

Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach

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Summary

1. Habitat fragmentation is involved in the present extinction crisis and is known to influence many aspects of population dynamics. The level of connectivity between populations is one of its components. In an experimental study on the common lizard (*Lacerta vivipara* Jacquin), we analysed in two contrasting habitats the influence of connection on dispersal patterns, on differences between dispersing and philopatric individuals, on population size, survival rates, and reproduction.

2. The experimental design consisted of eight two-patch units. Half of them were connected by dispersal. We performed this treatment in a grassland and a wood clearance, two habitats with different resource availability (respectively called 'rich' and 'poor' habitat).

3. We expected that the loss of connection would modify juvenile dispersal patterns, have a different effect on dispersing and philopatric individuals, negatively affect survival rates and fecundity by modifying social interactions and would have different consequences in 'rich' habitats compared to 'poor' ones.

4. Connection modified dispersal patterns. Two dispersal periods occurred in unconnected units, but only one occurred in connected ones. Moreover, dispersers of the second dispersal period were morphologically similar to philopatric individuals. The loss of connection probably caused the late dispersal of individuals which would have remained philopatric in a connected context. Dispersers of the second period seemed to have lower winter survival rates than philopatric individuals, as expected if these individuals had been 'forced' to disperse.

5. We found that connection modified demography through juvenile winter survival rates and female reproduction depending on habitat type. Connection led to higher juvenile survival rates in 'rich' habitats, whereas it was not the case in 'poor' habitats. The loss of connection decreased female reproductive rate whatever the type of habitat.

6. This study suggests that connection can directly modify demographic parameters depending on habitat quality and involving behavioural mechanisms. It confirms that conservation management, like installation of dispersal corridors, must take into account habitat characteristics and behavioural features.

Key-words: demographic parameters, habitat fragmentation, *Lacerta vivipara*, pattern and behaviour of dispersal, two-patch system.

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Introduction

Two main factors related to human activity are known to be involved in the present increase of species vulnerability and extinction. The first one, habitat destruction (Goodman 1986; Janzen 1986), induces both a decrease of the total habitat surface and a fragmentation of the landscape into small, more or less isolated patches (Wilcove, McLellan & Dobson 1986; Andr  n 1994). The second factor, global climatic change, modifies habitat characteristics (Holten 1990; Hunt *et al.* 1990; Woodward & Rochefort 1991).

The extent to which species may adapt to, or, suffer from such changes depends greatly on their ability to disperse, so that the study of dispersal is of prime importance to determine the level of connectivity and habitat quality required to ensure the survival of a given species.

Theoretical approaches to this question have led to a better understanding of the potential effects of fragmentation and habitat characteristics on species dispersion. In particular, spatially explicit models derived from percolation theory (Stauffer 1985) or the metapopulation approach show how patch size, and more importantly landscape connectivity, influence population and community dynamics (Andr  n 1994; Hanski & Thomas 1994; Kareiva & Wennergren 1995; Bascompte & Sol   1996). When fragmentation operates by a random and discrete destruction of suitable habitats (random landscapes), it was shown that, below a critical threshold of remnant original habitat (about 60%), patch size, species diversity and population extinction probability shift violently. A sudden loss of connectivity seems to be responsible for this step function corresponding to the moment where the disappearance of a patch prevents exchange of individuals between patches. Some models (Lande 1988; Wahlberg, Moilanen & Hanski 1996) have led to management rules for particular species meeting their assumptions, as for example, insensitivity to habitat heterogeneity or landscape global structure. However, they are insufficient to predict the ecological response of more complex biological systems (Wiens, Schooley & Weeks 1997). Models taking more details concerning the biology of species into account have been developed. This type of model shows that dispersal abilities and the level of specificity in habitat requirement modify the critical threshold of extinction (With 1995). In particular, habitat affinities can become an important factor at coarse scales of fragmentation (With, Gardner & Turner 1997).

These results underline the importance of collecting appropriate biological data to understand how dispersal and its interactions with habitat characteristics and connectivity influence population size. This can be achieved by investigating the role of connectivity on dispersal patterns and on demo-

graphic parameters (survival rates, fecundity) in different types of habitats.

Some experimental studies were designed to that end, showing that deteriorating connectivity can modify dispersal patterns (Andreassen, Ims & Stenseth 1996; Lecomte & Clobert 1996), and that the response to fragmentation may depend on the biological model. Fragmentation can either increase dispersal rate (fission response) or generate an aggregation (fusion response) (Lovejoy *et al.* 1986; Ims, Rolstad & Wegge 1993; Diffendorfer, Gaines & Holt 1995). Fragmentation can also modify the sex ratio (Aars, Andreassen & Ims 1995). The influence of connectivity on demographic parameters may also depend on the context. In a situation of exchanges between populations, Andreassen *et al.* (1996) found that disrupting connectivity and destroying habitat do not influence survival rates. In a context of colonization of empty patches, Johnson & Gaines (1987) showed that preventing dispersal can modify survival rates, and that frustrated dispersers had a lower survival rate than philopatric individuals or individuals allowed to disperse. Among these three classes, residents had the lowest fecundity. This diversity of results combined with the scarcity of such studies suggests that more experiments are required on the effect of fragmentation and habitat characteristics using different biological models.

Here, we test the influence of the level of connection on dispersal pattern, population size, and demographic parameters (survival rates, proportion of reproductive females, fecundity) in two different types of habitat. Our experimental design mimics recent fragmentation, either having or not having induced a total isolation of populations. Using two-patch systems, we contrasted two situations. Either exchanges between patches were possible through dispersal corridors, or exchanges were actively prevented. We performed this treatment in two contrasting habitats: a grassland, corresponding to a high level of resources for the studied species, and a wood clearance, which is a less suitable habitat (Pilorge 1987). For convenience, we call them, respectively, 'rich' and 'poor' habitats. The design allowed us to follow individual characteristics including morphological traits and movements between patches.

We expected that the loss of connection would:

1. modify dispersal patterns by changing dispersal determinants;
2. have a different effect on dispersing and philopatric individuals, because these two types of individuals may display different evolutionary strategies (Belichon, Clobert & Massot 1996; Lemel *et al.* 1997);
3. negatively affect survival rates and fecundity by modifying social interactions (Ims *et al.* 1993), which could lead to different population sizes;

4. have different consequences in 'rich' and 'poor' habitats (Clobert *et al.* 1994).

We used the common lizard (*Lacerta vivipara*), a small viviparous lacertid living in peat bogs and heathlands. This species was chosen for several reasons:

(a) we have a good knowledge of demographic processes in natural conditions (Clobert *et al.* 1994), which allowed us to compare our experimental results to natural situations;

(b) we have a long experience of this species and its behaviour (Massot 1992; Lecomte 1993) which allowed us to determine the relative suitability of the different types of habitats chosen (Pilorge 1987);

(c) field studies on natural populations have shown that dispersal is involved in mechanisms of population regulation in this species (Massot *et al.* 1992; Lecomte *et al.* 1994).

Methods

THE SPECIES

The common lizard is a widespread species, ranging from the polar circle to the parallel 50°N across Eurasia. It inhabits fragmented habitats like peat bogs and heathlands. It is a small viviparous lacertid lizard (adult snout-vent length 50–70 mm). In our experimental populations, individuals hibernate between mid-October and mid-March. Males are the first to emerge from hibernation and mating occurs soon after female emergence, at the end of April. Parturition occurs 2 months later. Females lay on average five eggs (range 1–12), which hatch within an hour after laying. Neonates are then autonomous (no parental care) and natal dispersal occurs within the first two weeks following birth. In this species, there is no apparent territoriality (Stamps 1977; Lecomte *et al.* 1994), although individuals may interact strongly for mates or food (L. Seitz, personal observation).

Long-term studies of natural populations on Mont Lozère, France (1420 m a.s.l., 44°30'N, 3°45'E), have shown that dispersal in this species is complex, involving social, behavioural and demographic determinants. By manipulating population size, dispersal appeared as an important factor regulating population size (Massot *et al.* 1992; Lecomte *et al.* 1994). Maternal ectoparasitism (Sorci, Massot & Clobert 1994), mother age (Ronce, Clobert & Massot 1998), nutrition during gestation (Massot & Clobert 1995), and social environment at birth (Léna *et al.* 1998) influence juvenile dispersal probability. In addition, dispersers and philopatric individuals differ behaviourally (Lecomte 1993; Clobert *et al.* 1994) and morphologically (Lecomte & Clobert 1996).

