Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction

DAVID SERRANO and JOSÉ L. TELLA

Department of Applied Biology, Estación Biológica de Doñana (CSIC), Pabellón del Perú, Avda Mª Luisa s/n, 41013 Sevilla, Spain

Summary

1. Factors governing dispersal rates have seldom been examined in spatially structured populations of vertebrates. We gathered information during 8 years on transfer rates between subpopulations in a spatially structured, growing population of colonial lesser kestrels *Falco naumanni*, and analysed the contribution of several variables related to spatial isolation and characteristics of both subpopulation of origin and destination on probabilities of dispersal.

2. Lesser kestrels were highly philopatric to their subpopulations, but first-breeders dispersed more often than adults (26% vs. 4%, $n = 1706$) because adults were reluctant to move from familiar areas. Frequency of subpopulation change was higher in females than in males (first-recruiters: 30% vs. 22%, $n = 987$; adults 5% vs. 1%, $n = 719$), according to their different breeding roles. However, all populational factors had an equal effect on individuals of different sex and dispersal status.

3. Movement rates decreased with inter-subpopulation distance – indicating that travelling to distant subpopulations may impose costs in terms of breeding prospects – and with the number of subpopulations, which increased during our study period.

4. Conspecific attraction strongly influenced the probability of dispersal: it was relatively higher in largely populated subpopulations, and individuals of large subpopulations were reluctant to change to others. These results were neither influenced by the size and breeding density of the subpopulations nor by habitat quality in terms of food availability or risk of predation, as indicated by breeding success of kestrels at each subpopulation. The number of conspecifics could be used by the kestrels as a cue of patch quality in terms of settlement options, and large subpopulations could be more easily detected by prospecting birds.

5. Our study highlights the fact that several assumptions of theoretical metapopulation modelling are often not fulfilled in nature. Both theoretical models and management strategies on spatially structured populations or metapopulations should thus consider the number, population size, and spatial distribution of local populations, as well as their relationships with the dispersal ability of the species.

Key-words: conspecific attraction, dispersal, *Falco naumanni*, intraspecific competition, isolation, metapopulations, spatially structured populations.

Introduction

The division of populations in spatially separated sub-populations or local populations may have profound

Correspondence: David Serrano, Department of Applied Biology, Estación Biológica de Doñana (C.S.I.C.), Pabellón del Perú, Avda Mª Luisa s/n, 41013 Sevilla, Spain. Fax: 34-95-4621125, E-mail: serrano@ebd.csic.es

effects on the dynamics and persistence of populations. One fundamental process underlying the demographic and genetic implications of fragmented populations is dispersal, since it is the process that binds local populations together (e.g. Hansson 1991; Hanski 1999). Dispersal implies two events linked by the movement process: emigration (when an individual leaves its 'home' subpopulation) and immigration (the settlement of the individual in any other subpopulation) (Ims &

Yoccoz 1997). Emigration and immigration rates are expected to have great impact on the dynamics and sizes of local populations, and thus on the regional risk of extinction. For instance, although small subpopulations may be more likely to go extinct as a result of demographic and environmental stochasticity (e.g. Soulé 1987), their persistence could greatly increase with the 'rescue' effect of immigration (*sensu* Brown & Kodric-Brown 1977). Thus, a popular idea is that dispersal from 'source' subpopulations in high-quality habitats may permit 'sink' subpopulations to exist in inferior habitats (Pulliam & Danielson 1991). Moreover, if a local population goes extinct, dispersal is the only way by which it may be recolonized. Thus, in the classical concept of metapopulation, the long-term persistence and stability of the system depends on the effects of dispersal rates on the balance between subpopulation extinction and colonization (Levins 1970; Hanski & Gilpin 1997). From an evolutionary perspective, and although it is known that very low rates of dispersal among subpopulations are sufficient for the system to behave as a panmictic population (Hoelzel & Dover 1991), rates of dispersal among subpopulations determine the level of gene-flow and could therefore affect processes such as local adaptation. For all these reasons, determining the dispersal ability of organisms and the factors by which it is affected is a key question to understand the dynamics of fragmented populations and is of central importance to develop successful management strategies (Hansson 1991; Macdonald & Johnson 2001).

The classical models of dispersal in spatially structured populations considered that all subpopulations were of equal size, quality and spacing, so organisms have equal probabilities of dispersing from one to any other (e.g. Levins 1970). Subsequent modelling has relaxed many of these simplifying assumptions, and has even allowed the incorporation of specific quantitative predictions about real dynamics such as distance-dependent movements, and number, size and specific location of the subpopulations (reviewed in Hanski & Simberloff 1997). Nevertheless, apart from the patch features stated above other characteristics have seldom been taken into account. For instance, the probability of settling in a given subpopulation could depend on whether it is already occupied by conspecifics (by 'social attraction', see Smith & Peacock 1990; Ray, Gilpin & Smith 1991; Stamps 1991) and even on the number of conspecifics (Serrano *et al.* 2001). Despite its potential importance, the effects of these social factors have been largely ignored, so extinction risks in some species could have been underestimated or overestimated. On the other hand, conspecifics could affect movements of individuals to and from subpopulations in opposite ways, i.e. promoting emigration or precluding immigration due to intraspecific competition (Dobson & Jones 1985). Dispersal has often been treated as a density-independent factor (e.g. Hanski, Kuussaari & Nieminen 1994; Lahaye, Gutiérrez

& Akçakaya 1994), which could also introduce unrealistic assumptions to the estimation of population trends and extinction risk.

Although a great amount of effort has been devoted to theoretical modelling of dispersal in spatially structured populations in recent years (Hanski & Gilpin 1997; Travis & Dytham 1998), there is very little empirical information, particularly in vertebrates, on factors affecting movement rates between subpopulations. Important theories or generalizations may be of little or no practical use for specific ecological or conservation problems, mainly because it is often impossible to estimate the relevant model parameters with the field data available (Doak & Mills 1994). This paucity of empirical information is because collecting data about transfer rates requires simultaneous surveying of a whole network of subpopulations during several years, which in practice presents substantial logistic problems (e.g. Spendelow *et al.* 1995; Lindberg *et al.* 1998). Even when intensive fieldwork has been made, dispersal distances are usually underestimated because long-distance dispersers are less likely to be detected than individuals dispersing short distances (Koenig, Vuren & Hooge 1996).

