

A demographic model for a population of the endangered lesser kestrel in southern Spain

FERNANDO HIRALDO, JUAN J. NEGRO, JOSE A. DONÁZAR and PILAR GAONA

Estación Biológica de Doñana, Spanish Council for Research (CSIC), Apdo 1056, 41080 Sevilla, Spain

Summary

1. The lesser kestrel (*Falco naumanni*) has experienced a dramatic decline in the last 20 years in the Western Palearctic. To help in making decisions for the recovery of the species, a matrix projection model has been developed using demographic data from an intensively monitored population in southern Spain in 1988–93. Survival rates were estimated using the Jolly–Seber modelling approach and Program SURGE.
2. The growth rate of the population was $\lambda = 0.959 \pm 0.04$. The upper 95% confidence limit of λ is 1.0398, and thus our estimate of λ is not significantly different from that of a stable population (i.e. $\lambda = 1$). Using the mean value for λ , the probability of extinction for this population, now consisting of ≈ 1000 breeding pairs, is 35% in 100 years and 98% in 200 years.
3. A sensitivity analysis indicates that population growth was most sensitive for changes in adult survival, followed by juvenile survival, productivity of fledglings, proportion of adults that attempt breeding and age at first breeding.
4. Adult and juvenile survival do not seem easily amenable to management, but the small improvement (8.5%) that could be reached enforcing protective laws substantially reduce the probability of extinction of the population.
5. Productivity is less than half its potential maximum due to massive nestling mortality. Increasing food availability around the breeding colonies through habitat management (e.g. leaving uncultivated strips around fields and favouring cereal crops), or introducing the species in areas containing suitable habitat may substantially increase productivity. Combining these measures with the achievable improvement (8.5% increase) in adult and juvenile survival maximizes the long-term survival of lesser kestrel populations.

Key-words: *Falco naumanni*, wildlife management, matrix projection model, Jolly–Seber, SURGE, population dynamics, mark–recapture study.

Journal of Applied Ecology (1996) **33**, 1085–1093

Introduction

The lesser kestrel (*Falco naumanni*) is a small colonial falcon distributed in southern regions of Eurasia (Brown & Amadon 1968). Lesser kestrels are migratory, wintering in Africa south of the Sahara desert (Cramp & Simmons 1980). Small numbers of wintering birds have also been reported in southern Spain (Negro, de la Riva & Bustamante 1991). In Europe, lesser kestrels usually breed in urban areas surrounded by farmlands with little or no tree cover. Its food consists of invertebrates, especially *Orthoptera* (Cramp & Simmons 1980). As with most raptor species (Newton 1979), females are larger than males. Adult birds exhibit a strong dichromatism (Negro &

Hiraldo 1992), with males showing a more colourful plumage.

The species has experienced a marked decline in its Western Palearctic breeding range in the last 30 years (Cramp & Simmons 1980; Biber 1990). Previously considered one of the most abundant raptors in Europe (Bijleveld 1974), the lesser kestrel has recently become extinct in several countries (e.g. Austria, Hungary, Poland) and has practically disappeared in others (e.g. France, Portugal, Bulgaria) (Biber 1990). The status of the species is unknown elsewhere.

The strongholds of lesser kestrels in the Western Palearctic are in Spain (Biber 1990). Nonetheless, the Spanish population has also suffered a precipitous decline, as it dropped from an estimated 20 000–50 000

pairs in the 1970s (Garzón 1977) to 4000–5000 breeding pairs in 1988 (González & Merino 1990).

Because lesser kestrels are predominantly insectivorous, it was long assumed that agricultural insecticides were responsible for the decline of the species (Cramp & Simmons 1980). Insecticides may have been a problem in the past, but a study on organochlorine and heavy metal content in eggs collected in 1988–91 reported concentrations unlikely to have negative effects on reproduction (Negro *et al.* 1993). The same study, however, reported a high nestling mortality due to starvation, and suggested that pesticides may reduce the availability of prey. Donázar, Negro & Hiraldo (1993) reported that preferred hunting habitat of the kestrels (i.e. cereal fields, meadows, grassy field margins) are being substituted by others (e.g. sunflower monoculture) where prey are scarcer and/or lesser kestrels hunt them less efficiently.

The lesser kestrel is currently a protected species in Spain, as in the other European Union countries. However, as most kestrels are urban breeders, there is not a single breeding colony located in a natural reserve and a management plan is urgently needed. The only conservation actions undertaken so far are the installation of nest-boxes in colonies where suitable cavities were scarce and a reintroduction programme using captive-bred individuals in Catalonia (Pomarol 1993).

To make sound decisions for the conservation of lesser kestrels, the population's response to different management should be studied. In this paper, we develop a matrix population model using demographic data from a population in southern Spain intensively colour-ringed and monitored during the period 1988–93. First, we used a deterministic version of our model to calculate the growth rate (λ) of the population, its standard error, as well as the sensitivity of λ to changes in the values of the demographic parameters. Secondly, we introduced demographic and environmental stochasticity (Shaffer 1981) in our matrix model to calculate the probability of extinction of the lesser kestrel population that we studied, and to evaluate the impact on the extinction probability of several management scenarios. Our ultimate goal was to identify those management strategies most likely to maximize survival of lesser kestrel populations.

