Habitat- and density-dependent demography of a colonial raptor in Mediterranean agro-ecosystems

4 authors:

Rosanna Di Maggio
Sapienza University of Rome
10 PUBLICATIONS   16 CITATIONS

SEE PROFILE

Daniela Campobello
Università degli Studi di Palermo
40 PUBLICATIONS   293 CITATIONS

SEE PROFILE

Giacomo Tavecchia
Mediterranean Institute for Advanced Studie…
93 PUBLICATIONS   1,896 CITATIONS

SEE PROFILE

Maurizio Sarà
Università degli Studi di Palermo
99 PUBLICATIONS   926 CITATIONS

SEE PROFILE

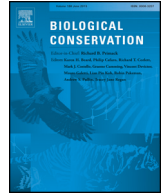Some of the authors of this publication are also working on these related projects:

Project   Practical actions for preserving the main European population of Lanner falcon' View project

Project   Animal PhotoId View project

Habitat- and density-dependent demography of a colonial raptor in Mediterranean agro-ecosystems

Rosanna Di Maggio [a,*], Daniela Campobello [a], Giacomo Tavecchia [b], Maurizio Sarà [a]

[a] Section of Animal Biology, Dept. STEBICEF — University of Palermo, Via Archirafi 18, Palermo, Italy
[b] Population Ecology Group, IMEDEA (CSIC-UIB), c. M. Marquès 21, 07190 Esporles, Spain

ARTICLE INFO

ABSTRACT

Agricultural intensification is considered the major cause of decline in farmland bird populations, especially in the Mediterranean region. Food shortage increased by the interaction between agricultural intensification and density-dependent mechanisms could influence the population dynamics of colonial birds. We used demographic data on lesser kestrels (*Falco naumanni*), a key species of Mediterranean pseudo-steppes, to understand the importance of land-use changes and density-dependent mechanisms in the light of its fluctuating conservation status in the Western Palearctic. Our analysis indicated an important influence of land uses (artichokes, arable and grassland fields) and colony size on kestrel survival rates. The strong habitat effect revealed the unsuitability of intensive arable lands with respect to extensive grasslands for lesser kestrels. Notably, artichokes, a winter-intensive crop, proved to be a high-quality habitat as they were associated with survival values equal to those of grassland. This is likely due to prey availability and reveals that non-traditional crops may provide suitable habitats for lesser kestrels. Information theory gave strong support to the negative influence of colony size on fecundity, albeit a small one, for its positive effect on survival probability. The estimated population growth rate was negative for all three habitats, indicating a decline over time and urging conservation actions in all of the areas studied. This decline was much higher in colonies surrounded by arable fields. In sensitivity analyses, λ indicated that adult survival was the parameter with the greatest effect on population growth, followed by survival of fledglings and fecundity. Our study showed how the costs and benefits of group living interact with agricultural intensification to drive species demography. In addition, we integrated significant information on one of the largest lesser kestrel populations to fine tune the most effective conservation strategy to prevent the collapse of the species in a relevant part of its range.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

The polarization of agriculture, with the intensification of farming practices in flat and coastal areas and the abandonment of less productive and marginal lands, is causing great landscape changes on a global scale (Donald et al., 2001; Baldi et al., 2013; Pe'er et al., 2014). This polarization is promoting wildlife-unfriendly farming systems (Brambilla et al., 2008), with a consequent loss of biodiversity in Europe, especially in regard to farmland birds (Butler et al., 2010; Sokos et al., 2013; Berg et al., 2015). Common Agricultural Policy (CAP) through the agri-environmental schemes (AES) provides the major mechanisms to support conservation actions in agro-ecosystems and faces the challenges of the expansion of the EU common market (Stoate et al., 2009; Sokos et al., 2013). Even if the EU recognizes biodiversity as a priority and modifies agricultural policies to stop and reverse the biodiversity loss (European Commission, 2006), agricultural intensification is still an ongoing process. The reformed CAP for 2014-20 provided new environmental prescriptions such as organic farming and protection of traditional rural landscape, which have been argued to be too weak to benefit biodiversity (Pe'er et al., 2014).

Dramatic modifications occurred in Mediterranean pseudo-steppes, a global biodiversity hotspot (Myers et al., 2000), such as the reduction in fallow land and field margins, removal of semi-natural patches, increase in irrigated lands, and abuse of biocides, all of which seem to contribute to the decline of farmland birds and other wildlife (Sirami et al., 2008; Gonzalez-Estebanez et al., 2011; Sokos et al., 2013; Chiantante et al., 2014).

It has been suggested that avian species breeding in pseudo-steppes and aggregating in breeding colonies would suffer the most from the current intensification of farming practices (Lane et al., 2001; Catry et al., 2012). The causal link between the decline of such avian species and agricultural changes has been proposed to operate via density-dependent mechanisms, where colony size plays a crucial role (Rodrıguez et al., 2006). In many cases, spatial arrangement between food and nest-site availability determines the number of breeders within colonies, i.e. colony size (Rodrıguez et al., 2006). Moreover, food

depletion due to intraspecific competition, a density-dependent mechanism, regulates colony size and, ultimately, the population growth rate (Lewis et al., 2001; Forero et al., 2002). It is thus likely that agricultural intensification would exacerbate density-dependent effects, so we might expect large colonies, characterized by higher food demand and increased levels of agonistic interactions (Serrano and Tella, 2007), to be more vulnerable to food depletion when placed in fast changing agro-ecosystems. In other words, the relationship between agricultural changes and colony size may have serious implications, still poorly known, for the understanding of population dynamics in colonial birds living in a pseudo-steppe habitat.

Here, we investigate how different agricultural habitats and colony sizes may drive the demography of the colonial lesser kestrel *Falco naumanni*, breeding in a pseudo-steppe of southern Italy. The lesser kestrel is an appropriate model for the study of species–habitat relationships because of its role as biological indicator for the monitoring of population dynamics of pseudo-steppe avian species (Bustamante, 1997). The demography of lesser kestrel populations was first investigated in Spain (Hiraldo et al., 1996) with the aim of estimating the probability of species extinction and evaluating different management actions. Monitoring lesser kestrel populations beyond the Iberian peninsula might provide further indications for preserving steppe wildlife and setting management strategies applicable not only on the local but also on the regional scale within Europe (Kolb, 2000; Sarà, 2010). The species has recently been downgraded from the 'Vulnerable' to the 'Least Concern' IUCN category (Iñigo and Barov, 2011) but population trends are highly variable across its range, including local cases of population decline (Iñigo and Barov, 2011). In reality, where management measures were applied, the lesser kestrel has improved its conservation status (Catry et al., 2012), while in areas of the Palearctic range (e.g. Italy), without effective conservation strategies, populations are fluctuating (Sarà, 2010). To allow full conservation recovery across the range, it would be necessary to identify, assess, and ultimately prevent the factors affecting the lesser kestrel's fluctuating demography, especially in rapidly human-altered environments and in the light of the six-year reporting cycle under Article 12 of the Birds Directive 2009/147/EC and the 2020 review of the European lesser kestrel Action Plan.