EXPERIMENTAL DESIGN

Enclosures

The experiment took place in the biological station of Foljuif (Ecole Normale Supérieure, Saint-Pierre-lès-Nemours, France). The experimental design comprised eight experimental units. Each experimental unit consisted of two enclosed patches (10 m × 10 m) connected by two one-way corridors (Fig. 1).

All units had the same orientation to limit micro-climatic and biotic heterogeneity. Nylon nets covered each unit to avoid avian predation. Plastic walls delimiting the enclosures were buried into the ground (30 cm) to limit predation by snakes and small rodents. Enclosures had a standardized habitat (Fig. 2) providing lizards with hiding and thermoregulation sites.

The two one-way corridors joining the two enclosures ended in a pitfall trap, which allowed the identification of individuals attempting to disperse (Fig. 3). A transparent plastic sheet hermetically closed each corridor (Fig. 3). The length of corridors (20 m) was chosen so that the distance between the centres of the two opposite patches of a unit corresponded to the upper limit of the confidence interval of an adult home range diameter (30 m, Massot 1992; Massot & Clobert 1995). In field conditions, juveniles or adults moving such a distance had a very small probability of returning to their site of origin (Strijbosch, VanRooy & Voesenec 1983; Lecomte 1993). The width of corridors (1 m) was chosen to fit with different constraints. The width had to be large enough to allow dispersing individuals to find the entrance of the corridor. It also had to be small enough to imply a discontinuity between the patches and to prevent any settlement in the corridors. Finally, the chosen width combined with the fence height (60 cm), had been calculated to imply a permanent shadow in the corridors, which was not a very attractive situation for ectothermic animals.

Experimental treatments

In four of the eight experimental units, lizards attempting to leave their patch were allowed to enter the patch they tried to reach. These units are called 'connected units'. In the other units, individuals attempting to disperse were returned to the patch from which they came. These units are called 'unconnected units'.

We investigated the effect of connection in two different types of habitats (Fig. 1) separated by 250 m. Four experimental units were situated in a grassland, whereas the four remaining units were situated in a wood clearance. To compare these two habitats, we used criteria defined by Pilorge (1987)

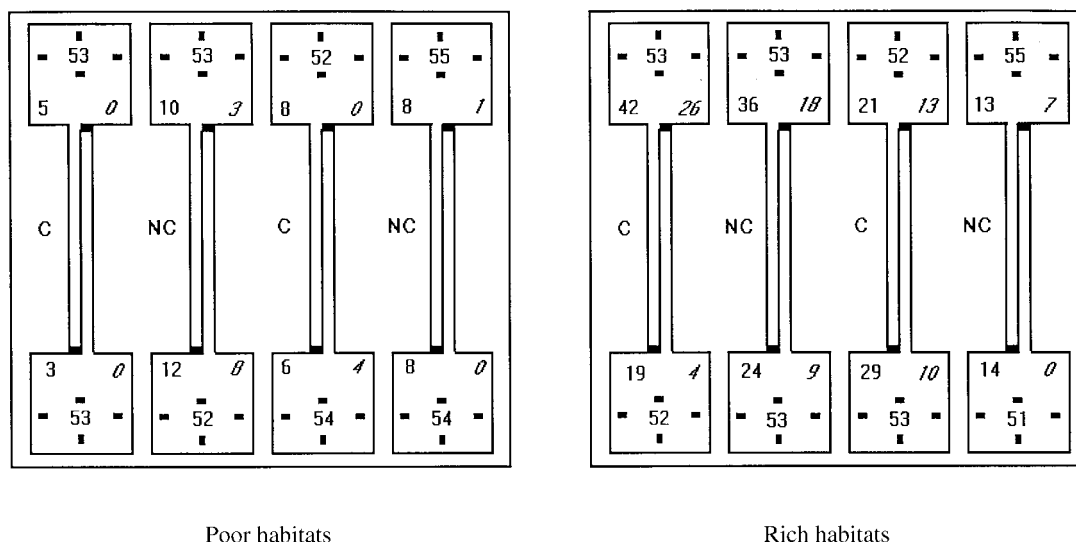


Fig. 1. Spatial organization of our experimental design and population sizes. C indicates connected units and NC unconnected units. Total population sizes appear in normal type and the number of juveniles in italics in the corner of each enclosure. The total number of individuals introduced is indicated in the middle of each enclosure. There are two replications of each treatment.

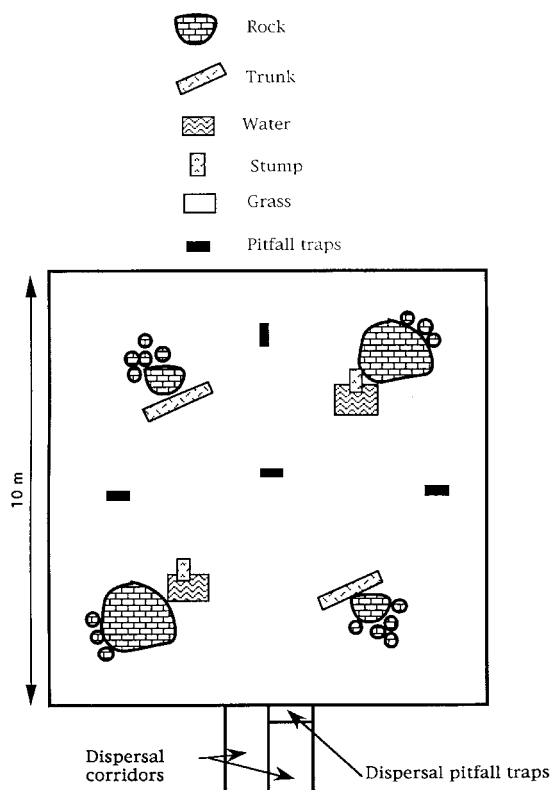


Fig. 2. Schematic representation of the standardized habitat in each patch. Each standardized habitat consists of grass and of four 'attractive' areas. Each area contains either a stump or a trunk, and rocks. Two of the four areas also contain a plastic box of water buried in the soil. Four pitfall traps are also homogeneously distributed in each habitat patch.

and Massot *et al.* (1992). Of these criteria, the most relevant for our experimental situation were dampness, insect abundance and sunshine period. We defined entomofauna abundance as the number of insects per species collected in pitfall traps during the first 2 months of the experiment. The entomofauna was less abundant in the wood clearance (4 Orders vs. 5; 25 individuals vs. 287). The wood clearance was less damp than the grassland, as indicated by the soil texture (more sandy and less silty) and the flora. The proximity of the wood also significantly reduced the daily period of sunshine. According to the biological characteristics of the common lizard (opportunistic insectivorous, ectotherm, peat-bog inhabitant), the grassland can be considered a more suitable habitat than the wood clearance. In the following text, the grassland will be referred to as 'rich' habitat, and the wood clearance as 'poor' habitat.

Validation experiment

This validation experiment was aimed at testing whether the experimental treatment in unconnected units (the manual return of dispersing individuals to their population of origin) corresponded to a natural behaviour. There are two behavioural interpretations of the unconnected treatment. The first interpretation is that, under natural conditions, individuals living in a patch surrounded by a hostile environment do not disperse at all. In this case, in our experiment, corridors and dispersal pitfall traps are just a means of identifying dispersers, as the cost

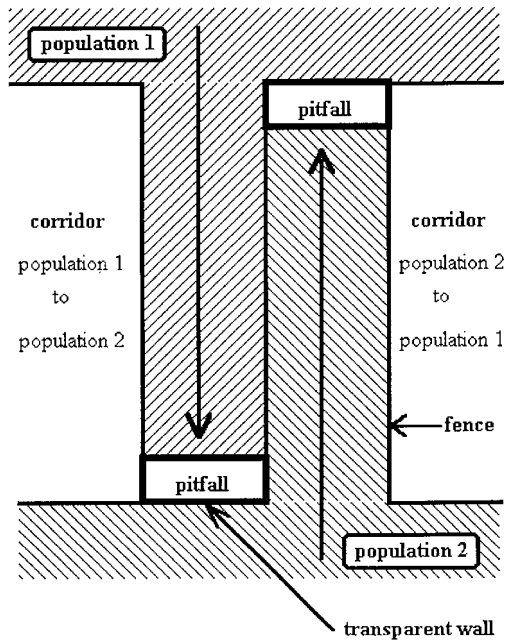


Fig. 3. Schematic representation of dispersal corridors of an experimental unit. Candidates for dispersal were caught when falling into the pitfall traps at the end of corridors. In connected units they were introduced into the population they were going to, whatever the direction considered. In unconnected units, they were returned to the population from whence they came.

