

SIMILARITIES IN DISPERSAL BEHAVIOUR AMONG SIBLINGS IN THE COMMON LIZARD (*LACERTA VIVIPARA*)

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■ INTRODUCTION

Little is known about processes that determine dispersal. A major finding, which has begun to be well documented in vertebrates, is that juvenile dispersal runs in family (see Massot *et al.*, 1994). A similarity of dispersal behaviour among siblings implies that certain factors act on dispersal at the level of the litter. Such factors can be of three types:

(i) Dispersal could be a heritable trait. Most theories on dispersal evolution assume a genetic basis of dispersal (Johnson and Gaines, 1990). A genetic polymorphism is more specifically assumed when variability within populations is discussed in adaptive terms (Waser and Jones, 1989). No evidence exists for genetic variance of dispersal in vertebrates (Johnson and Gaines, 1990).

(ii) Prenatal effects caused by the maternal environment during gestation could act on dispersal (Ims, 1990). An adaptive maternal control of offspring dispersal could promote offspring fitness in temporally predictable environments (Massot and Clobert, 1995). Conversely, prenatal effects could be maladaptive due to the time lag of response to selec-

tion (Kirpatrick and Lande, 1989). Two studies tested prenatal effects on dispersal in vertebrates. The first did not find such an effect (Ims, 1990), while the second (our previous works on the common lizard) found two prenatal effects acting on dispersal (parasitism: Sorci *et al.*, 1994; food: Massot and Clobert, 1995).

(iii) Postnatal conditions experienced at the natal site can influence dispersal (van Noordwijk, 1984; Arcese, 1989). In the studies of van Noordwijk (1984) and Arcese (1989), a significant resemblance among relatives was due only to a location effect.

To investigate processes that determine dispersal behaviour, we conducted a study on the common lizard (*Lacerta vivipara*). From 1989 to 1992, we tested the resemblance of dispersal behaviour among siblings, and the existence of pre- and postnatal effects. In 1996 and 1997, we tested interactions between processes at the origin of dispersal behaviour.

Lacerta vivipara is a small, live bearing lacertid lizard (adult snout-vent length from 50 to 70 mm). In the study populations located at the Mont Lozère (44° 30'N, 3° 45'E, Southern France), males emerge from hibernation in March-April, followed by one year-old individuals and adult females. Mating occurs at female emergence, and parturition usually lasts for two to three weeks starting in mid-July. On average, five eggs (with a thin and transparent shell) are laid, and hatching usually occurs within one or two hours. Mothers leave their offspring after having laid. The activity season ends in late September. A more detailed description of life history can be found in Avery (1975) and Pilorge (1987).

1989-1992'S STUDY

The study area is a moor mainly covered by grass and heath, but its heterogeneity is enhanced by trees and rocks. The site shows two contiguous zones with a different structural diversity of microhabitats: a zone with a high structural diversity (Z+, area=4300 m²) and a zone with a low structural diversity (Z-, area=4700 m²). This habitat heterogeneity is associated with a difference in lizard densities (700 adults ha⁻¹ in the zone Z+ versus 430 in the zone Z-). Except for postnatal effects (see below), we performed analyses only on Z+ individuals since dispersal was rare in the Z- area (Clobert *et al.*, 1994).

From 1989 to 1992, we captured pregnant females at the beginning of July, and maintained them in laboratory until they gave birth. This period corresponded to the second month of gestation. Females were housed in plastic terraria with damp soil, a shelter, and water *ad libitum*. They were exposed to natural daylight and were heated 6 hours per day with an electric bulb. At birth, offspring were sexed by counting ventral scales (Lecomte *et al.*, 1992) and individually marked by toe-clipping (no effect on maximal sprint speed in the common lizard [Sorci and Clobert, unpublished data] as in two other

lizard species [Huey *et al.*, 1990]). Offspring were released at the mother's capture point, except for the experiment on postnatal effects (see below). Offspring dispersal was inferred from their last recapture point (recapture by hand). A grid of sticks spaced out every 3 m allowed location of each recapture point with a 1 m precision. We defined as dispersers those individuals which moved more than the upper 95% confidence limit of the home range diameter (30 m), and as philopatric those juveniles which moved less than the average home range diameter (20 m) (Clobert *et al.*, 1994; Massot and Clobert, 1995). None of the individuals classified as dispersers were found to come back to their natal site.

