PII: S0006-3207(96)00136-X

*Biological Conservation* **80** (1997) 153–160
© 1997 Published by Elsevier Science Ltd
Printed in Great Britain. All rights reserved
0006-3207/97 $17.00+.00

# PREDICTIVE MODELS FOR LESSER KESTREL *Falco naumanni* DISTRIBUTION, ABUNDANCE AND EXTINCTION IN SOUTHERN SPAIN

Javier Bustamante

*Estación Biológica de Doñana, CSIC, Avda. María Luisa s/n, 41013, Sevilla, Spain*

(Received 9 March 1996; accepted 9 August 1996)

**Abstract**

*Environmental variables measured on 1:10,000 to 1:3,000,000-scale maps of southern Spain were used to build generalized linear models for presence/absence of lesser kestrel* Falco naumanni *colonies, extinction of colonies, and number of breeding pairs, in 6×6 km squares. Presence of breeding colonies in a square was positively associated with presence of urban areas, extent of non-irrigated cereal and sunflower crops, and mean annual rainfall, and negatively associated with extent of scrubland and forests. The model was statistically robust and had good predictive ability, correctly classifying 84% of the squares. Two alternative models were obtained for extinction of lesser kestrel colonies in a square. The first indicated extinctions where there were large areas of scrubland and low annual rainfall, and the second where there were very large or very small areas of non-irrigated cereal and sunflower crops. Although both were statistically significant, neither was very robust or had a good predictive ability. The number of lesser kestrel pairs breeding in a square showed a negative relationship with altitude, area of forest, and irrigated cultures, and a positive association with total length of rivers and streams. This model was not very robust and explained only 30·3% of the variance in kestrel numbers.*

*The models indicate that some climatic and land-use variables, as measured on the available maps, are good predictors of the presence of lesser kestrel colonies in southern Spain, but less good at predicting the probability of extinction of colonies or the number of breeding pairs. © 1997 Published by Elsevier Science Ltd. All rights reserved*

*Keywords:* lesser kestrel, southern Spain, predictive models, GLM models, extinction.

## INTRODUCTION

The lesser kestrel *Falco naumanni* is a small, hole-nesting, colonial falcon breeding in Europe in flat landscapes heavily transformed by agriculture (Cramp & Simmons, 1980). Breeding colonies tend to be located in buildings within towns and villages surrounded by cultivated landscapes (González & Merino, 1990).

During the last few decades, lesser kestrel populations in Europe have suffered a dramatic decline, including the Spanish population, which constitutes *c.* 60–70% of the western European population (Biber, 1990). At the end of the 1960s the Spanish population was estimated at 100,000 breeding pairs (Bijleveld, 1974). Apparently, there was a sharp decline during the 1970s with the population falling to 20,000–50,000 breeding pairs (González & Merino, 1990). By 1989 the estimated total breeding population in Spain had fallen to 5000 pairs, i.e. a loss of 95% in 20 years, with 42% of the population located in the Autonomous Community of Andalusia, southern Spain (González & Merino, 1990).

The causes of the decline are not well established. It has been attributed to a reduction in availability of nesting sites (caused by rehabilitation of old buildings and interspecific competition with other hole-nesting birds), to an increase in the use of agricultural pesticides, which are said to reduce egg fertility, and to changes in land use which are said to reduce the extent or the quality of foraging habitat (Cramp & Simmons, 1980; González & Merino, 1990). The influence of these factors on present lesser kestrel populations has been studied in detail in western Andalusia (Guadalquivir River Basin). The results of these studies indicate that reduction in nest availability (Forero *et al.*, 1997) and pollution with pesticides (Negro *et al.*, 1993*b*) are not the causes of the decline of lesser kestrels in this area. On the other hand, the reduction in the extent of adequate foraging habitats (natural pastures and fallow lands) during the recent decades (Donázar *et al.*, 1993*b*) could explain the decline of the species at a local scale in the Guadalquivir River Basin. It is important to know if these changes in land use are also responsible for the decline of the lesser kestrel at a regional scale.

If variables that identify land uses adequate for the lesser kestrel at a regional scale could be identified, it would be possible to predict how the population would respond to habitat modifications. This could help wildlife managers to evaluate the future effects of climate change or the Common Agricultural Policy of the European Union on this endangered species. Reintroduction projects that have already begun in some areas in Spain (Pomarol, 1993) could benefit from predictive models based on environmental variables that identify suitable areas for the release of the species.

This paper complements other works that studied habitat selection at a local scale in the same area (Donázar *et al.*, 1993*b*).

## STUDY AREA AND METHODS

The study area was the Autonomous Community of Andalusia, located in southern Spain. The area of 87,268 km$^2$ was divided into a regular 6×6 km square grid using the UTM grid reference system in zones 29 and 30 North. The size of the chosen grid square was based on the approximately 36 km$^2$ that constitute the foraging area of kestrels breeding at a colony of average size in the Guadalquivir River Valley (Negro *et al.*, 1993*a*).

To study the factors correlated with the present distribution of lesser kestrel colonies in Andalusia, I selected, at random, 51 squares among those thought to contain breeding colonies of the species in Andalusia based on the 1989 census (Negro *et al.*, 1990) and our knowledge of the area, and 50 squares among those thought not to contain breeding colonies. I had previously excluded from the sample all squares with a mean altitude >800 m above sea level (maximum altitude at which lesser kestrel colonies have been recorded in Andalusia) or with >25% of the square over the sea or outside the study area. In three of the 51 squares selected as with-kestrel areas no kestrels bred in 1993 or in 1994. In one of the 50 squares selected as without-kestrel areas, a colony was present in 1993 and 1994. Thus, the final sample consisted of 49 squares with kestrels and 52 without (Fig. 1).