of this dispersal attempt can be considered negligible compared to the distances covered by a lizard within a patch. A second interpretation is possible: under natural conditions, individuals attempt to disperse through an intermediate habitat (corresponding to our corridors with grass), hit a natural barrier (corresponding to dispersal pitfalls), are therefore prevented from dispersing and return to their patch of origin (corresponding to the manual return we imposed in unconnected units). Under natural conditions, lizards could adopt a third behaviour. They may attempt to disperse towards unsuitable habitats, try to settle there or even die in the course of their dispersal attempt, as assumed by source-sink models (Pulliam 1988). To test for the validity of these three possibilities, of which the third one may invalidate our design, in 1997 we built a new unit very near our experimental design comprising a patch of 'rich' habitat, and a patch being a forest fragment, habitat considered as a natural barrier for this species. Dispersal corridors had no vegetation and were shaded, which corresponds to a hostile habitat for this species (Pilorge 1987). In this experiment, lizards were only introduced into the patch with 'rich' habitat, which corresponds to the natural situation. The introduction timing and the number of individuals were similar to the main experiment. The year of introduction was different: 1997 for the

validation experiment and 1995 for the main experiment.

Lizard introduction

For the whole experiment, we transplanted the lizards from natural populations of Mont Lozère (southern France) to the biological station of Foljuif (central France). Two observations encouraged us to think that the transplantation would not modify the meaning of our results, at least for juveniles. First, a manipulation of density between two natural populations of Mont Lozère showed that introduction modified adult dispersal and behaviour, but not that of juveniles (Massot *et al.* 1992; Lecomte *et al.* 1994). That allowed us to think that juvenile movements observed in our experiment were actually dispersal events (and not movements in relation to a perturbation induced by adult introduction) and that the results concerning juveniles obtained in unconnected units compared to connected units did actually correspond to the effect of preventing dispersal. Secondly, a transplantation experiment from Mont Lozère to Bretagne (Paimpont, North-west of France) demonstrated the phenotypic plasticity of this species (Sorci, Clobert & Belichon 1996). That allowed us to transplant individuals into a new environment without having important consequences, such as selecting particular genotypes.

We collected all individuals (96 gravid adult females, 64 adult males, 80 subadult females and 80 subadult males) during the first week of July 1995 (30/6/97 for the validation unit) essentially from the same population on Mont Lozère. We kept gravid females in the laboratory until parturition to determine family relationships (in 1995: first parturition 27/7, last parturition 8/8; in 1997 for the validation experiment: first parturition 17/7, last parturition 29/7). All other lizards were also maintained in the laboratory until the first female hatched in order to limit heterogeneity in the date of introduction between adult females and other age classes. In the laboratory, gravid females were isolated in individual terraria (15 × 20 × 15 cm high), while adult males and yearlings were kept in groups in terraria (47 × 130 × 35 cm high, 15 lizards per terrarium). The floor of each terrarium was covered with damp peat moss. We provided water and crickets (*Acheta domesticus*) *ad libitum*. In addition to the natural photoperiod, lizards were exposed to the heat of an incandescent lamp 6 h per day, providing a thermal gradient from 25 °C to 30 °C, corresponding to the optimal temperature for this species (VanDamme, Bauwens & Verheyen 1991).

After having been marked individually, measured and weighted, individuals were randomly allocated to the 16 experimental patches (six adult females with their own litter, four adults males, five subadult

females and five subadult males per patch). The transplanted population in each patch had similar age and sex structure compared to natural populations (Massot *et al.* 1992). We verified that fecundity did not vary significantly between patches (ANOVA, $F_{1,15} = 0.21$, $P = 0.99$, mean fecundity = 5.6) and that population sizes after juvenile birth were homogeneous (log linear regression, $\chi^2_{12} = 0.54$, $N = 16$, $P = 1.00$).

We monitored individuals during the entire activity season (March to October in 1996; August to October in 1995 and in 1997 for the validation experiment). We caught them in the four pitfalls traps homogeneously distributed within each patch (Fig. 2) twice a day, and by hand capture once a month. This gave us sufficient data, without seriously disturbing the populations. Dispersal pitfalls traps were visited twice a day.

THE DATA AND THEIR TREATMENT

Definition of variables

At each capture, we recorded the date (day), sex, age, snout–vent length (mm), body mass (g), tail state (recently or not recently broken), and capture location.

Dispersers were defined as individuals which fell at least once into a dispersal pitfall.

Philopatric individuals were defined as individuals recaptured at least once in the season, but never in dispersal pitfall traps. We did not consider as philopatric individuals those which had never been captured after introduction, because the dispersal status of these probably short-lived individuals could not be determined. As the dispersal rate is less than 50%, this definition underestimated the number of philopatric individuals. However, it allowed us to know the dispersal status with certainty. So, it is the best definition to compare morphological traits of dispersal and philopatric individuals.

Population size was defined as the total number of individuals introduced in 1995 captured at least once before we reared gravid females in 1996. In connected units, dispersers were considered to belong to their arrival population. This is either an underestimation of population size at the start of 1996 or an overestimation of population size later in the season. However, we used this measure for two main reasons. First, capture probability was almost 1 for the entire season, and second, our measure of population size was comparable across populations and treatments.

Juvenile corpulence was defined as the ratio between body mass and snout–vent length, presumably a good indicator of body condition. We considered corpulence at two dates: at birth and during the last month before hibernation.

Juvenile corpulence increased linearly with time for the first 60 days of life (regression, $F_{1,124} = 23.88$, $r^2 = 0.16$, $P = 0.0001$), where *growth rate in corpulence* ($\text{g mm}^{-1} \text{day}^{-1}$) was calculated as corpulence at capture minus corpulence at birth divided by the number of days separating the capture from birth. We only considered captures separated by more than 15 days and individuals younger than 61 days. The interval of 15 days between birth and capture was chosen to minimize the influence of measurement error.

Dispersal rate was calculated as the ratio between the number of dispersers and the number of philopatric individuals, both having been recaptured after dispersal or introduction, respectively.

Fecundity was defined as the number of live neonates per female. We considered fecundity one year after introduction, that is in 1996.

Maternity success (MS) was defined as the probability of having at least one live neonate in 1996 for an adult female captured during that year. Given e_i , the number of mothers in the patch i , and n_i , the number of recaptured adult females in the patch i , MS corresponded to e_i/n_i .

Except for population size, fecundity and maternity success, all variables concerned 1995. Except when specified, age class mentioned referred to introduction in 1995.

Data analysis

For survival and capture probability estimations, after usual verifications for homogeneity (test 2 + 3, all χ^2 non significant) performed with the software RELEASE (Burnham *et al.* 1987), we used the software SURGE (Pradel, Clobert & Lebreton 1990; Pradel & Lebreton 1993). SURGE enabled us to create an array of models with various equality constraints between survival or capture probabilities, and to fit them in a similar way to variance-covariance analyses. In the general model, we took the effects of connectivity level, habitat type, time and all interactions into account. We did not include the replication as an effect in the general model because of the high number of populations (16). However, before performing analyses, we verified that there were no significant differences in survival or capture rates between the replicates of a given treatment, and then grouped the replicates of the same treatment together. The final model was chosen among the models nested in the general model on the basis of its Akaike Information Criterion ($\text{AIC} = \text{deviance} + 2 \text{ d.f.}$) (Akaike 1973). We selected the best models, which are those with the lowest AIC. Two models are considered as significantly different if their AIC differs by more than 2 units (Lebreton *et al.* 1992; Anderson & Burnham 1994). We generally considered three periods of cap-

ture (summer, from August to mid-October 1995; winter hibernation, from mid-October 1995 to mid-April 1996; prereproduction from mid-April to mid-June). We obtained independent estimations of survival and capture rates for the first two periods only (Clobert 1995). For the comparison between dispersers and philopatric individuals, we ignored survival of dispersers from introduction time to the first recapture because the first capture determines the status of the dispersing individuals (survival equal to 1).