In this study, we aimed to i) quantify the effect of land uses on fecundity and survival probability, and its potential interaction with colony size; ii) identify which demographic component was more important in determining the population growth rate; and iii) provide conservation guidelines to improve habitat suitability for one of the largest Italian populations of lesser kestrels.

Lesser kestrels tend to forage close to the breeding colony (García et al., 2006). As a consequence, we expect a direct influence of habitat around the colonies on survival and fecundity. In particular, we expect both parameters to be higher in territories characterized by extensive agriculture with expected high food availability (García et al., 2006). Previous works have found higher survival probability in large colonies compared with medium or small ones and concluded that colony size was the causative factor (see, for example, Serrano et al., 2005). Because for a given colony size, per capita food availability would depend on the total amount of resources, we also explored the simultaneous effect of colony size, habitat type and their interaction, i.e. the relative effect of colony size according to the habitat considered.

2. Methods

2.1. Study species and data collection

The lesser kestrel is a small raptor that lives in pseudo-steppes of the Western Palearctic and spends the winter in West Africa (Iñigo and Barov, 2011). It is a facultative colonial species that usually breeds in association with jackdaws *Corvus monedula* and rock pigeons *Columba livia* (Campobello et al., 2012, 2015). From spring to summer between 2004 and 2012 (with the exception of 2008), an average of 14 ± 4 (range 8–24; N = 28) colonies per year were visited in an area of 474 km^2 corresponding to the Gela Plain in southern Sicily (Italy, 37° 07′ N, 14° 19′ E). The Gela Plain hosts one of the most important lesser kestrel breeding populations in Italy, with colony sizes ranging from 1 to 45 pairs (Sarà et al., 2012). Since the 1950s, the human population has shifted from the villages to the main two cities in the area, and the rural past of the Gela Plain is characterized by several farmhouses and rural buildings, partially destroyed or abandoned, that currently host 84% of the lesser kestrel colonies occurring in the area (the remaining 16% nesting in cliffs; Sarà, 2010). We defined a breeding colony as a man-made building with at least one pair of kestrels performing some reproductive behavior at the site (i.e. a male delivering prey to a female, copulation or inspection of nest chambers) (Di Maggio et al., 2013; 2014). Visits to the colonies were conducted periodically, at the time of site occupation and egg-laying (April–May), incubation and hatching (May–June), and fledging (June–July). During these visits, we captured breeding adults in accessible nests, recorded reproductive parameters, and ringed nestlings using metal and darvic rings with unique alphanumeric codes. We carefully inspected colony buildings looking for dead birds, and checked their sex, age, and whenever possible, causes of death. During the same periods, 2 to 4 experienced observers conducted resighting sessions of one hour per colony with 20×60 spotting scopes to check lesser kestrels marked in previous years. Every year, the same observers conducted two to three resighting sessions per month in three roosts (one on a pine-tree, two on electric pylons) where most of the population gathered at night. Birds at the roosts were neither breeding juveniles of the past year nor breeding adults. Double records of the same birds, in the roost and at the colony, proved that many breeders spent the night outside of their colony. Adults were also observed there after having failed to reproduce (M. Sarà, unpublished results). We recorded the sampling effort as the number of days spent in the field per year, and used this covariate as a predictor of resighting probability. Since our data encompass both physical recaptures and resighting of individuals, we addressed them with the general term of 'encounters' (Serrano et al., 2005).

2.2. Habitat types

The Gela Plain, due to limited precipitation (350 mm/yr), is composed of a mosaic of pseudo-steppes dominated by artichoke fields (*Cynara* spp.), in rotation with wheat (*Triticum* spp.) and leguminous cultivations (80.9%, Triolo et al., 2011). The rest of the area contains pastures and xeric vegetation, predominantly graminaceous plants and Mediterranean shrubs (*Stipa capensis* and *Hyparrhenia hirta*; 10.7%) and small artificial Eucalyptus and pine stands (3.7%; Sarà et al., 2012). Previous landscape analysis revealed a strong decrease in Mediterranean shrublands and grasslands from 1867 to 2000, replaced by arable lands, vineyards and greenhouses (Russo et al., 2009). Historically, the cultivation of cotton was predominant in the area until the latter half of the past century when it was gradually replaced by artichokes in the 1960s–80s. Today, agricultural intensification is increasingly changing the core area of the Gela Plain with irrigated crops implanted after the artichoke harvest. Nonetheless, the Gela Plain includes a Special Protection Area (SPA, ITA050001) and a Site of Community Importance (SCI, ITA050011) and constitutes an Important Bird Area (IBA 166; Gariboldi et al., 2000). A Principal Component Analysis (PCA) was used to summarize the essential land-use characteristics within an area of radius 1 km around each colony (Bonal and Aparicio, 2008; online Appendix A1). Results indicated that the habitat surrounding the colonies was characterized by one of the three main habitat types (arable, artichoke or grassland (Table A1 and Fig. A1) and thus we assigned each colony to one of these habitats for survival and demographic modeling (Soliveres et al., 2011; Fig. A2). PCA was calculated using STATISTICA 8.0 (www.statsoft.com).

