

First-year and adult survival of the endangered Lesser Kestrel *Falco naumanni* in southern France

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Capsule Local first-year survival is higher in La Crau than in Spain with a high proportion of first-year birds returning to their natal area.

Aims To understand life history parameters that may be responsible for a population growth since the 1990s.

Methods Between 1994 and 1998, 342 birds were ringed as fledglings. From capture–recapture data, annual local survival and the proportion of first-year birds returning to their natal area were computed.

Results The annual survival probabilities of adult and first-year birds were constant during the study period (0.67 and 0.57, respectively). A high proportion (0.72) of birds ringed as fledglings returned to their natal area after one year. Of these, an estimated 53% bred in that first year. Local first-year survival is higher in La Crau than other areas in Spain.

Conclusion The high local survival rate, the product of survival and philopatry, might be responsible for the positive trend of the population. A peculiar aspect of the La Crau population is that ground nests have been increasingly common since the 1990s despite a higher risk of breeding failure.

The Lesser Kestrel *Falco naumanni* is a colonial trans-Saharan migratory Falcon, which breeds in suitable cavities near open and cultivated plains. Its European distribution is mainly confined to the Mediterranean region, particularly in Spain, the south of Italy and Greece. Although considered among the most abundant raptor species on the continent, the Lesser Kestrel has recently become extinct in several countries in central Europe (e.g. Austria, Hungary, Poland). Populations have also recently declined in their western Palearctic breeding range (Cramp & Simmons 1980, Del Hoyo *et al.* 1996, Bustamante 1997). The causes of this decline are still poorly understood. Different possibilities have been proposed, such as pesticides reducing prey (death by starvation) or reduced breeding success during years of intensive use of DDT and/or the loss of suitable habitats through the intensification of agriculture (Bustamante 1997).

Despite a general decrease in the number of Lesser Kestrels, a few European populations have shown the

opposite trend and their number of breeding pairs has been steadily increasing in the last decade. In southern France, the Lesser Kestrel nearly disappeared at the end of the 1970s (Cheylan 1991) and, today, the La Crau region accommodates the last French population of Lesser Kestrels (Choisy *et al.* 1999, Brun & Pilard 1999). After the low levels documented in the 1980s, when only a few pairs were breeding, the population has undergone a demographic expansion until 1997 (Pilard & Brun 1998). During the next two years, the population seemed to stabilize at around 50 breeding pairs (P. Pilard unpubl. data).

In 1994, a ringing programme began in La Crau with the aim of monitoring demographic parameters in this increasing population. Recently, Hiraldo *et al.* (1996) reported that the contribution of different life history parameters to Lesser Kestrel population growth was highest for adult survival, followed by juvenile survival, productivity of fledglings, proportion of adults that attempt breeding and finally age at first breeding. For the few increasing populations we expect that one of these demographic parameters, such as adult and/or yearling survival, must have higher values than in the decreasing populations. We estimated survival and the

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proportion of birds returning to their natal colony the year after birth by analysing capture–recapture data. By using this approach, we have to test whether the increasing number of pairs in the French population was due to an increase (or a general high value) of one of these parameters. We used the study of Hiraldo *et al.* (1996) for the population in southern Spain for comparison. In that study, observations suggested a 6% decrease in population size between 1989 and 1994 while the asymptotic population growth rate was not different from that expected of a stable population. Finally, we discuss results and the role of ground nesting in conservation implications for the La Crau population.

MATERIAL AND METHODS

Study area

We considered data collected in the La Crau region (43°N, southern France) in a population at the margin of the western European distribution of the species (Fig. 1). La Crau is a steppe plain where Lesser Kestrel nesting sites are rare (Pilard & Brun 1998). In the La Crau area, Lesser Kestrel nests were typically found clumped on barns or ruins, but since the 1990s ground nests under piles of stones have become increasingly common. Data for La Crau were collected on birds marked at fledging in nine small neighbouring colonies and have been treated as if collected from a single large population (Pilard & Brun 1998, Choisy *et al.* 1999).

