

Influence of spatial and temporal dynamics of agricultural practices on the lesser kestrel

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Summary

1. European agriculture is facing dramatic changes that are likely to have marked impacts on farmland biodiversity. There is an urgent need to develop land management strategies compatible with the conservation of biodiversity.

2. We applied a spatially explicit behaviour-based model to assess how farmland management and the pattern of events across the annual farming calendar influences the foraging decisions of lesser kestrels *Falco naumanni* in a cereal steppe landscape. Moreover, we simulated the most likely scenarios of future agricultural changes to predict its impacts on lesser kestrel breeding success. Lesser kestrels have been the subject of serious conservation concern and constitute a good model species to judge impacts on farmland species more widely.

3. Our results show that the location of cereal and fallow patches within a 2-km radius of a kestrel colony influences the total food supply delivered to the nestlings, explaining the differences in breeding success between years and colonies. Furthermore, the particular sequence in which patches are harvested by farmers is also predicted to influence offspring survival.

4. Agricultural intensification, simulated by increasing the proportion of cereal fields, is predicted to negatively influence breeding success. However, the field harvesting sequence can play an important role in alleviating the effects of the increased percentage of cereal, as demonstrated by the higher breeding success obtained when harvesting starts from patches farthest from the colonies. The replacement of cereal cultivation by low-intensity grazed fallows would not be detrimental for kestrels.

5. *Synthesis and applications.* Our results highlight the effectiveness of behaviour-based models to evaluate the interacting effect of spatial and temporal dynamics of agricultural landscapes and predict the response of populations to environmental change. To optimize food availability for lesser kestrels, land managers should implement long rotational schemes with < 60% of the area under extensive cereal cultivation in a 2-km radius around colonies. Harvesting should start in the cereal patches farthest from colonies. Ideally, the predominant land use around colonies should be fallows. These outcomes illustrate how behaviour-based models can be applied to identify specific management recommendations that would improve the effectiveness of agri-environmental schemes, the most accepted tool for maintaining farmland landscapes.

Key-words: agricultural intensification, breeding success, dynamic landscapes, *Falco naumanni*, farmland management, spatially explicit behaviour-based model

Introduction

Agriculture has become a major anthropogenic threat to biodiversity, and further intensification is expected to have profound negative impacts on species and habitats (e.g. Til-

man *et al.* 2001). In the European Union, lowland farmland holds the highest number of bird species with an Unfavourable Conservation Status, with the largest proportion concentrated in the Iberian cereal steppes (Suárez, Naveso & De Juana 1997). During recent decades, cereal steppe has changed rapidly as a result of the Common Agricultural Policy (CAP), the main instrument behind two divergent current

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trends: agricultural intensification in the best agricultural areas and land abandonment in less productive areas (Ostermann 1998). The dramatic impacts of the CAP on farmland birds (Donald, Green & Heath 2001) led to the introduction of agri-environmental schemes (AES) in 1992, which offer financial incentives to farmers to reward environment-friendly agriculture practices (Robson 1997). Recent studies show different efficiency amongst AES interventions (Kleijn & Sutherland 2003; Perkins *et al.* 2011; Whittingham 2011), suggesting incomplete knowledge of wildlife habitat requirements and species' responses to agriculture management. Therefore, understanding habitat–species relationships and the effect of changing landscape features on species' population dynamics is important to reverse the observed population declines.

The response of organisms to environmental changes, occurring at a variety of spatial and temporal scales, can be predicted by spatially explicit, behaviour-based models (Sutherland 2006). Based on adaptive decision-making by individuals, behaviour-based models allow robust predictions even under changing environmental conditions (Pettifor *et al.* 2000; Amano *et al.* 2007). This is particularly important in farmland landscapes, where changes in agricultural management often create a mosaic of different habitats. The abundance, quality and distribution of food resources are influenced by the spatial arrangement of different quality fields, which depend on farming management (Wolff 2005). Intensification and abandonment of traditional farming systems are both likely to have impacts on the quality of foraging patches and food availability (Donazar, Negro & Hiraldo 1993; Wolff 2005), thus affecting species' fitness components such as the number of offspring that parents are able to raise (e.g. Tella *et al.* 1998). Therefore, these models are becoming increasingly useful tools for conservation biologists and land managers (Dunning *et al.* 1995; Sutherland & Norris 2002).

In this study, we modelled the foraging and breeding success of the lesser kestrel *Falco naumanni* (L.) in a Portuguese cereal steppe landscape, where resource availability and distribution vary according to the temporal and spatial pattern of traditional agricultural practices. The lesser kestrel is a colonial migratory falcon that underwent rapid declines in Western Europe since 1950; the documented population decline has been mainly associated with agricultural changes, such as land abandonment, afforestation and agricultural intensification (Peet & Gallo-Orsi 2000). Lesser kestrels depend on the maintenance of a diverse agricultural mosaic, as promoted by the extensive cultivation of cereals in a rotational system (e.g. Tella *et al.* 1998; Franco *et al.* 2004). Previous studies showed that prey biomass and the probability of finding prey influence the behavioural decisions in each foraging bout and are important determinants of breeding success (Rodríguez, Johst & Bustamante 2006). As both factors are influenced by the spatial distribution and composition of crop types, and because lesser kestrels are central-place foragers highly dependent on nest-site availability, it has been suggested that land management should take into account not only the composition of crops but also the spatial relationships between foraging areas and

colonies (Franco *et al.* 2004; Rodríguez, Johst & Bustamante 2006).

