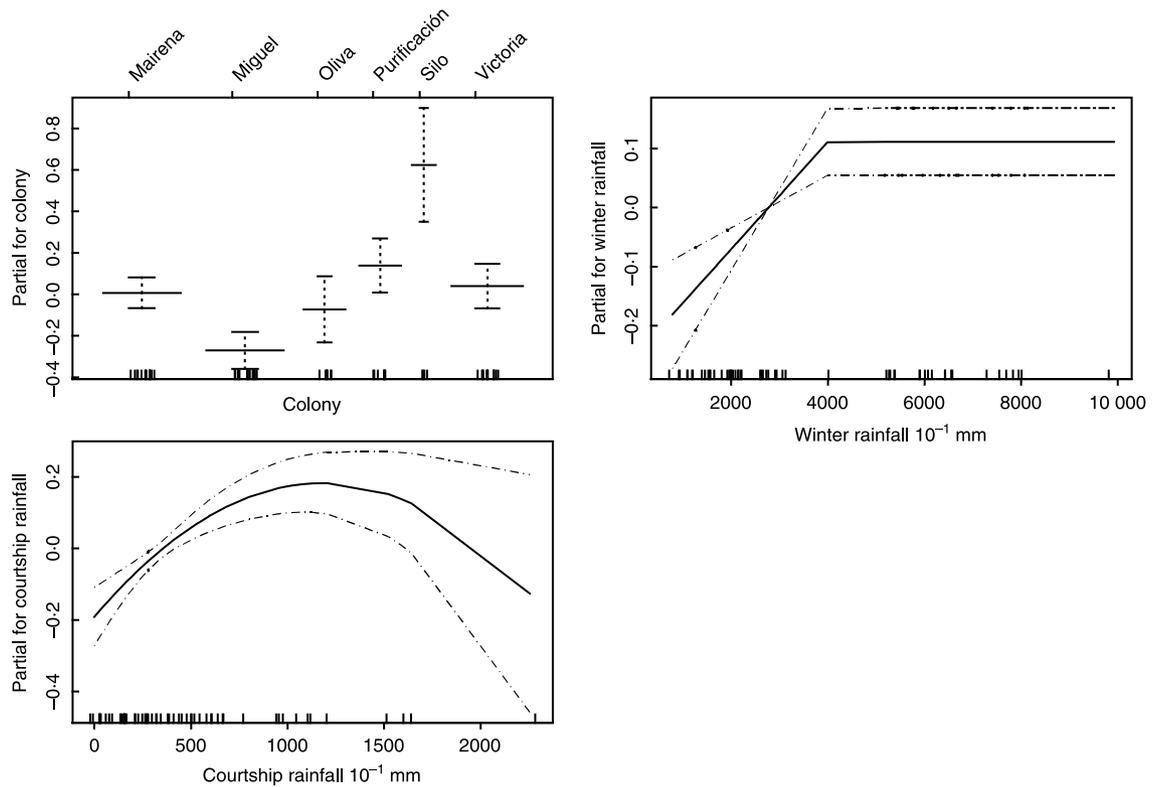


Fig. 5. Mean partial effect of each predictor in the best model for mean number of female chicks per adult female. Broken lines indicate the SE of the mean. The rugplot on the x-axes indicates the density of data points.

Table 6. Best model for nestling body condition

Explanatory variables	Parameter estimate	SE ¹	F	Δd.f.	P	% total deviance
	Intercept	-13.957	2.289			
	Mairena	aliased	aliased			
	Miguel	1.392	3.173			
Colony	Oliva	6.060	4.039	5.76	-5	0.0003
	Purificación	9.022	2.938			
	Silo	16.72	3.589			
	Victoria	8.215	2.840			
Courtship rainfall	6.67 e-3	2.22 e-3	9.03	-1	0.0042	9.61
Incubation rainfall	1.65 e-3	4.11 e-3	16.19	-1	0.0002	17.23

Null model deviance 231 994.6 with 55 d.f. Residual deviance 98 618.07 with 48 d.f.

not enter the models. The contrasting effect of rainfall in spring when comparing models for occupancy rate and for mean number of chicks per successful nest suggested some possible density dependence. We tested if the number of occupied nests or the fraction of females breeding had any influence on mean number of chicks per successful nest. Neither had a significant influence ($F_{1,46} = 0.04$, $P = 0.84$; $F_{1,46} = 0.02$, $P = 0.89$, respectively). All meteorological predictors in the minimum adequate model (Table 3) remained significant if number of occupied nests or the fraction of females breeding was included in the model to control for kestrel density.

PREDICTIVE ABILITY OF WINTER NAO INDEX AND ANNUAL RAINFALL

Winter NAO index and total annual rainfall (August–July) show a significant negative correlation for the period 1966–2000 in our study area (Pearson product-moment correlation $r = -0.644$, $P < 0.0001$, $n = 35$) ($r = -0.756$, $P < 0.0001$, $n = 35$, winter NAO index with rainfall from December to March). Years with positive values of the winter NAO index are dryer than those with negative values. For each response variable we tested the significance of the climatic predictor (winter NAO index or annual rainfall) by removal from a

GLM model containing colony, the climatic predictor and its interaction. There were no significant interactions between the colony and winter NAO index or annual rainfall. The winter NAO index was a significant predictor of mean number of chicks per successful nest ($F_{1,49} = 9.64, P = 0.003$), mean number of female chicks per occupied nest ($F_{1,49} = 10.46, P = 0.002$), mean number of female chicks per female ($F_{1,49} = 4.72, P = 0.03$), and nestling body condition ($F_{1,49} = 11.70, P = 0.001$) but not of occupancy rate ($F_{1,49} = 0.22, P = 0.6$) or nest success rate ($F_{1,49} = 3.34, P = 0.07$). Annual rainfall was a significant predictor of nest success rate ($F_{1,49} = 7.33, P = 0.009$), mean number of chicks per successful nest ($F_{1,49} = 21.78, P < 0.0001$), mean number of female chicks per occupied nest ($F_{1,49} = 25.74, P < 0.0001$), mean number of female chicks per female ($F_{1,49} = 16.16, P = 0.0002$) and nestling body condition ($F_{1,49} = 14.91, P = 0.0003$) but not of occupancy rate ($F_{1,49} = 0.17, P = 0.7$). For all response variables the winter NAO index explained less variance than annual rainfall, and the latter less variance than other meteorological predictors (rainfall or temperature), measured locally in periods related to the lesser kestrel breeding cycle (Table 7).