For all other analyses, we used the software SAS (SAS Institute 1990). For the influence of connection and habitat type on population size, we used a log-linear analysis (Genmod procedure, type 3 analyses, assumed distribution: Poisson, link function: log). The influence of habitat type and connection level on dispersal probability were tested by logistic regressions (Genmod procedure, type 3 analysis, assumed distribution: binomial, link function: logit). The test for each of the terms in both types of generalized linear models (McCullagh & Nelder 1989) is performed on likelihood ratio, which asymptotically follows a Chi-square. When the ratio of residual deviance of the model with all significant terms included by degrees of freedom (variance inflation factor) was significantly higher than 1 (overdispersion), we divided the chi-square value by the variance inflation factor. This corrected chi-square is reported as χ^2_{corr} . We only considered juvenile dispersal probabilities at the level of the family, since juveniles of the same litter are statistically dependent (Massot *et al.* 1994a): the probability of being disperser strongly depended on the clutch (logistic regression, clutch effect: $\chi^2_{78} = 170.35$, $N = 211$, $P < 0.0001$). The analysis of all other variables was performed with variance-covariance analyses (Glm procedure), Student tests (*t*-test procedure), and linear regression (Reg procedure). In most cases, conditions of application of linear models were verified (or else specified). When the variable body mass was involved, we excluded individuals that had recently lost their tail.

For each analysis, the replication effect was tested at the scale of the patch, and we verified that the same results had been found at the scale of the experimental unit (two populations + corridors). To take into account replication, different strategies were used. Whenever it was possible, we considered the replicate as the statistical unit. When it was not possible, we considered replication as a nested effect in the General Model [for example, GM: $Y = \text{connection} \times \text{habitat} \times \text{habitat replication} (\text{habitat} \times \text{connection})$]. In that case, the replication effect was always kept in the selected model, even if not significant. To compare dispersing and philopatric individuals, it was impossible to include the replication effect in the general model

because of low sample size. We tested replication effect separately. The same approach was used for survival analyses (see above). Exactly how we took the replicates into account will be detailed in the results for each analysis by giving the scale used (patch, clutch or individual), the general model, and the selected model.

We focused on juvenile dispersal for two reasons. First, dispersal occurs mainly at the juvenile stage in natural conditions. Second, introduction may have induced prospecting movements in the subadult and adult class, which should not be assumed to represent dispersal (Massot *et al.* 1994b).

Results

DISPERSAL

Validation experiment

While no juvenile dispersal ($N = 39$) was observed in the validation unit, juveniles attempted to disperse in all the other units in 1995 and 1997 (K. Boudjemadi, unpublished data). Only one adult female ($N = 6$), one adult male ($N = 4$) and one subadult male ($N = 5$) dispersed at the end of the summer, but they quickly returned to their population. This experiment showed that either individuals do not disperse towards an unsuitable habitat, or they attempt to disperse and return to their population of origin. This corresponds well to the situations mimicked by unconnected experimental units.

Dispersal patterns

Dispersal rates were not significantly different among age classes (logistic analysis, patch scale, General Model = Selected Model: number of dispersers in the age class i in the patch j /number of recaptured individuals in the age class i in the patch $j = \text{Age}$, $N = 406$ recaptured individuals, $\chi^2_{2\text{corr}} = 0.19$, $P = 0.91$). For subadults and adults, we did not detect any effect of time on dispersal pattern. Moreover, only one dispersing juvenile ($N = 30$) returned to its population of origin in connected units, whereas subadults, and more obviously adults, returned more frequently to their patch of origin (two of 13 subadults, five of 18 adults). All these returns were observed in 'poor' habitats. It suggests that juvenile movements were real dispersal, whereas it was less clear for other stages. We therefore concentrated on juvenile dispersal.

Dispersal probability (dp) did not significantly depend on connection, but was significantly higher in 'poor' habitats relative to 'rich' ones (logistic regression, clutch scale, GM: Number of dispersers by clutch/number of alive juveniles in that clutch = $\mathbf{H} \mathbf{C} \mathbf{H}^* \mathbf{C} \mathbf{P}(\mathbf{H}^* \mathbf{C})$, SM: $dp = \mathbf{H} \mathbf{P}(\mathbf{H}^* \mathbf{C})$, $N = 79$ clutches, Habitat effect: $\chi^2_{2\text{corr}} = 12.44$,

$P = 0.0004$; Replication effect: $\chi^2_{15\text{corr}} = 19.54$, $P = 0.19$).

We also investigated the timing of juvenile dispersal, taking into account the first time an individual was captured as a disperser. In natural populations, the peak of juvenile dispersal occurs within the 12 days following birth. In our experiment, this peak was observed both in connected and unconnected units. However, a second period of dispersal, almost as important as the first one, began later in the season in unconnected units, whereas very few individuals dispersed at the same time in connected units (Fig. 4, individual scale, Fisher exact test, $P = 0.06$). In a similar analysis, Lecomte & Clobert (1996) found the same tendency.

Morphological traits of philopatric and dispersing juveniles

All the following analyses were performed at the individual scale. Replication effects were tested before the analyses because sample sizes were too low when comparing the four patches of a given treatment. On the 24 analyses performed to test replication effects, we found only two $P \leq 0.05$. We therefore performed the analyses ignoring the replication effect.

Dispersers of the first peak and philopatric individuals showed no significant differences in corpulence at birth (Student's t -test, log(-log) transformation, $N = 100$, $t = -1.50$, $P = 0.14$). Philopatric individuals showed a tendency to grow faster than dispersers (Fig. 5, Student's t -test, $N = 106$, $t = 1.83$, $P = 0.07$, mean growth rate in corpulence for dis-

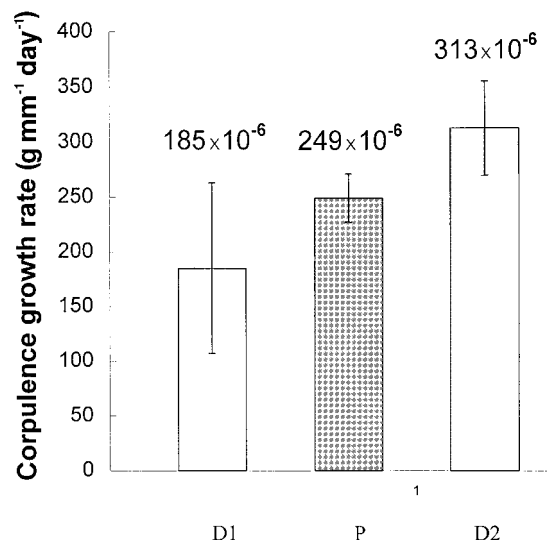


Fig. 5. Comparison of juvenile corpulence growth rates of dispersers of the first period (D1), philopatric individuals (P) and dispersers of the second period (D2) in unconnected units. Bars are standard errors. Values are growth rate in corpulence, expressed in g mm⁻¹ day⁻¹.

persers of the first period and, respectively, philopatric individuals: $185 \times 10^{-6} \pm 11 \times 10^{-6}$ g mm⁻¹ day⁻¹, $249 \times 10^{-6} \pm 39 \times 10^{-6}$ g mm⁻¹ day⁻¹, mean \pm SE). Consequently, philopatric individuals were more corpulent than dispersers of the first period in the last month before hibernation (Student's t -test, $N = 67$, $t = 2.64$, $P = 0.01$, mean corpulence for first peak dispersers: $183 \times 10^{-6} \pm 2 \times 10^{-6}$ g mm⁻¹, and

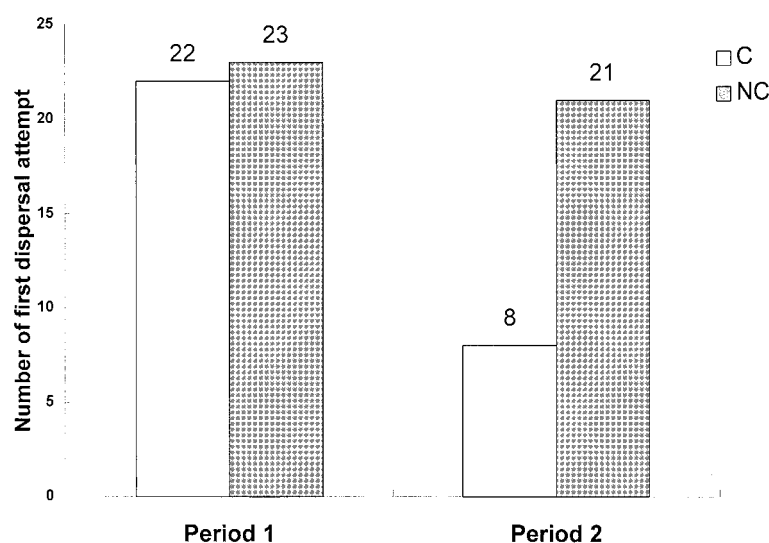


Fig. 4. Temporal organization of juvenile dispersal. Only the first dispersal attempt for a given individual was represented. Numbers are the sum of juveniles having attempted to disperse during a given period in connected (open bars) and unconnected units (shaded bars).

for philopatrics: $238 \times 10^{-4} \pm 6 \times 10^{-4} \text{ g mm}^{-1}$, mean \pm SE).

