

# How do crop types influence breeding success in lesser kestrels through prey quality and availability? A modelling approach

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## Summary

1. In the middle of the 20th century the colonial lesser kestrel *Falco naumanni* experienced a marked decline in its western palaeartic breeding range. Although this decline has been attributed to changes in land use influencing breeding success through lowering the abundance and quality of prey, a quantification of these effects has not yet been undertaken.
2. To study how these two key factors influence breeding success, we developed an individual-based model, which translates the hunting performance of each adult foraging trip into nestling growth and enables the effect of crop types on the breeding success of the lesser kestrel to be quantified. Both the authors' own field data and published inferential and experimental studies were used to parameterize and validate the growth model.
3. Model results demonstrated that adult provisioning rates provide very little information on the relation between prey availability and breeding success.
4. On the other hand, the model indicated that small differences in prey abundance among crop types cause large differences in breeding success, highlighting the importance of crop composition in the vicinity of lesser kestrel colonies.
5. Mean prey biomass is an even more important influence on breeding success. Our results indicated a minimum mean prey size of 0.6 g, below which colonies become population sinks.
6. *Synthesis and applications.* We developed an individual-based model that simulates the growth in body mass of a lesser kestrel brood as a function of prey abundance and prey size. These two key factors define a parameter space in which the conservation status of breeding colonies can be evaluated. We applied the model to six lesser kestrel breeding colonies with different mean prey size and different agricultural land use influencing prey abundance. Our model suggests that the habitat quality of two of these colonies is sufficient for population persistence, while management actions to increase habitat quality are required in the remaining four colonies. An increase in the availability of prey-rich habitats such as field margins would achieve this goal without imposing too great a cost on the local farming community.

*Key-words:* agri-environment schemes, farmland bird conservation, habitat management, individual-based model, nestling growth

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## Introduction

The intensification of agriculture is one of the main threats to biodiversity in Europe (Donald *et al.* 2002).

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Many farmland birds have suffered both population declines and contractions of distributional ranges because of modern agricultural practices (Tella *et al.* 1998; Donald, Green & Heath 2001; Johst, Brandl & Pfeifer 2001; reviewed by Ormerod & Watkinson 2000; Ormerod *et al.* 2003). Among them, the lesser kestrel *Falco naumanni* (Fleischer) experienced a marked decline in its western palaeartic breeding range in the

middle of the 20th century (Cramp & Simmons 1980; Biber 1990). Previously considered as one of the most abundant raptors in Europe (Bijleveld 1974), this migratory species became extinct in several countries (e.g. Austria, Hungary and Poland) and has practically disappeared in others (e.g. France, Portugal and Bulgaria). The Spanish population (the stronghold in the western palaeartic; Negro 1997) also suffered a precipitous decline, dropping from 20 000–50 000 pairs in the 1970s (Garzón 1977) to 4000–5000 breeding pairs in 1988 (González & Merino 1990). Thus, it is currently within the highest priority category among Species of European Conservation Concern (BirdLife International 2004).

The lesser kestrel is a colonial species that breeds in holes of old buildings, such as churches or castles, and also under roof tiles within urban areas in western Europe. It feeds on large invertebrates, mainly Orthoptera and Coleoptera (Franco & Andrada 1977; Rocha 1998; Lepley *et al.* 2000). High mortality rates among nestlings because of starvation have been identified as an important factor responsible for the decline of the Andalusian population (Negro, Donazar & Hiraldo 1993). In this species, low breeding success strongly influences population dynamics (Hiraldo *et al.* 1996) and has been attributed to low hunting performance in intensively used agricultural landscapes (Donazar, Negro & Hiraldo 1993; Tella *et al.* 1998).

The uptake of modern agricultural practices in Europe, linked to farmland bird declines, has been driven in part by European Union (EU) subsidies to encourage increased production (Donald, Green & Heath 2001; Donald *et al.* 2002). Recently, the EU decoupled subsidies from agricultural production and made agri-environment schemes, which can be used to benefit biodiversity, compulsory in all EU countries. In order to design appropriate agri-environmental schemes, the ecological benefit of certain land-use types must be known at both local and regional (landscape) scales (Johst, Drechsler & Wätzold 2002). Several changes in agricultural practices, such as the increase in insecticide treatments, decrease in field margins and grasslands, afforestation and increase of sunflower *Helianthus annuus* crops, have been linked to the population decline of the lesser kestrel (Donazar, Negro & Hiraldo 1993; Biber 1996; Franco & Sutherland 2004). However, data on the tolerance limits of the species to these changes, the threat level to particular colonies, and the response of population dynamics to habitat management is completely absent. These data are very difficult to obtain by means of experimentation or field observations on such a large scale, so a modelling approach is appropriate.

In this study, an individual-based model was developed that simulates the growth in body weight of a lesser kestrel brood as a function of daily food intake. Both individual variability and stochastic influences were considered. The main aim was to evaluate the mean breeding success of a set of broods (a colony)

with respect to hunting areas of different quality. Factors were identified that determine significant variations in hunting performance among different hunting habitats. By using these factors as inputs in the nestling growth model, different foraging scenarios and their influence on breeding success in lesser kestrels were simulated.

In order to test the model's reliability, parameter values were set within the range of variability documented for these factors in the existing literature and the authors' own field data. As reference systems, six lesser kestrel colonies were considered for which data on hunting performance and breeding success were available. The model was used to evaluate whether the breeding success of these colonies was constrained by particular land use-related factors and to disentangle the relative importance of different crop types on hunting performance.

## Materials and methods

### STUDY AREA

Data were collected in the Guadalquivir river basin in south-western Spain (from 5°25'W to 6°40'W, and from 36°55'N to 37°25'N), a predominantly flat pseudosteppe (altitude range 20–240 m) where traditional agrigrazing systems have been replaced by a system of continuous cropping with full mechanization and high input of chemical fertilizers and biocides (Fernández *et al.* 1992; Donazar, Negro & Hiraldo 1993). In this area, six urban lesser kestrel colonies (see Fig. S1 in the supplementary material) have been monitored since 1988, recording data on occupancy rate, nest success rate and mean number of chicks per successful nest (for more details see Rodríguez & Bustamante 2003). We also measured chick body mass (to the nearest 2 g) and length of the eight primary feather (the third outermost) to the nearest 0.5 mm, from which hatching dates were estimated (Negro 1991). Mean colony size was 21 occupied nests (range = 14–35).