TEMPORAL TRENDS IN CLIMATE

From 1966 to 2000 the total amount of rainfall in the period with some influence on lesser kestrel reproduction (October–June) has shown a marginally significant decline (regression slope $b = -26.68, F_{1,201} = 3.7, P = 0.056$). There is no significant difference in trend among colonies ($F_{5,196} = 0.33, P = 0.89$) nor a difference among colonies in mean rainfall ($F_{5,201} = 1.85, P = 0.10$). Rainfall in the winter period (October–January), before lesser kestrels arrive from their winter quarters, shows no particular temporal trend ($F_{1,201} = 1.17, P = 0.28$). Rainfall in spring (February–May), in the period from arrival to egg-laying, has declined very significantly ($b = -34.54, F_{1,201} = 37.84, P < 0.0001$) and rainfall in June has also declined significantly corresponding to incubation and nestling periods ($b = -5.7, F_{1,201} = 14.98, P = 0.0001$). Mean temperature in April–May (courtship period), the only temperature entering a model, has increased ($b = 0.25, F_{1,165} = 13.82, P = 0.0003$), but the trend differs significantly between colonies ($F_{5,164} = 9.33, P < 0.0001$).

TEMPORAL TRENDS IN PREDICTED POPULATION GROWTH RATE

The predictions of the different demographic models explained between 63.8 and 70.46% of the variation in observed population growth rate (λ) of our colonies from 1988 to 2000 (Appendix I). Mean predicted values of λ for each colony during the study period were significantly correlated with the slope of a linear regression fitted to the number of occupied nest ($r = 0.91, P = 0.01, n = 6$).

In the period 1966–2000 the predicted value of λ of the six lesser kestrel colonies we have studied has not declined significantly because of climate change (Fig. 6). According to Model 1 the decline in rainfall in the period February to June and the increase in temperature in April–May would have resulted in a significant increase in λ ($F_{1,164} = 7.51, P = 0.007$). All the other models indicate that there has been no significant change in λ attributable to the effect of climate change on fertility [Model 2 ($F_{1,196} = 0.13, P = 0.71$), Model 3 ($F_{1,196} = 0.002, P = 0.96$), Model 4 ($F_{1,196} = 0.0007, P = 0.98$)].

Discussion

Climate is one of the main factors influencing the geographical distribution of animals on Earth. Weather conditions have direct and indirect effects on survival and fertility and, by influencing demography, they can set the limits on where species can maintain stable populations.

The amount of variance of lesser kestrel breeding parameters explained by meteorological variables in our models (13.78–35.68%) indicates a very strong effect of weather on lesser kestrel fertility, taking into account that main effects in ecological models explain a mean 1.99–7.05% of variance (Møller & Jennions 2002). The amount of rain fallen during different parts of the lesser kestrel annual cycle is a good predictor of lesser kestrel fertility, but the influence of weather on breeding parameters is complex (Fig. 7). Rainfall has different effects depending on its amount and timing, and also influences differentially the three components of fertility we have considered: occupancy rate, nest success rate and mean number of chicks per successful nest. Considering these response variables independently

Table 7. Percentage of total (null) deviance explained by climatic variables when winter NAO index, annual rainfall or rainfall and temperature in different periods defined by the lesser kestrel phenology are used as predictors in GLM models for: OR = occupancy rate, NSR = nest success rate; CSN = chicks per successful nest; FCON = female chicks per occupied nest; FCF = female chicks per female, NBC = nestling body condition

Breeding parameters	OR	NSR	CSN	FCON	FCF	NBC
Winter NAO-index ¹	0.25	6.82	10.34	12.95	5.69	15.23
Annual rainfall	0.20	11.20	19.36	23.66	15.41	17.42
Rainfall & temperature in periods	13.79	35.68	35.58	33.57	29.78	26.84

¹Estimated from the increase in deviance when climatic variables were removed from a full model containing all significant climatic variables plus colony. Values in bold indicate models in which the corresponding climatic variables were statistically significant $P < 0.05$.