Dispersers of the first and second period in unconnected units did not show a significant difference in corpulence at birth (Student's *t*-test, $N = 44$, $t = 0.61$, $P = 0.55$). Dispersers of the second period grew faster than dispersers of the first period (Student's *t*-test, $N = 29$, $t = -3.12$, $P < 0.01$, mean for the first peak: $185 \times 10^{-6} \pm 39 \times 10^{-6} \text{ g mm}^{-1} \text{ day}^{-1}$ and for the second peak: $313 \times 10^{-6} \pm 22 \times 10^{-6} \text{ g mm}^{-1} \text{ day}^{-1}$). We did not detect any significant difference in corpulence between dispersers of the second and the first peak in unconnected units during the last month before hibernation (Student's *t*-test, $N = 20$, $t = -0.61$, $P = 0.55$), but this test was not very powerful because of low sample size.

There was no significant difference in the unconnected units between dispersers of the second peak and philopatric individuals for natal corpulence (Student's *t*-test, $N = 81$, $t = -0.64$, $P = 0.53$), growth rate in corpulence (Student's *t*-test, $N = 55$, $t = -0.81$, $P = 0.42$) and corpulence before hibernation (Student's *t*-test, $N = 42$, $t = 0.96$, $P = 0.34$).

Dispersers of the second peak, being more corpulent than those of the first peak, resembled philopatric individuals more than dispersers of the first peak.

INFLUENCE OF CONNECTION AND HABITAT TYPE ON DEMOGRAPHY

Population size analyses

Population size per unit (Fig. 1), all age and sex classes combined (except neonates of 1996), was

greater in 'rich' habitats than in 'poor' habitats, and the effect of connection seemed to depend on habitat type (Fig. 6, log-linear analysis, Poisson distribution assumed, patch scale, **GM = SM: Density = H C H*C**, $N = 16$ patches; Habitat effect: $\chi^2_{1\text{corr}} = 31.28$, $P < 0.0001$; Connection effect: $\chi^2_{1\text{corr}} = 0.40$, $P = 0.53$; Interaction effect: $\chi^2_{1\text{corr}} = 2.78$, $P = 0.10$). Separate analyses of population size by type of habitat showed that connection significantly decreases population size in 'poor' habitats (log-linear analysis, patch scale, **GM = SM: Density = C**, $N = 8$ patches; Connection effect: $\chi^2_1 = 4.32$, $P = 0.04$). A similar analysis for 'rich' habitats did not show a significant effect of connection (log-linear analysis, **GM = SM: Density = C**, $N = 8$ patches; Connection effect: $\chi^2_{1\text{corr}} = 0.66$, $P = 0.42$), but the observed tendency was a higher density in connected units (Fig. 6). This result, which is not significant, is probably in relation with the heterogeneity of population size observed across experimental units within the 'rich' habitat.

To test whether connection homogenized dynamics, we analysed the ratio $R = (N_1 - N_2)^2 / (1/2(N_1 + N_2))$ where N_1 and N_2 are the numbers of individuals in each patch of a unit. We found that connection did not homogenize population sizes, but that population sizes were more homogeneous in 'poor' habitats (log-linear analysis, unit scale, **GM: R = H C H*C**, **SM: R = H**, $N = 8$ units; Habitat effect, $\chi^2_{1\text{corr}} = 4.70$, $P = 0.03$).

Survival analysis

Survival analyses were performed at the individual scale, grouping all individuals of the same treat-

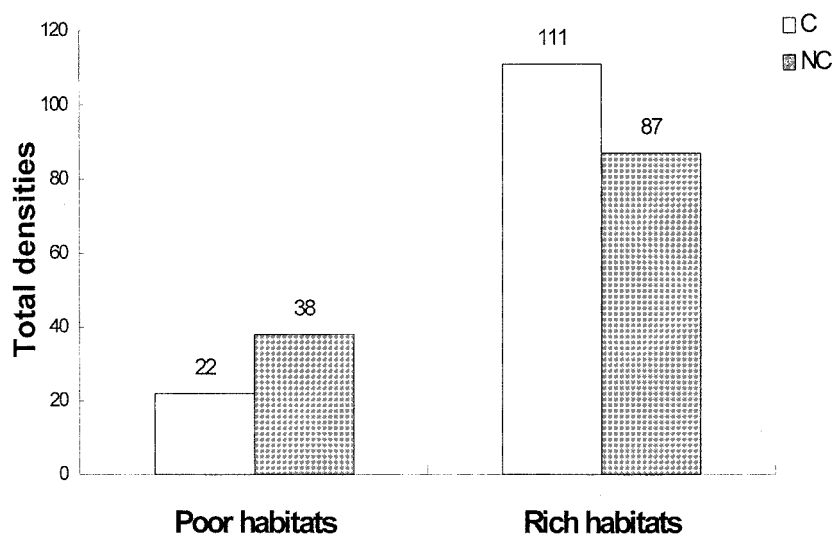


Fig. 6. Influence of level of connection and habitat quality on total density before reproduction in 1996 for all sex and age classes. Numbers are the cumulated densities for the two units of each treatment: connected (open bars) and unconnected units (shaded bars).

ment. Replication effects were tested before model selection to reduce the number of computed models.

No significant differences between replicates belonging to the same treatment were observed (deviance comparison, Chi-square, all $P > 0.05$).

For all age and sex classes, winter survival rate was significantly lower in 'poor' habitats than in 'rich' ones. For adults and subadults, connection did not significantly influence survival rates (Table 1). However, the selected model (Table 2) showed that the level of connection significantly influenced juvenile survival rates. Juvenile survival rates were significantly higher in connected experimental units when habitat was 'rich', while the converse was observed in 'poor' habitats (Fig. 7).

Comparison of survival between dispersers of the first period and philopatric individuals was difficult to interpret because of low sample size, and thus are not presented. However, the comparison between philopatric individuals and dispersers of the second period revealed significant differences between groups. In unconnected units, philopatric individuals recaptured at the time when dispersers of the second peak (g1) dispersed seemed to survive better

than dispersers of the second peak (g2) in all the selected models including the group factor (Table 3 for AIC values). It is for example the case for the most parsimonious model between the selected ones [Model $s = \text{dispersal}$, $c = \text{time}$; $N = 71$, $\text{AIC} = 142.99$, $s(g1) = 0.304$ in $(0.146-0.529)$, $s(g2) = 0.636$ in $(0.517-0.739)$].

Female reproduction

Fecundity was not age dependent (nested ANOVA, individual scale, $\text{GM} = \text{SM}$: Fecundity = Age $\text{P}(\text{H}^*\text{C})$, $N = 37$ mothers, 14 patches with a mother; Age effect: $F_{1,13} = 2.85$, $P = 0.12$; Replication effect: $F_{13,22} = 0.72$, $P = 0.71$).

Fecundity was not influenced by connection or habitat type (nested ANOVA, individual scale, $\text{GM} = \text{SM} = \text{H C H}^*\text{C P}(\text{H}^*\text{C})$, $N = 37$ mothers, 14 patches with a mother, Habitat effect: $F_{1,10} = 0.16$, $P = 0.70$; Connection effect: $F_{1,10} = 0.02$, $P = 0.89$; Interaction effect: $F_{1,10} = 0.19$, $P = 0.68$; Replication effect: $F_{10,23} = 0.86$, $P = 0.57$; Mean fecundity = 4.3, SE = 0.6, range 1–9).