### THE IMPACT OF CROP TYPES AND ITS QUANTIFICATION

During foraging, lesser kestrels do not use the available hunting area uniformly. Instead they actively select grasslands, crop margins and cereals. Areas planted with sunflowers are seldom used and olive groves *Olea europaea* are almost completely avoided in the study area (Donazar, Negro & Hiraldo 1993).

Field studies have found differences between preferred and avoided hunting habitats in the time devoted to capturing prey (Table 1) and in prey size (Tella *et al.* 1998; Rodríguez 2004). Thus both parameters should be considered when relating the breeding performance of the lesser kestrel to land use. The time devoted to capturing a prey item determines the maximum number of food items that a pair of kestrels can deliver to the nest daily, while the prey size (or biomass) determines

**Table 1.** Hunting performance in different crop types in terms of mean time taken to acquire a prey item. When available  $\pm$  SD is provided

Crop type	Time needed to get prey (min)	Source
Cereal	4.4	Donázar, Negro & Hiraldo (1993)
Cereal	3.1 $\pm$ 0.5	Tella <i>et al.</i> (1998)
Cereal stubble	3.9	Donázar, Negro & Hiraldo (1993)
Field margins	5.1	Donázar, Negro & Hiraldo (1993)
Field margins	5.6 $\pm$ 2.5	Tella <i>et al.</i> (1998)
Grasslands	6	Donázar, Negro & Hiraldo (1993)
Sunflowers	9	Donázar, Negro & Hiraldo (1993)

**Table 2.** Relative proportion of different crop types in a 3-km radius around the colonies (Negro, Donázar & Hiraldo 1993). Ranges account for the variability observed in the period 1999–2000. As an index of margins abundance, we calculated the number of intersections of two squares of 1.6-km and 3.2-km sides centred in the colony, with limits of agricultural plots on a cadastral map. 'Others' accounts for urban areas and crop types either not used by kestrels (orange trees, irrigated crops) or with negligible acreage

Crop type	Victoria	Oliva	Mairena	Purificacion	Miguel	Silo
Cereal	0.20–0.22	0.28–0.32	0.23–0.26	0.20–0.24	0.08–0.09	0.26–0.33
Sunflower	0.13–0.17	0.15–0.16	0.14–0.23	0.20–0.26	0.05–0.06	0.21–0.30
Grasslands	0.04–0.06	0.05–0.07	0.06–0.1	0.08–0.09	0.21–0.22	0.07–0.08
Olive groves	0.37–0.41	0	0.07	0.06	0.40–0.46	0.02
Margins 1.6 km	42	29	36	89	29	51
Margins 3.2 km	109	125	87	166	70	161
Others	0.19–0.20	0.46–0.50	0.41–0.42	0.40	0.19–0.23	0.34–0.35

the amount of food delivered per feed. The interaction between these two factors results in the final amount of food that parents are able to provide to their offspring and hence the maximum number of chicks they are able to rear.

None the less, the lesser kestrel diet is not based on a single prey type, nor are preferred hunting areas always available. Instead, the vicinity of each colony is characterized by a combination of crop types that ultimately determines mean breeding success through the mean prey weight (hereafter prey biomass) and the mean time between capture of successive prey items, expressed as the probability per minute of the bird finding a prey item (hereafter probability of finding a prey item).

The six lesser kestrel colonies studied were characterized by different proportions of crop types in the immediate vicinity of the nests (Table 2). Information was used from lesser kestrel radio-tracking studies undertaken in Spain, which measured the hunting performance of the lesser kestrel in different crop types (Table 1).

#### PREY DELIVERY RATES

This parameter integrated the distance between the colony and the hunting area, the adult intake rate and the probability of finding a prey item in the field, used as an indirect estimator of the probability of finding prey in the surroundings of the colony. In two of the six colonies of our study area, we recorded prey delivery rates (number of food items brought to the nest per hour) during observation periods of 3 h. Observations took place from 11 June to 7 July in Mairena (five nests

with two, three, three, four and four chicks) and Silo (five nests with two, three, four, five and five chicks). Four observation periods were spread evenly through the day to avoid biases as a result of the daily pattern of feeds: (i) early morning (8:00–11:00), (ii) late morning (11:00–14:00), (iii) afternoon (15:00–18:00) and (iv) evening (18:00–21:00). Three independent observations were performed for each period, giving a total of 12 observations per nest during the nestling period, from which we calculated the mean number of feeds per hour and adult in each colony.

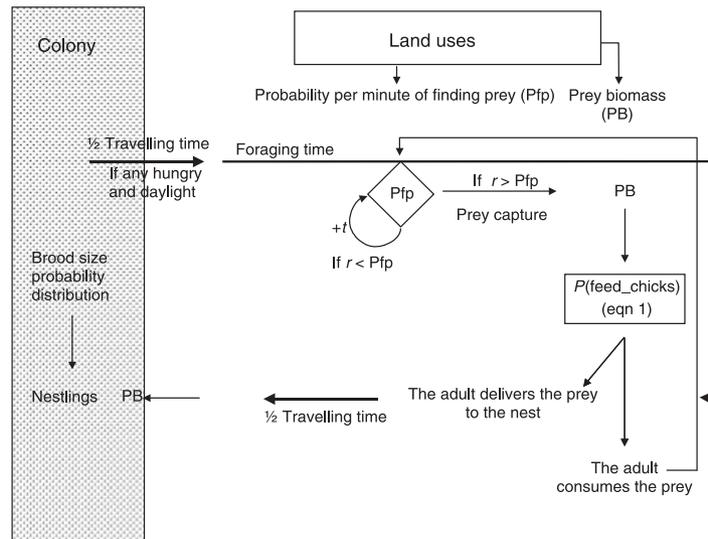
#### PREY BIOMASS AND DIFFERENCES AMONG CROP TYPES

Information was used from lesser kestrel dietary studies to quantify mean prey biomass (Franco & Andrada 1977; Rocha 1998; Choisy *et al.* 1999; Lopley *et al.* 2000; Kiény 2003; Rodríguez 2004). We used data from a 3-year Orthoptera sampling delivered in the main crops of the study area to quantify differences in prey biomass among crop types. Sampling methods followed Voisin (1980, 1986) and specific details are given in Rodríguez (2004). A representative subsample of individuals of different species was taken and weighed fresh after each sampling, allowing us to estimate the mean prey biomass in each of the sampled crops.

