Movement patterns of the common lizard
(*Lacerta vivipara*) in relation to sex and age

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Most of the existing empirical studies on dispersal have shown intraspecific differences between young and adults, and between males and females. However, they concern mostly birds and mammals, and very little is known about reptiles. This paper will present some preliminary results from a study on dispersal in the common lizard. It will focus on differences in age and sex which are probably two major components of the dispersal pattern.

If the common lizard is similar to most vertebrates, dispersal should involve mainly young individuals. Differences between sexes are less easy to predict as shown by the opposite trends observed in birds and mammals (GREENWOOD 1980). In birds, females are more likely to disperse, while in mammals, there is a male bias in dispersal. GREENWOOD argued that sex differences in reproduction costs and benefits due to mating system could explain this difference between birds and mammals. If males compete for resources to attract females (as in most birds), males should be philopatric, and females should disperse. If females compete for resources for reproduction (as in most mammals), they should be the philopatric sex. In the common lizard, the wider movements of males during the mating period is probably related to their search for mates (HEULIN 1984): males seem to compete directy for females. In females, reproduction appears to be influenced by density (MASSOT et al. in press): females are likely to compete for reproductive resources. As males seem less dependent on local resources, one should expect, on the basis of competition, a male bias in dispersal.

Material and methods

Movement patterns have been investigated on a population of the Mont Lozère (France) in 1989 and 1990. Hand captures constitute the bulk of the data. Each capture was localised to about 1 m on a grid composed of sticks placed every 3 m. Hand captures beyond the borders of the study area were less precisely recorded (to within about 5 m). The individuals going in and out of the three enclosed parts of the study area were also controled with pitfall traps buried along both sides of the enclosure.

In the literature, dispersal is usually defined as a change in position by more than one mean home range diameter. However, as many philopatric individuals move more than one mean home range, this overestimates the proportion of dispersers, especially in populations with few dispersers. Another possibility is to

define dispersal as a change in position by more than the value of the upper confidence limit of home range diameters. This way may cause the opposite bias: while most philopatric individuals will be correctly discriminated, some dispersers will be defined as philopatric. This latter bias will be stronger in populations with many dispersers. As dispersers are relatively few in the study population, the upper confidence limit discrimination was used.

Home range areas were estimated from hand captures and calculated using the convex polygon technique as worked out by JENNRICH & TURNER (1969). Successive captures were separated by at least 8 days to achieve their independence. Besides, as parturient females behave very differently from other females, they were removed from the female sample. Sample sizes were only satisfactory in 1990. Home range areas were logtransformed to normalize distributions and to homogenize variances. T-tests and ANOVAs were used to compare sex and age effects.

The distributions of distances between the first and the last captures (separated by at least 8 days) were compared by MANN-WHITNEY U tests. In this way, we compared all movements, whether dispersive or not. I used Chi-squares to compare proportions of dispersers alone.

Results

Home range

Adult and yearling males had a significant larger home range than females ($p= 0.001$). Average home range size did not vary significantly with age in males. Females more than 2 year old showed a significantly reduced home range size compared to 2 year old females ($p= 0.019$). Although a sample of only 5 juveniles did not allow any reliable statistic analysis, their home range size appeared relatively similar to that of other individuals. Finally, the maximum upper limit of all confidence intervals of home range sizes is about 700 m^2. This leads to an upper limit of 30 m for the diameter of the home range. This diameter will be used to segregate dispersers from philopatric individuals.

Dispersal pattern

Data on natal dispersal were recorded from juveniles hatched in the laboratory and released on their mother's capture spot. Natal dispersal is defined as the distance moved by an individual between its birth place and its first breeding site. To date, following common lizard's movements from hatching to its breeding place as an adult has not been achieved. In the framework of this study, I only disposed so far of 1990 recaptures as yearlings of 1989 juveniles, so that a part of the actual natal dispersal is missing. With this caveat in mind, dispersal patterns as well as proportions of dispersers did not differ significantly between male and female juveniles. In males, the mean distance moved is 24 m against 16 m in females, and 30% of males dispersed against 8% of females. Distances moved by neonates

between their release point and their successive recapture spots showed that most of dispersers moved during the 10 days following their birth, and that no juvenile recaptured at less than 30 m before 12 days is recaptured at more than 30 m before 12 days is recaptured at more than 30 m afterwards. In other words, juveniles appear to disperse immediately after birth or not at all.

In 1989 as well as in 1990, the dispersal patterns and the proportions of dispersers among yearlings and 2-year-old individuals did not differ between males and females. We found identical results for more than 2-year-old in 1989. In 1990 again, the proportions of dispersers did not differ significantly between males and females. However, dispersal patterns differed significantly (p= 0.002). The mean distance moved was 11 m in males against 5 m in females. This difference certainly reflects the difference in home range size which was significantly greater in males than in females.