Table 1. Survival and capture rate estimations for subadults, adult males and females. Connection did not influence adult and subadult survival rates, whereas habitat type had a strong effect (P for 'poor' habitats, R for 'rich' habitats). Local tests (comparison of deviance) were performed to test the influence of habitat type within a season. They showed that the difference between 'rich' and 'poor' habitats was especially strong in winter, S indicating it was significant in a season, NS indicating it was not. In winter, survival rates were significantly higher in 'rich' habitats. The selected models for subadults, adult males and adult females were $s = \text{habitat type} + \text{time}$ $c = \text{time}$

Habitat type	Period	Estimation	Confidence interval
Subadults			
<i>Survival rates</i>			
P (80)	Summer 1995	0.792	0.589–0.910 S
	Winter 1995–96	0.414	0.214–0.970 S
R (80)	Summer 1995	0.960	0.872–0.988
	Winter 1995–96	0.818	0.650–0.915
<i>Capture rates</i>			
	Summer 1995	0.663	0.557–0.755
	Winter 1995–96	0.575	0.443–0.697
Adult males			
<i>Survival rates</i>			
P (40)	Summer 1995	0.853	0.571–0.962 NS
	Winter 1995–96	0.420	0.251–0.610 S
R (40)	Summer 1995	0.988	0.920–0.98
	Winter 1995–96	0.917	0.775–0.972
<i>Capture rates</i>			
	Summer 1995	0.757	0.627–0.850
	Winter 1995–96	0.892	0.734–0.848
Adult females			
<i>Survival rates</i>			
P (48)	Summer 1995	0.916	0.466–0.992 NS
	Winter 1995–96	0.297	0.166–0.472 S
R (48)	Summer 1995	0.979	0.761–0.998
	Winter 1995–96	0.649	0.497–0.776
<i>Capture rates</i>			
	Summer 1995	0.637	0.505–0.750
	Winter 1995–96	0.458	0.313–0.611

Table 2. Influence of connection (c), habitat type (h) and time (t) on juvenile survival rates. Akaike Information Criterion (AIC) values and the number of parameters estimated are given for each model. s refers to survival rates while p refers to capture rate. * refers to the best models, for which AIC are the lowest. Connection, habitat type and interaction between these two factors are included in the two selected models. Only the results concerning the more parsimonious model ($p = t^*h$ s = c^*t^*h #2) will be given below. c^*t^*h #2 refers to the complete model containing the three factors c, t, h except for the interaction c^*t^*h .

p	c^*t^*h	c^*t^*h #2	c + t + h	c + t + h + c^*t	c + t + h	c + t	c + h	t + h	c^*t	c^*h	t^*h	c	t	h
s														
c^*t^*h	1298-00	1297-78	1299-35	1297-5	1295-63	1298-00	1325-32	1294-89	1299-82	1327-16	1293-17*	1327-31	1298-87	1324-03
	20	19	18	17	16	15	15	15	16	16	16	14	14	14
c^*t^*h #2	1296-38	1295-76	1297-95	1296-43	1294-83	1298-32	1318-11	1294-52	1300-19	1319-32	1292-08*	1325-32	1299-53	1317-41
	19	18	17	16	15	14	11	14	15	12	15	12	13	10
c^*t^*h	1303-76	1305-65	1308-46	1306-46	1302-69	1302-49	1332-65	1302-63	1304-3	1333-4	1301-86	1330-73	1303-26	1332-41
	18	17	16	15	13	2	11	12	13	12	14	10	11	10
$c^*t + h + c^*t$	1303-18	1304-57	1309-14	1311-8	1308-61	1307-72	1336-08	1307-72	1310-25	1338-07	1306-83	1332-09	1309-02	1337-52
	17	16	15	14	12	11	10	11	13	11	13	8	10	9
c + t + h	1306-67	1307-6	1311-08	1312-23	1308-86	1308-55	1338-18	1308-06	1311-74	1339-5	1307-37	1338-23	1308-89	1333-76
	16	15	13	12	10	9	8	9	11	9	11	7	8	7
c + t	1305-3	1306-3	1310-18	1314-25	1311-9	1369-66	1371-09	1310-2	1370-97	1368-15	1307-1	1396-92	1369-65	1370-27
	15	14	12	11	9	8	7	8	9	8	10	6	7	6
c + h	1307-12	1306-1	1309-56	1308-18	1306-87	1307-87	1390-33	1306-27	1311-22	1391-38	1306-69	1388-34	1308-64	1390-11
	15	13	10	9	8	7	6	7	9	7	9	5	6	5
t + h	1306-6	1308-66	1310-51	1310-25	1306-98	1306-55	1336-28	1306-44	1309-78	1337-77	1304-1	1334-3	1307-21	1335-34
	15	14	12	11	9	8	7	8	10	8	9	6	7	6
c^*t	1303-43	1304-02	1307-83	1312-08	1309-65	1367-02	1371-47	1308-43	1368-83	1370-23	1304-58	1393-93	1367-88	1369-67
	16	15	13	12	10	9	8	9	10	10	11	7	8	7
c^*h	1305-95	1305-29	1304-77	1302-8	1299-18	1299-99	1382-705	1299-46	1301-67	1383-88	1299-46	1380-86	1301-61	1382-27
	16	14	12	11	9	8	7	8	9	8	8	6	7	6
t^*h	1297-56	1301-26	1299-77	1302-97	1300-01	1301-07	1325-25	1296-55	1302-293	1325-25	1294-83	1327-33	1300-53	1323-27
	16	16	13	13	11	10	8	9	11	9	10	7	8	7
c	1306-64	1305-75	1323-43	1325-51	1326-36	1373-29	1420-75	1324-75	1374-44	1417-13	1307-54	1458-88	1373-35	1419-64
	14	12	10	9	7	6	5	6	7	6	8	4	5	4
t	1306-02	1308-2	1310-18	1313-94	1311-36	1367-68	1371-9	1309-42	1368-99	1371-25	1304-47	1395-38	1366-49	1369-94
	14	13	11	10	8	7	6	7	8	7	8	5	5	5
h	1308-65	1307-66	1309-79	1308-36	1305-00	1305-93	1388-37	1304-68	1309-22	1389-39	1305-28	1386-38	1306-98	1388-54

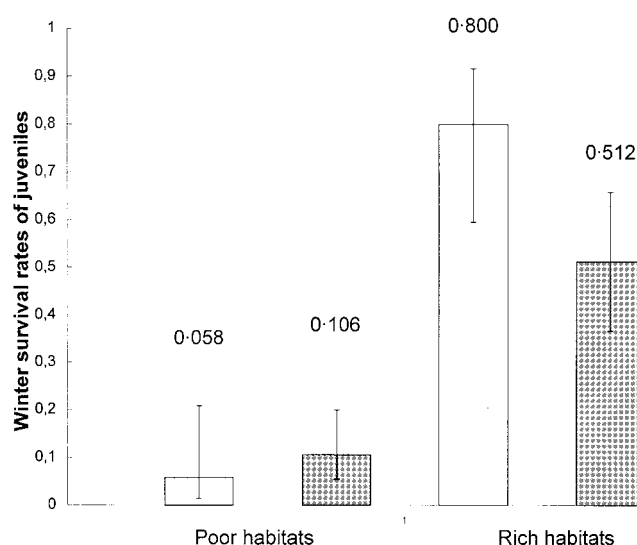


Fig. 7. Influence of connection and habitat type on juvenile winter survival rates. Numbers are estimates of juvenile winter survival rates in connected (open bars) and unconnected units (shaded bars). Bars represent the 95% confidence interval of each estimate.

Maternity success was significantly higher in the connected situation than in the unconnected one (logistic analysis, patch scale, **GM**: $e_i/n_i = \mathbf{H} \mathbf{C} \mathbf{H}^* \mathbf{C}$, **SM**: $e_i/n_i = \mathbf{C}$, $N = 80$ females; Connection effect: $\chi^2_{12} = 3.98$, $P = 0.05$, 61% of mothers in connected units, 38% in unconnected units), whereas habitat type did not significantly influence this variable.

Quality of juveniles is estimated by their corpulence. To take into account maternal effect, corpulence was averaged by clutch. Quality of juveniles did not depend on connection or habitat type (nested ANOVA, clutch scale, **GM** = **SM**: Mean cor-

pulence averaged by clutch = $\mathbf{H} \mathbf{C} \mathbf{H}^* \mathbf{C} \mathbf{P}(\mathbf{H}^* \mathbf{C})$, $N = 37$; Habitat effect: $F_{1,10} = 1.24$, $P = 0.30$; Connection effect: $F_{1,10} = 1.49$, $P = 0.25$; Interaction effect: $F_{1,10} = 1.19$, $P = 0.30$; Replication effect: $F_{10,23} = 0.84$, $P = 0.59$).