Description of the population model

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

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

where \mathbf{M} is the population projection matrix (Caswell 1989) incorporating data on fecundity, mortality and growth rate of each population stage. N_t is a vector

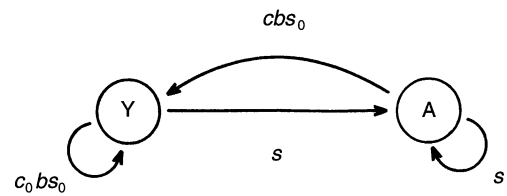


Fig. 1. Life-cycle graph for the lesser kestrel: Y = yearlings; A = adults (≥ 2 years old); b = female progeny per reproductive female; c_0 = proportion of yearlings attempting breeding; c = proportion of adults (2 years or older) attempting breeding; s_0 = juvenile survival (i.e. during the first year of life); s = adult annual survival.

with the abundance of individuals in each of the life-cycle stages (see Fig. 1).

To develop our matrix model we divided the population of female lesser kestrels into two age classes: yearlings and individuals 2 or more years old (Fig. 1). Our field observations indicate that both males and females typically start breeding when 2 years old, although about 12% of breeding pairs are composed by at least one yearling. Taking this data into consideration our model takes the form:

$$\begin{pmatrix} Y \\ A \end{pmatrix}_{t+1} = \begin{pmatrix} c_0bs_0 & cbs_0 \\ s & s \end{pmatrix} \times \begin{pmatrix} Y \\ A \end{pmatrix}_t \quad \text{eqn 2}$$

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

Estimation of demographic parameters

Colour-ringing and monitoring of breeding performance were conducted in 12 colonies in the Sevilla province (southern Spain) during 6 years (1988–93). All colonies were in the lower part of the Guadalquivir valley, which is intensively cultivated with cereals, sunflowers and olive trees.

BREEDING SUCCESS (b)

All the nests in the colonies were located and visited to determine brood size and to colour-ring the young. Nestlings were sexed by plumage characteristics according to Negro & Hiraldo (1991). The production of fledglings was estimated as the number of nestlings surviving until the age of ringing, which usually took place 7–10 days prior to fledging. The colonies were searched for dead nestlings at the end of the breeding season and fledgling success was re-estimated for those nests that had suffered documented losses. Most deaths were due to starvation and as there was no

Table 1. Mean number (\pm SD) of offspring per reproductive female in 1988–92

Year	Mean number	SD	<i>n</i> *
1988	2.16	1.37	112
1989	1.53	1.24	126
1990	1.80	1.17	125
1991	2.31	1.52	141
1992	1.50	1.90	122

* Number of broods.

evidence of scavengers, dead nestlings that went undetected were probably few.

Production of fledglings during the five breeding seasons of 1988–92 is given in Table 1. To estimate the mean number of fledgling females (*b* in the model), we first estimated the overall fledgling success of the five years and divided it by two (sex-ratios were balanced, Negro & Hiraldo [1992]). The mean value for *b* is given in Table 6.

ANNUAL SURVIVAL PROBABILITIES

Survival rates were estimated from capture and resight data of colour-ringed individuals in 1988–93. We used data from the three kestrel colonies located in the towns of Arahál, Morón, and Mairena del Alcor, respectively (all three in the province of Seville). Those colonies were the most intensively surveyed in our study, and the effort of capture and resight in each of them was comparable. Individuals were trapped at roosting sites or at the nests and were provided with colour rings displaying a two-character code which could be read using a telescope. Since the ringing programme started in 1988, considerable effort has been put into reading rings in the study area. Two full-time assistants have monitored the colonies with spotting scopes from the arrival of the first kestrels in February until the end of the breeding season in August. In addition, many ringed birds from previous years were re-trapped throughout the study. A small part of the return data (<1%) came from individuals found injured or dead by us or the public. Most resightings of adults (96%, Negro 1991) were done at the colonies where they had originally been ringed. We used the capture history data of 263 yearlings and adults (≥ 2 years old) (Table 2), as well as those of 996 individuals ringed as young (Table 3). Data for males and females were pooled, as sexual differences in survival were not significant (Negro 1991).

ANALYTICAL PROCEDURES FOR *S* AND *S*₀

To calculate survival rates, we used the Jolly–Seber modelling approach following Lebreton *et al.* (1992) and Paton (1994). Tests 2 and 3 from Program RELEASE (Burnham *et al.* 1987) were first utilized to assess the fit of the initial model (*S*, *P*), where

Table 2. Capture or resighting history matrix for lesser kestrels ringed as yearlings or adults (≥ 2 years old) in southern Spain from 1988 to 1993