To study the factors correlated with the extinction of breeding colonies we selected all squares for which historic records showed lesser kestrels breeding before 1989 and not breeding between 1989 and 1994; I rejected some squares in which the species may have bred sporadically between 1989 and 1994. This made a total of 30 squares that were compared with the 49 squares with kestrel colonies chosen at random (Fig. 1).

To study the factors correlated with lesser kestrel breeding density, a census was carried out in the spring of 1994 tallying the total number of lesser kestrel pairs breeding in the 51 squares chosen at random among those *a priori* with kestrels plus another seven neighbouring squares also holding breeding pairs. This made a total of 58 squares with information on breeding density. Where there was an estimate of the minimum and maximum number of breeding pairs in the

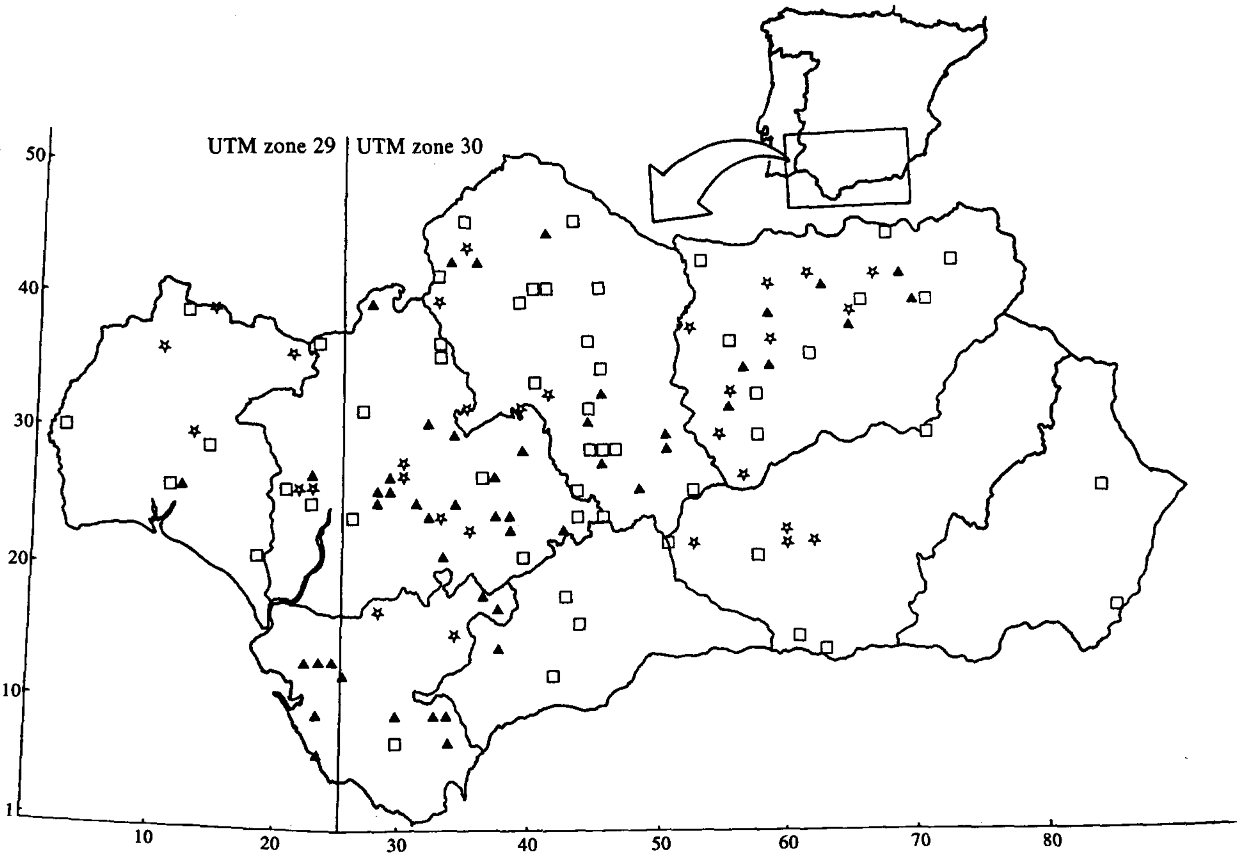

**Fig. 1.** Location of 49 squares with colonies (▲) and 52 without colonies (□), selected at random, and 30 squares with extinct colonies (☆).

square, I used the mean of these two values in the analyses.

### Census method

The census was carried out between 15 April and 7 May 1994. At this time females have yet to start incubating and males spend most of the time at the breeding colony defending their nest-hole, copulating with and courtship-feeding their mate. All places within the square capable of holding breeding pairs (cliffs, adequate buildings) were visited in the morning or in the evening. When all holes in the building or cliff were visible, the observers recorded the number of occupied nests. If not, they set off a firecracker, to make the kestrels fly. At some urban colonies in the Guadalquivir River Valley observations showed that occasional loud noises close to colonies made the birds fly for a short period of time without causing any other abnormal behaviour or detrimental effects. The number of breeding pairs at the colony was estimated as the maximum number of kestrels of the same sex or half the maximum number of unsexed kestrels counted simultaneously.