From 1993 to 2000, we studied an isolated population of lesser kestrels *Falco naumanni* (Fleischer) (Serrano *et al.* 2001; Serrano *et al.*, in press) that breeds in several discrete geographical areas, i.e. subpopulations. The intensive monitoring of marked kestrels in all subpopulations allowed us to examine the factors affecting the probability of dispersal with respect to characteristics of both subpopulation of origin and destination. In particular, our aims were: (i) to provide estimates of transfer rates among subpopulations for birds with different sex and dispersal status (i.e. natal and breeding dispersers); (ii) to identify the factors that determine subpopulation shift in relation to the ecological and social characteristics of both the subpopulations of origin and destination; and (iii) to examine to what extent these sources of variation differ between sexes and between natal and breeding dispersers.

Methods

Our study was based in a non-equilibrium, fast-growing population where no local population extinctions have been recorded. Subpopulations are separated by extensive areas with suitable habitat (in terms of both adequate nesting sites and foraging areas, Tella 1996), so the habitat is rather homogeneous and almost continuously distributed throughout the study area. For these reasons, our theory-based framework comes from models dealing with the evolution of animal movements (McPeek & Holt 1992; Johst & Brandl 1997; Travis & Dytham 1998), conspecific attraction (Smith & Peacock 1990; Ray *et al.* 1991; Reed & Dobson 1993), habitat selection (Fretwell & Lucas 1970), and intraspecific competition (Waser 1985; Rodgers & Klenner 1990), rather than from patch-occupancy

Table 1. Hypotheses and predictions tested to determine what factors affect dispersal between subpopulations of lesser kestrels of the Ebro Valley

Hypotheses	Predictions
Sex	Females should be more prone to disperse than males.
Dispersal status	Probability of dispersal should be higher in natal than in breeding dispersers.
Distance	Probability of dispersal should decrease with distance between subpopulations.
Conspecific attraction	Probability of dispersal should be higher the larger the subpopulation of destination and the smaller the subpopulation of origin.
Habitat quality	Individuals should disperse from low- to high-breeding performance subpopulations.
Intraspecific competition	(i) Individuals should disperse from high- to low-density subpopulations.
	(ii) Dispersal should increase the lower the growth rate in the subpopulation of origin and the higher the growth rate in the subpopulation of destination.
	(iii) Intraspecific competition should mainly operate in first-breeding individuals.
Availability of subpopulations	Probability of dispersal should be inversely related to the whole number of subpopulations.

models studying extinction probabilities and the fraction of patches occupied in a matrix of occupied and unoccupied suitable patches (e.g. Gilpin 1996).

Our hypotheses and predictions are summarized in Table 1. Distance among subpopulations has been said to influence movement rates, both in theoretical (e.g. MacArthur & Wilson 1967; Hansson 1991; Gilpin 1996) and empirical studies (e.g. Kindvall & Ahlén 1992; Sjögren 1994; Oro & Pradel 1999). Animals are not omniscient, and in the case of a migratory short- to medium-lived species like the lesser kestrel, it is expected that they do not have information about the location of all subpopulations at the same time. Long-distance movements could impose a cost on arriving at empty or unsuitable areas, thus leading to temporary or permanent losses from the breeding population. Furthermore, travelling from distant subpopulations could impose additional costs in terms of mortality (Johnson & Gaines 1990).

While distance has been widely recognized to constrain inter-subpopulation dispersal, other forces shaping dispersal in patchy populations have seldom been considered. Thus, once an individual leaves its 'home' patch, dispersal is usually treated as a stochastic event, so there is equal probability of settling in any patch located at a given distance. However, conspecific attraction has been recently hypothesized to determine settling patterns; animals would take their dispersal decisions based on the presence of conspecifics (Smith & Peacock 1990; Stamps 1991; Muller *et al.* 1997), especially in colonial species such as the lesser kestrel (Forbes & Kaiser 1994; Brown & Rannala 1995; Oro & Pradel 2000; Serrano *et al.* 2001). Conspecifics may increase the attractiveness for immigrants, therefore determining probability and direction of dispersal. The number of breeding pairs in a given subpopulation could reflect the number of potential nest sites and /or mates. Moreover, large numbers of breeding pairs could be more easily detectable by prospecting birds than small subpopulations. However, since population size could simply reflect other cues employed by the kestrels, such as habitat quality in terms of food availability or

risk of predation, we tested the alternative hypothesis that individuals tend to disperse from low quality to high quality patches, as predicted by models of habitat selection (Fretwell & Lucas 1970). Contrary to the conspecific attraction hypothesis, intraspecific competition for nest sites and /or mates could also affect dispersal rates by constraining dispersal decisions (Hansson 1991). In this way, dispersal rates have been said to be density-dependent both for the source and the recipient subpopulation (Andreassen & Ims 2001; Gundersen *et al.* 2001).

Dispersal rates may also be influenced by the availability of subpopulations. Since the number of subpopulations, i.e. the number of dispersal options, increased along the period of study, we expected dispersal rates between pairs of subpopulations to be inversely related to the whole number of subpopulations.

Finally, we tested whether dispersal probability differed between sexes and/or between birds with different dispersal status, i.e. individuals that may disperse between birth and first breeding (natal dispersers) and between two consecutive breeding attempts (breeding dispersers). Greenwood & Harvey (1980) suggested that in mating systems based on male defence of resources, as in lesser kestrels, a female-biased dispersal pattern would be expected. Accordingly, we predicted that females should be more prone to shift subpopulation than males. Since the benefits of philopatry are expected to be higher in adults than in young individuals (Pärt 1995), we also predicted that transfer rates should differ between natal and breeding dispersers.

Methods

Study species and study area

The lesser kestrel (*Falco naumanni*) is a migratory, facultative colonial falcon which breeds in Eurasia and winters south of the Sahara desert. Genetically strict monogamy is the predominant mating system. Males choose and defend nest sites against other males while displaying to attract females, and then they feed their

Table 2. Number of subpopulations, number of breeding pairs per subpopulation, and distance between subpopulations of lesser kestrels measured in the year of recruitment. Medians and ranges are shown

Year	Number of subpopulations	Distance between subpopulations (m)	Subpopulation size (breeding pairs)
1994	4	35979 (13464–82711)	42 (9–215)
1995	6	43094·5 (13464–94290)	35 (2–219)
1996	8	43710·5 (11597–95552)	27 (6–212)
1997	8	44003 (11903–95715)	34 (6–202)
1998	10	45260 (11903–122298)	41 (11–217)
1999	14	54383 (9859–199500)	25 (5–195)
2000	14	62250 (9859–199500)	33 (9–241)

mates during the prelaying period. Both sexes incubate and raise the young, but only females incubate and brood young chicks at night, and males invest more on feeding the chicks. First breeding of lesser kestrels occurs at 1–2 years. Average life span for the species is 3–4 years (see Negro 1997 for more information on the species).