For the reference system, we analysed 868 fresh lesser kestrel pellets collected at different nests and roosting places while monitoring colonies during the nestling periods of 1999, 2000 and 2001. This provided information about the mean diet composition for

**Table 3.** Mean prey biomass (in g) estimated in each colony–year combination. Mean growth rates ( $\lambda$ ) of colonies during 1988–2000 (Rodríguez & Bustamante 2003) are also given

Year	Victoria	Oliva	Mairena	Purificacion	Miguel	Silo	Mean
1999	0.6	0.8	0.6	1.1	–	1.2	0.86
2000	1.1	0.6	0.8	1.3	–	1.4	1.04
2001	1.1	0.9	1	1.6	1	1.7	1.22
Lambda	0.93	0.89	0.93	0.97	0.83	1.09	

**Fig. 1.** Flow chart showing the logic sequence followed by the most important events considered in the model.  $t$  is the time unit (min) and  $r$  is a random number between 0 and 1.

each colony and year. Prey remains from pellets were identified at the species or genus level by comparison with an insect collection from the same study area (Rodríguez 2004). Biomass estimates obtained during Orthoptera samplings (see above) were used to calculate mean prey biomass for each colony and year (Table 3).

#### SIMULATION MODEL OF NESTLING GROWTH

The individual-based model considered the daily growth in body mass of each nestling during the 37-day nestling period (Bustamante & Negro 1994). The basic event for the model is a feeding trip (Fig. 1), which is repeated throughout daylight hours (15 h). In the foraging area, the combination of different crop types provides prey of a given mean prey biomass and results in a given probability of finding a prey item. Nestlings that receive insufficient food will lose weight and die if they fall below a minimum weight. Daily food supply is the cumulative sum of biomass from prey items delivered to the nest each day. Throughout the day, the model records the amount of food consumed by each chick and, when it receives the maximum daily intake, the chick is set as 'full' and is not considered for further feeds until the next day. If both chicks and adults are 'full' the process is stopped until the next day.

Each simulation run starts with broods of different sizes randomly selected from the distribution of brood sizes recorded in the authors' long-term monitoring programme (see Appendix S1 in the supplementary material). Simulations were run on Delphi Professional V5.0 (copyright 1983, 1999, Borland Software Corporation, Tugford, Berkshire, UK).

#### FORAGING BY ADULTS

The travel time between the colony and the foraging area to supply one food item to the nest was set at  $8.2 \text{ min} \pm \text{SD} = 1.42$  in the main model. This was the mean travel time documented for urban lesser kestrels during which they covered a mean distance of 4.5 km (Liven-Schulman *et al.* 2004). Half and double this time were also simulated in the model to generalize results to colonies where distance to foraging areas differed substantially from the mean. Kestrels do not store prey and return to the nest each time they capture a prey item.

Adult metabolic cost during the period of highest energy requirements while rearing the chicks was estimated at around  $300 \text{ kJ day}^{-1}$  using double-labelled water (Tella 1996), which is approximately equivalent to 100 g of arthropods (Profus 1986). This was the value for maximum daily food intake per adult input to the model. None the less, adults lose weight during

the chick-rearing period (J. Bustamante & C. Rodríguez, unpublished data), indicating that they do not fulfil their daily metabolic requirements. In order to account for this, the model assumed around 50 g prey day<sup>-1</sup> adult<sup>-1</sup> as a minimum intake (see below). Once this minimum is assured, the final daily food intake of adults depends on the hunting conditions of the foraging area and the metabolic requirements of the brood (increasing with nestling body mass). As both parents feed the offspring, the model considered only one parent, integrating the parameters for both: daylight time and daily metabolic requirements were doubled and results (e.g. prey delivery rates and number of daily flights) were analysed taking this fact into account.

Once the adult catches the prey, it must decide whether to consume it or deliver it to the nest. This decision was modelled through a logistic function (equation 1): if the total adult intake ( $A_{\text{int}}$ ) is low, this function gives very low probabilities of the chicks being fed ( $P_{\text{feed}}$ ), thus ensuring that the adult gets the minimum food intake; otherwise the probability of feeding the chicks is high:

$$P_{\text{feed}} = \frac{0.99}{1 + e^{(8 - 0.074 \times A_{\text{int}})}} \quad \text{eqn 1}$$

The numerator of this equation defines the maximum probability that the chicks would be fed, while the exponent in the denominator modulates the shape of the logistic function, assuring a relatively quick transition between low and high probabilities of feeding the chicks. The point of inflection of this transition is located around the minimum food intake set per adult (50 g). For instance, the probability of feeding the chicks at a total adult food intake of 80 g (40 g adult<sup>-1</sup>) is 0.1, while at a total adult food intake of 140 g (70 g adult<sup>-1</sup>) the probability of feeding the chicks is 0.9. If the adult consumes the prey to account for its metabolic requirements, it must catch another prey item, which increases foraging time (Fig. 1). If it delivers the prey item to the nest, it must decide which of the nestlings will receive it. There is no information about how this process occurs in the lesser kestrel but results of previous studies suggest that a random distribution of food among nestlings should be expected because lesser kestrels do not recognize individual nestlings (Donázar, Negro & Hiraldo 1991; Bustamante & Negro 1994; Tella *et al.* 1997).

#### NESTLING BODY-WEIGHT GROWTH

Nestling growth curves follow the shape of a logistic function and have three main parameters characteristic of each species: asymptote, point of inflection and growth rate (Ricklefs 1967). A growth curve was designed for lesser kestrel nestlings, taking into account that the energy requirements of growing nestlings is the sum of two components: maintenance and growth, the first

being approximately proportional to the weight of the nestling (Ricklefs 1968). It was assumed that maintenance of the chick must be fulfilled daily, the remaining energy being used to grow to an upper limit set by the chick's maximum food intake capacity per day.