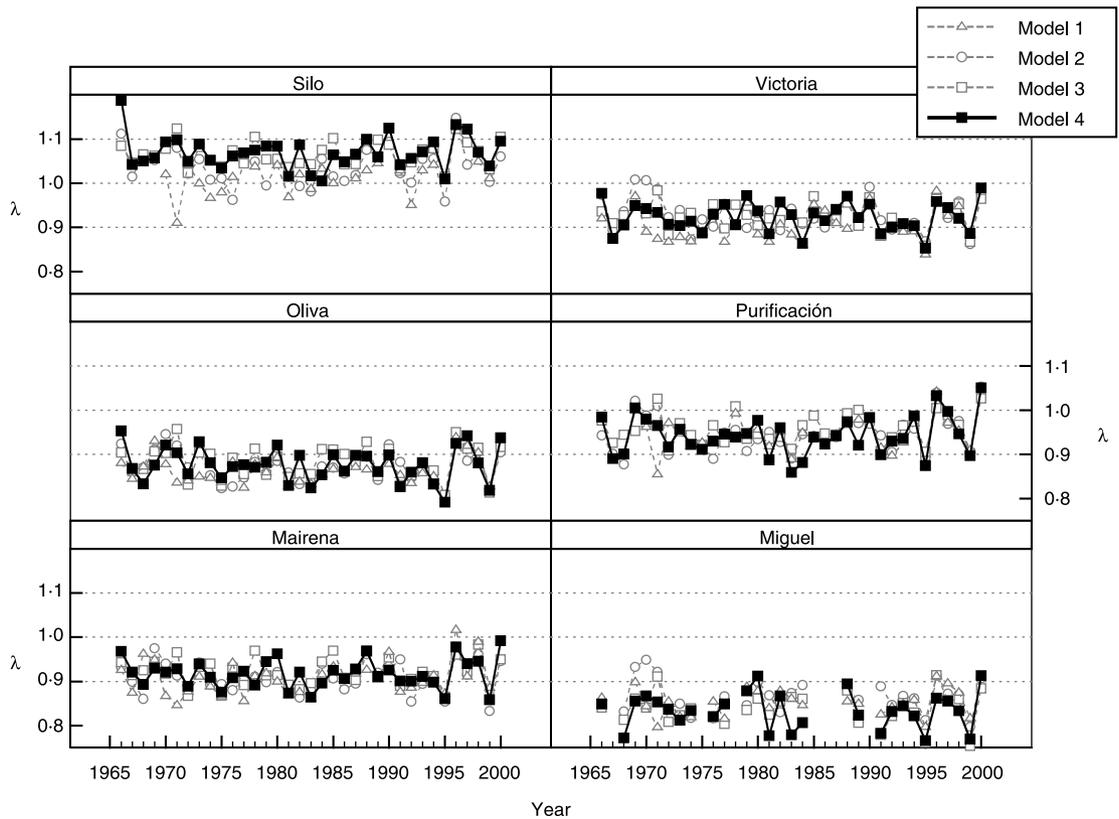


Fig. 6. Predicted λ for each year of the period 1966–2000 at the six lesser kestrel colonies. λ is estimated from a modification of Hiraldo *et al.*'s (1996) demographic model that incorporates the influence of weather on breeding success using the four different models described in Appendix I. The model with the highest explained variance (Model 4, $R^2 = 70.46\%$) is remarked. Gaps in the figure of Miguel colony are due to missing weather data.

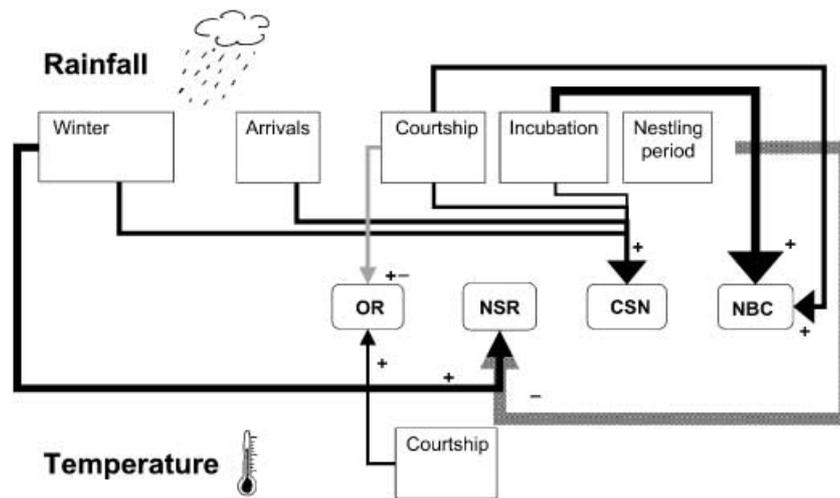


Fig. 7. Schematic diagram of the relationships among rainfall and temperature and lesser kestrel breeding parameters during the different periods of the breeding cycle. OR = occupancy rate, NSR = nest success rate, CSN = mean number of chicks per successful nest, NBC = nestling body condition. The arrow thickness is proportional to the amount of variance explained by each meteorological variable.

improves our understanding of the mechanisms by which weather influences breeding success. Occupancy rate indicates which fraction of potential nesting sites is used each year at a colony. Differences between colonies in mean occupancy rate as indicated

by our model are expected mainly due to differences in mean number and quality of available nesting sites and colony population size. A colony such as the Silo offers a relatively reduced number of very high quality potential nesting sites in an area of good foraging habitat and

tends to have occupancy rates close to 1, while the colony in the castle of Mairena offers a large number of potential sites of heterogeneous quality and mean occupancy rate is around 0.3. Annual variation in the relative occupancy rate of a colony could reflect fluctuations in population size or variations in the fraction of potential breeders that actually breed. It is known in raptors that not all potential breeders will initiate reproduction every year (Newton 1979; Newton 1989; Kenward *et al.* 2000). Most lesser kestrels start breeding at the age of 2 years. The fact that neither previous year productivity, nor productivity 2 years before, nor mean productivity of the two previous years (of the colony or of the metapopulation as a whole) had any influence in occupancy rate, suggest that occupancy rate does not reflect changes in colony population size – it does not respond to variations in the number of first breeders attempting to breed as a result of previous years reproductive success – and so there must be a variable fraction of nonbreeders in the population that varies with weather conditions in spring. According to our model, differences among colonies and weather during the courtship period, the period previous to egg laying, explain around 60% of the variation in occupancy rate. Occupancy rate increases with high minimum temperatures and moderate rainfall (up to 84 mm) during the courtship period. High minimum temperatures might speed up insect cycles and increase food available for the kestrels. Dry springs may be associated with limited vegetation growth and low prey abundance with the effect that some lesser kestrels would not reach the body condition necessary to start reproduction. An experiment by Frampton, Van den Brink & Gould (2000) in southern Britain, shielding agricultural parcels from rain, demonstrates that spring drought reduces the availability of arthropod prey in arable land. On the other hand, dry springs, despite prey abundance, could serve as a proximal cue for the kestrels to future poor breeding success, and some individuals could decide not to invest in breeding. Rainy springs, although predicting high breeding success (see models for chicks per successful nest and nestling body condition), have reduced occupancy rates. Heavy rainfall in spring could deteriorate foraging conditions or prey availability for the kestrels before egg laying, as it has been observed in other raptor species (Rijnsdorp *et al.* 1981; Dawson & Bortolotti 2000).