We developed a spatially explicit, behaviour-based model to investigate the impact of both spatial and temporal changes in land-use patterns on food supply for kestrel nestlings. Portuguese cereal steppes are highly dependent on AES and are threatened by changes in policy that affect traditional agricultural practices and, consequently, food supply for lesser kestrels. We simulate the effect of the most likely agricultural changes (land abandonment or agricultural intensification) on lesser kestrel hunting performance and breeding success. We use our results to provide recommendations for maximizing foraging opportunities for lesser kestrels and to identify land-use policies more compatible with its conservation. Finally, we discuss the application of the model framework to other species living in the same habitat.

Materials and methods

STUDY AREA

The study was conducted in the Castro Verde Special Protection Area, Southern Portugal. The region harbours almost 80% of the Portuguese lesser kestrel population, mainly breeding in old rural buildings and artificial nests (Catry *et al.* 2009). The landscape is dominated by extensive cereal cultivation within a rotation scheme: the fields are ploughed and cultivated in September–November; cereal fields are harvested in May and June and transformed into stubble. If the land is not cultivated in the following autumn, it remains fallow. After 2 years of cereal cultivation, fallows are left for 3–5 years. Both stubble and fallows are grazed by livestock. Since 1995, the area has benefited from the implementation of an agri-environmental scheme (see Appendix S1, Supporting Information).

The two largest lesser kestrel colonies (Bever and Pardieiro, with 70 and 65 pairs, respectively) were monitored on a weekly basis in 2008 and 2009 to assess laying date, hatching rate and breeding success.

THE MODEL

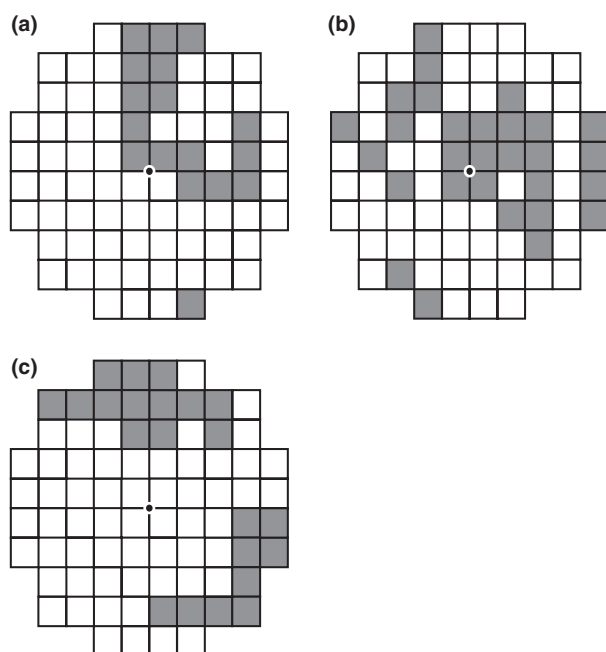
We developed a spatially explicit, behaviour-based model that simulates the total daily amount of food delivered by both parents during the nestling period, which ultimately defines the maximum number of chicks they are able to raise. Kestrels repeat foraging trips during daylight hours; in every trip, each individual selects a foraging patch based on the expected intake rate (EIR) in each available patch. Parents return to the nest each time they capture a single prey item; thus, the final amount of food delivered per day depends on the number of foraging trips, which are determined by the distance between the colony and foraging patches, the time required to capture a prey item and the biomass of captured prey. Data to estimate parameters in the model (Table 1) were collected in the Bever colony in 2009.

Spatial and temporal distribution of foraging patches

During the nestling period, most foraging trips take place within 2 km of the colony (Franco *et al.* 2004). For model simplicity, we created a grid of 16-ha patches ($n = 80$, Fig. 1a) based on the spatial distribution of foraging patches in the field and recorded temporal changes to patch distribution during the breeding season (see

Table 1. Value of input parameters in lesser kestrel foraging models

Parameters	Value
Land use	
Number of patches (16 ha) around the colony within a 2-km radius	80
Number of cereal patches (%)	17 (21)
Number of fallow patches (%)	63 (79)
Time	
Nestling period	37 days (1 June–7 July)
Mean hatching date	1 June
Day length (number of available hours to forage)	14 h
Start of harvest	15 June
Harvest time per day (h)	7.5
Foraging	
Mean (\pm SD) time needed to obtain a prey (s)	
Fallow	64.5 \pm 63.6
Cereal	185.2 \pm 141.1
Patch being harvest	40.8 \pm 42.8
Stubble	155.3 \pm 117.4
Prey size (proportion of captured preys in fallow, cereal, patch being harvest and stubble patches)	
Class 1 (0.4–0.8 g)	0.53; 0.06; 0.41; 0.44
Class 2 (0.8–1.5 g)	0.42; 0.44; 0.40; 0.42
Class 3 (1.5–3.0 g)	0.05; 0.5; 0.19; 0.14
Flight speed	7.14 m s ⁻¹
Probability of patch selection (er.rate = 1 random, er.rate = 0 patch with higher intake rate is selected)	0.5
Feeding	
Time spent for foraging	0.35
Expected weight of chicks as function of age	Weight = $\frac{143.67}{1 + e^{\left(\frac{77 - \text{age}}{2.94}\right)}}$
Metabolic requirements of chicks	Met Req = $7 + \log(\text{weight})^{1.6} + \frac{60}{1 + e^{-0.09 \times (\text{weight} - 139)}}$

**Fig. 1.** Distribution of cereal (grey squares) and fallow (white squares) patches within a 2-km radius around lesser kestrel colonies of Belver 2008 (b) and 2009 (a) and Pardieiro 2008 (c).