2.3. Survival and recapture probabilities

Marked birds were encountered near (i.e. roosts) or within their breeding colonies. We coded these observations in encounter histories (Burnham et al., 1987), in which for each year after the marking a "1" coded for an encounter event and a "0" indicated when a given bird was not seen. We used capture–recapture models to estimate local survival (φ) and recapture probabilities (p), from these histories (Burnham et al., 1987). We sorted birds into six groups according to age at marking (two groups, originally marked as fledglings and breeding adults are hereafter referred to as juveniles and adults, 'J' and 'A' subscripts in model notation, respectively) and habitat at marking (three levels were obtained from the PCA: arable, artichoke and grassland, noted 'ARA', 'ART' and 'GRA' in model notation, respectively). For birds marked as juveniles, we also considered two age classes, 1 yr old and >1 yr, noted 'Age' in model notation. A small quota (4.4% out of a total N = 2103) of juveniles was observed later as breeders. Possible change in habitat across individual lifespan could be accommodated into a multisite/multistate framework (e.g. Tavecchia et al., 2002). However, our data was too sparse to apply this modeling framework; therefore, the habitat at marking assigned to juvenile birds represented their natal habitat. A total of 72.3% of birds marked as breeders was faithful to its breeding habitat. The low breeding dispersal is congruent with findings in other populations (cf. Serrano et al., 2001 in which 71.6% of breeding lesser kestrels were recruited into the same colony or settled in colonies within their previous foraging habitats). Moreover, no cases of adult emigration to neighboring populations were detected during the study period, in spite of specific monitoring of the colonies outside the Gela Plain. As most records come from birds remaining in the same breeding colony or habitat, we considered their habitat at marking only and we were confident that the relatively few known dispersal cases ignored here would not bias our results. In addition to the effect of age and habitat effects, we considered two continuous covariates as predictors of survival and recapture probabilities, respectively: i) colony size ('Cs' in model notation) used to assess the potential density-dependent effects, and defined as the sum of the breeding pairs occupying a colony in each year; and ii) resighting effort, expressed as the decimal logarithm of the number of days of observation or capture carried out each year at lesser kestrel colonies ('Re' in model notation), and used to assess the sampling effort. The analysis began with a goodness-of-fit test (GOF) of the general Cormack–Jolly–Seber model (CJS) with software U-CARE 2.3 (Choquet et al., 2009). The CJS model assumes all parameters to be time dependent, so we introduced a 9-level factor corresponding to the years of study and implemented it for birds marked as fledglings as well as for those marked as adults. The GOF test includes components sensitive to different sources of heterogeneity, such as age, presence of transient animals (Test 3SR) or trap-heterogeneity (Test 2CT; Tavecchia et al., 2008). We then considered a candidate set of a priori defined multiple models, that we simultaneously compared using model information theory (IT, Grueber et al., 2011). In particular, we used the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson, 2002) for ranking the models coming from the considered predictors of survival and recapture probabilities. The model with the lowest AICc value was considered to provide the best fit between model deviance and model complexity. Models differing by less than two AICc points were considered to receive nearly identical support from the data (Burnham and Anderson, 2002; Grueber et al., 2011). In addition to AICc values, we estimated model deviances for each model and predictor weights. The latter two estimated the relative importance of each variable in the model set, and were obtained by summing the AIC weights of all models in which a given variable appeared (Symonds and Moussalli, 2011). To account for model selection uncertainty, we calculated the weighted average and the standard errors of parameter estimates by full-model averaging (Symonds and Moussalli, 2011). Model selection, parameter estimate, model deviance, AICc value, and

AIC weight were calculated using the program MARK 7.1 (White and Burnham, 1999).

Finally, only 10 of the 68 birds found dead (7.55 ± 4.69 per year, Table A2) were marked, so we were not able to correct for the recovery probability using capture–recapture-recovery methods (e.g. Tavecchia et al., 2012). Therefore, we investigated the relative importance of each cause of death conditional on the recovery event, i.e. using only birds that had been recovered. This conditional approach assumes that a dead bird is equally likely to be found regardless of the cause of death.

2.4. Fecundity

Breeding data were collected from 2004 to 2012 (except for 2008). Fecundity, i.e. the number of fledglings per nest, was modeled as a function of habitat (3-level factor), time (9-level factor) and colony size (covariate, 'Cs') using a Generalized Linear Mixed Model with a Poisson distribution (GLMM, McCullagh and Searle, 2000). As in survival modeling, we compared and selected models using the IT approach. GLMM was used to control for potential non-independence of data represented by fledglings and adults from the same nest and/or colony (Millar and Anderson, 2004; Zuur et al., 2013). To select which effect to include in the random part of the model, we evaluated nest and colony identities, first taken alone and then together, in order to select the random effect with the lowest AIC (Krackow and Tkadlec, 2001); the latter proved to be colony identity. Once the random structure was set, we modeled the fixed part as a function of year, colony size and habitat type (Zuur et al., 2013). We conducted all fecundity analyses in R 3.0.2 (R Development Core Team, 2011) with the R package lme4 (Bates et al., 2013). Both fecundity (expressed as the N of fledglings) and survival (0–1 probability) varied with colony size (see results). Therefore, they were standardized to their range [variable value, v = (v − min v) / (max v − min v)] to allow direct comparison on the same scale of the colony size effect (Milligan and Cooper, 1988).

2.5. Population modeling

To estimate the expected population growth rate in each habitat, we slightly modified the age-structured population model formerly reported for the species by Hiraldo et al. (1996) and Rodríguez and Bustamante (2003) by considering a post-breeding census. The general formulation for the matrix projection model takes the following form:

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

where $\mathbf{M}$ is the population projection matrix (Caswell, 2001, 2007) incorporating data on fecundity and survival probabilities of fledgling and older birds in a given habitat (Table A3). N_t is the vector with abundance of individuals in each class of the life-cycle ages at time t. The matrix $\mathbf{M}$ contains the age- and habitat-dependent survival and fecundity parameters as estimated from individual life-history and colony monitoring (Supplementary material, Table A3). We assumed a balanced sex ratio at fledgling (Negro and Hiraldo, 1992) and included a parameter for the proportion of juveniles and adults that attempted to breed, 'C_0' and 'C', respectively. These two parameters were estimated by raw data as in Hiraldo et al. (1996). For each habitat, we calculated the asymptotic population growth rate (λ) as the maximum real eigenvalue of $\mathbf{M}$, the stable age distribution, and the sensitivity and elasticity of λ to variations in demographic rates (Caswell, 2001). The stable age distribution represented the numerical contribution in terms of individuals of each age class to the stable age. The sensitivity of λ indicates which demographic parameter has the largest impact on the growth rate of our study population, whereas the elasticity of λ estimates the effect of a proportional change in a key demographic parameter (i.e. vital rate) on the population growth rate (Caswell, 2001). Matrix population models were analyzed using the package popbio (Stubben and Milligan, 2007) for program R (R Development Core Team, 2011). All results

obtained from survival, fecundity and population modeling are given as mean ± standard error, unless otherwise indicated.

3. Results

3.1. Habitat and colony size-dependent survival

We analyzed the encounter histories of 2103 lesser kestrels marked as fledglings (776 in colonies surrounded by arable fields, 548 by artichoke fields and 779 by grasslands) and 175 birds marked as adult breeders (75 in arable, 52 in artichoke and 48 in grassland colonies).

The result of the GOF test was not significant (GOF $\chi^2 = 41.50$, df = 73, $p = 0.99$), meaning that our data met the general assumption of the CJS model. Three models ranked within the two points of AICc and were equally considered to give the best support to lesser kestrel survival. The first model showed a relatively high AICc weight (0.35) with respect to the second (0.18) and third (0.14; Table 1). All of these models included a habitat effect in the survival probability of both juvenile and adult birds. Lesser kestrels living or born in colonies surrounded by arable habitat had a lower probability of survival than those in colonies surrounded by artichoke and grassland habitats (Models 1–3, Table 1). The latter two habitats had the same effect on the survival of both adults and juveniles and were treated together in further analyses. Average survival probability for adults was 0.30 ± 0.08 in arable colonies, 0.75 ± 0.07 in artichoke, and 0.66 ± 0.07 in grassland colonies. Similarly, survival probability for juveniles was lower in arable (0.13 ± 0.05) than in artichoke (0.23 ± 0.07) and grassland colonies (0.21 ± 0.07; Fig. 1).