Postnatal effects. Environmental influences after birth were tested in 1991 by releasing siblings in two naturally contrasted environments (the two zones of the study area, Z+ and Z-). We used 22 pregnant females captured close to our study area (100 m apart). We randomly assigned siblings to different terraria immediately after hatching. Juveniles of a same terrarium (c. 5 to mimic an average clutch size) were released at a same location in the study area (10 different release locations in Z+ and 5 in Z-). This allowed us to test for postnatal effects (Zone effect) independently from the genetic and prenatal ones.

Prenatal effects. We tested prenatal effects on offspring dispersal by manipulating maternal feeding during gestation in 1990, 1991 and 1992. We manipulated 99 females which came from the Z+ area. Females were offered two rates of food delivery: one larvae of *Pyralis farinalis* (average live weight \pm sd: 0.189 \pm 0.051 g, n=30 ; average dry weight \pm sd: 0.075 \pm 0.025 g, n=30) every week or every two weeks. Some of the females manipulated in 1990 and 1991 were respectively recaptured in 1991 and 1992, and again we manipulated their food supply. This allowed us to investigate a long-term prenatal effect (effect of the manipulation in year t on offspring dispersal in

year t+1) independently from the short-term prenatal effect (effect of the manipulation in year t+1 on offspring dispersal in year t+1).

1996/1997'S STUDY

Four new areas were studied in 1996 and 1997. We chose them with regard to their humidity level to contrast site effects. We chose humidity because this environmental constraint was shown as important in the common lizard (Lorenzon et al. 1999). However, differences between dry and humid sites could be due to other confound factors (life history traits of lizards, structure and composition of vegetation,...). Two dry areas were moors mainly covered by heath. They received only water from rain and dew. Two humid areas were clearings crossed by small streams and were largely flooded in spring. We temporarily removed 420 pregnant females from the 4 study sites: 107 females from the dry sites and 103 from the humid sites in 1996; 98 from the dry sites and 112 from the humid sites in 1997. Pregnant females of each study site were randomly assigned to four experimental treatments which contrasted conditions during gestation with respect to temperature and humidity. For temperature, we provided heat with electric bulbs during three hours a day in a "cold" group (206 females), and six hours in a "hot" group (214 females). For humidity, we wetted terraria with the following ratios (in arbitrary unit, respectively at 8h, 12h and 18h): 5, 0, 2 in a "dry" group (213 females), and 10, 5, 5 in a "humid" group (207 females). Offspring were released in the study areas within three days after birth. Each family was divided into two parts. One half was released in dry sites, and one half in humid sites. Juveniles were never released in the mother's site in order to avoid interaction with the mother and to strictly test for the release site effect. We identified the dispersal status of 181 juveniles from 1860 released juveniles. Our experimental design crossed three levels of environmental

influences: (i) the effect of the mother's site which may include long-term prenatal effects and genetic differentiation between sites, (ii) short-term prenatal conditions (temperature and humidity during gestation), and (iii) the postnatal environment (release site of offspring). These different effects were crossed in order to test their interactions.

STATISTICAL ANALYSES

Analyses of data involving siblings raises a statistical difficulty. Indeed, siblings cannot a priori be assumed as independent statistical units (Massot et al., 1994). A first step is therefore to evaluate whether dispersal run in families. If a family effect is present, data for siblings must be nested within families. However, as in most studies on dispersal, the small number of recaptured hatchlings per family prevented us from using nested analyses. Independence could be achieved by using only one offspring per family, but this procedure does not utilise most of the data. To maintain independence and make full use of data, we could use a numerical resampling technique based on one randomly selected offspring per family (Massot et al., 1994). We adopted here an easier and more direct method. We used generalised linear models in which we corrected for overdispersion of data (DSCALE option of the GENMOD procedure - SAS 1992) induced by the non-independence among siblings. We checked that this method gave us the same results than the numerical resampling technique.