Appendix S2, Supporting Information). The distance between the centre of each patch and the colony was assessed using ARCVIEW 3.2 (ESRI 1999).

Nestling period

Portuguese lesser kestrels usually return from their African wintering grounds in early February (Catry *et al.* 2011) and typically lay four to five eggs in April and May. Incubation takes 28 days, and after hatching, both parents feed the chicks for about 37 days (Bustamante & Negro 1994). The nestling period was set from 1 June (mean hatching date in the colony) to 7 July.

Foraging time

Based on observations of lesser kestrel activity, individuals in the model were assumed to be active during daylight (14 h). However, as in many other species (Herbers 1981; Masman *et al.* 1989), not all activity time is used for hunting prey. As it is extremely difficult to estimate the proportion of time spent hunting for the chicks accurately in the field, the foraging time allocation parameter was estimated by the calibration of the parameter value using observed prey delivery rates (see Appendix S3, Supporting Information). In the model, individuals were assumed to repeat foraging trips throughout the estimated time allocated for foraging.

Patch selection

Lesser kestrels actively select patches in the vicinity of the colony where hunting success is high (e.g. Donázar, Negro & Hiraldo 1993; Tella *et al.* 1998). During each foraging trip, individuals were assumed to select a patch with the highest expected intake rate (Max-EIR). However, it is accepted that foraging individuals lack perfect information on patch quality (Stephens & Krebs 1986). Thus, another parameter, patch selection error rate (er.rate), was introduced in the

model to account for the incomplete information (see Appendix S3, Supporting Information). Target patches were defined as the patches with an intake rate higher than $(1 - \text{er.rate}) \times \text{MaxEIR}$, and individuals were assumed to randomly select a patch from the defined target patches.

Expected intake rate

For each simulation day, the EIR in each patch was calculated as $a/(b + c)$, where a is the expected prey biomass, b the time required to catch a prey item and c the travelling time to the patch and back.

During the chick-rearing period, kestrels feed on invertebrates, mainly large Orthoptera (e.g. Lepley *et al.* 2000; Rodríguez *et al.* 2010) such as Tettigoniidae and Acrididae (I. Catry & A. Franco unpublished data). To assess the time expended in capturing prey in each habitat and the resulting prey biomass, hunting sequences were observed and Orthoptera were sampled (Table 1, see Appendix S4 and Fig. S1, Supporting Information). The expected prey biomass in each patch type was calculated as the sum of the proportion of each prey size category per patch multiplied by the mean fresh mass of each prey size category.

The travel time for each foraging trip was estimated by dividing the distance between the colony and the centre of the foraging patches by the lesser kestrels' flight speed (see Appendix S4, Supporting Information). The duration of each foraging trip determines the number of trips per day, and patch selection determines prey biomass captured in each foraging trip. Together, these parameters define the chicks' daily intake rate.

Nestling growth and metabolic requirements

The total energy required by a growing nestling is the sum of the energy needed for maintenance and growth (Ricklefs 1968). To estimate the daily metabolic requirements of nestlings (given by prey biomass) during the 37-day nestling period, we used the logistic equations fitted by Rodríguez, Johst & Bustamante (2006), as a function of chick mass (see Appendix S5 and Fig. S2, Supporting Information).

Breeding success

The total amount of food delivered per day per nest was divided by the amount of prey required by a chick per day to calculate the number of chicks that could be raised. The lowest value throughout the breeding period was defined as the maximum number of chicks raised.

Input parameters and model output

The input parameters are summarized in Table 1. During the 37-day nestling period, the model predicts the number of foraging trips to each habitat, distances travelled daily intake rate and the maximum number of chicks successfully fledged per nest. The simulation was run 100 times, and each model run simulated the behaviour of two individuals (i.e. parents). All simulations were performed using R 2.11.1 (R Development Core Team 2010).

Model validation

We analysed the ability of the model to predict the breeding success and proportion of trips to each habitat type and to each category of distances to the colony, using independent data collected around Belver and Pardieiro colonies in 2008. The validating data sets have a different proportion and distribution of cereal and fallow fields compared with Belver 2009, when the model was parameterized and calibrated (Fig. 1, Table 2) and thus constitute a good means of validating the model. The input parameters for the validation data sets are presented in Table 2. Using the same methods described above, we performed field observations to assess patch type and distance from the colony in each foraging trip ($n = 288$ and 235 for Pardieiro and Belver, respectively), which were used for the validation of model predictions.