Capture or resighting history*	Number of individuals
1 0 0 0 0 0	11
1 0 0 1 0 0	1
1 0 0 1 1 1	1
1 0 1 0 0 0	2
1 0 1 1 1 1	2
1 1 0 0 0 0	3
1 1 0 0 1 0	1
1 1 0 1 0 0	1
1 1 1 0 0 0	3
1 1 1 0 1 0	1
1 1 1 1 0 0	2
0 1 0 0 0 0	22
0 1 0 0 1 0	2
0 1 0 1 0 0	2
0 1 0 1 0 1	1
0 1 0 1 1 0	3
0 1 0 1 1 1	3
0 1 0 2 0 0	1
0 1 1 0 0 0	18
0 1 1 1 0 0	15
0 1 1 1 1 0	7
0 1 1 1 1 1	14
0 1 1 1 2 0	1
0 1 1 2 0 0	1
0 0 1 0 0 0	13
0 0 1 0 1 1	1
0 0 1 1 0 0	12
0 0 1 1 1 0	4
0 0 1 1 1 1	9
0 0 1 1 2 0	1
0 0 0 1 0 0	22
0 0 0 1 0 1	4
0 0 0 1 1 0	15
0 0 0 1 1 1	12
0 0 0 0 1 0	23
0 0 0 0 1 1	28

* Capture or resighting = 1; no capture or resighting = 0; found dead = 2. Each digit represents the situation in each of the 6 years between 1988 and 1993 (both included). As an example, the individual with history ‘1 1 1 0 1 0’ was ringed in 1988 and resighted in 1989, 1990 and 1992.

survival rates (*S*) and resighting probabilities (*P*) are both time (*t*) dependent. We assumed that recaptures and resightings were equivalent. We then used Program SURGE (Lebreton *et al.* 1992) for iterative model fitting and the computation of likelihood ratio tests. Model selection was based on Akaike’s Information Criterion (AIC). The model with the lowest AIC was selected as the best fitting model. The potential survival models that we examined for both juveniles and yearling-adults included four combinations of time for survival probabilities (*S*) and resighting probabilities (*P*) (Table 4).

We performed a goodness-of-fit test of data corresponding to lesser kestrels banded as young (Table 3) for the model (*S*, *P*). Tests 2 and 3 showed heterogeneity between and within groups (Test 2 + Test 3:

Table 3. Capture or resighting history matrix for lesser kestrels ringed as nestlings in southern Spain from 1988 to 1993. To calculate survival (s_0) with Program SURGE (see text) all individuals were removed from the population when first resighted (number '2' in all capture histories)

Capture or resighting history*	Number of individuals
1 0 0 0 0 0	110
1 0 0 0 0 2	1
1 0 0 0 2 0	6
1 0 0 2 0 0	10
1 0 2 0 0 0	7
1 2 0 0 0 0	22
0 1 0 0 0 0	168
0 1 0 0 0 2	1
0 1 0 0 2 0	1
0 1 0 2 0 0	3
0 1 2 0 0 0	13
0 0 1 0 0 0	183
0 0 1 0 0 2	3
0 0 1 0 2 0	11
0 0 1 2 0 0	22
0 0 0 1 0 0	201
0 0 0 1 0 2	18
0 0 0 1 2 0	37
0 0 0 0 1 0	148
0 0 0 0 1 2	32

* Capture or resighting = 1; no capture or resighting = 0; found dead or removed for analytical purposes = 2. Each digit represents the situation in each of the 6 years between 1988 and 1993.

$\chi^2_{12} = 149.3$, $P = 0.000$). This heterogeneity may arise because a large fraction of the juveniles do not return to the natal areas until they are 2 or more years old (Negro 1991). The whereabouts of those kestrels was unknown, but they may have stayed in the African wintering area.

To reduce heterogeneity, the survival of yearling and adults was estimated exclusively from the data

Table 4. Potential survival models for adult and young lesser kestrels in southern Spain. Best-fitting models in bold

Model*	np^\dagger	$-2 \ln L^\ddagger$	AIC§
Yearlings and adults			
S_t, P_t	10	817.6	837.6
S_t, P	6	830.4	842.4
S, P_t	6	826.8	838.8
S, P	2	840.2	844.2
Juveniles			
S_{at}, P_{at}	18	1223.5	1259.5
S_{at}, P_a	11	1231.5	1253.5
S_a, P_{at}	11	1223.5	1259.5
S_a, P_a	4	1272.7	1272.7

* S = annual survival probability; P = resighting probability; t = time dependency; a = age dependency.

† Number of estimable parameters.

‡ L = likelihood function.

§ Akaike's Information Criterion = $2np + -2 \ln L$.

Table 5. Annual survival rates for yearling-adults (s) and young (s_0) lesser kestrels in southern Spain between 1988 and 1993, calculated with Program SURGE (Lebreton *et al.* 1992). Parameter estimates were based on the Jolly-Seber model with a lower AIC. Survival probabilities (S) and resighting probabilities (P) were time-dependent for the adults (model S_t, P_t). For the young, S was age- and time-dependent, and P age-dependent, time constant

Years	s (model S_t, P_t)	s_0 (model S_{at}, P_a)
1988–89	0.677	0.382
1989–90	0.828	0.136
1990–91	0.687	0.281
1991–92	0.611	0.421
1992–93	0.745	0.481

corresponding to kestrels banded as breeders (Table 2). The survival of juveniles during their first year of life was estimated from data of kestrels banded as young, and modifying the capture history matrix according to Clobert *et al.* (1990) and Clobert *et al.* (1994).

The goodness-of-fit test for the model (S_t, P_t), the one with the lowest AIC for yearlings and adults (Table 4), was not rejected (Test 2 + Test 3, Program Release, $\chi^2_3 = 5.64$, $P = 0.58$). Therefore, our yearling-adult data were appropriate for a Jolly-Seber modelling approach. Annual survival rates are given in Table 5. For our population model we used the mean value of s during the period of study ($s = 0.7101$) (see Table 6).