The study area covers the whole Ebro Valley, NE Spain (*c.* 10 000 km²), an extensive plain mainly devoted to dry-farmed cereal crops and fallow. Lesser kestrels breed here in abandoned farmhouses, where they nest under tiled roofs (Tella 1996). Colonies during the study period gathered a variable number of pairs (1–43). Lesser kestrels select field margins and cereals for foraging, and home ranges during the chick-rearing period averaged 12·36 ± 8·28 km² (Tella *et al.* 1998). Adult lesser kestrels in the study area show philopatry to previous breeding colonies (72%), and dispersers tend to settle in a colony situated within their foraging areas (median dispersal distance = 1600 m; Serrano *et al.* 2001). Most juvenile lesser kestrels disperse from their natal colony when selecting the first breeding colony (83%); they were known to move distances of up 136 km, but most individuals tend to settle close to their natal colony (median = 7250 m; Serrano *et al.*, in press).

Each subpopulation is composed of a variable number of colonies. We delineated subpopulations, i.e. clusters of colonies, by considering the home range of radio-tracked breeding individuals (see Tella *et al.* 1998). We generated a home range of 2000 m around each colony and grouped colonies with overlapping home ranges into subpopulations. Using this method, colonies were clumped in well-delimited subpopulations (Fig. 1), holding from 1 to 61 colonies during the study period. Distances between neighbouring subpopulations ranged from 10 to 90 km, the most distant subpopulations being separated by 200 km (Table 2). The whole population size increased during the study period from 224 pairs in 1993 to 787 pairs in 2000.

A problem frequently encountered in studies of dispersal is the emigration of individuals outside of the study area (Koenig *et al.* 1996). Maximum and median breeding and natal dispersal distances in our studied
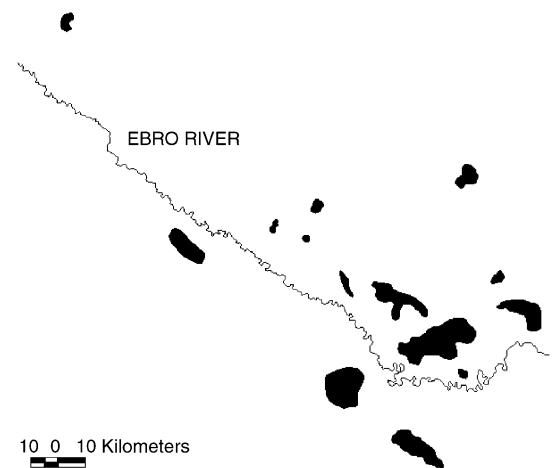
Fig. 1. Location of lesser kestrel subpopulations in the Ebro Valley, north-eastern Spain. This figure corresponds to the last year of study, when the population reached the highest number of breeding pairs.

population were considerably shorter than the distance separating the two farthest occupied colonies (Serrano *et al.* 2001; Serrano *et al.*, in press). Moreover, intensive sampling during the last decade of both close and distant populations of Spain, Portugal and France did not report any case of immigration from our population (M. de la Riva, C. Rodríguez, J. Bustamante, R. Bonal, P. Olea, L. de Brun, P. Nuno, C. Gutierrez and M. Alberdi, com. pers.). Therefore, we are confident that the population of the Ebro Valley is isolated.

n̄n̄ņŇņ ŏ̃æŏ̃ņņņǫæ̃ņǫ

Since 1993, lesser kestrels have been individually marked with plastic colour bands engraved with an alpha-numeric code that can be read with telescopes. As many birds as possible were banded each year, and hand recapture of hundreds of banded adults indicated that plastic band loss was absent. From February to July, regular surveys were carried out each year in all the study areas to locate colonies. Once the presence of the species was confirmed in a given building, we tried to read all bands from hides without disturbing the birds. At this stage, we mapped all nests to obtain colony size and plotted each identified bird in its nest.

Additionally, both colony size and recapture histories were completed during direct surveying of the colonies carried out to record breeding parameters. For the purposes of this study, we only considered those individuals that had bred in the colony where they were observed, i.e. those birds observed in a nest from 2 weeks preceding laying to the end of the fledgling dependence period (see Serrano *et al.* 2001 for further details). Therefore, we obtained accurate censuses of the whole breeding population each year, although not all breeding birds were individually identified. Nevertheless, all subpopulations contained a high proportion (60–90%) of known-age identified birds.

Measures reflecting characteristics of subpopulations

We measured 12 variables, reflecting characteristics of both subpopulation of origin and destination, measured in the year of recruitment (year *t*): (i) distance between subpopulations, as the straight-line distance from the centre of the subpopulation of origin to the nearest colony of the subpopulation of destination; (ii) number of breeding pairs in the subpopulation of origin; (iii) number of breeding pairs in the subpopulation of destination; (iv) mean number of young produced per breeding pair in the subpopulation of origin (see Serrano *et al.* 2001 for field procedures) – this variable reflects habitat quality in terms of food availability and risk of predation (Tella 1996); (v) mean number of young fledged per breeding pair in the subpopulation of destination; (vi) patch size of origin – boundaries of the subpopulations were defined by considering that individuals forage in a radius of 2 km around the colonies (Tella *et al.* 1998), and calculating the minimum convex polygon of the whole set of colonies of each subpopulation; (vii) patch size of destination, measured as above; (viii) breeding density in the subpopulation of origin (number of breeding pairs/ patch size); (ix) breeding density in the subpopulation of destination, calculated as above; (x) relative growth rate of subpopulation of origin, measured as N_t/N_{t-1}, where N_t and N_{t-1} were the local population size in years of recruitment and before recruitment, respectively. We assumed that subpopulation growth rate was inversely related to subpopulation saturation; (xi) relative growth of subpopulation of destination, calculated as above; and (xii) number of subpopulations in the whole metapopulation. Given that differential sampling effort between subpopulations could bias our estimates of patterns of dispersal, the percentage of individuals identified in each subpopulation with respect to its total number of breeding individuals was also included in the models.