SCENARIOS OF FUTURE AGRICULTURAL CHANGE

The impacts of future agricultural changes were evaluated by predicting changes in lesser kestrel breeding success under several scenarios of agricultural change. If EU cereal support decreases (as is

Table 2. Value of input parameters in lesser kestrel validation models. For the parameters not shown in this table, we used the same values as for the main model (see Table 1)

Parameters	Belver 2008	Pardieiro 2008
Land use		
Number of cereal patches (%)	22 (28)	29 (36)
Number of fallow patches (%)	58 (73)	51 (64)
Time		
Mean hatching date	1 June	24 May
Start of harvest	15 June	12 June
Foraging		
Time needed to obtain a prey (s)*		
Fallow	64.5 ± 63.6	75.62 ± 89.50
Cereal	185.2 ± 141.1	144.09 ± 115.55
Patch being harvest	40.8 ± 42.8	15.17 ± 7.52
Stubble	155.3 ± 117.4	154.07 ± 44.45
Prey size (proportion of captured preys in fallow, cereal, patch being harvest and stubble patches)*		
Class 1 (0.4–0.8 g)	0.53; 0.06; 0.41; 0.44	0.40; 0.03; 0.20; 0.39
Class 2 (0.8–1.5 g)	0.42; 0.44; 0.40; 0.42	0.35; 0.37; 0.41; 0.41
Class 3 (1.5–3.0 g)	0.05; 0.50; 0.19; 0.14	0.25; 0.60; 0.39; 0.20

*For Belver, we used the estimates achieved for the 2009 breeding season.

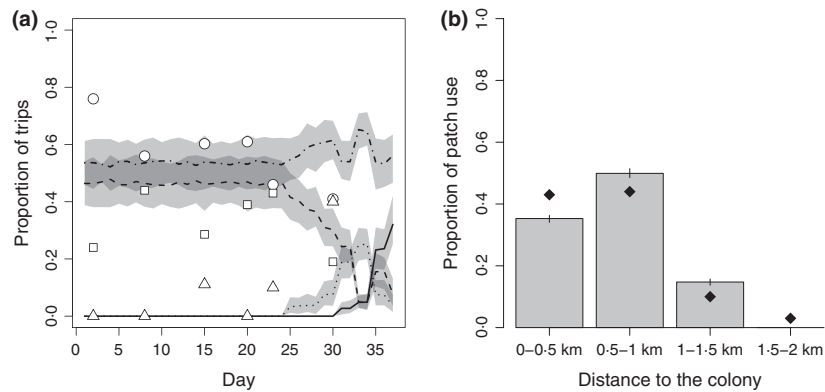


Fig. 2. Field observations (geometric shapes) and model predictions (lines and bars) for the proportion of lesser kestrel foraging trips (a) to each habitat (○--- fallow, □--- cereal, △— patch being harvested and ◇--- stubble) and (b) along a gradient of distance from the Belver colony in 2009. Shaded areas in panel a show 2.5 and 97.5 percentiles of the predictions for 100 simulations.

happening in the area, Franco & Sutherland 2004), the most likely scenarios include scrub encroachment because of land abandonment and tree plantations (both woody habitats are known to be avoided by foraging lesser kestrels; Franco *et al.* 2004) or an increase in fallow land grazed by livestock. In a further scenario, with increased intensification, there would be loss of fallow with either an increase in cereal fields or conversion to other crops, such as sunflowers. We simulated the replacement of cereal by grazed fallows and created a gradient of agricultural intensification by varying the proportion of cereal fields from 0 (100% fallow land, i.e. pastures) to 1 (all cereal fields). Those fields that were converted into cereal were randomly chosen with 100 simulations performed for each proportion of cereal fields. Moreover, because the order in which cereal patches are harvested can influence the food supplied to the nestlings, we considered three possible sequences of harvest for each landscape scenario: (a) starting from the farthest patch, (b) starting from the closest patch and (c) random sequences with respect to the location of the colony.

To evaluate the impacts of other scenarios (e.g. scrub encroachment, afforestation or sunflowers) for which we lack information on hunting performance and prey biomass, we assumed only one patch type (i.e. one habitat type) in the model and simulated a range of values.

Results

PARAMETER CALIBRATION

The best model fit was obtained by setting the time spent for foraging and the patch selection error rate at 0.35 and 0.50, respectively (see Fig. S3, Supporting Information). Thus, the model assumes that adult lesser kestrels spend 35% of their time hunting to feed their chicks and the remaining time spent foraging for themselves and on non-foraging activities. A patch selection error rate of 0.5 suggests that lesser kestrels can partly discriminate patch quality, selecting a target patch randomly from those patches with an EIR higher than 50% of the value in the highest quality patch.

Both the predicted proportion of foraging trips to each habitat type and relative patch use along a gradient of distances from the Belver colony in 2009 corresponded well with the field observations (Fig. 2). During most of the chick-rearing period, both cereal and fallow fields were used equally (Fig. 2a).

Harvest started on day 15, but given the high distance of harvested patches from the colony, an increase in the number of foraging trips to patches being harvested was predicted to occur only after day 30, when harvest reached the closer patches, which agreed with field observations. As harvest progresses, both predicted and observed trips to cereal fields significantly decline (Fig. 2a). Within the nestling period, around 80% of the foraging trips were predicted to take place within a 1 km of the colony, agreeing with field observations (Fig. 2b).