### Environmental variable selection

In every square, 19 environmental variables related to climate, topography, human influence, land cover and land use were measured (Table 1). These were chosen as having a direct or indirect influence on the species based on previous works (Donázar *et al.*, 1993*b*; Parr *et al.*, 1995) and could be measured from published maps so that the models could have a predictive use for managers.

### Statistical analyses

Initially I tested for differences in the average value of each environmental variable among squares with colonies, squares without colonies, and squares with extinct colonies, and for correlations between number of breeding pairs and environmental variables. The probabilities of the tests are given with and without a Bonferroni correction for multiple testing. I indicate which probabilities remained significant when multiplied by the number of variables tested simultaneously ($n = 21$).

I used Generalized Linear Models or GLMs (Nelder & Wedderburn, 1972; Dobson, 1983; McCullagh & Nelder, 1983) as a mathematical description of: (1) the presence/absence of lesser kestrel colonies in a square; (2) the probability that colonies in a square had become extinct before 1989; and (3) the number of lesser kestrel pairs breeding in one square.

GLM are a class of models of which the linear regression is a particular case. GLM allow for a greater

**Table 1. Descriptive statistics for variables that differed significantly between squares with colonies ($n = 49$), and squares without colonies ($n = 52$), or squares with extinct colonies ($n = 30$). For those variables not following a Normal distribution, the median, the lower quartile (LQ) and upper quartile (UQ) of the distribution are given. Differences between medians were tested with a Wilcoxon–Mann–Whitney Test (Siegel & Castellan, 1988). For variables not differing from a Normal distribution, mean and standard deviation (SD) are given and differences are tested with a students' *t*-test. The following additional variables were measured and tested in the models, but had no significant predictive capability: spring rainfall and temperature (April-July)[a], km of sealed and dirt roads[g], and percentage of olive groves, vineyards, irrigated cultures, and unproductive land[c]**

| | With colonies | | Without colonies | | | | Extinct colonies | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Variable | Median | (LQ–UQ) | Median | (LQ–UQ) | Z | *p* | Median | (LQ–UQ) | Z | *p* |
| *Annual rainfall* (mm)[a] | 500 | (500–700) | 600 | (500–600) | 1·04 | ns | 600 | (500–700) | 0·37 | ns |
| *Annual temperature* (°C)[a] | 18 | (17–18) | 17 | (16–18) | 2·18 | 0·03 | 17 | (15–18) | 1·95 | 0·05 |
| *Inhabitants*[b] | 6979 | (1738–16 570) | 1585 | (15–1650) | 5·82 | <0·001* | 4008 | (2131–9858) | 1·36 | ns |
| *Urban* (%)[cd] | 3·89 | (1·60–6·91) | 0·75 | (0·75–0·30) | 4·78 | <0·001* | 2·50 | (1·10–5·89) | 0·77 | ns |
| *Orchards* (%)[c] | 0·00 | (0·00–0·70) | 0·05 | (0·00–1·15) | 0·48 | ns | 0·75 | (0·05–3·10) | 2·30 | 0·02 |
| *Cereals* (%)[c] | 35·73 | (10·63–61·47) | 10·94 | (1·45–25·57) | 3·90 | <0·001* | 9·89 | (2·39–27·63) | 2·93 | 0·003 |
| *Vegetables* (%)[c] | 0·00 | (0·00–0·00) | 0·00 | (0·00–0·00) | 0·11 | ns | 0·00 | (0·00–0·30) | 2·18 | 0·03 |
| *Pastures* (%)[c] | 0·80 | (0·20–4·60) | 1·00 | (0·45–4·55) | 0·40 | ns | 3·04 | (0·90–8·63) | 2·01 | 0·04 |
| *Open land* (%)[ce] | 52·85 | (18·1–74·62) | 21·90 | (6·58–43·69) | 3·23 | 0·001* | 32·36 | (10·55–63·94) | 1·56 | ns |
| *Scrubland* (%)[c] | 3·50 | (0·50–9·41) | 21·90 | (3·60–59·37) | 3·71 | <0·001* | 5·28 | (0·60–41·63) | 1·51 | ns |
| *Forest* (%)[c] | 0·20 | (0·00–0·50) | 0·43 | (0·00–7·05) | 2·30 | 0·021 | 1·00 | (0·10–2·40) | 2·91 | 0·004 |
| *Suitability* (I)[f] | 27·54 | (9·62–41·86) | 12·19 | (4·29–26·24) | 2·95 | 0·003 | 11·84 | (5·24–32·33) | 2·02 | 0·04 |
| | Mean | (SD) | Mean | (SD) | *t* | *p* | Mean | (SD) | *t* | *p* |
| *Altitude* (m)[g] | 334·1 | (250·7) | 461·6 | (266·0) | 2·48 | 0·015 | 461·1 | (291·0) | 2·06 | 0·04 |
| *Rivers* (km)[g] | 31·4 | (13·1) | 39·0 | (16·5) | 2·58 | 0·011 | 33·2 | (7·1) | 0·70 | ns |

* Significant ($p < 0·05$) after Bonferroni correction considering the total of 21 variables tested.

[a] Data from 1:3,000,000 maps from Instituto Nacional de Meteorología (1983); means for 1931–1960.

[b] Estimated from the 1991 Spanish Population Census (Instituto Nacional de Estadística, 1993).

[c] Measured on 1:10,000 maps from Andalusia (Dirección General de Ordenación del Territorio, 1990–1992).

[d] Used in the models both as a continuous variable (*Urban*) and as binomial factor (*Presence of urban area*).