Statistical analyses

We used Generalized Linear Mixed Models (GLMMs, Littell *et al.* 1996) to identify simultaneously the factors affecting probability of dispersal between subpopulations while controlling for potential non-independence of observations. Our variable of interest was the number of individuals dispersing from a given subpopulation (origin) in year *t* – 1 to any other subpopulation (destination) in year *t*. This number is clearly influenced by the number of birds from the subpopulation of origin which still were present in the whole population in year *t*, i.e. the larger the number of birds available from subpopulation A, the larger the probability of one of them dispersing to subpopulation B. Therefore, we used a weighted logistic regression with a binomial distribution of errors and a logistic link function where the numerator was the number of birds dispersing from subpopulation A to subpopulation B, and the denominator the number of birds proceeding from A that returned to A, plus those proceeding from A that dispersed to the whole set of subpopulations (B, C, D, …) in year *t* (see Andreassen & Ims 2001 for the same approach). These numbers were obtained for each pair-wise combinations of subpopulations each year, and separately for each combination of sex and dispersal status (first breeders and adults). The identities of subpopulations of origin and destination as well as year were included as random factors to control for the potential non-independence of dispersal movements within years and subpopulations (Andreassen & Ims 2001).

In the case of adults, we only employed those birds identified in two consecutive years. However, individuals banded as fledglings recruited in the breeding population in their first or their second year of life. This could constitute a problem when an individual recruited in their first year of life escaped detection and was detected as a 2-year breeder, but in our population the probability of philopatry of adults to the subpopulation of first-breeding is extremely high (see Results), so this potential source of bias is negligible.

All explanatory variables, including quadratic and cubic terms to explore non-linear relationships, and their interactions were fitted into the GLMMs using the macro GLIMMIX of SAS. We used both backward and forward variable-selection procedures to obtain models which only included variables with significant effects. GLIMMIX automatically adjusts overdispersion by dividing the deviance by the extra-dispersion parameter. Hypotheses were tested using *F*-statistics for fixed effects and *Z*-statistics for random effects (see Littell *et al.* 1996 for more details).

Results

From the 4901 fledglings and 640 adults banded from 1993 to 1999, we obtained for analyses 987 individuals breeding for the first time in the population (456 males and 531 females) and 1143 records of adults breeding in consecutive years. However, the different records concerning the same adult in different years cannot be considered as independent statistical events (Serrano

Table 3. Generalized linear mixed model for probability of dispersal between subpopulations in the Ebro Valley

	Parameter estimate	Standard error	Test	P
Intercept	−2·1282	0·5644		
Percentage of individuals identified	1·9485	0·6732	$F = 8·38$	0·0039
Distance between subpopulations	−0·00003	0·000005	$F = 46·30$	< 0·0001
Number of breeding pairs in the subpopulation of origin	−0·0049	0·001123	$F = 13·28$	0·0003
Number of breeding pairs in the subpopulation of destination	0·006704	0·001581	$F = 17·98$	< 0·0001
Whole number of subpopulations	−0·1197	0·0534	$F = 11·47$	0·0007
Breeding dispersers	−2·1454	0·2780	$F = 59·54$	< 0·0001
Males	−0·3773	0. 1720	$F = 4·81$	0·0284
Year	0·007338	0·03092	$Z = 0·24$	0·4062
Subpopulation identity of origin	0	0	–	–
Subpopulation identity of destination	0·05219	0·09508	$Z = 0·55$	0·2915
Explained deviance (%)	46·67			
Residual deviance	619·0875			
Residual d.f.	1330			
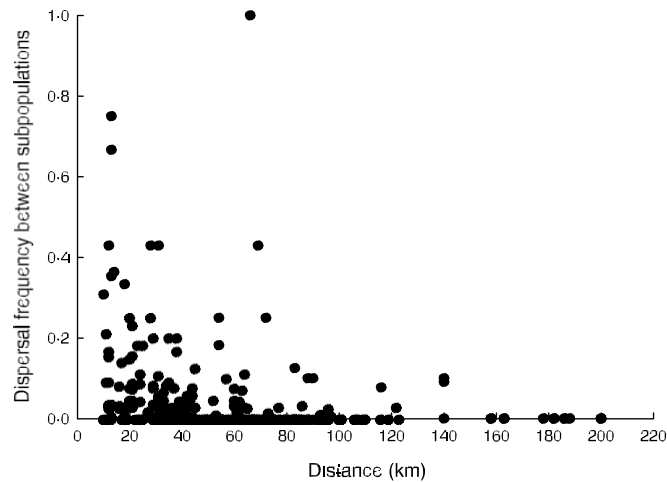
Fig. 2. Relationship between dispersal frequency between subpopulations and distance separating them. Note that this is a univariate trend (see Table 3 for multivariate tests).

et al. 2001), so we randomly selected a single record per individual, the final data set for adults including 719 individuals identified in two successive years (277 males and 442 females).

Univariate analyses showed that first-breeders moved from their 'home' to other subpopulations much more frequently than adults (26·3% vs. 3·6%; Yates corrected $\chi_1^2 = 152·34, P < 0·0001$). For both, first-breeders and adults, this frequency was higher in females than in males (first-recruiters: 30·1% vs. 21·9%, Yates corrected $\chi_1^2 = 8·09, P = 0·0045$; adults: 5·2% vs. 1·1%, Fisher exact test $P = 0·0034$).

Both the forward and the backward variable-selection procedures resulted in the same GLMM model (Table 3). Dispersal probability was affected by the percentage of birds identified in the recipient subpopulation. Controlling for this confounding variable, and consistently with the univariate tests, this model showed that dispersal between subpopulations was higher in natal than in breeding dispersers, and that females were more prone to disperse than males.

However, all categories of individuals appear to follow very similar cues for moving between subpopulations, since all interactions between sex, dispersal status, and the other variables were not significant and thus were not retained in the model.

Our results (Table 3) also showed that dispersal between subpopulations was inversely related to the distance separating them (see Fig. 2). In addition, the number of breeding pairs in both the subpopulation of origin and destination influenced the probability of dispersal, individuals being more prone to shift between subpopulations the smaller the subpopulation of origin (Fig. 3a) and the larger the subpopulation of destination (Fig. 3b). Finally, the number of subpopulations in a given year was negatively related to the probability of dispersal in any subpopulation.