CHICKS' DAILY INTAKE RATE AND BREEDING SUCCESS

The model estimated mean (2.5–97.5 percentiles) breeding success at 2.95 (2.69–3.15) fledglings per successful nest, taking into account the energy requirements of the nestlings (Fig. 3, dotted lines) and the input parameters assessed for the area (Table 1). This is similar to the observed mean (\pm SD) colony breeding performance (2.93 ± 0.9). In the first few days

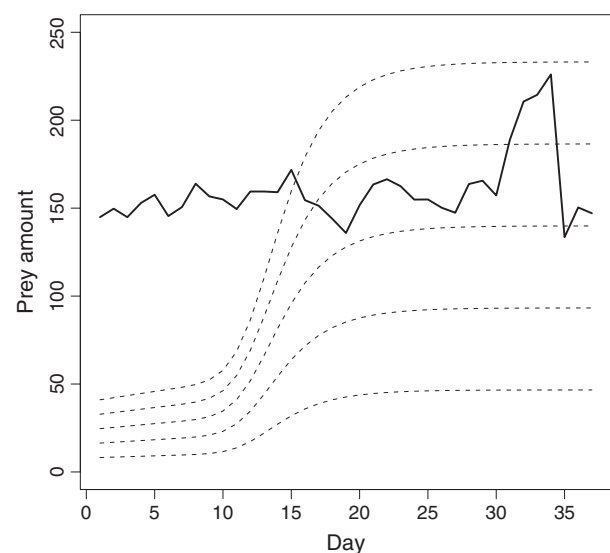


Fig. 3. Model predictions of daily food supply for lesser kestrel nestlings (the solid line exemplifies a typical simulation run) in relation to the metabolic requirements of one to five chicks (dotted lines) in Belver 2009.

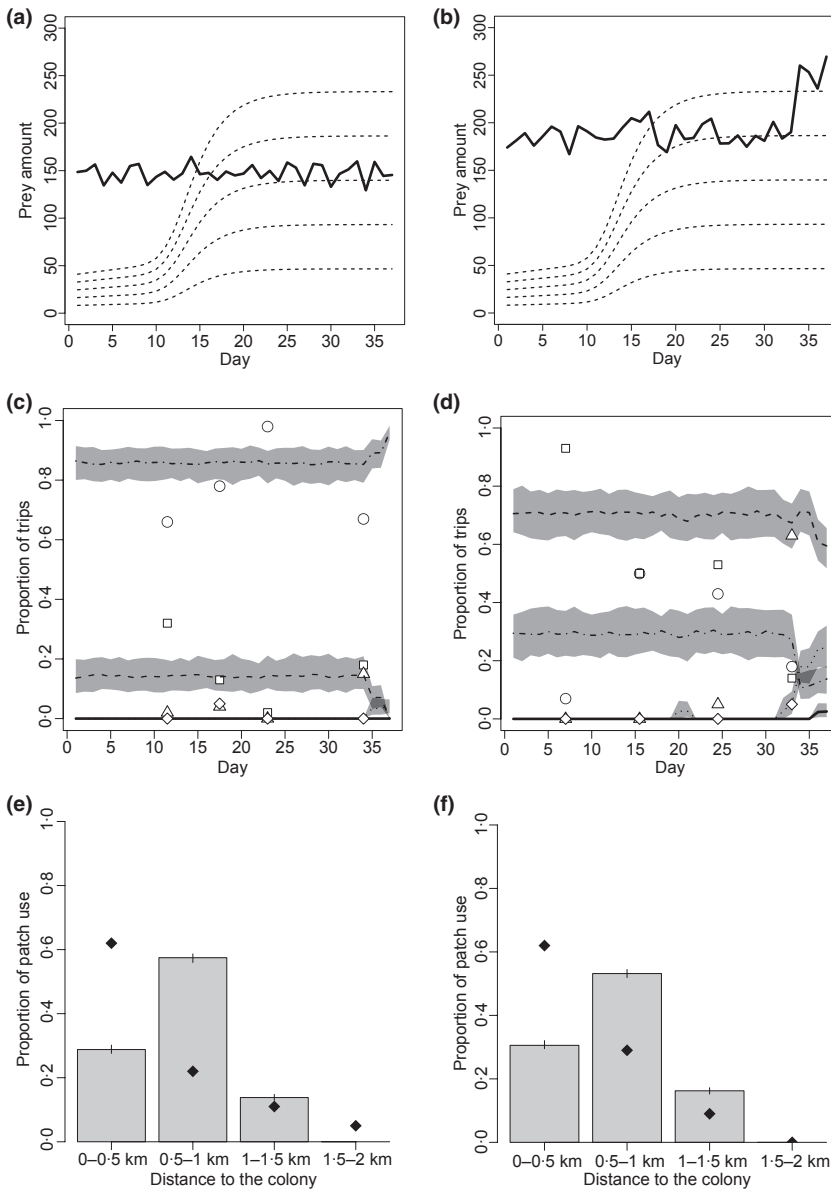


Fig. 4. Results of the validation analysis for Belver (left column) and Pardieiro (right column) lesser kestrel colonies in 2008. The graphs show model predictions of (a and b) daily food supply for nestlings (the solid line exemplifies one simulation run) in relation to the metabolic requirements of one to five chicks (dotted lines); (c and d) proportion of foraging trips to each habitat type (○--- fallow, □-- cereal, △— patch being harvest and ◇··· stubble) and (e) and (f) foraging distances. Field observations of patch use (dots and diamonds in panels c, d, e and f) are presented for comparison with predicted ones. Shaded areas show 2.5 and 97.5 percentiles of the predictions for 100 simulations.

following hatching, the daily food supply was sufficient to fulfil the energy requirements of five nestlings; subsequently, the same quantity of food would only be sufficient to feed three chicks because of their increased energy requirements during a period of fast growth. Harvesting the cereal crop significantly increases the potential food supply for the nestlings. More frequent delivery of prey items to the nests is clearly visible from day 30 (Fig. 3) when harvest took place nearby the colony. Despite the high value of patches being harvested near to the colony, its impact on food supply for the nestlings was ephemeral. Once replaced by stubble, the habitat quality around the colony declined rapidly and the daily food supply to nestlings was reduced (around day 35, Fig. 3).