[e] All land with herbaceous vegetation (i.e. *Pastures* + *Cereals* + *Vegetables* + *Irrigated cultures*).

[f] Index 'I' to evaluate the extent and adequacy of foraging habitat for kestrels in the square. The % of each land use was weighted with the inverse of the relative effort to obtain prey according to Donázar *et al.* (1993*b*): I = *Pastures* + 0·58 × *Cereals* + 0·69 × *Vegetables*.

[g] Measured on 1:50,000 topographic maps from the Instituto Geográfico Nacional.

range of relationships between the response and explanatory variables, and for the use of other error functions when the normal distribution is not applicable.

Three components must be defined for a GLM: a linear predictor, an error function, and a link function. A linear predictor (LP) is defined as the sum of the effects of the explanatory variables as follows

$$\mathrm{LP} = a + bx_1 + cx_2 + \dots, \qquad (1)$$

where $a$, $b$, $c$,... are parameters or constants to be estimated from the observed data and $x_1$, $x_2$,... are the explanatory variables and can be either continuous variables or factors. The parameters define the effect of the variables on the LP and, hence, on the predicted value of the response variable.

The error function depends on the nature of the response variable. For binary variables (0 or 1, presence/absence, etc.) a binomial function for the error is adequate. This was the error function used for the models: (1) presence/absence of colonies and (2) extinct vs present colonies.

The link function translates changes in the LP to changes in the response variable. One appropriate link function for a binomial distribution is provided by the logistic function that constrains the predicted values to lie between 0 and 1 (Crawley, 1993). The logistic link means that the probability of obtaining a positive response (presence of a colony in model 1, or extinction of a colony in model 2) is a logistic, s-shaped function when the linear predictor is a first-order polynomial, and for second-order polynomials will approximate a bell-shaped function. In its simplest form the logistic function can be expressed as:

$$p = (e^{\mathrm{LP}})/(1 + e^{\mathrm{LP}}) \qquad (2)$$

where $p$ is the probability of obtaining a positive response and $e$ is the base of the natural logarithm. can be transformed to a linear function:

$$\mathrm{Ln}[p/(1-p)] = \mathrm{LP}. \qquad (3)$$

The response variable for model 3 was the count of lesser kestrel breeding pairs in a square. The variance in the counts was much larger than the mean but did not fit a negative binomial distribution (Crawley, 1993) (Goodness of fit G test, $G = 1452$, d.f. = 54, $p < 0{\cdot}001$). A square-root transformation was therefore used giving a variable which did not differ significantly from a normal distribution (Kolmogorov Smirnov test, $\mathrm{DN} = 0{\cdot}074$, $p = 0{\cdot}99$, $\chi^2 = 4{\cdot}04$; $p = 0{\cdot}67$). So I used a normal error and an identity link for the models. The number of breeding pairs predicted by the model would be:

$$\begin{aligned} &No.\,pairs = LP^2 \ \forall\ \mathrm{LP} \geq 0 \\ &No.\,pairs = \ \forall\ \mathrm{LP} < 0 \end{aligned} \qquad (4)$$

**Analytical procedure**

I fitted each explanatory variable to the observations using the program GLIM (Baker, 1987) following a modification of a traditional forward stepwise procedure. Each variable was tested in turn for significance, and only those significant at the 5% level were included in the model.

If there was not a significant linear trend, a curvilinear response was tested by a second-degree polynomial. I also tested whether the addition of a quadratic or cubic term significantly improved a significant linear or quadratic model.

Recent papers have criticized automatic stepwise procedures as they are not necessarily able to select the most influential from a subset of variables (James & McCulloch, 1990). The modification of the stepwise modelling procedure employed involved testing the alternative models that were obtained when the second or the third most significant variable was included (provided that it was significant at the 5% level), instead of the most significant one at each of the steps. In each case, the only models explored were those in which the relationship between the response variable and the explanatory variable had some plausible ecological explanation. This Forward Stepwise Branching Modelling Procedure (Donázar *et al.*, 1993*a*) eventually produced a set of different models, but in most instances converged into a single model or a set of models from which similar causal relationships could be inferred.

One of the assumptions in regression analysis is that observations are independent, but this is not true for spatial data. For example, the occurrence of lesser kestrels in a square could mean that the probability of occurrence in neighbouring squares is increased (i.e. there is positive autocorrelation in the data). To test for spatial autocorrelation in the data and remove its effects I considered the geographical coordinates of the square as two new explanatory variables ($X$ and $Y$). Both variables and their interaction were tested in the models. When no significant spatial autocorrelation was found in a model, I also tested if all environmental variables remained significant when a linear relation with $X$ and $Y$ plus their interaction was included. The latter is equivalent to partial out the spatial component effect in the models (Legendre, 1993).

For each of the models obtained I estimated the percentage of correct classification and whether this classification was significantly better than random (Titus *et al.*, 1984). In addition, a residual analysis was undertaken for the best model or set of best models. Three diagnostic measures were used to evaluate the fit of the models to the data: a measure of the residual lack of fit, the potential influence and the coefficient of sensitivity (an approximate measure of the actual influence) of each observation. Definitions and procedures follow Pregibon (1981). Observations with a high residual, a high potential influence, or a high coefficient of sensitivity were checked for data errors or atypical observations. If data were correct the models were refitted excluding these observations, one at a time, to evaluate their influence on the coefficients and on the conclusions derived from the models.