Discussion

Our study showed the effects of connection and habitat type on population dynamics to be potentially multiple and complex. These two factors, acting independently or together, influenced both behaviour and demography. Juvenile dispersal rate was higher in the 'poor' habitat than in the 'rich' one. The effect of the level of connection was also qualitative. The absence of connection led to a second dispersal event involving individuals morphologically more similar to philopatric individuals. The fact that in unconnected units, dispersers of the second peak showed lower survival rates than philopatric individuals captured simultaneously confirmed the special nature of these late dispersers. Reproduction processes also seemed to be different in connected and unconnected units, females having higher maternity success in connected units. Connection modified juvenile winter survival rates depending on habitat type: connection enhanced survival in 'rich' habitats but decreased it in 'poor' habitats. This, in turn, entailed differences in total population size. Adult and subadult life-history traits were not dependent on the level of connection.

Table 3. Comparison of survival rates between dispersing individuals of the second peak (g1) and philopatric individuals recaptured during that period (g2). Akaike Information Criterion (AIC) values and the number of parameters estimated are given for each model. s refers to survival rate while p refers to capture rate models. * refers to the best models, for which AIC are the lowest

$\begin{matrix} p \rightarrow \\ s \downarrow \end{matrix}$	g^*t	$g+t$	t	g
g^*t	144.49 6	144.49 6	142.50* 5	148.98 6
$g+t$	144.49 6	144.49 6	142.50* 5	146.50 5
t	143.65* 5	144.65 5	145.27 3	146.22 4
g	146.14 6	144.14 5	142.20* 4	153.56 4

RELEVANCE OF THE EXPERIMENTAL
DESIGN

Individuals transplanted in our design essentially came from the same population (Mont Lozère), where natural density reaches, on average, a maximum of 1000 individuals per hectare. We introduced them into small patches, at high densities (about 2000 ind. ha⁻¹ before reproduction). This situation may correspond to an important and fast fragmentation forcing individuals to concentrate in small patches of suitable remnant habitat (fusion response, Lovejoy *et al.* 1986; Ims *et al.* 1993; Diffendorfer *et al.* 1995). Such a brutal fragmentation has actually been observed in two subpopulations situated in habitats of good quality at Mont Lozère. After the initial population was fragmented by the installation of a horse pasture in the middle of it, individuals from the pasture, which were individually marked, migrated to the two remaining subpopulations. However, as we do not have data from natural populations indicating to what extent a fragmentation would increase density in poor habitats, the density at introduction in 'poor' habitats could be abnormally important. The way it might influence our results will be discussed further.

Our experiment mimicked a situation where populations were completely isolated after fragmentation (unconnected units) and a situation where dispersal corridors still linked some patches (connected units). Unconnected units can correspond to two different behaviours likely to occur in isolated situations: either individuals living in a suitable habitat surrounded by an unsuitable habitat do not disperse at all, or they attempt to disperse through an intermediate habitat but come back to their patch of origin when encountering a natural barrier. The validation experiment showed that in an isolated situation (a suitable patch surrounded by fields and forest, which are unsuitable habitats), either individuals did not leave their patch, or they only left it for short visits to surrounding unsuitable habitat. It corresponds to the two behaviours supposed to occur in unconnected treatments. Therefore, unconnected treatments really mimicked a behaviour observed in a situation of isolated patches. Observations made on natural populations also support this interpretation because no exchanges of individuals have been observed for 10 years between two populations separated by a 30-m forest band (unsuitable habitat for the common lizard) (Massot *et al.* 1992).

The transplantation of individuals into a new environment could modify dispersal behaviour. Adult and subadult dispersal rates in our experiment were three times higher than in natural populations (about 0.15 instead of 0.05) (Clobert *et al.* 1994). The fact that an important amount of adults returned to their patch of origin in connected units

situated in 'poor' habitats suggests that these movements may correspond to prospecting movements. It may also indicate that larger adult home ranges including two opposite patches were used in 'poor' habitats. Even though it is less obvious for subadults, introduction could also have led to prospecting movements. Juvenile dispersal rates were low compared to those observed in natural populations (about 0.15 instead of 0.3–0.5). Our design, where only one dispersal direction is possible, may have allowed dispersal of the most motivated dispersers only. However, dispersal took place during a few days after birth in connected units, as observed in natural populations (Clobert *et al.* 1994; Massot & Clobert 1995), and only one dispersing juvenile returned to its patch of origin in connected units. This confirmed that observed movements were real dispersal. These two observations, showing that dispersal juvenile pattern observed in our patches corresponded to patterns of natural populations, seemed to indicate that transplantation and adult or subadult prospecting movements did not obviously modify juvenile dispersal behaviour in connected units. A previous study manipulating density also showed that adult movements did not change juvenile behaviour (Lecomte *et al.* 1994; Massot *et al.* 1992). Moreover, even if juvenile dispersal would have been modified by adult movements, our results may still be interpreted in terms of rapid fragmentation or reintroduction into a fragmented environment.

A restriction was inherent in the design of our experiment. We only had two units for each treatment, and in some cases we had to eliminate the experimental unit stratum from the analysis. This might diminish the generality of our results.

CONNECTION AND DISPERSAL

Although genetic bases of dispersal have not been clearly demonstrated in vertebrates (Hansson 1991), dispersal is widely supposed to have genetic and environmental components. Two main environmental factors are known to influence dispersal:

1. habitat heterogeneity in time and space;
2. the social environment, including competition and mate selection.

Dispersal rates have been predicted to be the expression of conditional strategies (McPeck & Holt 1992; Doncaster *et al.* 1997; Lemel *et al.* 1997), and the consequences on fitness of being philopatric or disperser have been shown to depend on species, populations, and time (Bélíchon *et al.* 1996). Hence, the motivations to move may be multiple, and different types of individuals differ in motivation. This is reflected by the distinction between forced and internally driven dispersal (Lidicker 1975; Stenseth 1983; Pärt & Gustafsson 1989; Pärt 1990); for exam-

ple, Léna *et al.* (1998) showed that competition with kin and those that were not kin did not lead the same individuals to disperse. Similarly, Lidicker (1975) found phenotypic differences between individuals which leave at peak of density and before this peak. Individuals forced to disperse differed from those dispersing naturally.

In our experiment, preventing dispersal in unconnected units led to a second peak of juvenile dispersal that was not observed in connected units. Individuals attempting to disperse for the first time during the second peak of dispersal would of course not have been able to disperse in a natural unconnected situation, but our design allowed us to identify them. Individuals of the second peak had characteristics of philopatric juveniles. A previous study testing the feasibility of our experimental design led to similar results (Lecomte & Clobert 1996), suggesting that our results are general. The loss of connection seemed to have generated the attempt at departure of individuals which otherwise would have been philopatric. These individuals had a lower winter survival rate than philopatric individuals. This is compatible with the hypothesis that these individuals were 'forced to disperse' either by the frustrated dispersers of the first dispersal period (juveniles or adult prospecting dispersers) or by other philopatric individuals. As the observed pattern could not be density-related in our design, we can conclude that it had a social origin. In fact, the loss of connection may have implied a global social perturbation leading some philopatric individuals to leave. Because the cost of travelling along dispersal corridors is supposed to be low, the difference observed in survival rate between philopatric individuals and dispersers of the second peak may reveal intrinsic differences, meaning that dispersers of the second peak could be a particular group of philopatric individuals, perhaps the less competitive ones. So the loss of connection could have a direct impact on naturally isolated populations by influencing the motivation of individuals to move. However, as habitat quality can also be involved in dispersal determinism, the influence of connection could depend on how habitat quality and connection interact and modify the motivation to move.

DISPERSAL AND HABITAT

Habitat type and availability are expected to influence dispersal rate; for example, the dispersal rate is expected to be larger in habitat of low quality, in particular when heterogeneity in habitat quality is reflected by differences in population size (McPeck & Holt 1992). However, in our experimental design population sizes and habitat type were equal in a given experimental unit, whatever habitat suitability. So, at a first glance, our experiment simulated 'intra-

habitat' more than 'interhabitat' dispersal. In natural conditions, it has been found that common lizards dispersed less in poor habitats than in rich habitats (Clobert *et al.* 1994), just the opposite of what we found here. However, 'poor' habitats also had low population size in natural conditions, which was not the case in our experiment, where we introduced the same number of individuals whatever the treatment. This induced a higher ratio of population size to carrying capacity in the 'poor' habitat units in comparison to the 'rich' habitat units. Dispersal is affected by both habitat type and density in the common lizard (Clobert *et al.* 1994; Léna *et al.* 1998). The overcrowded situation in the 'poor' habitat may have induced a higher dispersal propensity, an effect that can be distinguished from the effect of habitat type *per se*. This higher dispersal propensity can be linked to 'forced' dispersal. In that case, the cost of dispersal could be higher, not as a result of the travelling itself, but because some individuals not genetically or phenotypically prepared to move may have difficulties in settling in a new patch.