The above results were neither influenced by year nor by identities of both subpopulation of origin and destination (Table 3), although these variables were maintained in the model as random terms to control for the potential non-independence of the data.
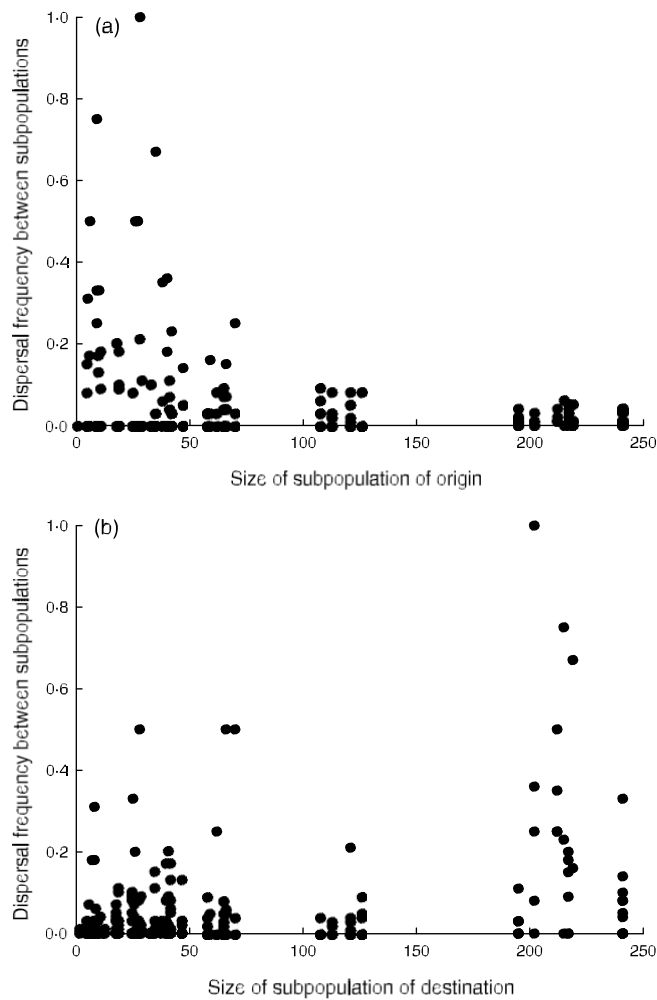
Fig. 3. Relationships between dispersal frequency between subpopulations and: (a) number of breeding pairs in the subpopulation of origin, and (b) number of breeding pairs in the subpopulation of destination. Note that these are univariate trends (see Table 3 for multivariate tests).

Discussion

ǫηɔ: M̄ǫ́η η̄ η̄ǫǒ̃η̃ǣǫM̄Ñ ǫǫM̄ǫǫǫ M̄ǫǫ̀v̄η̄ǫǣη̄η̄ǫ η̄ǫ́ η̄ η̄ǫǒ̃η̃ǣǫM̄Ñ ǣM̄ǫη̄ǫ

The lesser kestrel population in the Ebro Valley is structured in several discrete units connected demographically, but they are separated by distances exceeding the natal and breeding movements that most individuals perform during their life (Serrano *et al*. 2001; Serrano *et al*., in press). Subpopulations are mainly connected by natal dispersal, a result that is congruent with the widely accepted view that the longest dispersal distances are associated with dispersing away from the birth area (Greenwood & Harvey 1982), as has been reported in other fragmented populations of birds (Smith *et al*. 1996; Altwegg, Ringsby & Sæther 2000). Breeding dispersers, however, showed very low frequencies of intersubpopulation movements, which can be explained because the few adults that decide to change colony in consecutive years are reluctant to move to unfamiliar areas, and usually disperse to a neighbouring colony within their previous breeding

subpopulation where they can benefit from their experience of foraging areas (Serrano *et al*. 2001).

On the other hand, movement rates between subpopulations were higher in females than in males for both first-breeders and adults. This finding agrees with the hypothesis that gender-related differences in avian dispersal are related to the different role of each sex in acquisition and defence of resources (Greenwood & Harvey 1982). In the lesser kestrel, males compete intensively for nests at the beginning of the breeding season. Several lines of evidence suggest that unsettled males have to develop site-specific dominance relationships in order to exclude conspecific competitors (Tella 1996), so their probabilities of obtaining a good nest-site probably increases in their natal or previous breeding subpopulation. Males could hence benefit by settling in one of the first colonies they find in their 'home' subpopulation after coming back from the wintering grounds. Thus, they probably prefer to explore the area gradually, in small steps, until they can successfully settle within their natal or previous breeding subpopulation. Females, however, are not constrained by such pressures, so they could use an alternative strategy to

assess breeding sites and /or mates including both small steps and 'jumps' over much greater distances (see Orell *et al*. 1999); they are therefore more likely to move between subpopulations.

n̆n̆ŏN̆ŏN̄n̆ņM̄N̈ M̆ǫ́ņ ǫŏņn̄M̄N̈ n̄M̄ņǫŏ̆œ̆ǫ M̄n̄n̆ņņǫn̄ǫ́N̈ n̄ņǫŏ̆ņœ̆ǫM̄N̈ œ̆M̆ǫņǫ

Effects of subpopulation isolation

Dispersal rates in our population were distance-dependent, the probability of movement rates decreasing the further the distance between subpopulations. Thus, a subpopulation was not equally accessible to all dispersers, but dispersal patterns depended on the spatial distribution of local populations. This result could be explained if nearly all individuals tend to return to their local population of origin after wintering in Africa, but some of them, for whatever reason, emigrate later to other subpopulations. This would result in a distribution of dispersal distances similar to that described by geometric models of dispersal (e.g. Buechner 1987). In addition, it may indicate that the distance over which individuals can detect other subpopulations is small relative to average inter-subpopulation distance (see below for the effect of conspecific attraction). Although it seems obvious that distance separating occupied patches could constrain exchange of individuals between them, very little evidence has been reported for fragmented populations by studying individually marked birds (see Smith *et al*. 1996; Stith *et al*. 1996; Oro & Pradel 1999). Even immigration probabilities have been assumed to be unaffected by isolation in other fragmented populations (e.g. Margules, Higgs & Rafe 1982; Ambuel & Temple 1983), probably because distance separating subpopulations was not large enough with respect to movement abilities of the species under study (Spendelow *et al*. 1995). Although other authors have identified dispersal among subpopulations to be constrained by distance separating them, movements have been usually studied in a network of suitable habitat 'islands' embedded in a matrix of unsuitable habitat where resistance of the matrix, i.e. in terms of habitat suitability, strongly determines the dispersal capabilities of the species (e.g. Fahrig & Merriam 1994; Ricketts 2001). In the Ebro Valley, however, inter-subpopulation transfer of individuals is constrained by distance separating occupied subpopulations in spite of apparent habitat continuity, so distance 'per se' appears to constitute a strong determinant of dispersal among subpopulations.