Model averaging yielded the highest predictor weight of habitat ($w = 0.99$) on adult survival, followed by colony size ($w = 0.11$), which had no effect on survival. In the case of juveniles, the models in Table 1 included a time and age effect, together with habitat; survival was predicted from the model averaged effects of the year of study ($w = 0.99$, Fig. 1), age ($w = 0.99$) and habitat ($w = 0.93$). Nevertheless, information theory gave some support for a positive effect of colony size on predicting juvenile survival ($w = 0.29$, linear predictor: 0.012 ± 0.14 from model 2, Fig. 2); this factor was included only in the second ranked model. The inclusion of recapture effort led to a reduction of AICc value (Table 1), as the first model not including the recapture effort $[p_J(t)\ p_A(t)]$ ranked in the 12th position with a zero AICc weight. The logit-linear predictor for the recapture effort was 1.13 ± 0.38. Adults had a nearly 3-fold higher average recapture probability (0.18 ± 0.04) than juveniles (0.07 ± 0.02; Fig. A3). The most frequent cause of death among the 68 dead lesser kestrels was poisoning (26.47%) followed by birds that were stuck under unstable roof tiles (19.12%; Table A2).

3.2. Fecundity

The model selection procedure retained year as a significant source of variation in the number of fledglings, which passed from an average of 3.5 ± 0.19 fledglings in 2004 to 1.4 ± 0.10 in 2012 (Fig. A4). Contrary
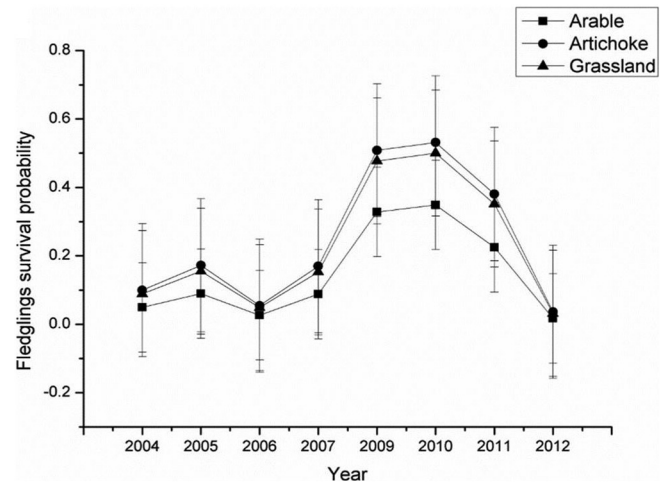

Fig. 1. Survival probability of juvenile lesser kestrels in the Gela Plain (N = 2103) in relation to natal habitat and year.

to survival analysis, the effect of habitat on the number of fledglings was not significant, and the best model with the lowest AICc (Model 1, Table 2) explained fecundity as a negative function of colony size and year but not of their interaction (Fig. 2, Table 2). In our study area, a colony size of around 18–20 pairs would produce the optimal trade-off between fecundity and juvenile survival.

3.3. Population modeling

Following the previous results, we also treated artichoke and grassland colonies together when modeling habitat-dependent growth. The estimated population growth rate (λ) for arable colonies was 0.38 ± 0.01, whereas for artichoke and grassland colonies it was 0.77 ± 0.02 (Fig. 3). Sensitivity and elasticity analyses indicated that the population growth rate showed the highest sensitivity and elasticity to adult survival, followed by changes in juvenile survival and then in adult fecundity in both habitat types (Table 3). The stable age distribution was dominated by the adult class and showed similar values in all colony habitats (proportion of adults: 0.59 for arable and 0.57 for artichoke and grassland).

4. Discussion

Mechanistic models linking land-use and demography can be used to explore population responses to land-use change if robust estimates of habitat-dependent vital rates are available (Stephens et al., 2003). This approach has the advantage that assumptions concerning ecological mechanisms are amenable to evaluation, and it identifies the most appropriate land-management strategy for biodiversity conservation (Mattison and Norris, 2005). Here, long-term colony monitoring and

Table 1
Capture–recapture models estimating survival and recapture probabilities of juveniles (ϕ_J and p_J, respectively) and adults (ϕ_A and p_A, respectively) lesser kestrels in different colony habitats of the Gela Plain. Only the first 10 top-ranked models have been reported. Model notation: colony size (Cs), time (t), age (Age), habitat: arable (ARA), artichoke (ART) and grassland (GRA), constant (.), additive effect (+), recapture effort (Re), N Par = number of model parameters.