## RESULTS

### Presence of lesser kestrel colonies in Andalusia

Statistical comparison of squares with and without lesser kestrel colonies in Andalusia showed that colonies occurred in squares with higher human population density (*Inhabitants*) than average, greater percentage of urbanized areas (*Urban*), greater percentage of land devoted to non-irrigated cultures (*Cereals*), smaller percentage of scrubland (*Scrubland*), smaller percentage of forested land (*Forests*), larger extension of land uses that denote open herbaceous vegetation (*Open land*), and higher values of the foraging suitability index (*Suitability*). They are also in areas with higher mean annual temperature (*Annual temperature*), lower altitudes (*Altitude*) and smaller total length of rivers and streams (*Rivers*) (Table 1). Differences in *Inhabitants*, *Urban*, *Cereals*, *Open land*, and *Scrubland* remained significant after a Bonferroni correction for multiple tests.

The set of environmental variables, which together best explained the presence and absence of lesser kestrel colonies in a GLM model, indicate that the probability of having a lesser kestrel colony increases with the presence of a village (*Presence of urban area*), with mean annual rainfall (*Annual rainfall*), and with *Cereals*, and decreases with *Scrubland* and *Forests* (Table 2). There was no significant improvement if the extent of the urban area was used instead of *Presence of urban area*, so the simpler model was used. There was no significant spatial autocorrelation in the presence of lesser kestrel colonies. If the spatial component effect was partialled out all variables except *Scrubland* (reduction in scaled deviance = 3·09, $p = 0{\cdot}078$) remained significant.

The model renders, for each square a probability of holding a kestrel colony. I considered the squares with a probability $> 0{\cdot}5$ classified as 'with colony' and those with a probability $< 0{\cdot}5$ classified as 'without colony'. The model correctly classified 84% of the squares (81·6% of the squares with colony and 86·6% of the squares without colony). This percentage of correct classification is 68·3% better than random (Kappa = 0·683, $Z = 6{\cdot}86$, $p < 0{\cdot}001$).

**Table 2. GLM model for presence of lesser kestrel colonies in 6×6 km squares in Andalusia using a binomial distribution of errors and a logistic link**

| | Parameter estimate | Standard error |
|---|---|---|
| Constant | −9·321 | 2·376 |
| *Presence of urban area* (1/0) | 3·228 | 0·9246 |
| *Annual rainfall* (mm) | 0·01126 | 0·00319 |
| *Forest* (%) | −0·2543 | 0·1183 |
| *Scrubland* (%) | −0·04900 | 0·02213 |
| *Cereals* (%) | 0·03640 | 0·01454 |
| Residual deviance | 73·48 | |
| d.f. | 95 | |

The residual analysis indicated that the model was robust. All the variables continued to be significant when the squares with the higher potential influence or the higher coefficient of sensitivity were eliminated in turn and the model refitted. The parameter estimate was relatively robust for all parameters except *Forests*. The elimination of squares with high potential influence produced a 7–15% change in the estimate of the parameter for *Forest* whereas the elimination of the square with the higher coefficient of sensitivity produced a 100% change in the parameter estimate for *Forests*.

### Extinction of lesser kestrel colonies in Andalusia

The squares in which lesser kestrel colonies became extinct before 1989 had higher percentages of the square devoted to orchards (*Orchards*), to vegetable crops (*Vegetables*), and higher values of *Altitude*, *Pastures* (including fallow land and pastures with scattered oaks 'dehesas'), and *Forests*, and lower values of *Annual temperature*, *Cereals*, and *Suitability* than squares holding colonies (Table 1). No variables remained significant after a Bonferroni correction.

The forward stepwise branching procedure for determining the set of environmental variables that best explained the extinction of lesser kestrel colonies produced two alternative GLM models. Both were statistically significant but neither was able to explain the whole variability in colony extinction. The first model (Table 3) indicated that the probability that colonies in a square had become extinct increased with *Scrubland* and decreased with *Annual rainfall*. This model correctly classified 72·2% of the squares (93·9% of the squares with extant colonies and 36·6% of the squares with extinct colonies). The model classification is 40·9% better than random (Kappa = 0·409, $Z = 3{\cdot}430$, $p < 0{\cdot}001$). The second model (Table 4) is a quadratic function of *Cereals*, and indicates that the probability of extinction reaches a minimum when values of *Cereals* are around 55%, but increases both with higher and lower values. This model correctly classifies 68·4% of the total squares (79·6% of the squares with extant colonies and 50% of the squares with extinct colonies) and is only 32·8% better than a random classification, although this

**Table 3. First GLM model for probability of extinction of lesser kestrel colonies in a 6·6 km square in Andalusia using a binomial distribution of errors and a logistic link**

| | Parameter estimate | Standard error |
|---|---|---|
| Constant | 2·024 | 1·181 |
| *Annual rainfall* (mm) | −0·005273 | 0·002115 |
| *Scrubland* (%) | 0·05527 | 0·002115 |
| Residual deviance | 92·13 | |
| d.f. | 76 | |

**Table 4. Second GLM model for probability of extinction of lesser kestrel colonies in a 6×6 km square in Andalusia using a binomial distribution of errors and a logistic link**

| | Parameter estimate | Standard error |
|---|---|---|
| Constant | 0·7308 | 0·4524 |
| *Cereals* (%) | −0·08432 | 0·03402 |
| *Cereals*$^2$ (%) | 0·0007632 | 0·0004023 |
| Residual deviance | 94·03 | |
| d.f. | 76 | |

difference is statistically significant (Kappa = 0·328, $Z = 2·753$, $p < 0·003$).