Nest success rate indicates the fraction of breeding attempts that do not fail completely. Complete breeding failure can be attributed mainly to nest desertion, hatching failures and nest predation (usually total failures). Weather is able to explain 36% of nest success rate; probably because losses due to predators and hatching failures are not related to weather. There were no significant differences between colonies. Our study colonies have few natural predators (Tella *et al.* 1996). However, they suffer disturbance by humans that is highly variable among years, depending on rehabilitation activities at each building. Disturbance leads to

clutch desertion and an increased mortality of recently hatched chicks. Hatching failures are probably not related to weather in spring because nesting sites are always sheltered from the rain and temperatures are mild. Winter rainfall may influence prey availability during incubation, and dry winters will increase the number of birds forced to quit incubation to forage when prey abundance is low. Rainfall during the nestling period has a negative influence on nest success rate. It is likely that rainy days at the time of hatching cause temporal declines in foraging activity, as has been seen in the American kestrel *F. sparverius* (Dawson & Bortolotti 2000) and in the hen harrier *Circus cyaneus* (Redpath *et al.* 2002), or in prey availability, causing mortality of complete clutches of recently hatched chicks.

Chicks per successful nest is the breeding parameter that our models predict the best. The lesser kestrel lays a relative constant clutch size (4–5 eggs) (Aparicio 1997), but fledges 1–5 chicks (the mean number of chicks per successful nest ranged from 1.1 to 4.3 in this study) depending on weather conditions. Rainfall is the main meteorological factor affecting the mean number of chicks per successful nest. Although total accumulated rainfall is a good predictor of this variable, a model that considers the amount of rainfall in different periods improves prediction in approximately 20% (Table 7). Most of the rainfall in our study area falls in winter (63% of annual rainfall) but the effect of 1 mm of spring rainfall on chicks fledged per successful nest is five times higher than the effect of 1 mm of rainfall in winter (Table 3). The lesser kestrel hunts frequently over margins of roads, crop edges, stream banks and fallow lands (Donázar, Negro & Hiraldo 1993), where annual plants can be found. Winter rainfall percolates to deep soil strata, where is less available for the short roots of annual plants. Spring rainfall occurs just when most annual plants are growing from seeds, being more available than water stored at deeper soil layers. As kestrels feed mainly on Orthoptera, which are mainly herbivorous insects (Bock, Bock & Grant 1992), the higher the growth of annual plants the higher the availability of prey. There was a negative but not significant effect of rain during the nestling period on the number of chicks per successful nest, probably because rain at this time is very rare (on average 1 rainy day or 9 mm of accumulated rainfall during the whole period), and large chicks will eventually recover from a short temporal reduction in prey availability (Negro, Chastin & Bird 1994). Differences among colonies in mean number of chicks per successful nest could be attributed to differences in land-use that result in differences in the proportion of good foraging habitats around each colony.

Nestling body condition is probably a good indicator of survival probability (Magrath 1991; Møller 2002). Colony together with weather (especially spring rainfall) explain 50% of the variation in condition. Late spring rainfall (courtship and incubation) is more relevant than winter or early spring precipitation (arrivals) in determination of fat reserves in nestlings. Once

corrected for weather conditions, differences among colonies in nestling body condition show a positive, although not significant, correlation because of the small sample size (Spearman's rank correlation $r_s = 0.71$, $P = 0.11$, $n = 6$), with the differences observed in chicks fledged per successful nest. Differences in land-use around the colonies could be responsible for the quality of foraging habitat and lead to differences in the average number and in body condition of chicks raised.

In general, rainfall has a positive effect on lesser kestrel breeding success (as can be deduced from the models based on annual rainfall or winter NAO index), and this agrees with the geographical distribution of the species in Mediterranean Spain, which tends to disappear progressively towards the more arid south-east (González & Merino 1990). A predictive model for lesser kestrel distribution in Andalusia, southern Spain (Bustamante 1997), also showed that the annual rainfall showed a positive correlation with the probability of colony presence and a negative correlation with the probability of colony extinction. This positive effect of rainfall on lesser kestrel reproduction is in contrast with most previous studies of the effect of rainfall on raptors, that have found only negative effects (Cavé 1968; Davis & Newton 1981; Newton 1986; Kostrzewa & Kostrzewa 1991; Dawson & Bortolotti 2000), even for species in arid ecosystems (Gargett 1977; Olsen & Olsen 1992; Steenhof *et al.* 1999), with only a few exceptions in desert areas (Hustler & Howells 1986, 1989; Bahat & Mendelsohn 1996). This highlights the importance of considering weather along a complete annual cycle, as rainfall and temperature can have contrasting effects. Indirect effects of previous weather conditions may override the effect of weather during the breeding season. Equivalent contrasting effects of climatic conditions on the demography of a species have been found in some species. Barbraud & Weimerskirch (2001) found in the emperor penguin *Aptenodytes forsteri* that when sea surface temperature (SST) increases and sea ice extent decreases, adult survival decreases but breeding success at the colony increases. Years with harsh winter weather, with a positive winter NAO index, are associated with lower fertility in Soay sheep *Ovis aries* in St Kilda, but individuals born after a harsh winter benefit from lower population density and better foraging conditions and have higher survival and lifetime reproductive success (Forchhammer *et al.* 2001).

It is to be expected that rainfall will have a net positive effect on fecundity in arid climates by influencing food abundance (Sillet, Holmes & Sherry 2000), and recent studies with passerines (Grant *et al.* 2000; Morrison & Bolger 2002) indicate that this is so. Also in Mediterranean ecosystems, rainfall is the main factor limiting productivity (Valverde 1967; Soriguer 1981).