| Model	Survival	Recapture	AICc	ΔAICc	AICc w	Deviance	N Par
1	**φ_J (ARA + ART = GRA + t + Age), φ_A (ARA + ART = GRA)**	**p_J (Re) p_A(Re)**	**1772.6**	**0**	**0.35**	**1732.2**	**20**
2	φ_J (ARA + ART = GRA + t + Age + Cs), φ_A (ARA + ART = GRA)	p_J (Re) p_A(Re)	1773.9	1.36	0.18	1731.5	21
3	φ_J (ARA + ART + GRA + t + Age), φ_A (ARA + ART = GRA)	p_J (Re) p_A(Re)	1774.4	1.88	0.14	1732.1	21
4	φ_J (ARA + ART = GRA + t + Age + Cs), φ_A (ARA + ART = GRA + Cs)	p_J (Re) p_A(Re)	1774.8	2.23	0.11	1730.4	22
5	φ_J (ARA + ART + GRA + t + Age), φ_A (ARA + ART + GRA)	p_J (Re) p_A(Re)	1775.4	2.88	0.08	1731.0	22
6	φ_J (ARA = ART = GRA + t + Age), φ_A (ARA + ART = GRA)	p_J (Re) p_A(Re)	1776.8	4.22	0.04	1738.5	19
7	φ_J (ARA = GRA + ART + t + Age), φ_A (ARA + ART = GRA)	p_J (Re) p_A(Re)	1776.8	4.24	0.04	1736.5	20
8	φ_J (ARA = ART + GRA + t + Age), φ_A (ARA + ART = GRA)	p_J (Re) p_A(Re)	1777.7	5.11	0.03	1737.3	20
9	φ_J (ARA = ART = GRA + t + Age), φ_A (ARA + ART + GRA)	p_J (Re) p_A(Re)	1777.8	5.21	0.03	1737.4	20
10	φ_J (ARA = GRA + ART + t + Age), φ_A (ARA + ARA = GRA)	p_J (Re) p_A(Re)	1787.5	14.89	0	1747.1	20
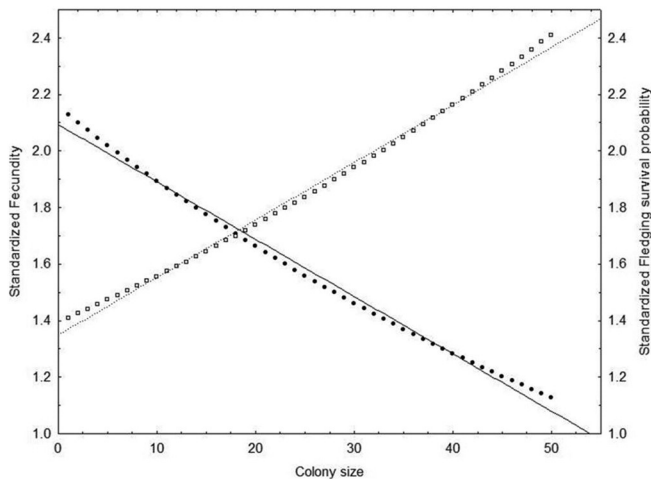
Fig. 2. Relationship between colony size and juvenile survival probability (Model 2, Table 1, N = 2103, solid line and black dots) and fecundity (Model 1, Table 2, N = 1001, dotted line and white squares). Juvenile survival probability and fecundity were standardized dividing by range to have both variables with the same order of magnitude and to plot them on colony size.
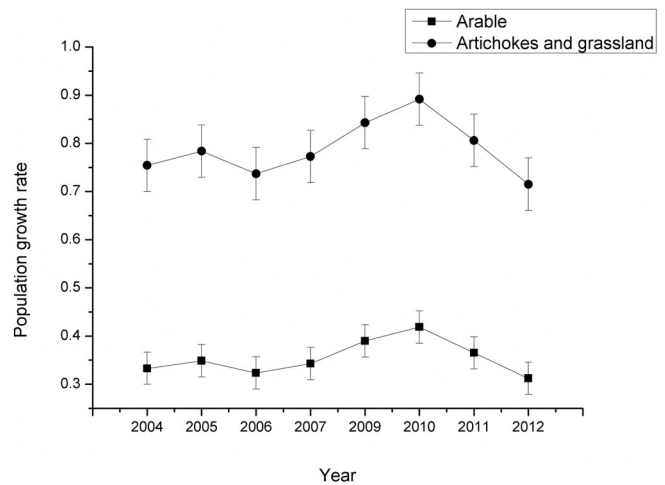

Fig. 3. Estimated lesser kestrel population growth rate in 2004–2012 (with the exception of 2008) for artichoke, grassland and arable habitats.

individual capture–recapture data were used to identify the effect of land use on fecundity and survival probabilities of lesser kestrels. In our study area, both survival and recapture probability changed positively with age (see also Prugnolle et al., 2003). This is probably due to age-dependent access to reproduction in high quality colonies (Bellia et al., 2011; Serrano and Tella, 2007), and to the effect of annual rainfall patterns on age-dependent mortality in overwintering areas (Mihoub et al., 2010). Not surprisingly, the demography of migratory birds mostly depends on both wintering and breeding habitat quality (see below), which is critical in determining individual fitness (e.g. Gunnarsson et al., 2005). Population growth of farmland birds is often habitat specific (e.g. Arlt et al., 2008) and yet, density dependence plays a crucial role in colonial species (Serrano et al., 2005).

4.1. Effect of colony size on lesser kestrel demography

Sociality elicits a complex interplay of costs and benefits (Danchin and Wagner, 1997; Campobello and Hare, 2007; Di Maggio et al., 2013), and the unequal fitness payoffs of living in a group drive the variation in avian colony size (Brown et al., 2000). Our findings confirm colony size as an important driver of population dynamics of colonial birds as summarized here for a renowned model species such as the lesser kestrel.

Lesser kestrels living in larger colonies acquire fitness benefits that prevail over the costs of both the increased competition for resources (Bonal and Aparicio, 2008) and the increased risk of transmission of parasites and diseases associated with group living (Serrano et al., 2004). Further benefits of living in large colonies include the reduced risk of

predation for adults and their offspring (Serrano et al., 2005) and the reduction of individual investment in vigilance (Campobello et al., 2012). Moreover, colony size regulates the dispersal of lesser kestrels, which use the number of conspecifics as a cue to colony quality and tend to move to large colonies (Serrano et al., 2001; Serrano and Tella, 2003). Earlier studies found colony size to be positively associated with reproductive success in this species (Serrano and Tella, 2007), and nestling survival was higher in large colonies (Serrano et al., 2001), due to the interaction between nest distance and breeder abundance (Di Maggio et al., 2013). On the other hand, living in large groups imposes significant costs (e.g. Szostek et al., 2014), as lesser kestrels experience density-dependent food depletion in large colonies (Bonal and Aparicio, 2008). First-breeding birds are forced to emigrate from natal sites due to social interactions with adults in colonies at carrying capacity (Serrano and Tella, 2007), and the increase in colony size beyond a certain threshold exerts a negative effect because of its repercussions on nest distance (Serrano et al., 2004).

Opposite selection pressures are thus acting on colony size as in common terns *Sterna hirundo*, where large colonies promote higher survival but reduce the quality of chicks (Minias et al., 2015). Similarly, we detected an opposite colony size effect in juvenile survival and fecundity. In juveniles, colony size plays a small positive effect on survival; however, colony size has a negative effect on fecundity, as the number of fledglings decreased more in large colonies than in small ones. Alternatively, juveniles born into large colonies might be more philopatric than those born into small ones. This hypothesis cannot be ruled out but in view of the negative effect of colony size on fecundity, it would

Table 2

Results of GLMM testing for the role of colony size, habitat and year on fecundity (N = 1001 nests). In bold the model with the lowest AIC value. Colony Id was fitted as a random term. Interactive effect marked as * and additive effect as +; N Par = number of model parameters.

Rank	Model	AIC	ΔAIC	AIC w	N Par
1	**Fecundity ~ year + colony size**	**3679.5**	**0**	**0.619**	**2**
2	Fecundity ~ year + colony size * habitat	3681.0	1.5	0.293	3
3	Fecundity ~ year + colony size + habitat	3683.4	3.9	0.088	3
4	Fecundity ~ habitat + year	3696.9	17.4	0.000	2
5	Fecundity ~ year	3793.4	113.9	0.000	1
6	Fecundity ~ colony size	3848.4	168.9	0.000	1
7	Fecundity ~ habitat + colony size	3851.6	172.1	0.000	2
8	Fecundity ~ habitat	3884.4	204.9	0.000	1

Table 3

Sensitivity and elasticity of different vital rates on population growth rates for lesser kestrels living in arable, artichoke and grassland habitats of the Gela Plain. Estimates and definitions of vital rates are given in online Table A3.