There was no significant spatial autocorrelation in the extinction of colonies. If the spatial component effect was partialled out from the first model *Annual rainfall* was no longer significant. If it was partialled out from the second model the quadratic term of *Cereals* was no longer significant, and the new model indicated a negative linear correlation with *Cereals*.

The residual analyses indicated that neither model was very robust. The elimination of one of the most influential squares in the first model produced a 4–70% change in the parameters, although both variables—*Annual rainfall* and *Scrubland*—remained significant. In the second model the quadratic term of *Cereals* was no longer significant if either of the two most influential squares was eliminated from the model. In this case the model indicated also a significant decrease in the probability of extinction with the increase in *Cereals*.

### Lesser kestrel breeding density

The number of lesser kestrel breeding pairs in a square had a significant positive correlation with *Cereals*, and *Rivers*, and a significant negative correlation with *Scrubland*, *Forests*, and *Altitude* (Table 5), but no correlations remained significant after a Bonferroni correction.

The best GLM model explaining the number of lesser kestrel breeding pairs in a square indicated a negative relation with *Altitude*, *Forest* and *Irrigation* (percentage of the square devoted to irrigated cultures) and a positive relation with *Rivers*. The model, however, explained only 30·3% of the variance in lesser kestrel numbers (Table 6).

**Table 5. Spearman rank correlations ($r_s$) between number of lesser kestrel pairs breeding in the 58 squares in the census and the environmental variables. Only significant correlations or correlations with variables included in the model in Table 6 are given. No probabilities remained significant after a Bonferroni correction considering the total of 21 variables tested**

| Variable | $r_s$ | $p$ |
|---|---|---|
| *Cereals* | 0·285 | 0·032 |
| *Irrigated cultures* | −0·073 | ns |
| *Scrubland* | −0·265 | 0·046 |
| *Forest* | −0·319 | 0·016 |
| *Altitude* | −0·240 | 0·070 |
| *Rivers* | 0·268 | 0·043 |

There was no significant spatial autocorrelation in the number of lesser kestrel breeding pairs. If the spatial component effect was partialled out, all the variables, except for *Altitude*, continued to be significant.

The residual analysis of the model indicated that the model was not very robust. The variable *Irrigation* was no longer significant if one of the most influential squares was eliminated from the model. Also, the estimate of the parameter of *Forests* changed by 40% when another very influential square was eliminated.

## DISCUSSION

The overall results of the three models indicate a positive association of the lesser kestrel with urban areas, non-irrigated cultures (mainly cereals) and annual rainfall, and negative association with altitude, scrubland, forests and irrigated cultures in southern Spain. A land-use variable, *Cereals*, showed a positive correlation with all three measures of kestrel success (presence, survival of colonies, and density), while another two, *Scrubland* and *Forests*, showed a negative correlation with all three. These three variables have a good predictive ability and each appears in two of the four models developed (Tables 2 and 3, Table 4 and Table 6). *Altitude* showed a negative correlation with all three indicators of kestrel sucess, but is included only in the model for kestrel density. *Annual rainfall* showed no direct correlation with presence, colony survival or density, but was positively associated with kestrel presence and colony survival when considered simultaneously with other variables in predictive models (Tables 2 and 3). These results agree with those of Parr *et al.* (1995), who found that flat topography and cereal crops were the best predictors of presence of lesser kestrel colonies in central Turkey. They also indicate that land use and land cover are the main factors affecting the distribution of the species in southern Spain, and agree with the hypothesis of Donázar *et al.* (1993*b*) that land-use changes are responsible for the general decline of the species in the last few decades.

The model for presence/absence of colonies was relatively strong and coincides with previous knowledge that the species preferentially nests in buildings in urban areas (González & Merino, 1990), and avoids foraging

**Table 6. GLM model with Normal distribution of errors and identity link for square root of the number of lesser kestrel pairs estimated breeding in a 6×6 km square in Andalusia**

| | Parameter estimate | Standard error |
|---|---|---|
| Constant | 3·547 | 0·8588 |
| *Altitude* (m) | −0·003517 | 0·001258 |
| *Forest* (%) | −0·3135 | 0·1258 |
| *Rivers* (km) | 0·06882 | 0·02329 |
| *Irrigated cultures* (%) | −0·0648 | 0·02543 |
| $R^2$ | 30·27% | |

in scrubland or forested areas (Donázar *et al.*, 1993*b*). The high predictive ability of *Presence of urban area* suggests that the species is absent from some suitable foraging habitats because buildings, the preferred sites for nesting, are lacking. The selection of urban areas for breeding has been advantageous for the species because of reduced nest predation (Tella *et al.*, 1996), but also because the open uncultivated grasslands adequate for foraging were interspersed with agricultural fields surrounding towns and villages. Nowadays, the intensification of agriculture in Andalusia (Fernández Alés *et al.*, 1992) has reduced the extent of foraging areas close to towns or villages and kestrels are therefore forced to fly long distances from the colony (up to 16 km) to forage (Negro *et al.*, 1993*a*). In areas with low-intensity agriculture, like Monegros (northern Spain), kestrels tend to forage close to the colony (< 3 km) (J.L. Tella, J.A. Donázar and F. Hiraldo, unpublished data). If kestrels, like other raptors (Cade & Bird, 1990; Cade & Jones, 1993) and, in general, other birds (Klopfer & Ganzhorn, 1985; Morton *et al.*, 1991), have an imprinted image of the habitat in which they were born it could be expected that individuals will tend to breed in urban areas even if the quality of the surrounding foraging habitats has declined. It would be interesting to find out if adequate foraging habitat is present far from villages and if these areas are not colonized because of low availability of adequate nesting sites.