It might be argued that long-distance migratory birds are unlikely to suffer problems by dispersing to distant patches, but a similar distance-dependent dispersal pattern has been found in other long-distance migratory species (Doncaster *et al*. 1997; Oro & Pradel 1999; Hames *et al*. 2001). This could be explained because dispersal and migration are likely to be triggered by different behavioural cues. Moreover, the

different nature of dispersal and migration events in terms of grouping, height, and speed of flight, could be associated with different fitness constraints. Finally, our results also support the hypothesis that colonization probabilities of unoccupied patches could be strongly related to their degree of isolation. Since the number of immigrants proceeding from a particular subpopulation declined with increasing distance from it, the formation of new subpopulations is also expected to be distance-dependent (Hanski *et al*. 1994).

ǫN̄ņ n̄n̆n̆ņņǫ ŏn̄ ǫŏņn̄M̄N̈ M̄ǫǫœ̆M̄ņǫn̄ŏǫ́

The most novel result of our study is that dispersal was shaped by the number of breeding pairs in both subpopulation of origin and destination. In this way, individuals were more prone to disperse from low- to highly populated subpopulations. Although the potential effect of conspecific attraction at a metapopulation scale has been previously suggested (Smith & Peacock 1990; Ray *et al*. 1991; Reed & Dobson 1993), to our knowledge this is the first study supporting empirically that conspecific attraction operates in a fragmented system of vertebrates (see Kuussaari, Nieminen & Hanski 1996 for a fragmented population of butterflies). The fact that subpopulation size affected dispersal, rather than patch area, breeding density or breeding success, indicates that lesser kestrels were actually cueing on the number of conspecifics and not on other confounding factors. High numbers of breeding pairs in a given subpopulation not only facilitates the detection of occupied patches by prospecting birds, but also provides cues about habitat quality in terms of settlement options, which increases the probability of recruiting successfully. In addition, the number of breeding pairs within the subpopulation of origin was inversely related to the probability of recruiting elsewhere, suggesting that individuals deciding or being forced to disperse away from their 'home' colony were reluctant to emigrate to other subpopulations when there were a high number of dispersal options within their own subpopulation (see also Oro & Pradel 2000). These results concur with the suggested negative relationship between dispersal rate and local population size (McPeek & Holt 1992; Doncaster *et al*. 1997; Roland, Keyghobadi & Fownes 2000), so the random-dispersal assumption of many models is violated. In this sense, future modelling attempts should consider interpatch dispersal patterns being shaped by such a deterministic factors in addition to probabilistic processes.

On the other hand, intraspecific competition could promote dispersal. Both theoretical (e.g. Travis, Murrell & Dytham 1999) and empirical (e.g. Veit & Lewis 1996; Andreassen & Ims 2001) studies have emphasized the role of density dependence in the amount of dispersing individuals between subpopulations. Furthermore, subpopulation carrying capacity or habitat saturation are other sources of variability in

the probability of dispersal (e.g. Nager *et al.* 1996; Lindberg *et al.* 1998). However, neither subpopulation density nor subpopulation growth rate (as measures of subpopulation saturation) affected dispersal rates in our study. It is possible that, in our fast-growing population, no subpopulations have yet reached their equilibrium stability in terms of density or carrying capacity, so heterogeneity is not large enough to affect movement rates between subpopulations.

ṇo̊ọ̣ṇ̃ẽõ̊Mǭn̊o̊ǫ̣ n̄vǒN̈n̠Mǫn̊o̊ǫ̣

Lesser kestrel populations have suffered a high decline in the last decades, being thus classified as a 'globally threatened' species (Tucker & Heath 1994). This decline has been related to recent changes in agricultural practices, intensification of cultivation in pseudo-steppes being the main cause of habitat loss (Tella *et al.* 1998). The population of lesser kestrels in the Ebro Valley has increased dramatically during the study period due to the general maintenance of traditional agro-grazing practices (Tella *et al.* 1998). However, current agricultural trends, as in many other populations of lesser kestrels, include widespread intensification of farming practices, such as irrigation, that are incompatible with the requirements of the species (Tella *et al.* 1998; Tella & Forero 2000). Thousands of hectares of traditional farmlands are being, or are planned to be, transformed into irrigated cultures, affecting most colonies in at least three subpopulations and separating the rest by unprofitable habitats. Therefore, the present spatially structured population will become a true metapopulation (*sensu* Hanski & Gilpin 1997), where occupied habitat patches will be separated by a matrix of unsuitable habitat. This ongoing process is expected to limit and even to reduce the number and size of subpopulations, and could therefore modify the dispersal pattern observed by altering distances between occupied patches and attractiveness for immigrants. On the other hand, it is worth noting that the spatial structure of the lesser kestrel population in the Ebro Valley is similar to that exhibited by many populations of the species (Negro 1997), in which habitat reduction and fragmentation have already restricted its distribution to discrete patches of suitable habitat. However, it cannot be ignored that dispersal measured in the relatively contiguous habitat present nowadays in the study area may overestimate the dispersal capabilities of the species in a much more transformed scenario, since individuals could refuse to move along hostile habitats (Dunning *et al.* 1995; Kindvall 1999; Roland *et al.* 2000), or may move at different degrees depending on the profitability of the intervening matrix types (Gustafson & Gardner 1996; Ricketts 2001). In this sense, transfer rates between patches could be lower in populations where the habitat is fragmented by agricultural changes.

One essential result of this study is that dispersal events are more deterministic than has been previously considered in the metapopulation literature; individuals are attracted to the presence of high numbers of conspecifics in nearby patches, and as a result they are distributed in clumps with much suitable habitat left unused, in spite of the positive population trends and the relatively high rates of transfer of individuals among subpopulations. When conspecific attraction is operating, dispersal to small and isolated subpopulations is less frequent than could be expected based on a random pattern of dispersal or on the simple presence of conspecifics, so processes of rescue immigration are less likely to occur. To the extent that this is true for patch colonization processes, such social attraction may reduce patch-colonization and recolonization probabilities and make populations more sensitive to fragmentation (Ray *et al.* 1991; Sæther, Engen & Lande 1999). In addition, our findings suggest that emigration rates are relatively higher from small than from large subpopulations, a process that could also have negative effects on population trends (Kindvall 1999; Dale 2001). Isolated and particularly small subpopulations may thus be subject to the detrimental effects of inbreeding, genetic drift and mutation accumulation (Mills & Smouse 1994; Lande 1995; Lynch, Conery & Bürguer 1995; Hames *et al.* 2001), or may be more prone to extinction without the reinforcement process of immigration from other subpopulations through the cumulative effects of chance demographic events and environmental stochasticity (e.g. Soulé 1987; Gabriel & Bürguer 1992; Lande 1993). In this sense, it should be noted that some of the smallest subpopulations per year in this study contained less than 10 breeding pairs.