To estimate survival of the young we followed methodology outlined in Clobert *et al.* (1990) and Clobert *et al.* (1994). These authors proposed a method to estimate the local immature survival rate, and the age-specific proportions of breeders in bird populations where individuals from the same cohort do not breed for the first time at the same age. This method assumes that the first resight of an individual in its natal area coincides with its first breeding attempt. This is not necessarily true in lesser kestrels and thus we cannot use this method to calculate the

Table 6. Life history parameters used in the population model

Parameter	Mean	SD
b	0.9321	0.1828
c_0	0.3847	0.0716
c	0.9250	0.0811
s_0	0.3409	0.1200
s	0.7101	0.0726

b = female progeny per reproductive female.

c_0 = proportion of yearlings attempting breeding.

c = proportion of adults (2 years or older) attempting breeding. s_0 = juvenile survival, i.e. during the first year of life.

s = adult annual survival.

age-specific proportion of breeders (we estimate this parameter of the model by other means, see below). We can estimate, however, the local immature survival rate.

We modified the original capture and resighting history matrix for the young (Table 3) to create a new one in which all individuals are considered as removed from the population at the time of its first capture. The goodness-of-fit test of the new data set for the initial model (S_t, P_t) was not rejected. Test 3 could not be carried out due to the structure of the data. Test 2 did not show heterogeneity ($\chi^2_3 = 8.6136, P = 0.1255$). Therefore, the new data set for the young was appropriate for the Jolly–Seber modelling approach.

Of the four models tested with SURGE (all of them age-dependent, corresponding with the first age class of the juveniles), the best fitting model was (S_{at}, P_a) (Table 4). Annual survival rates calculated from this model are given in Table 5. For the population model, we used the mean value $s_0 = 0.3409$ (see Table 6).

PROPORTION OF ADULTS (C) AND YEARLINGS (C_0) THAT ATTEMPT BREEDING

c was estimated for the years 1989, 1990 and 1992. During those years a sector of the breeding colony at Mairena del Alcor (Sevilla province) was monitored at least twice a week throughout the breeding season. Out of 40 monitored pairs, 37 (92.5%) laid eggs (see also Table 6).

c_0 was estimated according to the following expression:

$$c_0 = \frac{2 \times p_t \times y}{f_{t-1} \times s_0} \quad \text{eqn 4}$$

where p_t is the number of breeding pairs in year t (multiplied by 2 to standardize to individual birds); y is the proportion of yearlings in the population of breeders in year t ($y = 0.120$, averaging data from 1988 to 1992); f_{t-1} is the number of fledglings in year $t-1$; s_0 is the juvenile survival. The c_0 value used in the model is given in Table 6.

Population projections

According to the projection matrix in eqn 2, the growth rate of the population that we studied was $\lambda = 0.9594$. The stable age distribution (w) is dominated by the adults (0.74 adults vs. 0.26 juveniles). The reproductive values (v) are also higher for the adults (0.82 adults vs. 0.69 juveniles).

CONFIDENCE LIMITS FOR λ

To calculate confidence limits for λ we have first calculated its sampling variance using the following equation (Lande 1988):

$$\sigma_\lambda^2 = \sum (\partial\lambda/\partial\pi)^2 \sigma_\pi^2 \quad \text{eqn 5}$$

Table 7. ‘Elasticity’ and ‘sensitivity’ of λ to the different demographic parameters (π , see Table 6 for definitions). The contribution of each parameter to the sampling variance of λ from eqn 5 (see text) is also given

	Elasticity	Sensitivity ($\partial\lambda/\partial\pi$)	Contribution to σ_λ^2 ($\times 10^{-3}$)
b	0.2362	0.2295	0.0405
c_0	0.0729	0.0292	0.0071
c	0.2077	0.2002	0.0748
s_0	0.6458	0.2295	0.0934
s	1.0411	0.7705	1.4000
Total (σ_λ^2) = 1.6168×10^{-3}			

where π represents each of the parameters in our model (i.e. b, s, s_0, c, c_0), σ_π^2 is the sampling variance of π estimated from N_π individuals in the population (Kendall & Stuart 1977). The expression in parentheses represents the ‘sensitivity’ of λ to small changes in π (see below and Table 7).

The standard error of the estimate of λ is $\sigma_\lambda = 0.0402$. Thus, λ 's upper 95% confidence limit is 1.0398 and our estimate of λ is not significantly different from that of a stable population ($\lambda = 1$).

OBSERVED POPULATION TRENDS

Annual population surveys in the study area indicate a 6% decrease in the size of the population between 1989 and 1994. This rate of decline is in fact very close to our estimated value of λ (Fig. 2).

SENSITIVITY ANALYSIS

The sensitivities of λ with respect to changes in the demographic parameters indicate which of the parameters has the largest impact on the growth rate of the population (Lande 1988). Sensitivity can be measured both in absolute terms (‘sensitivity’ *sensu strictu*) or in relative terms (‘elasticity’) (Kroon *et al.* 1986; Caswell 1989). The sensitivity analysis (Table 7) indicates which changes (both absolute and relative) in the adult annual survival have the largest impact on the population growth rate. An increment of 5.2% in the current adult survival (from 0.710 to 0.749) would stabilize population growth ($\lambda = 1$), whereas first-year survival and breeding success should increase around 16% (0.340–0.404, and 0.932–1.110, respectively) for stable growth to be reached.