Comparison of adult local survival of Lesser Kestrel in Spain and in France

Local adult survival of Lesser Kestrel in France was estimated using resightings of birds ringed as fledglings and recaptured as adults (> 1 year old) from 1995 to 1999 in La Crau (southern France, Fig. 1). In order to compare the adult survival in La Crau to that in the Andalusia region (southern Spain, Fig. 1), we retrieved the capture histories of breeding birds for 1988–93 published in Hiraldo *et al.* (1996) and carried out a joint analysis of the two data sets. This allowed us to compare survival rates between the two regions assuming survival to be constant over time. Estimates were obtained by maximum likelihood from capture–resighting histories (Lebreton *et al.* 1992) considering that resightings were equivalent to recaptures. We used the software MARK1.9 (White & Burnham 1999) for the iterative fitting of models with different parameter-



Figure 1. Breeding distribution of Lesser Kestrel in Spain and France (●) and location of study areas where capture–recapture data were collected (for the Spanish population, data from Hiraldo *et al.* 1996).

izations for survival and/or recapture probabilities. Model selection procedure was based on a modified Akaike's information criterion (AICc; Burnham & Anderson 1998).^a

Local survival and proportion of first-year birds returning to their natal area

The first-year local survival probability and the proportion of birds present in their native area one year after birth were estimated only for the French population because full data were not available for the Spanish population. Model construction and selection were performed as described in the previous section.^b

RESULTS

Adult local survival of Lesser Kestrel in Spain and in France

The capture histories of 104 adult Lesser Kestrels breeding in La Crau and 582 adults breeding in Spain were used to calculate survival. A test of the goodness-of-fit of the general model [$\phi_F(t) p_F(t); \phi_S(t) p_S(t)$] was not significant ($\chi^2_{14} = 10.80$, $p = 0.7013$) suggesting that the data met the general assumptions of capture–recapture models. According to the best fitting model

Table 1. Eliminating non-significant effects from the model $\phi_F(t) \phi_S(t) p_F(t) p_S(t)$ assuming time-dependent survival and recapture probabilities for adult Lesser Kestrel in France (La Crau) and in southern Spain. Retained model is in bold.

Model number	Model	AICC	Np	Deviance
1	$\phi_F(t) \phi_S(t) p_F(t) p_S(t)$	1062.20	16	62.274
2	$\phi_F(t) \phi_S(t) p_F(t) p_S(\cdot)$	1067.44	13	73.822
3	$\phi_F(t) \phi_S(t) p_F(\cdot) p_S(t)$	1069.48	14	73.769
4	$\phi_F(t) \phi_S(\cdot) p_F(t) p_S(t)$	1065.26	13	71.642
5	$\phi_F(\cdot) \phi_S(t) p_F(t) p_S(t)$	1058.53	14	62.814
6	$\phi_F(\cdot) \phi_S(\cdot) p_F(t) p_S(t)$	1061.64	11	72.182
7	$\phi(\cdot) p_F(t) p_S(t)$	1059.66	10	72.278

F, France; S, Spain; t , time; \cdot , constant; Np, number of estimable parameters in the model; AICC, modified Akaike's information criterion.

$[\phi_F(\cdot) p_F(t); \phi_S(t) p_S(t)]$, recapture probability changed significantly over time in both populations (Table 1). Survival probability varied significantly over time in Spain but not in France. Local adult survival probability in La Crau was (mean \pm se) 0.67 ± 0.06 . Nonetheless, the model $[\phi(\cdot) p_F(t) p_S(t)]$ assuming the same constant survival parameter in both populations was within two points of AICC of the best model (Table 1) and indicated that the adult survival did not differ significantly between the two populations (Fig. 2).