The relationship with rainfall indicates that in an area like Andalusia, with low mean rainfall, the species avoids the more arid areas even if there are apparently suitable habitats. This coincides with the general distribution of the species in Spain, which declines progressively towards the more arid southeast (González & Merino, 1990). This could be due to the lower productivity of vegetation in these areas influencing the availability of invertebrate prey for the kestrel.

Uncultivated grasslands are the preferred foraging habitat for the lesser kestrel (Donázar *et al.*, 1993*b*), but differences between squares with colonies and squares without were not significant in the value of *Pastures*, and this variable had little predictive power. This could be because the category pastures and grasslands on the land-use maps available is a very broad classification of land-cover types with little or no agricultural use, and included land-cover types with very different value from the point of view of foraging habitat for kestrels. This could also explain why the suitability index, which combined information on land-cover type extension and suitability for foraging according to a study by Donázar *et al.* (1993*b*), had a low predictive power.

*Forests* and *Scrubland*, although significantly negatively correlated with *Cereals* ($r_s = -0{\cdot}25$, $p = 0{\cdot}004$, and $r_s = -0{\cdot}66$, $p < 0{\cdot}0001$), add predictive ability to the model. These broad vegetation categories represent inadequate foraging habitats for the lesser kestrel (Donázar *et al.*, 1993*b*) and are adequately represented on land-cover maps.

The lack of a significant spatial component effect in the extinction of colonies indicates no clear range contraction in the lesser kestrel distribution in southern Spain. There is also no relation between extinction and *Presence of urban area*. This indicates that extinctions have similarly affected colonies in and outside villages. The two predictive models, although not very robust, point in the same direction. Colonies seem to have disappeared from areas with low annual rainfall; they were probably never adequate for the species and might have been colonized only at times when the population was increasing or in periods of high rainfall. The relation with *Scrubland* can indicate that the species has also disappeared in areas of former marginal agriculture where scrubland cover has increased in recent decades (Fernández Alés *et al.*, 1992; Cámaras Agrarias de Andalucía, pers. comm.). The alternative model, a quadratic relation with *Cereals* with low extinction probability at intermediate values, could reflect the ways in which agriculture has changed in Andalusia. Rural areas with marginal agriculture have suffered from progressive depopulation with a decline in the extent of cereal crops and an increase in scrubland, whereas the more productive areas have suffered from intensification with reduction in field edges, increased irrigation and introduction of sunflowers *Helianthus annuus* (Fernández Alés *et al.*, 1992). Although both phenomena seem to have been negative, the statistical evaluation of the model indicates that pattern of extinction is more clearly associated with areas of marginal agriculture than with areas that have suffered intensification. Both models suggest the importance of land-use change in explaining the dramatic decline of the species.

The low predictive ability of these models indicates that the causes of extinction of particular colonies cannot be derived easily from present land uses. Variables that measured the changes in land use at the time these colonies disappeared would have a better predictive ability. It is also possible that the reasons for extinctions were particular to each colony (e.g. local persecution, rehabilitation of buildings, etc.).

The model for lesser kestrel breeding density points toward a set of factors similar to the other models. Forested areas and irrigated cultures, indicating areas of intensified agriculture, are avoided. Higher areas are associated with an increase in scrubland, and lower mean temperatures, which could influence the abundance and seasonal availability of Orthoptera, the main prey of the lesser kestrel. A positive relationship with river length could be due to the presence of riverine grasslands, that are selected by the species for foraging according to Donázar *et al.* (1993*b*). The low predictive ability of the model could be due to the lack of variables measuring nest-site availability, but also because the land-use classification was too coarse to evaluate precisely the availability of foraging habitat.

Thus, neither the probability of extinction of a certain colony or colony size are easy to predict accurately with present land-use and land-cover maps. However, all models indicate that the present trend of intensifying agriculture in some areas while setting aside or reforesting others is detrimental for the lesser kestrel. Future work should evaluate if it is possible to increase predictability with other kinds of models, more precise maps, or by including temporal information about land-use and land-cover changes.

## ACKNOWLEDGEMENTS

I am very grateful to the following people and groups who assisted with the fieldwork: M. de la Riva, Y. Menor de Gaspar, J. M. Bermúdez, G. de la Riva, F. Hiraldo, J. A. Donázar, Grupo Ornitológico Jerezano (GOJ), Sociedad Ornitológica Larus, Grupo Ecologista Jacaranda, Grupo Naturalista Otis tarda, Grupo Ornitológico de Defensa y Estudio de las Aves (GODESA), and Grupo de Observación Defensa y Estudio de la Naturaleza (GRODEN). I. Llach, Y. Menor de Gaspar, J. Pérez, J. M. Bermúdez, M. de la Riva y M. González Forero extracted the environmental infomation from maps and other sources. A. Green, F. Hiraldo, J. A. Donázar, J. J. Negro, J. L. Tella and L. Carrascal made helpful comments on a previous version of the manuscript. S. Nadeau helped with corrections of the English text. Funding was provided by SEO-BirdLife, CICYT project PB 90-1021 and a postdoctoral fellowship from CSIC to the author.

## REFERENCES

Baker, R. J. (1987). *GLIM 3.77 reference manual* (2nd edn). Numerical Algorithms Group, Oxford.