To estimate both the metabolic requirements of nestlings ( $F_{\text{met}}$ ) and their maximum daily food intake ( $F_{\text{max}}$ ), two experimental studies were used (Lacombe, Bird & Hibbard 1994; Negro, Chastin & Bird 1994) which were carried out on American kestrel *Falco sparverius* (Linneo) nestlings, a falcon of a size similar to the lesser kestrel. On the basis of these experiments, we fitted logistic equations to data obtained from these studies to describe the metabolic requirements ( $F_{\text{met}}$ ) and the maximum food intake ( $F_{\text{max}}$ ) of nestlings as a function of their weight ( $w$ ) (see Appendix S2 and Appendix S3, respectively, in the supplementary material):

$$F_{\text{met}} = 7 + \log(w)^{1.6} + \frac{60}{1 + e^{-0.09 \times (w - 139)}} \quad \text{eqn 2}$$

$$F_{\text{max}} = 6 + \ln(w)^{1.75} + \frac{45}{1 + e^{-0.095 \times (w - 142)}} \quad \text{eqn 3}$$

Experiments carried out by Lacombe, Bird & Hibbard (1994) and Negro, Chastin & Bird (1994) provided nestling growth and food intake in grams. Previous results showed that there is a positive correlation between breeding success and mean prey biomass ( $F_{1,15} = 23.9$ ,  $P = 0.0002$ , 64% of explained variance; Rodríguez 2004) and both the digestive costs and nutritional value of different food items are difficult to calculate (Johnston 1993; Borg & Toft 2000). For these reasons weight rather than energy units were used to estimate metabolic requirements and intakes.

#### MINIMUM WEIGHT FOR SURVIVAL/ STARVATION OF A NESTLING

To estimate the minimum weight necessary for a nestling to remain alive as a function of age ( $a$ ) in days, the authors used their own data from more than 3800 lesser kestrel nestlings of different ages weighed in the field. From these data a function called 'threshold weight for death' ( $W_{\text{thr}}$ ) was developed, which is the weight in g below which no chick of a particular age is found alive. As lesser kestrel nestlings spend a mean period of 37 days in the nest, although some chicks may leave the nest sooner (Bustamante & Negro 1994) this threshold was considered constant from day 33 onwards. The field data were best described by a linear function between the threshold weight for death and the age of nestlings (for ages ranging 1–33 days and considering day of birth as 1):

$$W_{\text{thr}} = 5 + 2.5 \times (a) \quad \text{eqn 4}$$

This equation assumes a minimum daily growth rate of 2.5 g, which is slightly below the minimum daily growth rate recorded for lesser kestrel nestlings (Liven-Schulman

**Table 4.** Range of simulated conditions for each model parameter. The values for probability of finding a prey item were derived from the times needed to get a prey item

Parameter	Lower limit	Upper limit	Step unit	Source
Prey biomass (g)	0.4	3	0.1	Rodríguez (2004)
Probability of finding prey	0.06	0.27	0.01	
Time needed to get a prey item (min)	17	3.7		Donazar, Negro & Hiraldo (1993)
Initial nestling weight (g)	7.5	18.26		
Fledgling weight (g)	90.1	144.48		

**Table 5.** Main lesser kestrel prey species and their relative importance in different dietary studies in terms of biomass proportion (BP). Mean biomass of these species is also given. When different age classes for prey (juvenile and adult) were documented, the information is given as a range of means

Prey species	BP in kestrel diet	Kestrel diet source	Mean prey biomass (g)	Biomass source
<i>Decticus albifrons</i>	0.34	Lepley <i>et al.</i> (2000)	3.1	Rodríguez (2004)
<i>Decticus albifrons</i>	0.20	Rocha (1998)	3.1	Rodríguez (2004)
<i>Ephippiger ephippiger</i>	0.62	Rodríguez (2004)	2.7	Rodríguez (2004)
<i>Ephippiger ephippiger</i>	0.12	Rocha (1998)	2.7	Rodríguez (2004)
<i>Gryllotalpa gryllotalpa</i>	0.68	Choisy <i>et al.</i> (1999)*	0.7–2.5	Choisy <i>et al.</i> (1999)
<i>Gryllus campestris</i>	0.48	Franco & Andrada (1977)	0.3–0.6	Franco & Andrada (1977)
<i>Gryllus campestris</i>	0.74	Rodríguez (2004)	0.95	Choisy <i>et al.</i> (1999)
<i>Locusta migratoria</i>	0.19	Rodríguez (2004)	–	–
<i>Locusta migratoria</i> ♂	–	–	0.79	Rodríguez (2004)
<i>Locusta migratoria</i> ♀	–	–	1.6	Rodríguez (2004)

\*Also described as an important food item for the lesser kestrel in Israel (Liven-Schulman *et al.* 2004).

*et al.* 2004). If any chick was below this level during the growing period, it was set as dead in the model.

#### INPUT PARAMETER RANGES AND SENSITIVITY ANALYSES

Each combination of parameters (prey biomass and probability of finding a prey) was simulated 100 times within the range of values described in the existing literature and observed in the study area (a total of 594 different combinations; Table 4) and the mean breeding success was calculated.

For the range of mean prey biomass, published information about lesser kestrel food habits was used (Table 5), comprising our own data within this range (Table 3 and Fig. 2). Although the lesser kestrel diet is almost never based on a single prey type, but rather on a combination of prey items of different weights, the lower and upper limits of the range (Table 4) considered monodiets based on the smallest and largest common prey species, respectively (Table 5). In addition, conditions were also simulated well above and below these limits to ensure that the model remained robust under these extreme conditions (e.g. the model was tested by simulating feeds with extremely large prey, such as small mammals, that actually only account for 2% of prey items in the study area; Rodríguez 2004).

For the range of probabilities of finding a prey item, data were used from radio-tracking studies where the hunting profitability of different crop types was calcu-

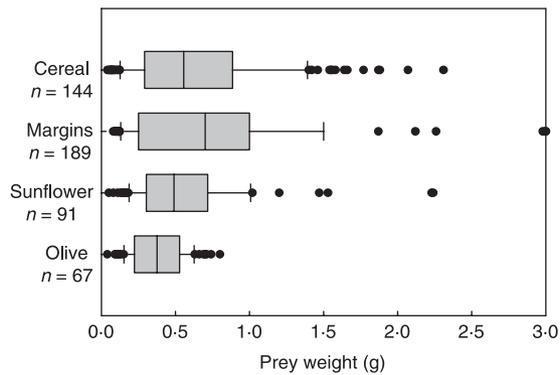
lated (Table 1). As the lesser kestrel does not hunt over some crop types (such as olive groves; Donazar, Negro & Hiraldo 1993) but these crop types could be present in the vicinity of the colony, the lower limit of the probability of finding prey was set below the level of the worst hunting habitat (0.11 in sunflowers; Table 1). For the upper limit of the range, the probability of finding prey was set as that for the best habitat according to Donazar, Negro & Hiraldo (1993).