Matrix element	Definition	Sensitivity	Elasticity
A) Arable			
1-year bird fecundity	C0FS0	0.034	<0.001
Adult fecundity	CFSad	0.249	0.140
First-year survival probability	S0	0.597	0.141
1-year bird survival probability	Ssub	0.096	0.140
Adult survival probability	Sad	0.717	0.576
B) Artichoke and grassland			
1-year bird fecundity	C0FS0	0.014	<0.001
Adult fecundity	CFSad	0.116	0.074
First-year survival probability	S0	0.396	0.075
1-year bird survival probability	Ssub	0.103	0.074
Adult survival probability	Sad	0.851	0.776

imply a maladaptive behavior. Our findings more likely indicated a trade-off between the survival probability of offspring and fecundity, with a lower number of high-quality juveniles (i.e. with a small survival advantage in the first year) produced in larger colonies. The combination of density-dependent fertility with the small effect that density has on juvenile survival allowed us to quantify the optimal colony size. This is almost a midpoint value conditional on the range of colony sizes settled by lesser kestrels in the Gela Plain under the environmental conditions of 2004–2012. Nevertheless, it establishes a baseline for further experimental design on the selection of a medium colony size, such as the optimal size for group living in farmland birds.

4.2. Effect of land uses on lesser kestrel demography

The elevated biodiversity in Mediterranean agro-ecosystems requires special management practices on a local scale (Sokos et al., 2013). In our study we found that land use had a very strong effect on adult survival probability and population growth rate. Adult lesser kestrels living in colonies surrounded by grassland and artichoke fields had 50% higher survival probabilities than conspecifics living in arable colonies. Though grasslands and artichoke fields are quite different land uses, adult lesser kestrels experienced equivalent survival probabilities in these two habitats. Grasslands, including set-aside and fallow lands, are extensive landscape elements of traditional farming particularly important for the lesser kestrel (Franco et al., 2004) and wildlife conservation (Moreira et al., 2005; Zamora et al., 2007). In contrast, the artichoke field is a distinctive crop type of the study area, and is an unusual foraging habitat for the lesser kestrel in Southern Europe (García et al., 2006; Catry et al., 2014). The temporal dynamics of cultivation (Catry et al., 2012), makes artichoke fields suitable for lesser kestrels. During the winter, when lesser kestrels are absent from the area, artichoke fields are disturbed by the human activities related to intensive cultivation, such as preparation of the field, artichoke planting, and heavy use of fertilizers and biocides (Lo Giudice et al., 2014). The fields are abandoned after the harvest in late April to early May, and provide an abundance of prey and biomass to lesser kestrels during the breeding season (Di Maggio et al., unpublished results).

In our study area, cereal fields grant the lowest survival to lesser kestrels, confirming the poor quality of this land use due to tall vegetation cover that provides low accessibility to prey, and to biocide use, mechanical plowing, and mowing, which reduce prey biomass (Garcia et al., 2006; Catry et al., 2012). Only during harvesting, cereals represent a good foraging habitat for the ephemeral increase in food supply (Catry et al., 2014). In our study area, arable fields prove to be the land use providing the lowest invertebrate and vertebrate richness and biomass (Di Maggio et al., unpublished results).

4.3. Conservation implications and management of farmland habitats

The current values of vital rates found in the Gela Plain predict a decline of the lesser-kestrel population. As in Hiraldo et al. (1996), our findings suggest that lesser kestrel demography is driven by the adult class (but see Prugnolle et al., 2003). Adult survival is the vital rate contributing the most to the sensitivity and elasticity of the population growth rate, followed by juvenile survival and adult fecundity. Conservation practices working on the basis of explicit factors affecting adult survival would thus be the most decisive for correct population management of the lesser kestrel across the Palearctic range (Ehrlén et al., 2001; Sarà et al., 2014). Adult survival probabilities in grassland and artichoke colonies (0.66–0.75) are comparable to those of other lesser kestrel populations (0.67–0.72: Hiraldo et al., 1996; Prugnolle et al., 2003; Serrano et al., 2005). Contrarily, adult survival in arable colonies (0.30) of the Gela Plain is the lowest recorded in demographic studies of the species so far. The asymptotic growth rate indicated a negative population trend ($\lambda < 1$) across the study period for every land-use, although it was much more marked in the arable colonies. Agricultural intensification in the Gela Plain is reducing the extent of grasslands, and extending the irrigated crop season with a much more massive use of biocides. Their use is particularly dangerous in June, when lesser kestrels are raising their nestlings as indicated by the large number of poisoned females recorded dead inside failed nests. Accordingly, the most effective strategy to prevent the collapse of the lesser kestrel population in the Gela Plain should be based on land-use management and on the direct causes of adult mortality, to return to the extensive agricultural practices observed at the beginnings of the study. Although maintaining low-intensity farming is still the main recommendation for this species (García et al., 2006; Catry et al., 2012), the positive effects of irrigated non-traditional crops, such as artichoke in the Gela Plain, or alfalfa *Medicago sativa* fields in Spain (Ursua et al., 2005), on lesser kestrel demography bring forward new management options when socio-economics pressure makes irrigation unavoidable. Conservation actions should be encompassed in an AES implemented to reduce agricultural intensification and human disturbance and enhance habitat heterogeneity (Whittingham, 2007). Specifically, the AES should promote organic farming in the area and artichoke cultivation with low input of biocides to make more compatible irrigated crops with lesser kestrel conservation. Uncut strips of cereals and grasslands should be left as buffers around arable colonies to improve prey availability and reduce adult and nestling starvation (Catry et al., 2014). Because there was no interaction between habitat type and colony size, all of these conservation actions would be equally effective when applied to all colonies, irrespective of colony size.

Experimental manipulations of land uses with simultaneous monitoring of pseudo-steppe species, such as the lesser kestrel, would provide fine-tuned indications, not only for wide-scale conservation strategies on one bio-indicator of a vulnerable habitat but also for management actions able to improve sustainability in agricultural practices.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.11.016.

References

Arlt, D., Forslund, P., Jeppsson, T., Pärt, T., 2008. Habitat-specific population growth of farmland bird. PLoS One 3, e3006.

Baldi, A., Batary, P., Kleijn, D., 2013. Effects of grazing and biogeographic regions on grassland biodiversity in Hungary — analysing assemblages of 1200 species. Agr Ecosyst Environ 166, 28–34.

Bates, D., Maechler, M., Bolker, B., 2013. lme4: linear-mixed effects models using S4 classes. Available at: http://cran.r-project.org/package=lme4.