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, London.

Cade, T. J. and Bird, D. M. (1990). Peregrine falcons, *Falco peregrinus*, nesting in an urban environment: a review. *Can. Field Nat.* **104**, 209–218.

Cade, T. J. and Jones, C. G. (1993). Progress in restoration of the Mauritius kestrel. *Conserv. Biol.* **7**, 169–175.

Cramp, S. and 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, Oxford.

Dirección General de Ordenación del Territorio (1990–1992). *Mapa topográfico de Andalucía.* Consejería de Obras Públicas y Transportes, Junta de Andalucía, Sevilla.

Dobson, A. J. (1983). *Introduction to statistical modelling.* Chapman and Hall, London.

Donázar, J. A., Hiraldo, F. and Bustamante, J. (1993*a*). Factors influencing nest site selection, breeding density and breeding success in the bearded vulture (*Gypaetus barbatus*). *J. Appl. Ecol.* **30**, 504–514.

Donázar, J. A., Negro, J. J. and Hiraldo, F. (1993*b*). Foraging habitat selection, land-use changes and population decline in the lesser kestrel *Falco naumanni. J. Appl. Ecol.* **30**, 515–522.

Fernández Alés, R., Martín, A., Ortega, F. and Alés, E. E. (1992). Recent changes in landscape structure and function in a Mediterranean region of SW Spain (1950-1984). *Land. Ecol.* **7**, 3–18.

Forero, M. G., Tella, J. L., Donázar, J. A. and Hiraldo, F. (1997). Can the interspecific competition and nest site availability explain the decrease of lesser kestrel populations? *Biol. Conserv.*

González, J. L. and Merino, M. (1990). *El cernícalo primilla (*Falco naumanni*) en la Península Ibérica. Situación, problemática y aspectos biológicos.* ICONA, Madrid.

Instituto Nacional de Estadística (1993). *Nomenclátor de las ciudades, villas, lugares, aldeas y demás entidades de población con especificación de sus núcleos. Censos de Población y Viviendas 1991.* INE, Madrid.

Instituto Nacional de Meteorología (1983). *Atlas climático de España.* INM, Madrid.

James, F. C. and McCulloch, C. E. (1990). Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Ann. Rev. Ecol. Syst.* **21**, 129–166.

Klopfer, P. H. and Ganzhorn, J. U. (1985). Habitat selection: behavioral aspects. In *Habitat selection in birds*, ed. M. L. Cody. Academic Press, San Diego, CA, pp. 435–53.

Legendre, P. (1993). Spatial autocorrelation-trouble or new paradigm? *Ecology* **74**, 1659–1673.

McCullagh, P. and Nelder, J. A. (1983). *Generalised linear modelling.* Chapman and Hall, London.

Morton, M. L., Wakamatsu, M. W., Pereyra, M. E. and Morton, G. A. (1991). Postfledging dispersal, habitat imprinting, and philopatry in a montane, migratory sparrow. *Orn. Scand.* **22**, 98–106.

Negro, J. J., de la Riva, M., del Junco, O. *et al.* (1990). Situación en la Comunidad Autónoma de Andalucía. In *El cernícalo primilla (*Falco naumanni*) en la Península Ibérica. Situación, problemática y aspectos biológicos*, ed. J. L. González and M. Merino. ICONA, Madrid, pp. 35–45.

Negro, J. J., Donázar, J. A. and Hiraldo, F. (1993*a*). Home range of lesser kestrels *Falco naumanni* during the breeding season. In *Biology and conservation of small falcons. Proc. of the Hawk and Owl Trust conf. Canterbury*, ed. M. K. Nicholls and R. Clarke. The Hawk and Owl Trust, London, pp. 144–150.

Negro, J. J., Donázar, J. A., Hiraldo, F., Hernández, L. M. and Fernández, M. A. (1993*b*). Organochlorine and heavy metal contamination in non-viable eggs and its relation to breeding success in a Spanish population of lesser kestrels (*Falco naumanni*). *Environ. Pollut.* **82**, 201–205.

Nelder, J. A. and Wedderburn, R. W. M. (1972). Generalised linear models. *J. R. Stat. Soc. A* **135**, 370–384.

Parr, S., Collin, P., Silk, S., Wilbraham, J., Williams, N. P. and Yarar, M. (1995). A baseline survey of lesser kestrels *Falco naumanni* in central Turkey. *Biol. Conserv.* **72**, 45–53.

Pomarol, M. (1993). Lesser kestrel recovery project in Catalonia. In *Biology and conservation of small falcons*, ed. M. K. Nicholls and R. Clarke. The Hawk and Owl Trust, London, pp. 24–28.

Pregibon, D. (1981). *Logistic regression diagnostics. Ann. Statist.* **9**, 705–724.

Siegel, S. and Castellan, N. J. Jr (1988). *Nonparametric statistics for the behavioral sciences.* McGraw–Hill, New York.

Tella, J. L., Hiraldo, F., Donázar, J. A. and Negro, J. J. (1996). Cost and benefits of urban nesting in the lesser kestrel. In *Raptors in human landscapes: adaptations to built and cultivated environments*, ed. D. M. Bird, D. Varland and J. J. Negro. Academic Press, London, pp. 53–60.

Titus, K., Mosher, J. A. and Williams, B. K. (1984). Chance-corrected classification for use in discriminant analysis: ecological applications. *Amer. Midl. Nat.* **111**, 1–7.