## Results

#### PREY DELIVERY RATES AND PREY BIOMASS

During 2001 a total of 737 provisioning events was recorded in the two colonies studied. The mean number of prey delivered per hour and adult in Mairena was 1.44 (SD = 0.38,  $n = 472$ ) and in Silo 1.08 (SD = 0.24,  $n = 265$ ).

A total of 11 467 prey items was identified by pellet analyses, of which 67% (78% of prey biomass) were Orthoptera. The mean number of prey items for each year and colony combination was 647 (range 406–1137). For each colony and year, we calculated the mean prey biomass from pellets (Table 3), which differed among colonies (ANOVA  $F_{3,12} = 4.2$ ,  $P = 0.03$ ). We collected 491 Orthoptera individuals as potential lesser kestrel prey during insect samplings carried out in different crop types in the six study colonies. The distribution of mean prey weight differed among crop types (ANOVA  $F_{3,487} = 6.13$ ,  $P = 0.0004$ ; Fig. 2).



**Fig. 2.** Distribution of individual prey weight in the sampled crop types. Median, first and third quartiles are in grey boxes. Whiskers correspond to the fifth and 95th percentiles. Outliers are represented as black dots. Number of individuals sampled in each crop is shown on the y-axis.

## MODEL VALIDATION

### Comparison between observed and simulated breeding performance

Prey delivery rates and mean prey biomass obtained in two of the studied colonies in 2001 were introduced in the model as inputs, thus representing real hunting conditions experienced by these colonies: the mean prey biomass in Mairena was 1 g in 2001 (Table 3), and this value was entered in the model. We set the probability of finding a prey item at 0.104, because this value best approached the prey delivery rates observed in this colony. Under these conditions the model calculated a breeding success of  $2.52 \pm 0.03$  [95% confidence interval (CI)] fledged chicks successful nest<sup>-1</sup>. The mean prey biomass in Silo was 1.7 g (Table 3) and the probability of finding a prey item was set at 0.063. Under these conditions, the model predicted a breeding success of  $3.1 \pm 0.03$  (95% CI) chicks successful nest<sup>-1</sup>. The values of breeding performance calculated by the model for the two colonies were very close to those observed in the field during colony monitoring. In Mairena the number of chicks per successful nest in 2001 was  $2.4 \pm 0.3$  (95% CI), and in Silo we recorded  $3.3 \pm 0.5$  (95% CI) chicks successful nest<sup>-1</sup>. As prey delivery rates and breeding success of particular colonies were not used to parameterize the nestling growth model, the concordance between the simulated and observed breeding success constituted a good source of validation for the model.

### Comparison between observed and simulated nestling growth curves

In addition to crop types, annual weather conditions play an important role in lesser kestrel breeding success (through ecosystem productivity; Rodríguez & Bustamante 2003), resulting in either low breeding success (bad years) or years with high breeding success (good years). Therefore, both good and bad hunting condi-

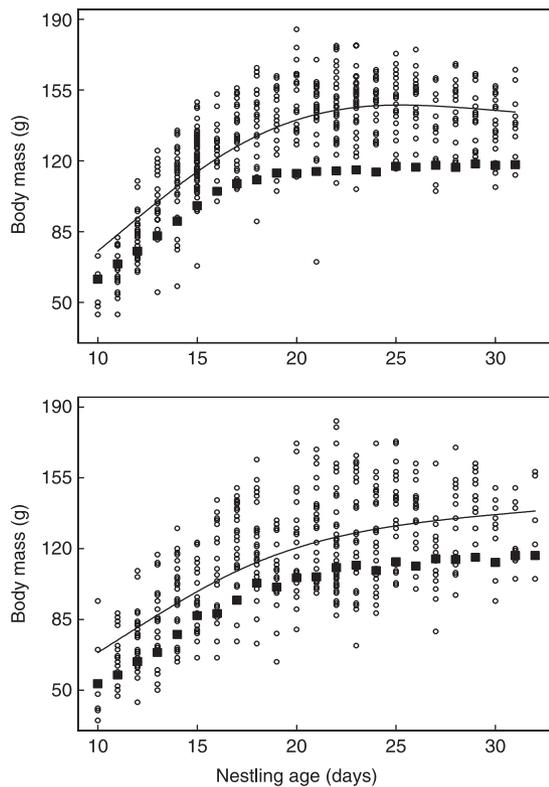
tions can be simulated by setting the mean prey biomass in the model equal to the mean value obtained for the study colonies during a good year (2001, mean prey biomass 1.22) and during a bad year (1999, mean prey biomass 0.86) (Table 3). In both cases, an intermediate probability of finding a prey of 0.12 was used. Model results for nestling growth curves in a good year were within the range obtained by Lacombe, Bird & Hibbard (1994) (see Appendix S2 in the supplementary material) when chicks were fed *ad libitum* and a 10% reduced diet. Growth curves simulating a bad breeding year agreed best (the lowest value of the sum of squared differences between curves) with those obtained with a 20% reduced diet. Accordingly, the resulting mean breeding success for the bad year simulations was relatively low (2.0 chicks successful nest<sup>-1</sup>; 95% CI 0.08) but was relatively high for the good year simulations (4.2 chicks, 95% CI 0.2).

Thus, the model correctly ranked the breeding success for bad and good foraging conditions and produced both appropriate breeding success values and realistic growth curves. None the less the simulations slightly underestimated the mean body mass of lesser kestrel nestlings compared with real data. This could be because the maximum food intake ( $F_{\max}$ ) was derived from the slightly smaller American kestrel (Fig. 3).

## INFLUENCE OF LAND USE ON BREEDING SUCCESS

Figure 4 shows that increasing mean prey biomass and increasing the probability of finding prey results in an increase in lesser kestrel breeding success (see the isolines; Fig. 4). Interestingly, mean prey biomass seems more important than the probability of finding prey, as it is possible to have high breeding success (> 4 chicks per brood) with large prey (> 2 g) at any value of the range of probabilities of finding prey, while the effect of the latter is very dependent on mean prey biomass. The prey delivery rate at the nest increases up to a maximum of around seven feeds h<sup>-1</sup>, obtained at high values of probability of finding prey (0.25) and intermediate values of mean prey biomass (1–2 g). Note that a further increase in the mean prey biomass reduced the provisioning rate.