The NAO has a profound influence on the climate of western Europe in winter and many recent studies have used the winter NAO index as a proxy of annual weather conditions to study its effect on demography of birds (Przybylo *et al.* 2000; Sanz 2002b) or mammals

(Forchhammer *et al.* 2001). Although the NAO has a significant influence on rainfall in the Mediterranean, the winter NAO index is a significant but poor predictor of kestrel fertility, and some demographic parameters (e.g. occupancy rate), that seem to be influenced by weather conditions, cannot be predicted directly from the winter NAO index. Annual rainfall recorded locally at the colony is a better predictor than the winter NAO index, probably because it takes into account local differences in rainfall among colonies. Our models indicate that predictions improve substantially when both the amount and the timing of rainfall in relation to the lesser kestrel annual cycle are considered, probably because in this way the contrasting effects of rainfall in reproduction are accounted for. In a similar way, Ringsby *et al.* (2002) found that in an insular metapopulation of house sparrows *Passer domesticus* differences in the onset of breeding among populations influenced the way in which the autocorrelated daily weather conditions affected the demography of each subpopulation.

Rainfall pattern in our study area has changed during the last 35 years. The reduction in spring rainfall observed agrees with an observed general reduction in annual rainfall in the Mediterranean from 1901 to 2000 (IPCC 2002) and also with what the climate change models predict for this area (IPCC 2002). According to Borén *et al.* (2000), the climatic models for the Iberian Peninsula indicate that rainfall will increase in winter and decrease in spring, summer and autumn. From a simplistic point of view, any reduction in rainfall should be considered negative for the lesser kestrel, and a model based on annual rainfall (or in the winter NAO index) would predict a negative effect on demography of a reduction in rainfall (or a positive winter NAO phase). Rainfall has decreased in spring, a period in which rain has contrasting effects on demography. Too much or too little rain in spring has a negative effect on reproduction (mainly by influencing the fraction of females that start breeding). Rain has also decreased in June, a time in which rain has apparently only negative effects. By using our models to predict the expected population growth rate of the different colonies in the last 35 years we observe that the reduction in spring rainfall has not had any significant effect in lesser kestrel demography, and so the recorded species decline must have been due to other factors.

Conclusions

The relationship between annual weather and lesser kestrel breeding success has been documented and parameterized in this paper. Rainfall is an important predictor of various breeding parameters having, in general, a positive effect on reproduction. This is something that was expected because rainfall is the main limiting factor of productivity in Mediterranean climates. Dry winters are associated with high rates of total breeding failure while dry springs will result in low number of chicks at successful nests and chicks

fledging in poor body condition. Rainfall, despite having a net positive effect on lesser kestrel breeding, has contrasting effects in certain periods. The proportion of females attempting to breed is negatively affected by rainfall in the period previous to egg laying if the amount of rainfall goes over a 84-mm threshold. However, rain in spring is positive for the number of chicks fledged at successful nests and especially for nestling body condition. This contrasting effect of rainfall is probably responsible for the lack of influence on the lesser kestrel demography of the reduction in rainfall in spring that has been observed in the last 35 years.

Acknowledgements

We thank Fernando Hiraldo, José Antonio Donázar and Juan José Negro for access to historical breeding data of some of the colonies. Manuel de la Riva, Yolanda Menor, José María Bermúdez, Juan Luis Barroso, Adolfo Osés and Manuel Calvo helped us during the fieldwork. The Instituto Nacional de Meteorología (Spain) provided meteorological information. This research has been funded partially by the projects PB96-0855, PB97-1154 and REN2001-2134/GLO of CICYT and FEDER funds of the EU. C.R. was supported by a doctoral fellowship from the Spanish Ministerio de Ciencia y Tecnología. We also thank David Serrano, Gary Bortolotti, Javier Seoane, José Luis Tella, Juan José Negro, Miguel Delibes and Ricardo Díaz-Delgado for their valuable comments on a previous version of the manuscript.