MODEL VALIDATION

The models successfully predicted the breeding success in the two colonies in 2008 [mean: 2.88, 2.5–97.5 percentiles: 2.68–

3.03 and 3.06 ± 1.1 (SD) in Belver and 3.72 (3.43–3.92) and 3.5 ± 0.7 in Pardieiro, for predicted and observed fledged chicks per pair, respectively]. The model predictions quantitatively corresponded with habitat choice for Belver 2008 and qualitatively for Pardieiro 2008 (Fig. 4c,d). In Belver 2008, cereal patches were located relatively far from the colony (Fig. 1b), and kestrels were predicted to forage mostly on fallow land, which was similar to the observed pattern of patch use (Fig. 4c). In contrast, cereal patches were fairly common near the Pardieiro colony (Fig. 1c) and were both predicted and observed to be most used (Fig. 4d). In Belver, the predicted use of patches being harvested was very low (Fig. 4c), whilst in Pardieiro, the harvesting of cereals after day 30 significantly increased the amount of food delivered to the nestlings (Fig. 4b). When the model results are compared with the observed data, both models show that patch use in relation to the distance from the colony was underestimated at 0–0.5 km and overestimated at 0.5–1 km (Fig. 4e,f).

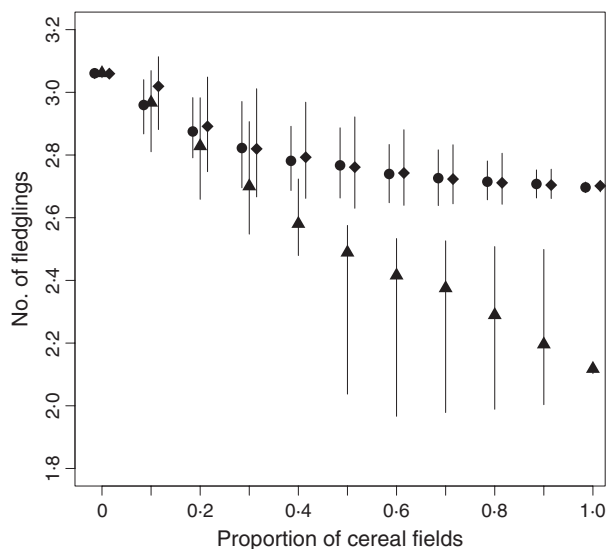


Fig. 5. Predicted number of lesser kestrel fledglings along a gradient of agricultural intensification. The scenario with replacement of cereal patches by grazed fallow (100% fallow) is represented when the proportion of cereal is zero. Three possible sequences were considered in relation to the distance from the colony: starting from the closest patch (triangles), starting from the farthest (diamonds) and at random (circles). Symbols represent the mean value of 100 simulations, and error bars the maximum and minimum values amongst all simulations.

LANDSCAPE SCENARIOS AND LESSER KESTREL BREEDING PERFORMANCE

Figure 5 illustrates the predicted variation in breeding success as a result of an increase in the proportion of cereal patches, from 0% to 100%, around the colony. The highest breeding success is predicted to occur when all cereal patches are replaced by grazed fallow (100% pasture). An increase in cereal patches (intensification scenario) leads to a reduction in the number of fledglings. When cereal patches are harvested in a random order or sequentially from the farthest to the closest field (Fig. 5, circles and diamonds, respectively), there is a slight decline in the predicted number of fledgling, but when patches are harvested sequentially from the closest field to the furthest field (Fig. 5, triangles), the predicted decline is pronounced (because of the poor quality of stubble patches).

Both a decrease in prey size and an increase in the time required to find a prey item are predicted to have a negative impact on the final food supply for the nestlings and, consequently, on breeding success (Fig. 6). With a mean hunting time of 5 min, lesser kestrels cannot raise more than two chicks, independently of the prey size. However, if hunting time does not exceed 3 min, an increase in prey size would improve kestrels' breeding success.