By means of a matrix projection model, Hiraldo *et al.* (1996) estimated that 2.3 fledglings breeding pair<sup>-1</sup> are necessary for population maintenance in the long term. Given some total breeding failures (around 18% of breeding attempts,  $n = 2427$  nests), this value corresponded to 2.82 fledglings successful nest<sup>-1</sup> and was plotted in Fig. 4 (white line) as a reference line to distinguish between sufficient and insufficient breeding success for colony survival. From the diet composition perspective, the results suggested a minimum mean prey biomass of about 0.6 g, below which colonies would be unable to reach the breeding success threshold. On the other hand, mean prey biomass above 1.6 g practically guaranteed population survival, regardless of how

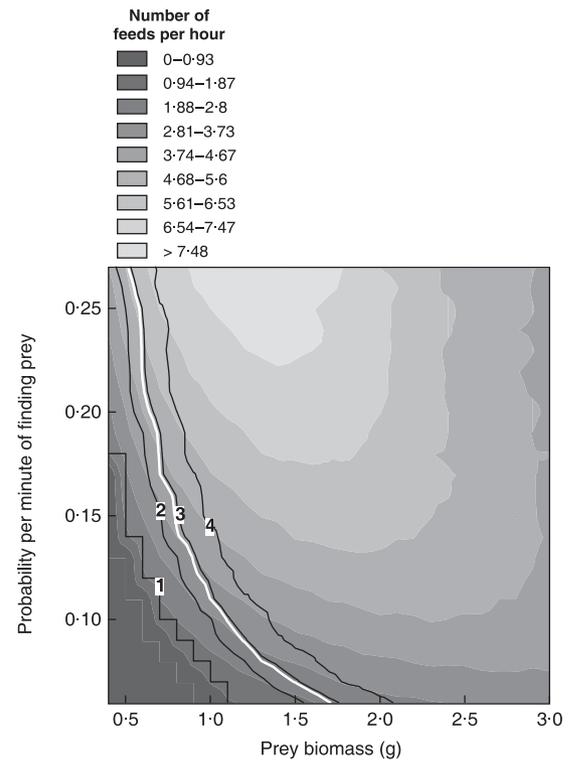


**Fig. 3.** Comparison between mean values of nestling body mass simulated by the model (solid squares) and real data from nestlings weighed in the field at different ages (empty circles). A smoothing spline is used on real weights to obtain a mean trend. The top graph corresponds to good foraging conditions (mean prey biomass 1.22) and nestlings belonging to colony years in the fourth quartile of mean breeding success. The bottom graph corresponds to bad foraging conditions (mean prey biomass 0.86) and nestlings belonging to colony years within the first quartile of mean breeding success.

long (within a reasonable range) kestrels need to find prey. With respect to crop types, cereals and, especially, cereal stubbles offer very good hunting conditions in terms of a high probability of finding prey (0.23 and 0.26, respectively). On the other hand, if the hunting habitat mainly comprises sunflowers, the probability of finding prey is lower (around 0.11) and a minimum mean prey biomass of 1.1 g is needed to ensure population survival. Taking into account our reference system, three out of the six colonies never reached this value, and only two consumed prey of a mean biomass regularly above this limit (Table 3).

Figure 5 allows evaluation of whether or not the colonies of our study system were able to persist in the long term, using the same parameter space as in Fig. 4 and also including the reference isoline of 2.82 fledglings successful nest<sup>-1</sup> (broad black line). Additionally, distance effects of the hunting habitat are visualized in terms of half and double the assumed mean travelling time of 8.2 min from a colony to the hunting area by means of two additional isolines above and below the reference line.

In order to estimate the conservation status of the six colonies of our study system, we investigated whether

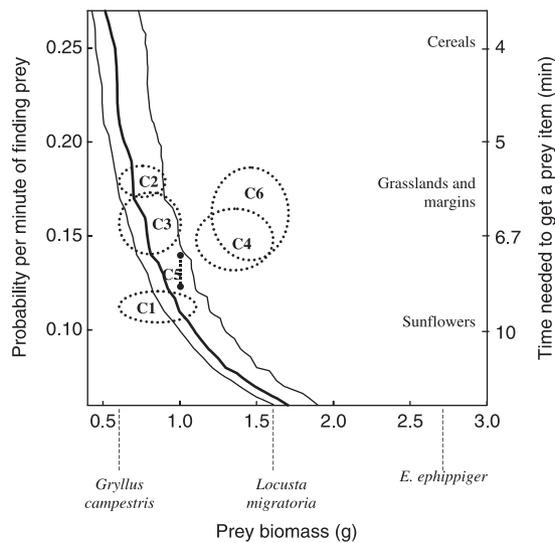


**Fig. 4.** Isolines of the mean number of fledged chicks per successful nest (one, two, three and four) and nest provisioning rates (grey-scaled background detailed in the legend) as a function of the mean prey biomass and the probability per minute of finding prey. The white isoline represents the breeding success calculated by Hiraldo *et al.* (1996) to reduce the extinction risk of the population to 1.4% in 200 years.

kestrels in these colonies are constrained by the foraging conditions they experience. This was done by positioning them on Fig. 5 (dotted-line ellipses) according to their mean prey biomass (Table 3) and the relative proportion of crop types in their vicinity (Table 2). Considering 8.2 min of travelling time as the reference for our study system (Negro, Donazar & Hiraldo 1993), two colonies (Purificacion and Silo) were above the breeding success threshold calculated by Hiraldo *et al.* (1996). The remaining colonies only reached the threshold in the upper limit of their hunting conditions range. Crop compositions around Oliva and Mairena were probably adequate in terms of the probability of finding prey, but they provided small prey items. In contrast, the high proportion of inadequate hunting habitats (olive groves and sunflowers) in the vicinity of the Victoria and Miguel colonies (Table 2) probably led to long hunting times. In accordance with these results, mean real lambda values for these colonies were below 1, lower than for Purificacion and Silo, which were characterized by lambda values very close to or above 1 (Table 3).