In essence, conservation strategies should be focused on allowing the flow of individuals among subpopulations by maintaining a sufficient number of nearby habitat patches on stepping-stone critical areas, and to maintain the size of subpopulations large enough to prevent not only the negative effects of demographic and environmental stochasticity, but also processes of extinction resulting from high rates of emigration. However, relationships between habitat loss and population size are complex (e.g. Andrén 1994), so estimating the effect of habitat fragmentation on population viability, and designing the number, extent and spatial distribution of habitat patches would require specific, spatially explicit modelling approaches that reflect the dispersal ability and habitat preferences of the species to be preserved.

References

Altwegg, R., Ringsby, T.H. & Sæther, B.-E. (2000) Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows *Passer domesticus. Journal of Animal Ecology*, **69**, 762–770.

Ambuel, B. & Temple, S.A. (1983) Area dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology*, **64**, 1057–1068.

Andreassen, H.P. & Ims, R.A. (2001) Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. *Ecology*, **82**, 2911–2926.

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in island biogeography: effect of inmigration on extinction. *Ecology*, **58**, 445–449.

Brown, C.R. & Rannala, B. (1995) Colony choice in birds: models based on temporally invariant site quality. *Behavioral Ecology and Sociobiology*, **36**, 221–228.

Buechner, M. (1987) A geometric model of vertebrate dispersal: tests and implications. *Ecology*, **68**, 310–318.

Dale, S. (2001) Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos*, **92**, 344–356.

Doak, D.F. & Mills, L.S. (1994) A useful role for theory in conservation. *Ecology*, **75**, 615–626.

Dobson, F.S. & Jones, W.T. (1985) Multiple causes of dispersal. *American Naturalist*, **126**, 855–858.

Doncaster, C.P., Clobert, J., Doligez, B., Gustafsson, L. & Danchin, E. (1997) Balanced dispersal between spatially varying local populations: an alternative to the source–sink model. *American Naturalist*, **150**, 425–445.

Dunning, J.B., Borgella, R., Clements, K. & Meffe, G.K. (1995) Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology*, **9**, 542–550.

Fahrig, L. & Merriam, G. (1994) Conservation of fragmented populations. *Conservation Biology*, **8**, 50–59.

Forbes, L.S. & Kaiser, G.W. (1994) Habitat choice in breeding seabirds: when to cross the information barrier. *Oikos*, **70**, 377–384.

Fretwell, S.D. & Lucas, H.L. (1970) On territorial behavior and other factor influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16–36.

Gabriel, W. & Bürguer, R. (1992) Survival of small populations under demographic stochasticity. *Theoretical Population Biology*, **41**, 44–71.

Gilpin, M. (1996) Metapopulations and wildlife conservation: approaches to modeling spatial structure. *Metapopulation and Wildlife Conservation* (ed. D.R. McCullough), pp. 11–27. Island Press, Washington, D.C.

Greenwood, P.J. & Harvey, P.H. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.

Greenwood, P.J. & Harvey, P.H. (1982) The natal and breeding dispersal in birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.

Gundersen, G., Johannesen, E., Andreassen, P. & Ims, R.A. (2001) Source–sink dynamics: how sinks affect demography of sources. *Ecology Letters*, **4**, 14–21.

Gustafson, E.J. & Gardner, R.H. (1996) The effect of landscape heterogeneity on the probability of patch colonization. *Ecology*, **77**, 94–107.

Hames, R.S., Rosemberg, K.V., Lowe, J.D. & Dhondt, A.A. (2001) Site reoccupation in fragmented landscapes: testing predictions of metapopulation theory. *Journal of Animal Ecology*, **70**, 182–190.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford.

Hanski, I. & Gilpin, M.E. (1997) *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego.

Hanski, I., Kuussaari, M. & Nieminen, M. (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia. Ecology*, **75**, 747–762.

Hanski, I. & Simberloff, D. (1997) The metapopulation approach, its history, conceptual domain, and application to conservation. *Metapopulation Biology. Ecology, Genetics and Evolution* (eds I. Hanski & M.E. Gilpin), pp. 5–26. Academic Press, San Diego.

Hansson, L. (1991) Dispersal and connectivity in metapopulations. *Biology Journal of the Linnean Society*, **42**, 89–103.

Hoelzel, A.R. & Dover, G.A. (1991) *Molecular Genetic Ecology*. Oxford University Press, Oxford.

Ims, R.A. & Yoccoz, N.G. (1997) Studying transfer processes in metapopulations. *Metapopulation Biology. Ecology, Genetics and Evolution* (eds I. Hanski & M.E. Gilpin), pp. 247–265. Academic Press, San Diego.

Johnson, M.L. & Gaines, M.S. (1990) Evolution of dispersal: theoretical models and empirical test using birds and mammals. *Annual Review of Ecology and Systematics*, **21**, 449–480.

Johst, K. & Brandl, R. (1997) Evolution of dispersal: the importance of the temporal order of reproduction and dispersal. *Proceedings of the Royal Society of London, Series B*, **264**, 23–30.

Kindvall, O. (1999) Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tettigoniidae). *Journal of Animal Ecology*, **68**, 172–185.

Kindvall, O. & Ahlén, I. (1992) Geometrical factors and metapopulation dynamics of the bush cricket *Metrioptera bicolor* Philippi (Orthoptera: Tettigonidae). *Conservation Biology*, **6**, 520–529.

Koenig, W.D., Vuren, D.V. & Hooge, P.H. (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution*, **11**, 514–517.

Kuussaari, M., Nieminen, M. & Hanski, I. (1996) An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia. Journal of Animal Ecology*, **65**, 791–801.

Lahaye, W.S., Gutiérrez, R.J. & Akçakaya, H.R. (1994) Spotted owl metapopulation dynamics in Southern California. *Journal of Animal Ecology*, **63**, 775–785.

Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, **142**, 911–927.

Lande, R. (1995) Mutation and conservation. *Conservation Biology*, **9**, 782–791.

Levins, R. (1970) Extinction. *Some Mathematical Questions in Biology* (ed. M. Gerstenhaber), pp. 77–107. American Mathematical Society, Providence, R. I.