References

- Aparicio, J.M. (1997) Cost and benefits of surplus offspring in the lesser kestrel (*Falco naumanni*). *Behavioural Ecology and Sociobiology*, **41**, 129–137.
- Bahat, O. & Mendelsohn, H. (1996) The long-term effect of precipitation on the breeding success of golden eagles in the Judean and Negev deserts, Israel. *Eagle Studies* (eds B.-U. Meyburg & R.D. Chancellor), pp. 517–522. WWGBP, London/Paris.
- Barbraud, C. & Weimerskirch, H. (2001) Emperor penguins and climate change. *Nature*, **411**, 183–185.
- Bernis, F. (1980) *La Migración de Las Aves En El Estrecho de Gibraltar*. Universidad Complutense de Madrid, Madrid.
- Biber, J.P. (1990) *Action Plan for the Conservation of Western Lesser Kestrel Falco Naumanni Populations*. ICBP, Cambridge.
- Bijleveld, M. (1974) *Birds of Prey in Europe*. Macmillan Press, London.
- Bock, C.E., Bock, J.H. & Grant, M.C. (1992) Effects of bird predation on grasshopper densities in an arizona grassland. *Ecology*, **73**, 1706–1717.
- Borón, R., Ribalaygua, J., Benito, L. & Balairón, L. (2000) Escenarios climáticos. 3. Escenarios de alta resolución para España a partir de un experimento HadCM2. *El Cambio Climático* (ed. L. Balairón), pp. 459–462. Servicio de Estudios del BBVA, Madrid.
- Bradley, M., Johnstone, R., Court, G. & Duncan, T. (1997) Influence of weather on breeding success of peregrine falcons in the Arctic. *Auk*, **114**, 786–791.
- Bustamante, J. (1997) Predictive models for lesser kestrel *Falco naumanni* distribution, abundance and extinction in southern Spain. *Biological Conservation*, **80**, 153–160.
- Bustamante, J. & Negro, J.J. (1994) The post-fledging dependence period of the lesser kestrel (*Falco naumanni*) in southwestern Spain. *Journal of Raptor Research*, **28**, 158–163.
- Caswell, H. (1989) *Matrix Population Models*. Sinauer, Sunderland, MA.
- Cavé, A.S. (1968) The breeding of the kestrel, *Falco tinnunculus* in the reclaimed area of Oostelijk Flevoland. *Netherlands Journal of Zoology*, **18**, 313–407.
- Clarke, J.A. & Johnson, R.E. (1994) The influence of spring snow depth on White-tailed ptarmigan breeding success in the Sierra Nevada. *Condor*, **94**, 622–627.
- Cramp, S. & Simmons, K.E.L. (1980) *Handbook of the Birds of Europe, the Middle East and North Africa*. Oxford University Press, Oxford.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Cucco, M., Malacarne, G., Orecchia, G. & Boano, G. (1992) Influence of weather conditions on pallid swift *Apus pallidus* breeding success. *Ecography*, **15**, 184–189.
- Davis, P.E. & Newton, I. (1981) Population and breeding of red kites in Wales over a 30-year period. *Journal of Animal Ecology*, **50**, 759–772.
- Dawson, R.D. & Bortolotti, G.R. (2000) Reproductive success of American kestrels: the role of prey abundance and weather. *Condor*, **102**, 814–822.
- Donázar, J.A., Negro, J.J. & Hiraldo, F. (1992) Functional analysis of mate-feeding in the lesser kestrel *Falco naumanni*. *Ornis Scandinavica*, **23**, 190–194.
- Donázar, J.A., Negro, J.J. & Hiraldo, F. (1993) Foraging habitat selection, land-use changes and population decline in the lesser kestrel *Falco naumanni*. *Journal of Applied Ecology*, **30**, 515–522.
- Dufva, R. & Allander, K. (1996) Variable effects of the hen flea *Ceratophyllus gallinae* on the breeding success of the great tit *Parus major* in relation to weather conditions. *Ibis*, **138**, 772–777.
- Erikstad, K.E. & Andersen, R. (1983) The effect of weather on survival, growth rate and feeding time in different sized willow grouse broods. *Ornis Scandinavica*, **14**, 249–252.
- Erikstad, K.E. & Spidso, T.K. (1982) The influence of weather on food intake, insects prey selection and feeding behaviour in willow grouse chicks in northern Norway. *Ornis Scandinavica*, **13**, 176–182.
- Forchhammer, M.C., Clutton-Brock, T.H., Lindström, J. & Albon, S.D. (2001) Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology*, **70**, 721–729.
- Forchhammer, M.C., Post, E. & Stenseth, N.C. (2002) North Atlantic Oscillation timing of long- and short-distance migration. *Journal of Animal Ecology*, **71**, 1002–1014.
- Frampton, G.K., Van den Brink, P.J. & Gould, P.J.L. (2000) Effect of spring drought and irrigation on farmland arthropods in southern Britain. *Journal of Applied Ecology*, **37**, 865–883.
- Franco, A. & Andrada, J. (1977) Alimentación y selección de presa en *Falco naumanni*. *Ardeola*, **23**, 137–187.
- García, J. (2000) Dispersión premigratoria del Cernicalo Primilla *Falco naumanni* en España. *Ardeola*, **47**, 197–202.
- Gargett, V. (1977) A 13-year population study of the black eagles in the Matopos, Rhodesia, 1964–76. *Ostrich*, **48**, 17–27.
- Garzón, J. (1977) Birds of prey in Spain. The present situation. *World Conference on Birds of Prey. Report of Proceedings* (ed. International Council for Bird Preservation), pp. 159–170. International Council for Bird Preservation, Cambridge, UK.
- González, J.L. & Merino, M. (1990) El cernicalo primilla (*Falco naumanni*) en la Península Ibérica. *Situación, Problemática Y Aspectos Biológicos*. ICONA, Madrid.
- Grant, P.R., Grant, B.R., Keller, L.F. & Petren, K. (2000) Effects of El Niño events on Darwin's finch productivity. *Ecology*, **81**, 2442–2457.

- Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized Additive Models*. Chapman & Hall, London.
- Hiraldo, F., Negro, J.J., Donazar, J.A. & Gaona, P. (1996) A demographic model for a population of the endangered lesser kestrel in southern Spain. *Journal of Animal Ecology*, **33**, 1085–1093.
- Hurrell, J.W. & van Loon, H. (1997) Decadal variations in climate associated with the North Atlantic Oscillation. *Climate Change*, **36**, 301–326.
- Hustler, K. & Howells, W.W. (1986) A population study of tawny eagles in the Hwange National park, Zimbabwe. *Ostrich*, **57**, 101–106.
- Hustler, K. & Howells, W.W. (1989) Habitat preference, breeding success and the effect of primary productivity on tawny eagles *Aquila rapax* in the tropics. *Ibis*, **131**, 33–40.
- Intergovernmental Panel of Climate Change (IPCC) (2001) *Climate change 2001: the scientific basis. Third Assessment Report of Working Group I* (eds D.L. Albritton & L.G. Meira Filho). Cambridge University Press, Cambridge.
- Intergovernmental Panel of Climate Change (IPCC) (2002) *Climate Change and Biodiversity. IPCC Technical Paper V* (eds H. Gitay, A. Suárez, T. Watson & D.J. Dokken). WMO-UNEP. <http://www.ipcc.ch/pub/tpbiodiv.pdf>
- Kenward, R.E., Walls, S.S., Hodder, K.H., Pahkala, M., Freeman, S.N. & Simpson, V.R. (2000) The prevalence of non-breeders in raptor populations: evidence from radio-tagging and survey data. *Oikos*, **91**, 271–279.
- Kostrzewa, R. & Kostrzewa, A. (1991) Winter weather, spring and summer density, and subsequent breeding success of Eurasian kestrels, common buzzards, and northern goshawk. *Auk*, **108**, 342–347.
- Lamb, P.J. & Pepler, R.A. (1987) The North Atlantic Oscillation: concept and application. *Bulletin of the American Meteorological Society*, **68**, 1218–1225.
- Leslie, P.H. (1945) On the use of matrices in certain population mathematics. *Biometrika*, **33**, 67–118.
- Lewis, E.G. (1942) On the generation and growth of a population. *Saukhya: the Indian Journal of Statistics*, **6**, 93–96.
- Magrath, R.D. (1991) Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *Journal of Animal Ecology*, **60**, 335–351.
- McCullagh, P. & Nelder, J.A. (1989) *Generalised Linear Modelling*, 2nd edn. Chapman & Hall, London.
- Mearns, R. & Newton, I. (1988) Factors affecting breeding success of peregrines in South Scotland. *Journal of Animal Ecology*, **57**, 903–916.
- Milsom, T.P. (1987) Aerial insect-hunting by hobbies *Falco subbuteo* in relation to weather. *Bird Study*, **34**, 179–184.
- Møller, A.P. (2002) North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *Journal of Animal Ecology*, **71**, 201–210.
- Møller, A.P. & Jennions, M.D. (2002) How much variance can be explained by ecologists and evolutionary biologists? *Oecologia*, **132**, 492–500.
- Morrison, S.A. & Bolger, D.T. (2002) Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia*, **133**, 315–324.
- Moss, R., Oswald, J. & Baines, D. (2001) Climate change and breeding success: decline of the capercaillie in Scotland. *Journal of Animal Ecology*, **70**, 47–61.
- Murray, D.L., Keith, L.B. & Cary, J.R. (1998) Do parasitism and nutritional status interact to affect production in snowshoe hares? *Ecology*, **79**, 1209–1222.
- Negro, J.J. (1991) *Ecología de Poblaciones Del Cernicalo Primilla Falco Naumanni*. PhD thesis, Universidad de Sevilla, Sevilla.
- Negro, J.J., Chastin, A. & Bird, D.M. (1994) Effects of short-term food deprivation on growth of hand-reared American kestrels. *Condor*, **96**, 749–760.
- Negro, J.J., de la Riva, M.J. & Bustamante, J. (1991) Patterns of winter distribution and abundance of lesser kestrels in Spain. *Journal of Raptor Research*, **25**, 30–35.
- Negro, J.J., Donazar, J.A. & Hiraldo, F. (1992) Copulatory behaviour in a colony of lesser kestrels: sperm competition and mixed reproductive strategies. *Animal Behaviour*, **43**, 921–930.
- Negro, J.J. & Hiraldo, F. (1992) Sex ratios in broods of the lesser kestrel, *Falco naumanni*. *Ibis*, **134**, 190–191.
- Negro, J.J. & Hiraldo, F. (1993) Nest site selection and breeding success in the lesser kestrel. *Bird Study*, **40**, 115–119.
- Negro, J.J., Hiraldo, F. & Donazar, J.A. (1997) Causes of natal dispersal in the lesser kestrel: inbreeding avoidance or resource competition? *Journal of Animal Ecology*, **66**, 640–648.
- Newton, I. (1979) *Population Ecology of Raptors*. T. & A.D. Poyser, Berkhamsted.
- Newton, I. (1986) *The Sparrowhawk*, 1st edn. T. & A.D. Poyser, Calton.
- Newton, I. (1989) *Lifetime Reproductive Success in Birds*. Academic Press, London.
- Olsen, P.D. & Olsen, J. (1989a) Breeding of the peregrine falcon *Falco peregrinus*. III. Weather, nest quality and breeding success. *Emu*, **89**, 6–14.
- Olsen, P.D. & Olsen, J. (1989b) Breeding of the peregrine falcon *Falco peregrinus*. II. Weather, nest quality and the timing of egg laying. *Emu*, **89**, 1–5.
- Olsen, P. & Olsen, J. (1992) Does rain hamper hunting by breeding raptors? *Emu*, **92**, 184–187.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C. & Stenseth, N.C. (2001) Ecological effects of the North Atlantic Oscillation. *Oecologia*, **128**, 1–14.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tonnent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.
- Peñuelas, J., Filella, I. & Comas, P. (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology*, **8**, 531–544.
- Przybylo, R., Sheldon, B.C. & Merilä, J. (2000) Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *Journal of Animal Ecology*, **69**, 395–403.
- Redpath, S.M., Arroyo, B.E., Etheridge, B., Leckie, F., Bouwman, K. & Thirgood, S.J. (2002) Temperature and hen harrier productivity: from local mechanisms to geographical patterns. *Ecography*, **25**, 533–540.
- Rijnsdorp, A., Daan, S. & Dijkstra, C. (1981) Hunting in the kestrel, *Falco tinnunculus* and the adaptive significance of daily habits. *Oecologia*, **50**, 391–406.
- Ringsby, T.H., Sæther, B., Tufto, J., Jensen, H. & Solberg, E.J. (2002) Asynchronous spatiotemporal demography of a house sparrow metapopulation in a correlated environment. *Ecology*, **83**, 561–569.
- Sæther, B., Tufto, J., Engen, S., Jerstad, K., Røstad, O.W. & Skåtan, J.E. (2000) Population dynamical consequences of climate change for a small temperate songbird. *Science*, **287**, 854–856.
- Sakamoto, Y., Ishiguro, M. & Kitigawa, G. (1986) *Akaike Information Criterion Statistics*. D. Reidel Publishing Co., Tokyo.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Hueneke, L.F., Jackson, R.B., Kinzing, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global diversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Sanz, J.J. (2002a) Climate change and birds: have their ecological consequences already been detected in the Mediterranean region? *Ardeola*, **49**, 109–120.
- Sanz, J.J. (2002b) Climate change and breeding parameters of great and blue tits throughout the Western Palearctic. *Global Change Biology*, **8**, 409–422.
- Sillet, T.S., Holmes, R.T. & Sherry, T.W. (2000) Impacts of a

- global climate cycle on population dynamics of a migratory songbird. *Science*, **288**, 2040–2042.
- Soriguer, R.C. (1981) Biología y dinámica de una población de conejos (*Oryctolagus cuniculus* L.) en Andalucía occidental. *Doñana, Acta Vertebrata*, **8**, 1–379.
- Steen, J.B., Steen, H., Stenseth, N.C., Myrberget, S. & Marström, V. (1988) Microtine density and weather as predictors of chick production in willow ptarmigan, *Lagopus l. lagopus*. *Oikos*, **51**, 367–373.
- Stenhof, K., Kochert, M.N., Carpenter, L.B. & Lehman, R.N. (1999) Long-term prairie falcon population changes in relation to prey abundance, weather, land uses, and habitat conditions. *Condor*, **101**, 28–41.
- Tella, J.L., Hiraldo, F., Donazar, J.A. & Negro, J.J. (1996) Cost and benefits of urban nesting in the lesser kestrel. *Raptors*

- in Human Landscapes: Adaptations to Built and Cultivated Environments* (eds D.M. Bird, D. Varland & J.J. Negro), pp. 53–60. Academic Press, London.
- Valverde, J.A. (1967) *Estructura de Una Comunidad de Vertebrados Terrestres*. CSIC, Madrid.
- Village, A. (1990) *The Kestrel*. T. & A.D. Poyser, London.
- Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wiklund, C.G. & Stigh, J. (1986) Breeding densities of snowy owls *Nyctea scandiaca* in relation to food, nest sites and weather. *Ornis Scandinavica*, **17**, 268–274.