## Discussion

In this study the probability of finding prey and the prey biomass are considered as the two key factors characterizing lesser kestrel hunting performance in



**Fig. 5.** Schematic location of studied colonies (dotted-line ellipses) in the range of model parameter values. The position of each ellipse on the  $y$ -axis was set in accordance with the difference between the relative surface of used and avoided crop types (cereals and grasslands vs. sunflowers and olive groves) (Table 2). Differences were then normalized with respect to the smallest one for which the smallest probability per minute of finding a prey item observed in any crop type was considered (Table 1). The position on the  $x$ -axis and width of ellipses corresponds to the observed range of mean prey biomass in each colony (Table 3). The height of the ellipse was set in accordance with the relative interannual variability of crop composition. Black isolines correspond to the breeding threshold of 2.82 chicks successful nest<sup>-1</sup> with travelling times between the colony and the hunting area of 4.1, 8.2, and 16.4 min (from left to right). The  $y$ -axis on the right translates the probability values ( $y$ -axis on the left) into values for time needed to get prey (Table 1). The mean weights of common prey items in the study area are also shown along the  $x$ -axis. Colonies: Victoria (C1), Oliva (C2), Mairena (C3), Purificación (C4), Miguel (C5) and Silo (C6).

agricultural landscapes with different crop types and compositions. By means of a combined approach of individual-based modelling and field investigations, we studied the impact of different combinations of these key factors on nestling growth. This allows first a general evaluation of the mean breeding success as a function of crop composition around a colony within the ranges observed in the field (Tables 1–4), and secondly a specific evaluation of the effect of both current land use and future changes for the colonies studied.

The results in Fig. 4 reveal that even relatively small differences in the probability of finding a prey item (determined by prey abundance) between preferred and avoided crop types (around 6 min between preferred cereals and avoided sunflowers; Donázar, Negro & Hiraldo 1993) significantly influence the breeding success of a colony. This supports the findings of Donázar, Negro & Hiraldo (1993), who identified the reduction of grasslands, extensive cereals and field margins in favour of sunflower fields as land-use changes associated with

the lesser kestrel population decline. According to our results, the hunting performance in the preferred habitats is sufficiently good (probability of finding prey between 0.2 and 0.26) to allow high breeding success even when feeding on small prey (Fig. 4).

Besides the mean abundance of prey, the model results highlight the importance of the mean prey biomass for breeding success, as other studies on large farmland birds have also suggested (Potts 1986; McCracken & Bignal 1998). Relatively small differences in mean prey biomass (Table 3) between colonies with similar crop composition (i.e. similar probabilities of finding a prey) will affect whether a colony is above or below the breeding success threshold calculated by Hiraldo *et al.* (1996) (Figs 4 and 5). The fact that lesser kestrels reduce the provisioning rate when feeding on large prey is also shown in the model. Figure 4 shows that colonies with similar provisioning rates can have very different breeding success depending on prey size. For example 3.5 prey items h<sup>-1</sup> can occur in colonies with a mean breeding success ranging from two to four chicks depending on mean prey biomass.

The distribution of prey weight in the crop types sampled showed that although the simulated range of prey biomass is realistic, large prey items are less abundant and most of the Orthoptera sampled ranged from 0.2 to 1 g. This poses an interesting trade-off between the probability of finding prey and its biomass. In hunting habitats with a high probability of finding prey (e.g. cereal stubbles) suboptimal prey items are more frequent, while in habitats with lower probabilities to find prey (e.g. field margins) larger prey items are more frequent. Such trade-offs may also influence the behavioural decisions in each foraging bout and could be studied by a spatially explicit model.

Combining the simulation results with field investigations of the particular hunting conditions experienced by the six colonies of our study system (Fig. 5), we were able to estimate the conservation status of these colonies in terms of their potential breeding success. Our approach also allowed identification of the constraints in the foraging conditions of each colony (whether agricultural land use mainly caused insufficient prey abundance or insufficient prey of adequate size). For two of the study colonies (Purificación and Silo), habitat quality is high enough for population maintenance (Fig. 5). On the other hand, for the remaining colonies (Mairena, Miguel, Oliva and Victoria) the hunting habitat seems to constrain foraging efficiency in different ways. Kestrels at the Oliva and Mairena colonies hunted very small prey items. The expansion of areas supporting large prey items, such as field margins (Tella *et al.* 1998; Fig. 2), would improve hunting conditions for these colonies and hence their breeding success. In contrast, kestrels in Victoria (and probably in Miguel, although diet information was only available for a single year) must cope with a high proportion of olive groves and other unsuitable habitats (up to 76%; Table 2) in their hunting area,

resulting in long hunting trips and long times between prey captures. Thus, although kestrels were able to obtain relatively large prey items (at least during some years; Table 3 and Fig. 5), the results suggest that an increase in good hunting habitats, such as cereals, in the vicinity of these colonies would increase the probability of finding prey and would increase breeding success. Kestrels prefer to hunt over field margins, which provide good hunting opportunities even in irrigated areas (Ursúa, Serrano & Tella 2005). These areas could be enlarged to benefit kestrels and other wildlife (Table 1 and Fig. 2).

These kinds of agri-environmental schemes have been implemented to benefit other farmland species, such as the ciril bunting *Emberiza cirilus* in England (Ovenden, Swash & Smallshire 1998), leading to population recoveries of around 83% among breeding individuals (Peach *et al.* 2001). The enlargement of grass field margins and development of in-field strips are currently part of the so-called 'broad and shallow' agri-environmental options promoted in recent UK policy (Benton, Vickery & Wilson 2003). None the less, further field and modelling investigations in a spatially explicit context are necessary to understand fully the role of margins in agricultural landscapes (Atkinson *et al.* 2005; Holland *et al.* 2005).

The modelling conducted in this study reveals that prey biomass and the probability of finding prey are important determinants for the breeding success of the lesser kestrel in the agricultural landscapes of Spain (Figs 4 and 5). Our work also suggests that these factors are important in determining the relative success of individual colonies and that habitat manipulation to provide greater foraging opportunities could be a valuable conservation measure. As both factors are influenced by the spatial distribution and composition of crop types around a colony together with the foraging behaviour of the kestrels, further analysis of the relationship between the spatial pattern of crop types around the colonies and prey abundance and biomass would be valuable. It is essential to identify critical habitat not only for the lesser kestrel but also for other farmland birds that are constrained by prey availability, e.g. partridge *Perdix perdix* (Potts 1986), chough *Pyrrhocorax pyrrhocorax* (Blanco, Tella & Torre 1998), little bustard *Tetrax tetrax* (Wolff *et al.* 2001) and corn bunting *Miliaria calandra* (Brickle *et al.* 2000).