Lindberg, M.S., Sedinger, J.S., Derksen, D.V. & Rockwell, R.F. (1998) Natal and breeding philopatry in a black brant, *Branta bernicla nigricans*, metapopulation. *Ecology*, **79**, 1893–1904.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute, Cary, USA.

Lynch, M., Conery, J. & Bürguer, R. (1995) Mutation accumulation and the extinction of small populations. *American Naturalist*, **146**, 489–518.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princenton University Press, Princenton, New Jersey.

Macdonald, D.W. & Johnson, D.D.P. (2001) Dispersal in theory and practice: consequences for conservation biology. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 358–372. Oxford University Press, New York.

Margules, C., Higgs, A.J. & Rafe, R.W. (1982) Modern biogeographic theory: are there any lessons for nature reserve design? *Biological Conservation*, **24**, 115–128.

McPeek, M.A. & Holt, R.D. (1992) The evolution of dispersal in spatially and temporally varying environments. *American Naturalist*, **140**, 1010–1027.

Mills, L.S. & Smouse, P.E. (1994) Demographic consequences of inbreeding in remnant populations. *American Naturalist*, **144**, 412–431.

Muller, K.L., Stamps, J.A., Krishnan, V.V. & Willits, N.H. (1997) The effects of conespecifics attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist*, **150**, 650–661.

Nager, R.G., Johnson, A.L., Boy, V., Rendon-Martos, M., Calderón, J. & Cézilly, F. (1996) Temporal and spatial variation in dispersal in the greater flamingo (*Phoenicopterus rubber roseus*). *Oecologia*, **107**, 204–211.

Negro, J.J. (1997) Lesser kestrel *Falco naumanni*. *BWP Update*, **1**, 49–56.

Orell, M., Lahti, K., Koivula, K., Rytkönen, S. & Welling, P. (1999) Immigration and gene flow in a northern willow tit (*Parus montanus*) population. *Journal of Evolutionary Biology*, **12**, 283–295.

Oro, D. & Pradel, R. (1999) Recruitment of Audouin's gull to the Ebro Delta colony at metapopulation level in the western Mediterranean. *Marine Ecology Progress Series*, **180**, 267–273.

Oro, D. & Pradel, R. (2000) Determinants of local recruitment in a growing colony of Audouin's gull. *Journal of Animal Ecology*, **69**, 119–132.

Pärt, T. (1995) The importance of local familiarity and search costs for age- and sex-biased philopatry in the collared flycatcher. *Animal Behaviour*, **49**, 1029–1038.

Pulliam, H.R. & Danielson, B.J. (1991) Sources, sinks and habitat selection: a landscape perspective on population dynamics. *American Naturalist*, **137**, 50–66.

Ray, C., Gilpin, M. & Smith, A.T. (1991) The effect of conspecific attraction on metapopulation dynamics. *Biology Journal of the Linnean Society*, **42**, 123–134.

Reed, J.M. & Dobson, A.P. (1993) Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution*, **8**, 253–256.

Ricketts, T.H. (2001) The matrix matters: effective isolation in fragmented landscapes. *American Naturalist*, **158**, 87–99.

Rodgers, A.R. & Klenner, W.E. (1990) Competition and the geometric model of dispersal in vertebrates. *Ecology*, **71**, 818–822.

Roland, J., Keyghobadi, N. & Fownes, S. (2000) Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology*, **81**, 1642–1653.

Sæther, B.-E. Engen, S. & Lande, R. (1999) Finite metapopulation models with density-dependent migration and stochastic local dynamics. *Proceedings of the Royal Society of London Series B*, **266**, 113–118.

Serrano, D., Tella, J.L., Donázar, J.A. & Pomarol, M. (in press) Social and individual features affecting natal dispersal in the colonial lesser Kestrel. *Ecology*.

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. *Journal of Animal Ecology*, **70**, 568–578.

Sjögren, P. (1994) Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology*, **75**, 1357–1367.

Smith, A.T. & Peacock, M.M. (1990) Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology*, **4**, 320–323.

Smith, J.N.M., Taitt, M.J., Rogers, C.M., Arcese, P., Keller, L.F., Cassidy, A.L.E.V. & Hochachka, W.M. (1996) A metapopulation approach to the population biology of the song sparrow *Melospiza melodia*. *Ibis*, **138**, 120–128.

Soulé, M.E. (1987) *Viable Populations for Conservation*. Cambridge University Press, Cambridge.

Spendelow, J.A., Nichols, J.D., Nisbet, I.C.T., Hays, H., Cormons, G.D., Burger, J., Safina, C., Hines, J.E. & Gochfeld, M. (1995) Estimating annual survival and movement rates of adults within a metapopulation of Roseate Terns. *Ecology*, **76**, 2415–2428.

Stamps, J.A. (1991) The effect of conspecifics on habitat selection in territorial species. *Behavioral Ecology and Sociobiology*, **28**, 29–36.

Stith, B.M., Fitzpatrick, J.W., Woolfenden, G.E. & Pranty, B. (1996) Classification and conservation of metapopulations: a case study of the Florida scrub jay. *Metapopulation and Wildlife Conservation* (ed. D.R. McCullough), pp. 187–215. Island Press, Washington D.C.

Tella, J.L. (1996) *Ecological constraints, costs and benefits of coloniality in the lesser kestrel*. PhD Thesis. University of Barcelona, Spain.

Tella, J.L. & Forero, M.G. (2000) Farmland habitat selection of wintering lesser kestrels in a Spanish pseudosteppe: implications for conservation strategies. *Biodiversity and Conservation*, **9**, 433–441.

Tella, J.L., Forero, M.G. & Hiraldo, F. & Donázar, J.A. (1998) Conflicts between lesser kestrel conservation and European Agricultural Policies as identified by habitat use analysis. *Conservation Biology*, **12**, 593–604.

Travis, J.M.J. Murrell, D.J. & Dytham, C. (1999) The evolution of density-dependent dispersal. *Proceedings of the Royal Society of London Series B*, **266**, 1837–1842.

Travis, J.M.J. & Dytham, C. (1998) The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. *Proceedings of the Royal Society of London Series B*, **265**, 17–23.

Tucker, G.M. & Heath, M.F. (1994) *Birds in Europe: Their Conservation Status*. BirdLife International (BirdLife Conservation Series no. 3), Cambridge.

Veit, R.R. & Lewis, M.A. (1996) Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *American Naturalist*, **148**, 255–274.

Waser, P.M. (1985) Does competition drive dispersal? *Ecology*, **66**, 1170–1175.