Bellia, E., Campobello, D., Sarà, M., 2011. Great tit (*Parus major*) breeding in fire-prone oak woods: differential effects of post-fire conditions on reproductive stages. Int. J. Wildland Fire 20, 605–611.

Berg, A., Wretenberg, J., Zmihorski, M., Hiron, M., Pärt, T., 2015. Linking occurrence and changes in local abundance of farmland bird species to landscape composition and land-use changes. Agr Ecosyst Environ 204, 1–7.

Bonal, R., Aparicio, J.M., 2008. Evidence of prey depletion around lesser kestrel *Falco naumanni* colonies and its short term negative consequences. J. Avian Biol. 39, 189–197.

Brambilla, M., Guidali, F., Negri, I., 2008. The importance of an agricultural mosaic for Cirl Buntings *Emberiza cirlus* in Italy. Ibis 150, 628–632.

Brown, C.R., Brown, M.B.B., Danchin, E., 2000. Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. J. Anim. Ecol. 69, 133–142.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer Verlag.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C., Pollock, K.H., 1987. Design and analysis of fish survival experiments based on capture-release. Am. Fish. Soc. Monogr. 5, 1–437.

Bustamante, J., 1997. Predictive models for lesser kestrel *Falco naumanni* distribution, abundance and extinction in southern Spain. Biol. Conserv. 80, 153–160.

Butler, S.J., Boccaccio, L., Gregory, R.D., Vorisek, P., Norris, K., 2010. Quantifying the impact of land-use change on European farmland bird populations. Agr Ecosyst Environ 137, 348–357.

Campobello, D., Hare, J.F., 2007. Information transfer determined by association of neighbours in European bee-eater (*Merops apiaster*) colonies. Ethol. Ecol. Evol. 19, 237–243.

Campobello, D., Sarà, M., Hare, J.F., 2012. Under my wing: lesser kestrels and jackdaws derive reciprocal benefits in mixed species colonies. Behav. Ecol. 23, 425–433.

Campobello, D., Hare, J.H., Sarà, M., 2015. Social phenotype extended to communities: expanded multilevel social selection analysis reveals fitness consequences of interspecific interactions. Evolution. http://dx.doi.org/10.1111/evo.12629.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer Associates.

Caswell, H., 2007. Sensitivity analysis of transient population dynamics. Ecol. Lett. 10, 1–15.

Catry, I., Amano, T., Franco, A.M.A., Sutherland, W.J., 2012. Influence of spatial and temporal dynamics of agricultural practices on the lesser kestrel. J. Appl. Ecol. 49, 99–108.

Catry, I., Franco, A.M.A., Moreira, F., 2014. Easy but ephemeral food: exploring the trade-offs of agricultural practices in the foraging decisions of lesser kestrels on farmland. Bird Study 1, 1–10.

Chiantante, G., Brambilla, M., Bogliani, G., 2014. Spatially explicit conservation issues for threatened bird species in Mediterranean farmland landscapes. J. Nat. Conserv. 22, 103–112.

Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M., Pradel, R., 2009. U-CARE: utilities for performing goodness of fit tests and manipulating capture–recapture data. Ecography 32, 1071–1074.

Danchin, E., Wagner, R.H., 1997. The evolution of coloniality: the emergence of new perspectives. Trends Ecol. Evol. 12, 342–347.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Di Maggio, R., Campobello, D., Sarà, M., 2013. Nest aggregation and reproductive synchrony promote lesser kestrel *Falco naumanni* seasonal fitness. J. Ornithol. 154, 901–910.

Di Maggio, R., Mengoni, C., Mucci, N., Campobello, D., Randi, E., Sarà, M., 2014. Do not disturb the family: roles of colony size and human disturbance in the genetic structure of lesser kestrel. J. Zool. 295, 108–115.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. Lond. B. 268, 25–29.

Ehrlén, J., van Groenendael, J., de Kroon, H., 2001. Reliability of elasticity analysis: reply to mills et al. – conserv. Biol. 15, 278–280.

European Commission, 2006. Halting the loss of biodiversity by 2010 — and beyond, sustaining ecosystem services for human well-being Accessed 1 Dec 2013. http://ec.europa.eu/environment/.

Forero, M.G., Tella, J.L., Hobson, K.A., Bertellotti, M., Blanco, G., 2002. Conspecific food competition explains variability in colony size: a test in Magellanic penguins. Ecology 83, 3466–3475.

Franco, A.M.A., Catry, I., Sutherland, W.J., Palmeirim, J., 2004. Do different habitat preference methods produce the same conservation recommendations for lesser kestrels? Anim. Conserv. 7, 291–300.

García, J.T., Morales, M.B., Martínez, J., Iglesias, L., García de la Morena, E., Suárez, F., Viñuela, J., 2006. Foraging activity and use of space by lesser kestrel *Falco naumanni* in relation to agrarian management in central Spain. Bird Conserv. Int. 16, 83–95.

Gariboldi, A., Rizzi, V., Casale, T., 2000. Aree importanti per l'avifauna in Italia. LIPU-Birdlife.

González-Estébanez, F.J., García-Tejero, S., Mateo-Tomás, P., Olea, P.P., 2011. Effects of irrigation and landscape heterogeneity on butterfly diversity in Mediterranean farmlands. Agr Ecosyst Environ 144, 262–270.

Grueber, C.E., Laws, R.J., Nakagawa, S., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711.

Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M., Sutherland, W.J., 2005. Seasonal matching of habitat quality and fitness in a migratory bird. Proc. Biol. Sci. 272, 2319–2323.

Hiraldo, F., Negro, J.J., Donázar, J.A., Gaona, P., 1996. A demographic model for a population of the endangered lesser kestrel in southern Spain. J. Appl. Ecol. 33, 1085–1093.

Iñigo, A., Barov, B., 2011. Action Plan for the Lesser Kestrel *Falco naumanni* in the European Union. SEO-BirdLife, BirdLife International for the European Commission.

Kolb, K.H., 2000. Are umbrella and target species useful instruments in nature conservation? Experiences from a black grouse habitat in the Rhon Biosphere Reserve. Cah. Ethol. 20, 481–504.

Krackow, S., Tkadlec, E., 2001. Analysis of brood sex ratios: implications of offspring clustering. Behav. Ecol. Sociobiol. 50, 293–301.

Lane, S.J., Alonso, J.C., Martin, C.A., 2001. Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? J. Appl. Ecol. 38, 193–203.

Lewis, S., Sherratt, T.N., Hamer, K.C., Wanless, S., 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature 412, 816–819.

Lo Giudice, A., Mbohwa, C., Clasadonte, M.T., Ingrao, C., 2014. Life cycle assessment interpretation and improvement of the Sicilian artichokes production. Int. J. Environ. Res. 8, 305–316.