■ RESULTS

1989-1992'S STUDY

Resemblance among siblings. Juvenile dispersal was family-dependent for both sexes (Family effect: $\chi^2_{44}=88.6$ $P=0.0001$; Family*Sex: $\chi^2_{44}=22.4$ $P=0.9972$). We found this family effect for the different study years (1989: $\chi^2_7=13.1$ $P=0.0696$; 1990: $\chi^2_5=15.2$ $P=0.0097$; 1991: $\chi^2_{17}=32.5$ $P=0.0129$; 1992: $\chi^2_{14}=30.5$ $P=0.0065$).

Postnatal effects. In 1991, we released juveniles of 22 litters in two different environments (Zones Z+ and Z-: see Materials and methods). We found a significant interaction between the release zone and the sex of juveniles ($\chi^2_1=4.50$ $P=0.034$). Males dispersed more frequently in Z+ than in Z-, whereas females dispersed at a low rate whatever the zone (fig. 1). The postnatal environment appeared therefore to influence offspring male dispersal.

Prenatal effects. We manipulated the feeding rate of 99 mothers in 1990, 1991 and 1992 in order to test the effect of the maternal feeding during gestation on offspring dispersal. Juvenile males and females were influenced in the same way by the maternal feeding (non significant interactions for Feeding*Sex and Feeding*Sex*Year). However, we found that their dispersal behaviour was influenced by

the maternal feeding in a different way depending on the year ($P=0.010$ for Feeding*Year - fig. 2). Some females were manipulated for their feeding rate in two consecutive years. We therefore examined the effect of the manipulation in year t on offspring dispersal in year t+1. In spite of the small sample size (fig. 3), we found a marginally significant P value for the interaction between long- and short-term maternal feeding effects ($P=0.070$). The trend was an increased dispersal for well fed females compared to those that were less well fed in year t+1 when females were less well fed in year t, and the reverse when females were well fed in year t (fig. 3).

1996/1997'S STUDY

Here, we tested interactions between processes at the origin of offspring dispersal (generalised linear models with the 4 experimental effects and their first-order interactions). All experimental effects influenced offspring dispersal, but in non-independent ways. The postnatal environment (i.e., the release site of juveniles) interacted with the temperature during gestation for males in 1997 ($P=0.0184$), and for females in 1996 ($P=0.0007$). However, the postnatal effect directly acted on males in 1996

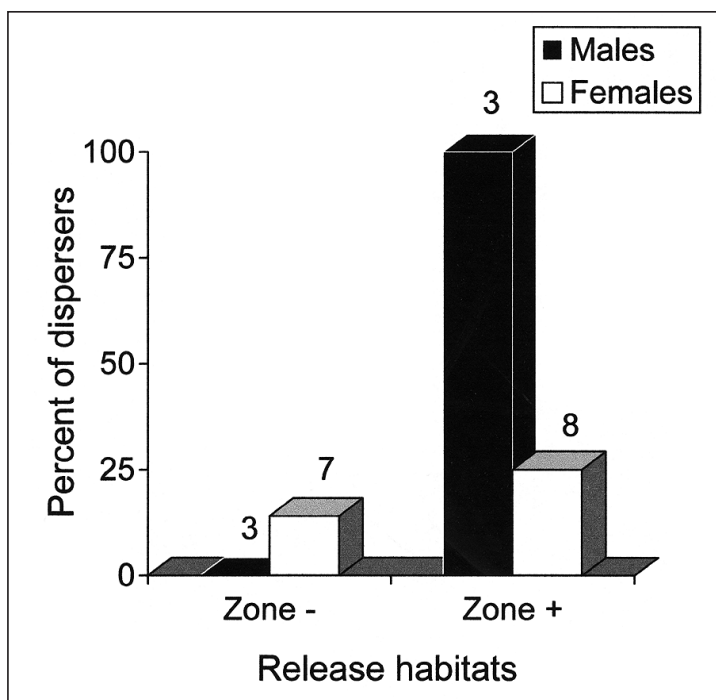


Fig. 1: Postnatal influence on offspring dispersal tested by a release habitat effect independently from other family effects. Siblings were released in two different habitats: Zone - = lower structural diversity, Zone + = higher structural diversity. Sample sizes above bars.