Simulation of different management scenarios

To estimate the extinction probability of the lesser kestrel population we introduced environmental stochasticity (Shaffer 1981) into our model. Survival rates and productivity were considered as random variables with a normal distribution. In each simu-

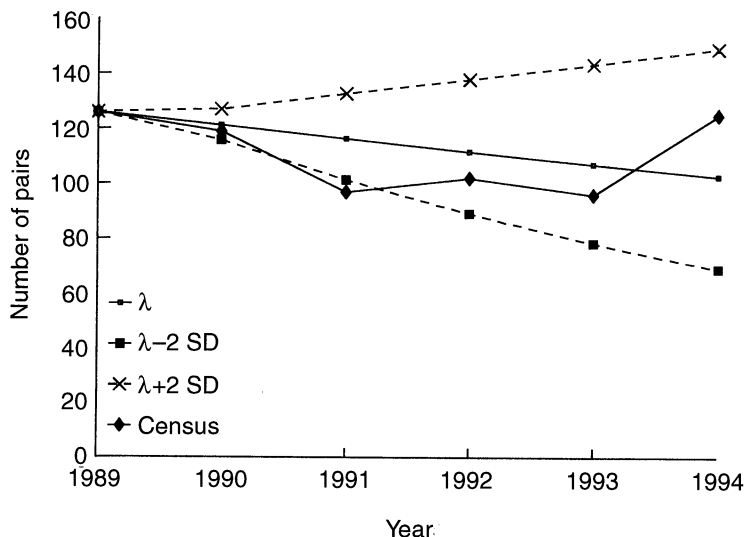


Fig. 2. Observed population trend in 1989–94 for a lesser kestrel population in southern Spain, and values projected by the demographic model. Projections for the mean value of $\lambda = 0.9594$ and its lower and upper 95% confidence limit are included.

lation the annual value of the parameters is given by the following expression:

$$x(i) = x + (s \times d) \quad \text{eqn 6}$$

where x is the mean value of any given parameter, s is its standard deviation and d is the normal standard deviation. The value of d varies randomly in each simulation.

Following Akçakaya (1991), demographic stochasticity was introduced by sampling a Poisson distribution to obtain the number of juveniles produced each year, and by sampling binomial distributions to find out the sex of the juveniles and the number of survivors each year. The results of the simulations indicate that the probability of extinction of the population is 35% in 100 years, and 98% in 200 years (Fig. 3).

The conservation strategies that could be applied to lesser kestrel colonies in the study area were evaluated through their effect on the probability of extinction of the whole lesser kestrel population in the Guadal-

quivir valley in 1988 (929 pairs, González & Merino 1990). Management scenarios were simulated 1000 times; each simulation was 200 years in duration.

REDUCTION OF ADULT MORTALITY

According to the sensitivity analysis, adult survival has the highest impact on λ . However, the success of a management plan focused on a single parameter would depend on whether that parameter is currently altered in relation to that of a healthy population (see Green & Hirons 1991), and also on whether that parameter is amenable to human alteration (Crouse *et al.* 1987). No data on adult survival in stable populations of lesser kestrels are available. However, the adult annual survival that we estimated ($s = 0.71$) is similar or higher than those reported for other falconids of similar size whose populations are not endangered (European kestrel *Falco tinnunculus*: 0.58–0.65; American kestrel *F. sparverius*: 0.51–0.53 [in Newton 1979]; merlin *F. columbarius*: 0.71 [James,

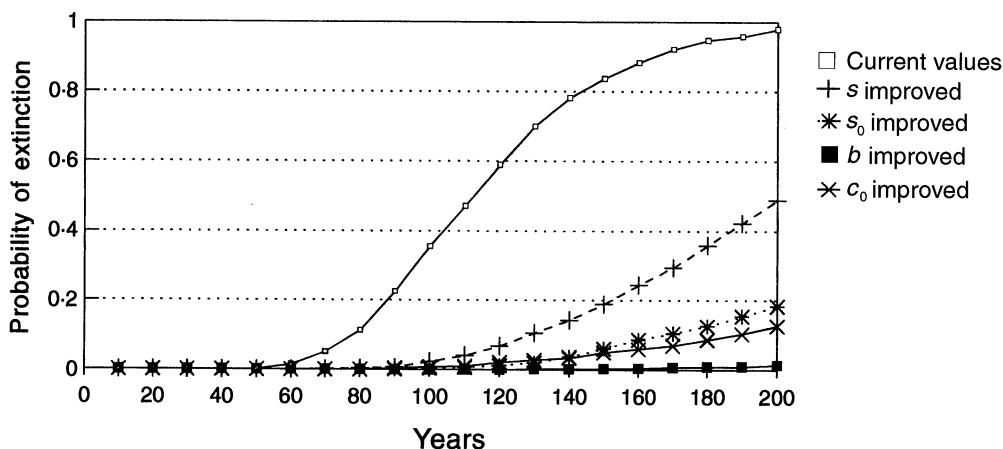


Fig. 3. Simulation of the changes in the probability of extinction for the lesser kestrel population in the Guadalquivir valley (southern Spain). Simulations of improvements of individual life history parameters are also represented.