Received 7 February 2003; accepted 6 May 2003

Appendix I

Details of the models used to incorporate the effect of annual weather conditions in the period 1966–2000 in the demographic model from Hiraldo *et al.* (1996).

MODEL 1

In this model ($R^2 = 64.29\%$) c in eqn 2 is substituted by the fraction of adults females that breed at colony i in year t , $c_{i,t} = OR_{i,t}/OR_{i,maximum}$, $OR_{i,t}$ being the predicted occupation rate and $OR_{i,maximum}$ the maximum occupation rate recorded in colony i in the period 1998–2000, and the female fertility b is substituted by: $b_{i,t} = NSR_{i,t} * CSN_{i,t} * 0.5$, $NSR_{i,t}$ being the predicted nest success rate and $CSN_{i,t}$ the mean number of chicks per successful nest at colony i in year t . Other demographic parameters are assumed to be colony and time invariant and taken from Hiraldo *et al.* (1996): $c_0 = 0.3847$, $s_0 = 0.3409$, $s = 0.7101$. The models used for OR , NSR and CSN are linear models equivalent to those in Tables 1–3, after refitting the parameters to rainfall records using monthly values and using mean temperature in April–May (T April.May) instead of courtship mean minimum temperature. Rainfall (R) October–January substitutes winter rainfall, rainfall February–March substitutes arrival rainfall, rainfall April–May, substitutes courtship rainfall, rainfall May substitutes incubation rainfall and rainfall June substitutes nestling period rainfall. So new models are:

$$OR = Colony + poly(R \text{ April.May}, 2) + T \text{ April.May}$$

$$NSR = R \text{ October.January} + R \text{ June}^1$$

$$CSN = Colony + R \text{ October.January} \\ + R \text{ February.March} + R \text{ April} + R \text{ May}$$

¹ The effect of $R \text{ June}$ is constant when > 20 mm.

MODEL 2

In this model ($R^2 = 63.80\%$) demographic parameters in eqn 2 are the same as in Model 1. To consider the possibility that the effect of rainfall was not linear and

not independent of when it took place, within each period, the models for OR , NSR and CSN use cubic smoothing splines with 3 d.f. to fit the response to rainfall in each month independently, so that $s(R \text{ October}, 3)$ indicates the fitting of a cubic smoothing spline with 3 d.f. to rainfall in October.

$$OR = Colony + s(R \text{ April}, 3) + s(R \text{ May}, 3) \\ + \text{Courtship minimum temperature}^2$$

$$NSR = s(R \text{ October}, 3) + s(R \text{ November}, 3) \\ + s(R \text{ December}, 3) + s(R \text{ January}, 3) \\ + s(R \text{ June}, 3)$$

$$CSN = Colony + s(R \text{ October}, 3) + s(R \text{ November}, 3) \\ + s(R \text{ December}, 3) + s(R \text{ January}, 3) \\ + s(R \text{ February}, 3) + s(R \text{ March}, 3) \\ + s(R \text{ April}, 3) + s(R \text{ May}, 3)$$

² We assume that courtship minimum temperature is invariant.

MODEL 3

In this model ($R^2 = 64.22\%$) the term cb in eqn 2 is estimated directly from FCF (the model for number of female chicks per adult female, Table 5) and c_0b , the number of female chicks per yearling female is estimated as $FCF * (0.3409/0.9250)$, assuming that the ratio yearling/adult females (c_0/c) breeding at the colony is constant and the same observed by Hiraldo *et al.* (1996), $c = 0.9250$, $c_0 = 0.3409$. Other demographic parameters are assumed to be colony and time invariant and also taken from Hiraldo *et al.* (1996), $s_0 = 0.3409$, $s = 0.7101$. The model used for FCF is the linear equivalent to the one in Table 5, after refitting the parameters to rainfall records as monthly values. Rainfall (R) October–January substitutes winter rainfall, and rainfall April–May substitutes courtship rainfall. So the new model is:

$$FCF = Colony + R \text{ October.January}^3 \\ + poly(R \text{ April.May}, 2)$$

³ The effect of $R \text{ October.January}$ is constant when > 400 mm.

MODEL 4

In this model ($R^2 = 70.46\%$) the term cb in eqn 2 is estimated directly from FCF and c_0b , the number of female chicks per yearling female is estimated as $FCF * (0.3409/0.9250)$, as in model 3, assuming that the ratio yearling/adult females (c_0/c) breeding at the colony is constant and the same observed by Hiraldo *et al.* (1996), $c = 0.9250$, $c_0 = 0.3409$. Other demographic parameters are assumed to be colony and time invariant and also taken from Hiraldo *et al.* (1996), $s_0 = 0.3409$, $s = 0.7101$.

To consider the possibility that the effect of rainfall was not linear and not independent of when it took place, within each period, the model used for FCF uses cubic smoothing splines with 3 d.f. to fit the response to rainfall in each month independently, so that $s(R\ October, 3)$ indicates the fitting of a cubic smoothing spline with 3 d.f. to rainfall in October. The new model is:

$$FCF = Colony + s(R\ October, 3) \\ + s(R\ November, 3) + s(R\ December, 3) \\ + s(R\ January, 3) + s(R\ April, 3) + s(R\ May, 3)$$