CONNECTION AND DEMOGRAPHY

In many models, the lack of connection is supposed to influence long-term population dynamics by amplifying demographic and environmental stochasticity, in particular when environmental conditions are not spatially autocorrelated (for example, Fahrig & Merriam 1985). Other models considering more particular types of dynamics (Gillenberg, Söderbacka & Ericsson 1993; Gonzalez-Andujar & Perry 1993; Hastings 1993; Doebeli 1994) suggested that connection can stabilize complex dynamics, especially in the case of strong intraspecific competition (McCallum 1994; Stone 1995). This underlines that connection would modify social interactions, which in turn could modify long-term average demographic parameters. However, existing models did not take into account any direct costs of the absence of connection on demographic parameters.

We did not find that connection stabilizes the dynamics by homogenizing densities. This result should be viewed with care because we only analysed the first year of the experiment. However, we found that connection influenced demographic parameters.

Connection did not modify mean female fecundity or juvenile quality, but increased the proportion of successfully reproductive adult females. As all patches contained at least one pregnant female and a surviving adult male, this result was not a result of the absence of potential mates in unconnected patches. This can be seen as a kind of Allee effect (Allee 1931, 1951). In unconnected units, the sample of potential partners is reduced compared to connected units, and the risk of incompatibility between

partners is increased; for example, as female receptivity is time constrained in this species, sexual asynchrony between partners is more likely. So stochastic (probability of encounter of an adult of the opposite sex) as well as behavioural (probability of finding a 'suitable' partner) processes could have been involved. This interpretation is supported by the theoretical work from Legendre *et al.* (1999), where the effect of population sizes on extinction dynamics was considered. This work showed that decreased mating is expected at low density due to purely stochastic demographic processes and that it should increase extinction probability. Experimental evidence for Allee effects in animals are scarce (Pearl, Miner & Parker 1927; Frank, Boll & Kelly 1957; Saether, Ringsby & Roskaft 1996), but some observations suggest an Allee effect, for example in colonial birds, where lifetime reproductive success can decrease when the colony size is low (Brown, Stutchbury & Walsh 1990). In plants, experimental studies manipulating density and 'mate choice' through pollinators showed that both stochastic and behavioural mechanisms (through the pollinator) were involved (Kunin 1993; Sabat & Ackerman 1996). However, in our experiment, an Allee effect (stochastic or behavioural) cannot be the main mechanism involved in the decrease in recruitment. It could have been the case if maternity success had been especially lower in 'poor' habitats, where density was very low, compared to 'rich' habitats. As connection was the only factor influencing maternity success, we hypothesize that connection by itself can modify recruitment. Frustrating adult movements (dispersal or prospecting) could have modified costs of reproduction. However, based on our results, it is too early to propose a precise mechanism.

We also found that the lack of connection decreased juvenile winter survival rates in 'rich' habitats. As density was similar in all patches at the beginning of the experiment and mortality was very low in summer, this result cannot be explained by a density effect just before hibernation. However, the modification of social interactions the second peak of dispersal in unconnected units might reveal could be one of the mechanisms involved in this decrease in survival rates. However, we did not find a simple effect of connection on juvenile survival rate. This effect may depend on habitat type, the connection having a positive effect in 'rich' habitats and a negative effect in 'poor' habitats. The positive influence of connection in 'rich' habitats seemed to be compensated for in 'poor' habitats. It could be in relation to the higher cost of dispersal in 'poor' habitats hypothesized in the previous paragraph.

Johannessen & Ims (1996) did not find that fragmentation influenced survival rates in the root vole. This difference can result either from differences in the level of plasticity relative to fragmentation of

the two species or from differences in the experimental design; for example, the scale of fragmentation considered was different. In the root vole experiment, distance between patches was much smaller than the dispersal abilities of this species, while it is not so obvious in our case.

The decrease in juvenile survival observed in 'rich' connected units is consistent with that of female reproductive success. These results suggest that connection could modify population size not only by decreasing demographic stochasticity in the long term, as predicted by existing models. The lack of connection could also render small isolated populations prone to extinction through direct costs on individuals.

CONSIDERATIONS ABOUT CONSERVATION BIOLOGY

The common lizard is a useful model for conservation biology and more especially for studying the effects of habitat fragmentation because of its conservation status and its life cycle. This species is not directly threatened in the short term in France, so it is possible to take samples from locally abundant populations and to study the effects of habitat fragmentation using experimental approaches. The lizard's life cycle is long enough to be consistent with the life cycle of endangered species and short enough to consider the evolution of an experimental situation over several generations. Such experimental approaches constitute a fundamental approach of conservation biology, allowing a general understanding of the mechanisms which modify population dynamics when habitat fragmentation occurs. This study is included in that context and its general impact lies in its comparison with other experimental studies investigating the same aspects in different groups and species. Unfortunately, such studies remain, to our knowledge, very scarce (Aars *et al.* 1995; Andreassen *et al.* 1996; Johannessen & Ims 1996). Our study could have a more particular interest for the management of the threatened species in the genus *Lacerta*, as for example the 11 species covered by the Convention on the Conservation of European Wildlife and Natural Habitats. In addition to its interest as a study for a fundamental approach to conservation biology, the common lizard is directly affected by habitat fragmentation in some countries such as Belgium and Holland, at least in the long term. The common lizard is a protected species in France and inhabits heathlands and peat bogs, which are very sensitive to habitat fragmentation. The conclusions of our study could help towards management of this species in the future.

We found that connection had a positive effect on juvenile survival rate in 'rich' habitats, whereas this positive effect was not observed in 'poor' habitats.

Our results suggest that dispersal corridors would be useful for the common lizard in a fragmented landscape containing patches of 'rich' habitats. It would not be the case in 'poor' habitats, i.e. when fragmentation led to an important degradation of habitat. However, these conclusions must be related to the particular conditions of the experiment. The density at introduction into 'poor' habitats could be abnormally high compared to that observed in poor habitats under natural conditions. This could have led to exceptionally noticeable dispersal rates. Consequently, as dispersal cost might be higher in 'poor' habitats, it could have induced higher mortality rates in the connected unit of 'poor' habitat compared to the case in the natural situation. So the detrimental effect of connection observed in 'poor' habitats could not occur in a natural context. In the future, we will be able to account for the long-term effects of connection in 'poor' habitats for several years (1995–1999).

Another feature of our design is the limitation of predation both in patches and in corridors. The effect of predation in patches can be considered as a component of habitat quality. However, it has been shown that the impact of predation in corridors during the transient stage can be particularly high compared to that observed in patches (Hobbs 1992). Therefore, predation might undermine the positive effect of connection in 'rich' habitats and amplify an eventual negative effect of connection in 'poor' habitats. To sum up, the positive effect of connection on survival rates observed in 'rich' habitats would rather correspond to a natural situation where predation is low, whereas the negative effect of connection in 'poor' habitats would rather correspond to a situation where dispersal rates and predation are important.

Our study underlines the importance of the interaction between connection and habitat characteristics in population dynamics, at least in the short term, and confirms the importance of taking into account habitat characteristics in the context of introduction of a species to it (Griffith *et al.* 1989). Moreover, the influence of connection on dispersal and reproduction confirms that studying behaviour and mating systems has a direct interest to species conservation (Berger 1996; Saether *et al.* 1996; Legendre *et al.*, 1999).

Conclusions

Our study experimentally confirmed that the level of connection and habitat type can modify population size, as predicted by recent models (With 1995; With *et al.* 1997). This modification was the result of an alteration of the survival rate of the dispersing age class and of the maternity success of adult females during the season following the loss of connection.

A good knowledge of habitat requirements, dispersal strategies and social interactions seems to be required to understand the role of dispersal corridors more precisely and to define reintroduction strategies. Finally, this study supported the potential importance of social interactions on population dynamics even for species with low levels of social organization, such as the common lizard, suggesting that the effect of fragmentation could be more important than predicted by models, which are not taking this aspect into account.

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