Warkentin & Oliphant 1989)). This interspecific comparison suggests that the opportunities to further reduce the current adult mortality rate are small. Nonetheless, urban lesser kestrels suffer much less predation than their rural counterparts (Tella *et al.* 1996) and thus urban populations might have a different population dynamics (e.g. lower mortality rates) than that expected for a bird of their size.

Only mortality due to direct human intervention in the breeding grounds (e.g. shooting, netting during restoration work in the colonies) seems to be avoidable. Human-related mortality might be eliminated by patrolling colony areas and enforcing existing protective laws, as well as conducting educative programmes in the areas of concern. However, even if that is accomplished, we estimate using data on mortality causes in Negro (1991) that the overall mortality rate would be reduced to a maximum of 8.5%. Given this reduction in mortality, survival would increase from 0.710 to 0.734 (i.e. a 3.25% increase in the survival rate).

Reducing the adult mortality by 8.5%, the probability of extinction of the population in 200 years (see Fig. 3) is half the value obtained using our current estimation for $s = 0.71$. Therefore, management for a reduction of the adult mortality during the breeding season in the Guadalquivir valley, increases substantially the long-term survival of the lesser kestrel population inhabiting the area.

REDUCTION OF JUVENILE MORTALITY

As with adult survival rates, no data are available on survival of juveniles in a stable population of lesser kestrels. Data for other small Falconiformes (e.g. European and American kestrels, and sparrowhawks *Accipiter nisus*) are between 0.30 and 0.50 (see review in Newton 1979). Our estimation of 0.34 is thus in the lower range for small raptors. An excessive juvenile mortality could then be responsible, at least partly, for the decline of the lesser kestrel. However, opportunities to increase survival while acting in the breeding areas are possibly similar to that with the adults. A reduction in juvenile mortality of 8.5%, the same reduction simulated for the adults, would increase s_0 from 0.34 to 0.39 (i.e. a 12.8% increase). Model simulations using the new value indicate that the probability of extinction of the population in 200 years is reduced fivefold compared to the simulation with current values (Fig. 3). If adult and juvenile mortality were simultaneously reduced by 8.5%, the probability of extinction would be further reduced and, according to our simulations, the probability of extinction of the population in 200 years is close to zero.

INCREASE IN PRODUCTIVITY

Mean clutch size (4.11 eggs) and hatching rate (81%) in the study area are average for the species (Cramp

& Simmons 1980; Negro *et al.* 1993). Productivity, however, is less than half the number of chicks that actually hatch. Thus, the parameter of the population model most susceptible to improvement is nestling mortality, which is extremely high due to starvation (Negro *et al.* 1993). This situation may be related to scarcity of prey during the nestling-rearing period (Donazar *et al.* 1993). Lesser kestrels prefer to hunt in uncultivated areas and cereals, which have decreased drastically and have been replaced by new crops avoided by the kestrels.

We have simulated an increase in productivity from the current 1.86 to 2.31 fledglings per breeding pair (a 24% increase), which was the productivity in 1991 (Table 1), the highest recorded during the period of study. Even though λ shows less sensitivity to productivity than to adult or juvenile survival (Table 7), the important increase in productivity that we simulated reduces the probability of extinction of the population to 1.4% in 200 years (Fig. 3). When we simulated a 24% increase in productivity and 8.5% reductions in both adult and juvenile mortality, the probability of extinction in 200 years is zero, as the population would actually increase.

Of the two remaining parameters of the model, c is already close to its maximal value (92.5% of adults attempted breeding) and hardly amenable to management. In principle, c_0 could increase markedly. However, we cannot predict to what extent this parameter would change in response to management strategies. If yearlings bred in the same proportion as adults do (92.5%), the probability of extinction of the population would be 12.7% in 200 years (Fig. 3).

Discussion

We are very confident of our estimates of adult survival because adults tend to reneest in the same colonies year after year. Productivity and proportion of birds that attempt breeding were calculated by direct observation and with large sample sizes and, therefore, we believe they must also be very accurate. However, we could have underestimated juvenile survival, and λ in turn, if a significant fraction of the juveniles dispersed outside the study area. This is unlikely, because the number of individuals dispersing decreases exponentially with distance from the birthplace (Negro 1991). In fact, most resightings of birds ringed as nestlings were at their natal colonies (71% and 63% of resightings for males and females, respectively).

The sensitivity analysis indicated that the contribution of the different life-history parameters to population growth was highest for adult survival, followed by juvenile survival, productivity of fledglings, proportion of adults that attempt breeding and age at first breeding. Exactly the same sequence has been proposed for other relatively long-lived animals (Crouse *et al.* 1987), including several raptors such as the peregrine falcon (*Falco peregrinus*) (Wootton &

Bell 1992), imperial eagle *Aquila adalberti* (Ferrer & Calderón 1990; Ferrer & Hiraldo 1991; Gaona 1993) and northern spotted owl (*Strix occidentalis caurina*) (Lande 1988). These authors emphasized, and we agree with them, that the most effective strategy to ensure the long-term survival of these species is to reduce mortality of adults and juveniles. In the case of the lesser kestrel in the Guadalquivir valley, the elimination of avoidable mortality of both juveniles and adults reduces significantly the probability of extinction of the population.