Discussion

The cultivation of cereals under a rotational system provides high-quality habitat for lesser kestrels (Tella *et al.* 1998; Franco & Sutherland 2004). Nonetheless, there is limited

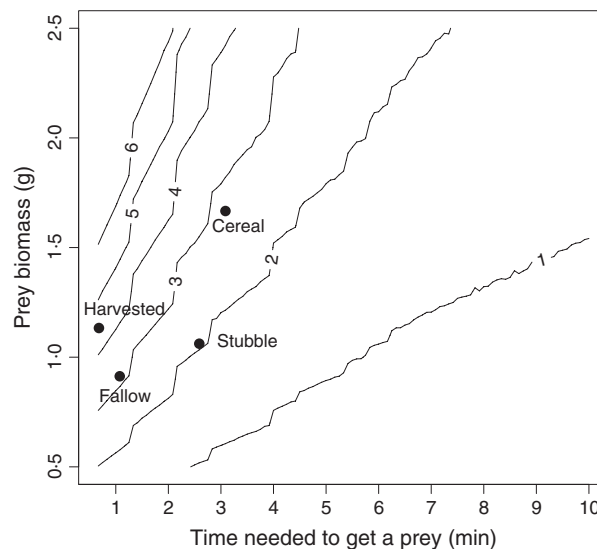


Fig. 6. Model predictions of mean number of lesser kestrel fledglings as a function of the time required to catch prey and prey biomass. Simulations were run assuming a single patch type and various combinations of prey biomass and time required to catch prey. Observed values in each habitat type around the Belver colony are shown (solid circles) for comparison.

evidence for positive associations between specific management options and population breeding success. Using a behaviour-based model, we suggest that farmland management (composition, spatial distribution of habitat patches and harvesting sequence) influences the food supply for nestlings and, consequently, lesser kestrel breeding success.

MODEL VALIDATION

Our model successfully predicted the breeding success and habitat use of lesser kestrels in 2 years and two colonies. However, the model failed to predict the distance of foraging trips undertaken within a 1-km radius around either Belver or Pardieiro colonies in 2008. The actual number of foraging trips observed in the field was higher than the predicted number of foraging trips to the closest patches, although the difference might partly be due to the choice of patch resolution (400 × 400 m). Overall, the good fit of the model suggests that the assumptions of the model structure are reasonable and the parameters are sensible, supporting our main findings. Moreover, the model performance reinforces the importance of including the assumption of incomplete information on patch quality in foraging models.

INFLUENCE OF SPATIAL AND TEMPORAL DISTRIBUTION OF PATCHES ON FOOD SUPPLY FOR THE NESTLINGS

The pattern of cereal rotation means that the landscape around the colonies is modified every breeding season, influencing individual foraging decisions and patch use. When the availability of cereal fields near the colony is high (as in Belver 2009 and in Pardieiro 2008), our model predicts that they will be

highly used (Figs 2b and 4d); when cereal fields are located further from the colony, the model predicts that they will be used less frequently (Belver 2008, Fig. 4C). The predicted difference in the number of nestlings fledged in Belver in two consecutive years (2.88 and 2.95 in 2008 and 2009, respectively) shows the effect of a small increase in the proportion of cereal patches near the colony.

Within a given year, during the nestling period, cereal fields are harvested and subsequently transformed into stubble. Our results highlight the differences in foraging opportunities presented by each of the three 'cereal stages' (cereal, fields being harvested and stubble) and its impact on breeding success. During harvest, cereals become a high-quality foraging habitat owing to an increase in prey accessibility (temporary prey flush) caused by the sudden removal of vegetation cover; if located close to the colony, the predicted number of foraging trips and the food supply for the nestlings significantly increases (Figs 2a and 4b). However, as patches being harvested are turned into stubble, the food supply to the nestlings is predicted to decrease owing to the lower quality of this habitat or to the longer distances that kestrels have to travel to reach higher-quality patches (Fig. 2a). The sequence in which patches are harvested is predicted to influence the total amount of food delivered to chicks and annual breeding success.

FUTURE SCENARIOS

Cereal steppes in Portugal represent an economically marginal farming system, with yields less than half the average European Union yields and, consequently, land use is likely to change in the future (Suárez, Naveso & De Juana 1997; One possible scenario would be for cereal crops to be replaced by fallow land used for livestock grazing (Franco *et al.* 2004). Under this scenario (100% pastures), our results show no negative effects on lesser kestrel breeding success, even suggesting a small increase in productivity (Fig. 5). We should stress, however, that the long-term ecological consequences of transformation of fallow into permanent pastures were not evaluated.

The impact of intensification was modelled by increasing the proportion of cereal around the colony. In low productivity areas, such as our study site in Castro Verde, a large increase in the area under cereal is unlikely because the soil is very poor. Nonetheless, the foraging range around a kestrel colony can be exclusively cereal habitat in any given year. Our model simulations suggest that breeding success will decline as cereal production intensifies in the vicinity of colonies, especially when harvest starts in the closest patches (Fig. 5). In this scenario, where cereal fields exceed 50% of the available habitat, kestrels would have to forage on stubble during a significant part of the chick-rearing period, making it difficult to collect sufficient food to raise more than two nestlings. We stress that the order of harvesting can play an important role in alleviating the negative effect of an increase in cereal production, although we have not accounted for the likely reduction in prey diversity, abundance and size because of an increase in the use of pesticides and loss of habitat heterogeneity (e.g. van Wingerden,

van Kreveld & Bongers 1992; Fenner & Palmer 1998). In our area, vegetation density and height in cereal patches are very low and no pesticides are used. Moreover, small rocky areas in the middle of these patches are left uncultivated, creating suitable conditions for large Orthoptera (I. Catry pers.obs.).