Local survival and proportion of first-year birds returning to their natal area

We analysed 342 recapture histories of Lesser Kestrel banded as fledglings in France. The general model assuming time- and age-dependent parameters $[\phi(a^*t)]$

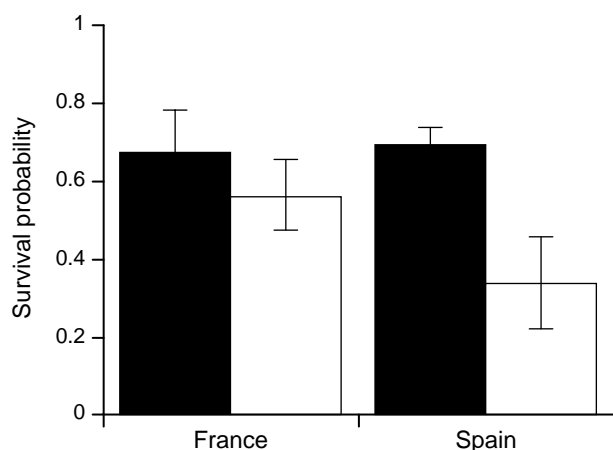


Figure 2. First-year (□) and adult (■) survival probability (\pm 95% CI) in France between 1995–99 and Spain between 1988–93.

Table 2. Eliminating non-significant effects from the model $\phi(a^*t) p(a^*t)$ assuming survival and recapture probability dependent on time and age (two age-classes) in France (La Crau). A variance inflator factor of 1.0976 was used to correct model deviance and model AICC. Retained model is in bold.

Model number	Model	QAICC	Np	mDeviance
1	$\phi(a^*t) p(a^*t)$	584.485	16	24 286
2	$\phi_Y(t) \phi_a(\cdot) p(a^*t)$	580.676	14	28 265
3	$\phi_Y(t) \phi_a(\cdot) p(a + t)$	579.998	12	32 957
4	$\phi_Y(t) \phi_a(\cdot) p(t)$	580.758	9	44 967
5	$\phi_Y(t) \phi_a(\cdot) p(a)$	586.749	8	29 918
6	$\phi_Y(\cdot) \phi_a(\cdot) p(a + t)$	573.038	8	32 470
7	$\phi(\cdot) p(a + t)$	573.275	7	24 286

QAICC, corrected model Akaike's information criterion; Np, number of estimable parameters in the model; mDeviance, corrected model deviance; γ , juvenile survival; subscript a , adult survival; t = time; \cdot , constant; a , age.

$p(a^*t)$ suggested a small extra-multinomial variation (bootstrap goodness-of-fit on 100 simulations: $p = 0.11$). Nevertheless, because this could be due to the simulation method, we corrected the model deviance by a \hat{c} value of 1.0976 estimated as the ratio between the \hat{c} of the fitted model and the average one of the simulated data set. We found that both time and age significantly influenced capture probabilities. However, their effects could be considered to be additive (model $\phi_Y(t) \phi_a(\cdot) p(a + t)$) (see Table 2). The local survival for first-year birds was estimated as 0.57 ± 0.05 . This value, although very different from that found for the Spanish population (0.34 ± 0.12), only approached significance (Z-test: $P = 0.07$). The proportion of first-year Kestrels returning to La Crau estimated as the ratio of yearling and adult capture probabilities was 0.72 ± 0.014 (standard error estimated by the δ -method as in Seber 1982, p.7) and constant over time. Among birds that returned to La Crau at one year old, only 53% were resighted as breeders. Therefore, the proportion of first-year breeders is approximately $0.38 (0.72 \times 0.53)$.

DISCUSSION

Causes of population increase

During recent decades, Lesser Kestrel numbers have declined dramatically over the species' European distribution range. In contrast to this general trend, the La Crau population (southern France) has shown a steady increase in number of breeding pairs since the 1990s. Hiraldo *et al.* (1996) showed that the population growth rate was more sensitive to variations in

adult and yearling survival probabilities than to those in breeding output. In agreement with this finding, the breeding output of the two populations was similar despite census data showing an opposite demographic trend. We found that adult survival in La Crau was also similar to that found in the Spanish population. In contrast, our results suggest that local first-year bird survival (Fig. 2) is higher in La Crau than in Spain.