Productivity has a lower influence on the population growth than the survival of adults or young. However, current productivity in our population is far from its potential maximum, and thus may suffer a much higher proportional increase than survival. This situation clearly indicates that to derive management implications from population models the sensitivity analysis is not enough. It is also necessary to consider the actual possibilities in hand to modify the different demographic parameters.

A conceivable strategy to reduce nestling mortality due to starvation would be to promote the culture of crops favoured by the kestrels, e.g. cereals, legumes and melons (Donazar *et al.* 1993), and to leave uncultivated strips of land around crop fields (Sotherton, Boatman & Rands 1989). This strategy would also increase populations of small game such as red-legged partridges (*Alectoris rufa*) (Rands 1987) and Iberian hares (*Lepus granatensis*), which reproduce and shelter in grassy field margins, and might be financially supported by local hunter associations. Nowadays, game populations in monoculture areas are not self-sustaining and hunters release captive-bred stock at a very high cost (authors' unpublished observations). Government subsidies or public donations could also help to compensate for revenue loss (if any).

Habitat management for increased productivity may also increase juvenile survival. In other raptors it has been reported that pairs able to rear more offspring also produce healthier ones (Ferrer 1993). Our own data indicate that years of higher productivity were followed by relatively higher returns. Food supplementation of some nests could be also attempted to determine (i) whether more fledglings can be produced by artificially increasing the provisioning rates, and (ii) whether an experimental increase in productivity would result in higher return rates of yearlings. This latter strategy, even if successful, would require a tremendous commitment in terms of personnel and funds.

Another approach could be to reintroduce the species in areas where the kestrels disappeared due to human persecution or lack of nesting cavities, but that contain suitable habitat. Cereal-producing regions in south and central Spain may provide excellent conditions for lesser kestrels. Interesting precedents of very successful re-introduction programmes of *Falco* species are the peregrine falcon in eastern North America,

now with a self-sustaining population (Cade *et al.* 1988), and the Mauritius kestrel (*Falco punctatus*), whose population has recovered from less than a dozen individuals to more than 100 in a few years (Jones & Owadally 1985). Captive breeding of lesser kestrels is relatively easy (Pomarol 1993) and captive-bred birds can be released by the hacking method (Newton 1979). In fact, a re-introduction programme is already in progress in north-eastern Spain. Some hacked birds have returned to the release areas and have started breeding, although the success of the project has been moderate so far (Pomarol 1993). An additional source of birds for hacking could be starving nestlings that fall to the ground from their nests. These nestlings die if not recovered and moved to a raptor rehabilitation centre. A network of colonies could be searched for fallen nestlings. In captivity, recovery of nestling kestrels following starvation is usually quick and with no long-term effects on development (see Negro *et al.* 1994). Further research would be needed, however, to identify areas where self-sustaining populations of lesser kestrel can be established.

Acknowledgements

We thank M. de la Riva, Y. Menor de Gaspar and J.M. Bermudez for their assistance in the field work. The CSIC-CICYT (project PB87-0405) provided financial support. JJN benefitted from a postdoctoral fellowship from the CSIC.

References

- Akçakaya, H.R. (1991) A method for simulating demographic stochasticity. *Ecological Modelling*, **54**, 133–136.
- Biber, J.P. (1990) *Action Plan for the Conservation of Western Lesser Kestrel Falco naumanni Populations*. ICBP Study Report 41. Cambridge, UK.
- Bijleveld, M. (1974) *Birds of Prey in Europe*. Macmillan Press, London.
- Brown, L.H. & Amadon, D. (1968) *Eagles, Hawks and Falcons of the World*. Country Life Books, London.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987) *Design and analysis methods for fish survival experiments based on release-recapture*. American Fishing Society Monograph 5, Bethesda, MD.
- Cade, T.J., Anderson, J.H., Thelander, C.G. & White, C.M. (eds) (1988) *Peregrine Falcon Populations. Their Management and Recovery*. The Peregrine Fund, Boise, Idaho.
- Caswell, H. (1989) *Matrix Population Models*. Sinauer, Sunderland, Massachusetts, USA.
- Clobert, J., Lebreton, J.-D. & Marzolin, G. (1990) The estimation of local immature survival rate and of age-specific proportions of breeders in bird populations. *Population Biology of Passerine Birds* (ed. J. Blondel), pp. 199–213. Springer-Verlag, Berlin, Heidelberg.
- Clobert, J., Lebreton, J.-D., Allainé, D. & Gaillard, J.M. (1994) The estimation of age-specific breeding probabilities from recaptures or resighting in vertebrate populations. II. Longitudinal models. *Biometrics*, **50**, 375–387.
- Cramp, S. & Simmons, K.E.L. (1980) *The Birds of the Western Palearctic*, Vol. II. Oxford University Press, Oxford.