In intensively managed crops (e.g. sunflowers and other irrigated crops), prey items are usually smaller and hunting time is higher. For example, median prey size and mean time required to obtain a prey item was 0.5 g and 9 min, respectively, in sunflower crops (Donázar, Negro & Hiraldo 1993; Rodríguez, Johst & Bustamante 2006). Either a decrease in prey size or an increase in hunting time could reduce breeding success to a single nestling (Fig. 6). Similarly, if fallow is not grazed, agricultural abandonment may result in scrub encroachment. Another possible scenario would be afforestation, given its higher economic profitability. Both scrub encroachment and afforestation would generate changes in vegetation structure, significantly reducing prey accessibility and increasing hunting time (Tella *et al.* 1998; Franco *et al.* 2004; Rodríguez & Bustamante 2008) with concomitant detrimental effects on breeding success (Fig. 6).

MANAGEMENT IMPLICATIONS

Lesser kestrels need to raise at least 2.4 fledglings annually to maintain a viable population (accounting for total breeding failure of 38% of breeding attempts, $n = 1532$; population growth rate was estimated at 1.01 with 1.6 fledgling per breeding pair; Catry, Franco & Sutherland 2011). Therefore, the proportion of cereal fields within 2 km around the colony should be below 60% to ensure population persistence. Where the surrounding area is exclusively under extensive cereal production, the kestrel population could still be viable if harvest started at the farthest patches from the colony (Fig. 5). Nonetheless, to enhance breeding success, our results suggest that fallow land should occupy the highest proportion of habitat around the colony, whilst extensive cultivation of cereals, if under the agri-environmental restrictions (see Appendix S1, Supporting Information) and at low levels (< 20%), would not be detrimental to lesser kestrels. Moreover, cereal fields may act as reservoirs of large prey, and the high quality of patches being harvested can represent an important food resource for inexperienced nestlings after fledging. Under all scenarios, breeding success is predicted to improve if harvest does not start from the cereal patches closest to the colony location.

The habitat quality of our study colonies is high enough to guarantee population persistence. Nonetheless, differences between colonies in the final number of fledglings suggest that habitat quality might be improved to achieve higher breeding success. Higher productivity areas, such as old fallows, are known to support larger prey (Blake *et al.* 1994), suggesting that the maintenance of long rotation schemes (5 or 6 years) are favourable for foraging birds. Grazing pressure greatly influences invertebrate occurrence and accessibility (Lepley *et al.* 2000). A previous study around the Pardieiro colony (Cordeiro *et al.* 2005) showed that lesser kestrels positively selected fallows with 0.25–0.5 stock units ha^{-1} , whilst fallows

exceeding 0.75 stock units ha⁻¹ were clearly rejected. Therefore, the maintenance of very low levels of grazing and the implementation of non-grazed patches, in-field strips or field margins (Rodríguez, Johst & Bustamante 2006), which could act as prey reservoirs and corridors, would enhance adult foraging performance.

THE VALUE OF MECHANISTIC MODELLING APPROACHES IN AGRICULTURAL LANDSCAPES

Evidence for the impact of land-use change and agricultural intensification in the decline of farmland birds has often come from temporal and spatial correlations between particular types of land-use change and particular changes in species-richness or abundance (e.g. Chamberlain *et al.* 2000; Wretenberg, Pärt & Berg 2010). Nonetheless, the underlying ecological processes of observed population trends are still poorly understood (Butler *et al.* 2010), and correlation-based studies, however useful, have important limitations when used to predict changes in biodiversity under future land-use scenarios. Behaviour-based modelling provides a method for understanding the mechanistic links between land use, food resources and the response of organisms (Stephens *et al.* 2003). Behaviour-based models are particularly relevant in farmland landscapes, where agricultural practices often cause spatial and temporal heterogeneity in habitats and food resources, which in turn impact on many species (e.g. Johst, Brandl & Pfeifer 2001). Although field data are necessary to estimate the model parameters for a single species, similar models can be applied to other species.

In this study, the considerable impact of the order in which cereal patches are harvested highlights the interacting effect of spatial and temporal resource dynamics, which are likely to affect the foraging and breeding success of many species that are central-place foragers during the breeding season. Moreover, behaviour-based models are especially relevant for species such as the lesser kestrel that are strongly limited by nest-site availability and cannot, therefore, respond to changes in agricultural land-use patterns simply by changing nest-site location. In contrast to ground or shrub-nesters, building and hole-nesters (e.g. roller *Coracias garrulus*, little owl *Athene noctua* and barn owl *Tyto alba*, common kestrels *Falco tinnunculus*, jackdaws *Corvus monedula*, hirundines) may experience greater limitation in such dynamic landscapes. By modifying land use and the distribution of patches around the colony/nest, our model can be used to assess the species' response to changes in resource distribution under future scenarios of land use and/or management. Moreover, the model framework is applicable to other cereal steppe areas (e.g. where field size is different) by changing the grid size.

Agri-environment schemes are a widely accepted management tool to increase biodiversity in farmed landscapes (Siriwardena 2010). Nevertheless, their re-evaluation, particularly with respect to spatial organization and temporal scale, is crucial to improve their effectiveness (Siriwardena 2010). This study demonstrates that behaviour-based models can contribute to this goal.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Distribution of Orthoptera prey weight according to their size.

Fig. S2. Daily metabolic requirements and growth curves of nestlings.

Fig. S3. Parameter calibration: foraging time allocation and patch selection error.

Appendix S1. Castro Verde agri-environmental scheme.

Appendix S2. Land-use setting.

Appendix S3. Parameter calibration.

Appendix S4. Expected intake rate.

Appendix S5. Metabolic requirements of the nestlings.

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