To sum up (Fig. 1), proportions of dispersers did not differ between males and females whatever the age class considered, although they were greater in males in 6 cases on 7. Otherwise, juvenile males dispersed more than older males in 1989 (p< 0.001). It was not the case in females (p= 0.7461). Finally, the difference between
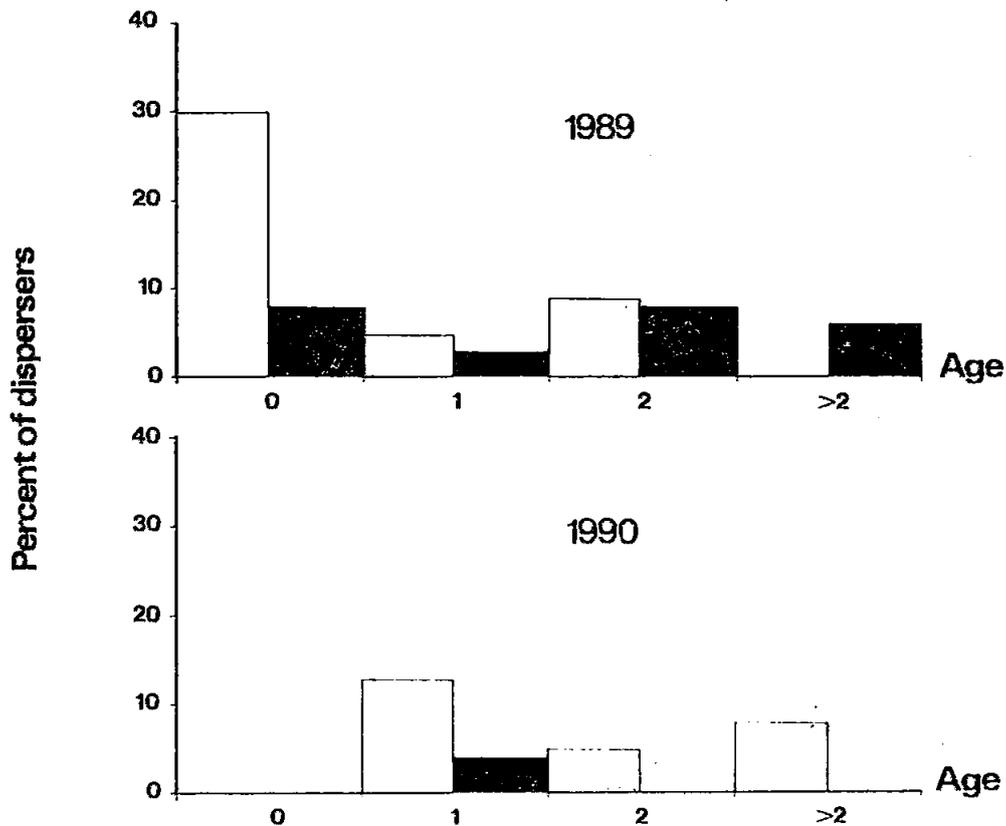

Fig. 1. Proportion of males (open bars) and females (filled bars) that dispersed in relation to age (N above the bars)

sexes was opposite between 1989 and 1990 in individuals older than 2 years (p= 0.002).

Discussion

Environmental stability affects the adaptative value of dispersal. When local environment is deteriorating while better conditions persist elsewhere, dispersing will be advantageous. Therefore, everything else being equal, dispersal must be more common in unstable environments than in stable ones. In the studied population, the environment looks fairly stable, so that the relatively low dispersal rates estimated are not surprising.

In any case, some individuals do disperse, particularily in juvenile males. In other categories, there is no more than one tenth of the individuals dispersing. Whereas there is clearly an effect of age on dispersal, the effect of sex in juveniles is not obvious. However, this lack of a significant difference in juveniles might be due to the small sample size of juvenile females. The present results only allow to say that juveniles disperse more than older individuals, and that juvenile dispersal might be male-biased.

Two hypotheses are usually considered to explain the fact that juvenile disperse more than older individuals. Either competition is more expensive than dispersal in young, but not in adult, or there is a parent/offspring conflict. In the latter case, offspring dispersal can be advantageous to their parents, even in the case of a strong cost of dispersal. Inclusive fitness is indeed less affected with a lower competition within progeny, and with a lower competition between parent and offspring.

About the possible male-bias in juvenile dispersal, it would be compatible with GREENWOOD's hypothesis (1980) based on competition. Females competing for resources for reproduction and males competiting for females, males are less dependent of the local resources than females and therefore more able to take the risk to change habitats.

An interesting point emphasized by this study is that juveniles disperse immediately after birth. This may be due to climatic constraints since the probablity of finding favorable conditions decreases rapidly during the short time lag between hatching and entry into hibernation. However, this alone does not tell us why young do not wait until the next activity season to disperse. Juvenile competition, or competition with adults, might be too strong to allow such a delay in dispersal. In a population in Brittany, HEULIN (1984) found long-range movements mainly in juveniles and yearlings. Yearling dispersal in this population could mean that competition in juveniles is low enough to make dispersal after hibernation possible. Besides, predation on young by *Vipera berus*, and lower densities than in our population make this hypothesis plausible.

In the study population, a density experiment previously showed that dispersive movements were involved in regulation processes (MASSOT et al., in press). After an increase of density, immigration stopped, and after a decrease, immigration

increased. This agrees with the previous hypotheses about the role of competition in the determinism of dispersal in the common lizard.

References

GREENWOOD, P. J. (1980): Mating systems, philopatry, and dispersal in birds and mammals. – *Animal Behavior* 28: 1140-1162.

HEULIN, B. (1984): Contribution à l'étude de la biologie des populations de Lacerta vivipara: stratégie démographique et utilisation de l'espace dans une population du massif forestier de Paimpont. – Thèse docteur troisième cycle, Université de Rennes I, Rennes.

JENNRICH, R. I. & TURNER, F. B. (1969): Measurement of noncircular home range. – *J. Theoret. Biol.* 22: 227-237.

MASSOT, M. CLOBERT, J. PILORGE, T. LECOMTE, J. & BARBAULT, R. (in press): Density-dependence in the common lizard: demographic consequences of a density manipulation. – *Ecology*

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