- Crouse, D.T., Crowder, L.B. & Caswell, H. (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, **68**, 1412–1423.
- Donázar, J.A., Negro, J.J. & Hiraldo, F. (1993) Foraging habitat selection, land-use changes and population decline in the lesser kestrel *Falco naumanni*. *Journal of Applied Ecology*, **30**, 512–522.
- Ferrer, M. (1993) *El Aguila Imperial*. Ed. Quercus, Madrid, Spain.
- Ferrer, M. & Calderón, J. (1990) The Spanish Imperial Eagle *Aquila adalberti* C.L. Brehm 1861 in Donana National Park (South West Spain): a study of population dynamics. *Biological Conservation*, **51**, 151–161.
- Ferrer, M. & Hiraldo, F. (1991) Evaluation of management techniques for the Spanish Imperial Eagle. *Wildlife Society Bulletin*, 436–442.
- Gaona, P. (1993) *Modelos demográficos para el águila imperial ibérica e implicaciones para su conservación*. PhD thesis, Universidad Autónoma de Madrid, Spain.
- Garzón, J. (1977) Birds of prey in Spain. The present situation. *World Conference on Birds of Prey. Report of Proceedings* (ed. International Council for Bird Preservation). ICBP, Cambridge, UK.
- González, J.L. & Merino, M. (1990) *El cernicalo primilla (Falco naumanni) en la Península Ibérica*. Serie Técnica, ICONA, Madrid, Spain.
- Green, R.E. & Hirons, G.J.M. (1991) The relevance of population studies to the conservation of threatened birds. *Bird Population Studies* (eds C. M. Perrins, J. D. Lebreton & J. M. Hirons), pp. 593–633. Oxford University Press, Oxford, UK.
- James, P.C., Warkentin, I.G. & Oliphant, L.W. (1989) Turnover and dispersal in urban merlins *Falco columbarius*. *Ibis*, **131**, 426–447.
- Jones, C.G. & Owadally, W. (1985) The status ecology and conservation of the Mauritius kestrel. *Conservation Studies on Raptors* (eds I. Newton & R.D. Chancellor), pp. 211–222. ICBP Technical Publication No. 5. ICBP, Cambridge, UK.
- Kendall, M. & Stuart, A. (1977) *The Advanced Theory of Statistics*. Vol. 1. *Distribution Theory*, 4th edn. Macmillan, New York.
- Kroon, H. de, Plaisier, A., van Groenendael, J. & Caswell, H. (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology*, **67**, 1427–1431.
- Lande, R. (1988) Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). *Oecologia*, **75**, 601–607.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D. (1992) Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Leslie, P.H. (1945) On the use of matrices in certain population mathematics. *Biometrika*, **33**, 183–212.
- Lewis, E.G. (1942) On the generation and growth of a population. *Saukhya: the Indian Journal of Statistics*, **6**, 93–96.
- Negro, J.J. (1991) *Ecología de poblaciones del cernicalo primilla (Falco naumanni)*. PhD thesis, Universidad de Sevilla, Spain.
- Negro, J.J. & Hiraldo, F. (1992) Sex ratios in broods of the lesser kestrel *Falco naumanni*. *Ibis*, **134**, 190–191.
- Negro, J.J., Chastin, A. & Bird, D.M. (1994) Effects of short-term food deprivation on growth of hand-reared American kestrels. *Condor*, **96**, 749–760.
- Negro, J.J., de la Riva, M. & Bustamante, J. (1991) Patterns of winter distribution and abundance of lesser kestrels (*Falco naumanni*) in Spain. *Journal of Raptor Research*, **25**, 30–35.
- Negro, J.J., Donázar, J.A., Hiraldo, F., Fernández, L.M. & Fernández, M.A. (1993) Organochlorine and heavy metal contamination in non-viable eggs and its relation to breeding success in a Spanish population of lesser kestrel. *Environmental Pollution*, **67**, 201–205.
- Newton, I. (1979) *Population Ecology of Raptors*. T. & A.D. Poyser, Berkhamsted, UK.
- Paton, P.W. (1994) Survival estimates for snowy plovers breeding at Great Salt Lake, Utah. *Condor*, **96**, 1106–1109.
- Pomarol, M. (1993) Lesser kestrel recovery project in Catalonia. *Biology and Conservation of Small Falcons* (eds M. K. Nicholls & R. Clarke), pp. 24–28. The Hawk and Owl Trust, London.
- Rands, M.R.W. (1987) Hedgerow management for the conservation of partridges *Perdix perdix* and *Alectoris rufa*. *Biological Conservation*, **40**, 127–139.
- Shaffer, M.L. (1981) Minimum population sizes for species conservation. *BioScience*, **31**, 131–134.
- Sotherton, N.W., Boatman, N.D. & Rands, M.R.W. (1989) The 'conservation headland' experiment in cereal ecosystems. *The Entomologist*, **108**, 135–143.
- Tella, J.L., Hiraldo, F., Donázar, J.A. & Negro, J.J. (1996) Costs and benefits of urban nesting in the lesser kestrel (*Falco naumanni*). *Raptors in Human Landscapes* (eds D. M. Bird, D. Varland & J. J. Negro). Academic Press, London.
- Wootton, J.T. & Bell, D.A. (1992) A metapopulation model of the peregrine falcon in California: viability and management strategies. *Ecological Applications*, **2**, 307–321.

Received 6 December 1994; revision received 17 November 1995