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### Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

**Appendix S1.** Brood size distribution.

**Appendix S2.** Metabolic requirements of the nestlings

**Appendix S3.** Maximum food intake.

**Figure S1.** Study area.

## Appendix S1

### BROOD SIZE DISTRIBUTION

The lesser kestrel lays a relatively constant clutch of 4-5 eggs (Negro *et al.* 1993; Aparicio 1997). In our study the mean, median and mode was 4 eggs, the recorded distribution being as follows: 1 egg: 0.3%; 2 eggs: 2%; 3 eggs: 16.8%; 4 eggs: 47.8%, 5 eggs: 31.9%, and 6 eggs: 1.3%,  $n = 615$  nests in which clutches were monitored. Brood predation in these colonies is negligible (2 out of 334 broods; Tella *et al.* 1996), and recent studies have demonstrated that hatching failure influence less the most frequent clutch sizes of 4 eggs (6.43% of hatching failure), and more both bigger, and smaller clutch sizes (9.23%, and 10.88%, respectively. Serrano, Tella & Ursúa 2005). After applying these rates to the observed clutch size distribution, the resulting brood size distribution did not deviate from the simulated by the model (Wilcoxon rank-sum test  $Z = 1.6$ ;  $P = 0.12$ ). Initial weights of nestlings (Table 4) also accounted for the slight hatching asynchrony of the species.

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## Appendix S2

### METABOLIC REQUIREMENTS OF THE NESTLINGS

To estimate the metabolic requirements of chicks, an experiment carried out by Lacombe *et al.* (1994) with American kestrel nestlings was used. In this experiment, the nestlings were grown under four different diets: *ad libitum* and diet reductions of 10, 20, and 30%. The authors indicated the daily amount of food they provided to nestlings in each treatment, and they also showed the mean growth curves of treatments. Using the *ad libitum* treatment, daily metabolic requirements ( $F_{req}$ ) were considered as the amount of food consumed that was not transformed into growth. It was calculated using the following equation:

$$F_{req} = \text{Daily food intake} - \text{Daily growth} \quad \text{eqn S1}$$

Then, a logistic function was fit to the Lacombe *et al.* data to obtain eqn 2. At fledgling weights (140 g Bijlsma *et al.* 1988; authors' unpublished data), this function provides metabolic requirements of around 40 g, comparable to those calculated for captive Eurasian kestrels (Yalden & Yalden 1985).

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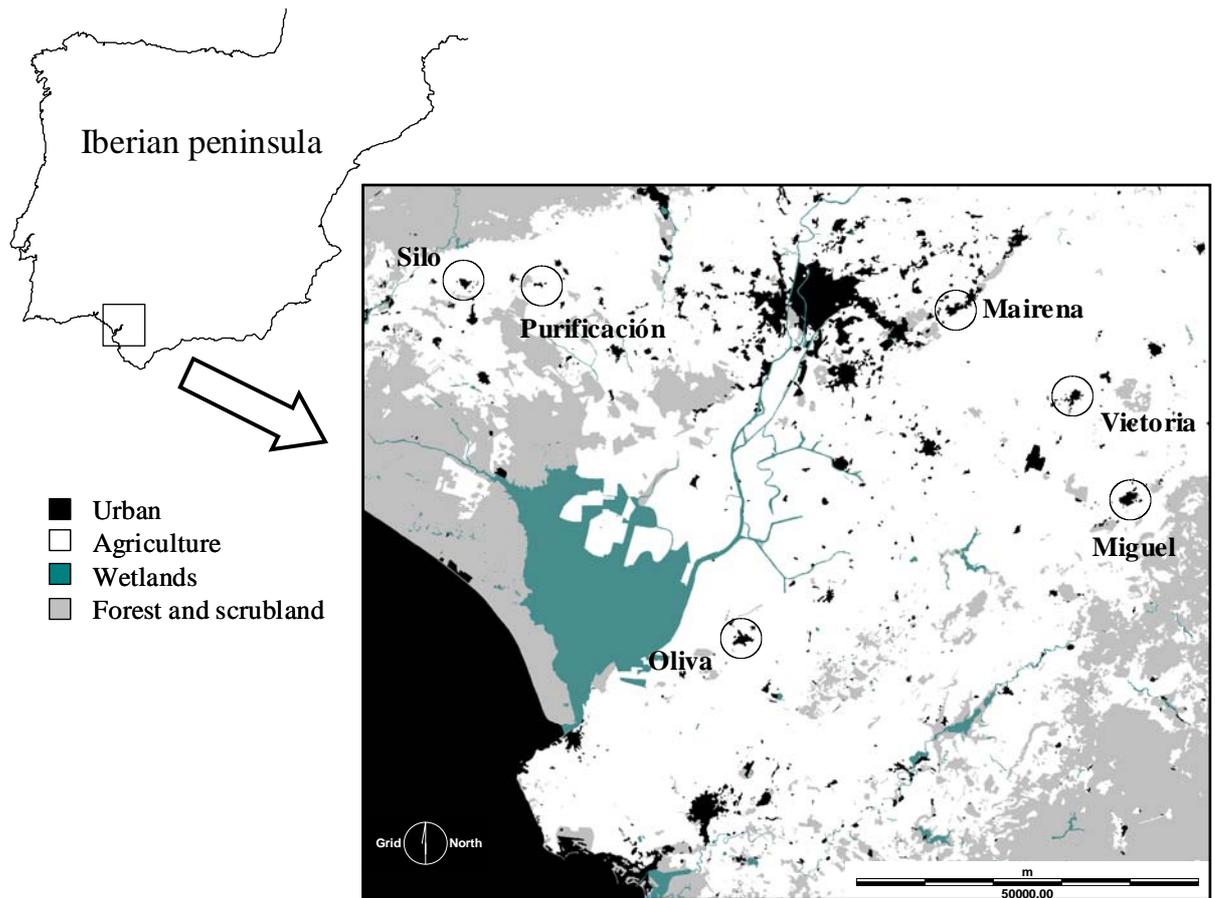
## Appendix S3

### MAXIMUM FOOD INTAKE

The maximum food intake for nestlings was calculated using an experiment carried out by Negro *et al.* (1994) with American kestrel nestlings that were starved at different ages and during periods of up to 48 h. After starvation, chicks were fed *ad libitum* and they were able to recover control weights in 2-4 d by means of maximum daily growth rates. Since it can be assumed that nestling growth during these post-starvation periods was the maximum they are able to reach, the maximum daily food intake ( $F_{max}$ ) was calculated using the following equation:

$$F_{max} = \text{Maximum daily growth} + \text{Daily metabolic requirements} \quad \text{eqn S2}$$

Where daily metabolic requirements ( $F_{req}$ ) were calculated as a function of the chick weight using *eqn 2*. A logistic function was fitted to the distribution of  $F_{max}$  and obtained the *eqn 3*.



**Figure S1**

Location of the six study colonies. Distribution of land use on a regional scale is also provided.