The observed increase in the number of Lesser Kestrels in La Crau are probably a consequence of a high rate of local first-year survival, but whether this results from an enhanced survival or from an increased philopatry is unknown. An alternative explanation for the observed population increase in La Crau is immigration. In our population, we documented two cases of adult birds ringed elsewhere (in 1996 a male with a ring from an unknown country and a female with a Portuguese ring). Although these anecdotal observations document some long-distance exchange, we do not know their extent. A previous study on Lesser Kestrel post-natal movements in southern Spain has shown a high degree of philopatry of individuals, with most juveniles breeding within 30 km of the natal site (Negro *et al.* 1997). Such a high level of philopatry in the Spanish colonies suggests that unmarked breeders in the La Crau colony might have been born in undetected or inaccessible breeding sites within the study area. Lesser Kestrel numbers in Spain are recovering and long distance movements might have been underestimated previously (J. Negro pers. comm.). Because natal dispersal distance increases with population density (Negro *et al.* 1997), we cannot definitely exclude a higher contribution of immigrants from southern populations in recent years.

Use of a new nest niche

Nest-site availability is known to be an important limiting factor for population number and breeding success of birds of prey (Newton 1979, 1998). For the Kestrel, this is also supported by the recent findings of Fargallo *et al.* (2001) which demonstrated that an increase in nest availability enhanced population size. The Lesser Kestrel preferentially nests in buildings probably because of reduced nest predation (Forero *et al.* 1996). In the La Crau population, such nest-sites are rare (Pilard & Brun 1998). Kestrel numbers began to increase when birds progressively selected ground nests in stone piles more often, a nest-site very common in La Crau (Brun & Pilard 1999). The selection of a vacant nesting habitat might have been the factor

sustaining the increase of the breeding population size over the period 1992–97 through an augmented philopatry by reducing both inter-specific competition (e.g. with Jackdaws *Corvus monedula*; Brun & Pilard 1999) and intra-specific competition (Negro *et al.* 1997) for suitable breeding sites. This scenario, although not the only possible one, is consistent with the high value of local survival of first-year birds and with the fact that natal dispersal distance increases with breeding density (Negro *et al.* 1997).

Management implications

Artificially increasing nest availability with the use of nestboxes in order to augment the degree of philopatry or the yearling survival, could be an effective management strategy. Further work should focus on the balance between costs and benefits associated with the different types of nest in La Crau.

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ENDNOTES

a. Two models with a difference in the AICc < 2 were considered statistically indistinguishable and biological considerations took precedence. In such cases, the more interpretable or meaningful model in biological terms was retained. The model selection procedure started by assessing the goodness-of-fit of the general model $\phi_F(t) p_F(t)$; $\phi_S(t) p_S(t)$ which assumes both survival, ϕ , and resighting, p , probabilities changing over time (t); subscripts F and S denote parameters for France and Spain respectively (when the suffix is absent, parameters are assumed to be the same in both populations). When the estimates were close to the boundary values of 0 or 1, we investigated upper (when estimates were close to 0) and lower (when estimates were close to 1) confidence interval limits by the profile likelihood method. This was done by successively fixing the parameters at different values each time further from the maximum likelihood estimates until the deviance increased significantly (by more than 3.84).

b. We considered as a starting point the model $\phi(a*t) p(a*t)$ that assumed survival and recapture probabilities dependent on time (t) and age (a ; two age classes: first-years and birds > 1 year old); an asterisk shows the presence of interaction among the age and time effects whereas a plus sign would indicate its absence, i.e. additive effects (Lebreton *et al.* 1992). Model deviances were corrected using a variance

inflator factor (method described in Lebreton *et al.* 1992) to account for extra-multinomial variance. When models assumed a different structure according to age, we used the subscripts 'y' and 'a' to denote parameters for first-year and adult birds, respectively. For example the model $\phi_y(t) \phi_a(.) p(t)$ would assume a common time-dependent recapture probability but a time-dependent survival in first-year birds only. The proportion of birds hatched in La Crau and present in their natal area one year later was estimated as the ratio between first-year and adult recapture probabilities following Clobert *et al.* (1994).

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