Mattison, E.H.A., Norris, K., 2005. Bridging the gaps between agricultural policy, land-use and biodiversity. Trends Ecol. Evol. 20, 610–616.

McCullagh, P., Searle, S.R., 2000. Generalized Linear and Mixed Models. Wiley-Interscience.

Mihoub, J., Gimenez, O., Pilard, P., Sarrazin, F., 2010. Challenging conservation of migratory species: Sahelian rainfalls drive first-year survival of the vulnerable lesser kestrel *Falco naumanni*. Biol. Conserv. 143, 839–847.

Millar, R., Anderson, M.J., 2004. Remedies for pseudoreplication. Fish. Res. 70, 397–407.

Milligan, G.W., Cooper, M.C., 1988. A study of standardization of variables in cluster analysis. J. Classif. 5, 181–204.

Minias, P., Włodarczyk, R., Janiszewski, T., 2015. Opposing selective pressures may act on the colony size in a waterbird species. Evol. Ecol. 29, 283–297.

Moreira, F., Beja, P., Morgado, R., Reino, L., Gordinho, L., Delgado, A., Borralho, R., 2005. Effects of field management and landscape context on grassland wintering birds in Southern Portugal. Agr Ecosyst Environ 109, 59–74.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Negro, J.J., Hiraldo, F., 1992. Sex ratios in broods of the lesser kestrel *Falco naumanni*. Ibis 134, 190–191.

Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbe, A., Wulf, F., Scott, A.V., 2014. EU agricultural reform fails on biodiversity. Science 344, 6188.

Prugnolle, F., Pilard, P., Brun, L., Tavecchia, G., 2003. First-year and adult survival of the endangered lesser kestrel *Falco naumanni* in southern France. Bird Study 50, 68–72.

Rodríguez, C., Bustamante, J., 2003. The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines? J. Anim. Ecol. 72, 793–810.

Rodrıguez, C., Johst, K., Bustamante, J., 2006. How do crop types influence breeding success in lesser kestrels through prey quality and availability? A modelling approach. J. Appl. Ecol. 43, 587–597.

Russo, P., Carullo, L., Tomaselli, G., 2009. Analisi del paesaggio rurale delle aree "natura 2000" di Gela per la comprensione delle dinamiche storiche di trasformazione. Ricerca ed innovazione nell'ingegneria dei biosistemi agro territoriali. Doppiavoce, pp. 1–10.

Sarà, M., 2010. Climate and land-use changes as determinants of lesser kestrel *Falco naumanni* abundance in Mediterranean cereal steppes (Sicily). Ardeola 57, 3–22.

Sarà, M., Campobello, D., Zanca, L., 2012. Effects of nest and colony features on lesser kestrel (*Falco naumanni*) reproductive success. Avian Biol. Res. 5, 209–217.

Sarà, M., Campobello, D., Zanca, L., Massa, B., 2014. Food for flight: pre-migratory dynamics of the lesser kestrel *Falco naumanni*. Bird Study 61, 29–41.

Serrano, D., Tella, J.L., 2003. Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. J. Anim. Ecol. 72, 400–410.

Serrano, D., Tella, J.L., 2007. The role of despotism and heritability in determining settlement patterns in the colonial lesser kestrel. Am. Nat. 169, 53–67.

Serrano, D., Tella, J.L., Forero, M.G., Donázar, J.A., 2001. Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. J. Anim. Ecol. 70, 568–578.

Serrano, D., Forero, M.G., Donázar, J.A., Tella, J.L., 2004. The role of dispersal and conspecific cues on breeding site selection and colony dynamics of lesser kestrels. Ecology 85, 3438–3447.

Serrano, D., Oro, D., Ursua, E., Tella, J.L., 2005. Colony size selection determines adult survival and dispersal preferences: allee effects in a colonial bird. Am. Nat. 166, 22–31.

Sirami, C., Brotons, L., Burfield, I., Fonderflick, J., Martin, J.L., 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. Biol. Conserv. 141, 450–459.

Sokos, C.K., Mamolos, A.P., Kalburtji, K.L., Birtsas, P.K., 2013. Farming and wildlife in Mediterranean agroecosystems. J. Nat. Conserv. 21, 81–92.

Soliveres, S., García-Palacios, P., Castillo-Monroy, A.P., Maestre, F.T., Escudero, A., Valladares, F., 2011. Temporal dynamics of herbivory and water availability interactively modulate the outcome of a grass–shrub interaction in a semi-arid ecosystem. Oikos 120, 710–719.

Stephens, P.A., Freckleton, R.P., Watkinson, A.R., Sutherland, W.J., 2003. Predicting the response of farmland bird populations to changing food supplies. J. Appl. Ecol. 40, 970–983.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe — a review. J. Environ. Manage. 91, 22–46.

Stubben, C.J., Milligan, B.G., 2007. Estimating and analyzing demographic models using the popbio package in R. J. Stat. Softw. 22, 1–23.

Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's Information Criterion. Behav. Ecol. Sociobiol. 65, 13–21.

Szostek, K.L., Becker, P.H., Meyer, B.C., Sudmann, S.R., Zintl, H., 2014. Colony size and not nest density drives reproductive output in the common tern *Sterna hirundo*. Ibis 156, 48–59.

Tavecchia, G., Pradel, R., Lebreton, J.D., Biddau, L., Mingozzi, T., 2002. Sex-biased survival and breeding dispersal probability in a patchy population of the Rock sparrow *Petronia petronia*. Ibis 144, 79–87.

Tavecchia, G., Minguez, E., De León, A., Louzao, M., Oro, D., 2008. Living close, doing differently: small-scale asynchrony in demography of two species of seabirds. Ecology 89, 77–85.

Tavecchia, G., Adrover, J., Muñoz Navarro, A., Pradel, R., 2012. Modelling mortality causes in longitudinal data in the presence of tag loss: application to raptor poisoning and electrocution. J. Appl. Ecol. 49, 297–305.

Triolo, S., Campobello, D., Sarà, M., 2011. Diurnal habitat suitability for a Mediterranean steppeland bird, identified by Ecological Niche Factor Analysis. Wildl. Res. 38, 152–162.

Ursua, E., Serrano, D., Tella, J.L., 2005. Does land irrigation actually reduce foraging habitat for breeding lesser kestrels? The role of crop types. Biol. Conserv. 122, 643–648.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, 120–129.

Whittingham, M.J., 2007. Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? J. Appl. Ecol. 44, 1–5.

Zamora, J., Verdú, J.R., Galante, E., 2007. Species richness in Mediterranean agro-ecosystems: spatial and temporal analysis for biodiversity conservation. Biol. Conserv. 134, 113–121.

Zuur, A.F., Hilbe, J.M., Ieno, E., 2013. A Beginner's Guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists. Highland Statistics.