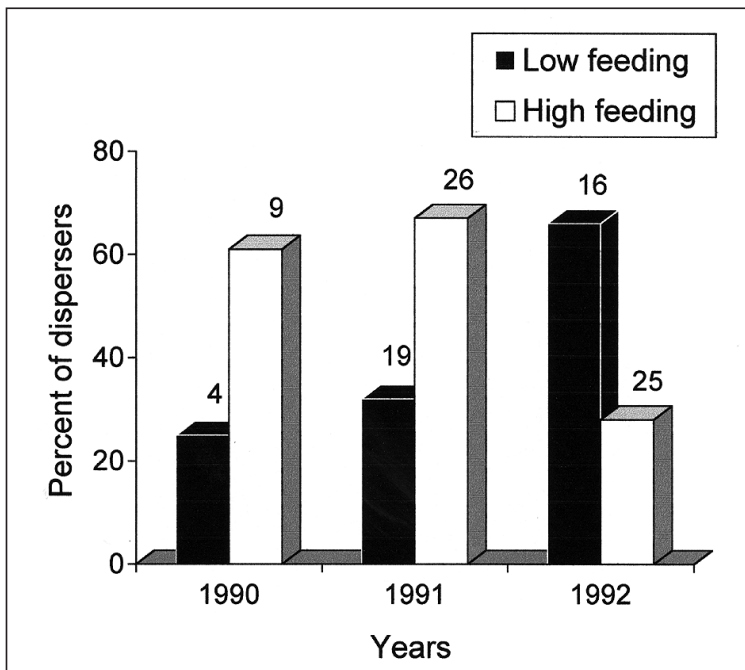


Fig. 2: Effect of maternal feeding on offspring dispersal. Sample sizes above bars.

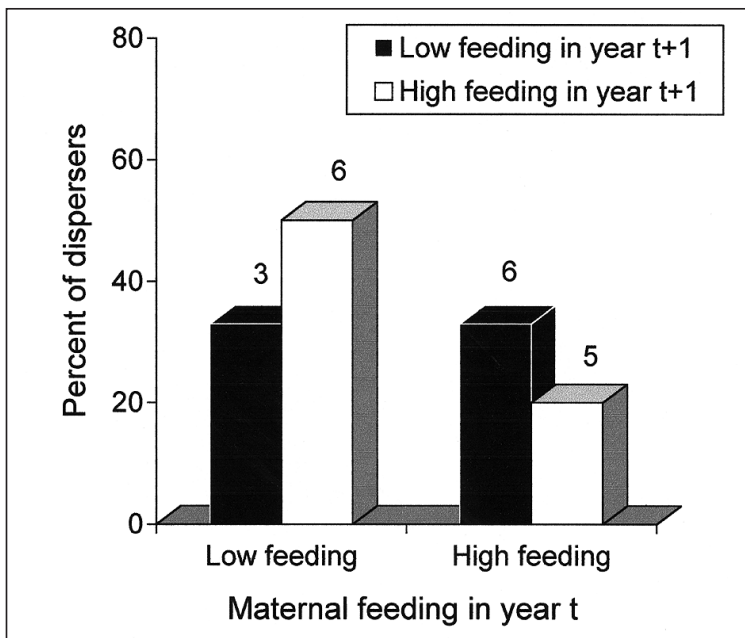


Fig. 3: Effect of maternal feeding in year t on offspring dispersal in year t+1, in interaction with the maternal feeding in year t+1. Sample sizes above bars.

($P < 0.0001$), and on females in 1997 ($P = 0.0229$). The humidity during gestation interacted with the habitat of origin of mothers for males in 1997 ($P = 0.0006$), and for females in 1996 ($P < 0.0001$).

More frequent dispersal events were related to bad as well as good environmental conditions. Dispersal was more frequent for offspring released in dry sites than for those released in humid sites (fig.4). However, this response was modulated by the temperature during gestation as indicated by significant interactions for males in 1997 and females in 1996: the release effect was higher in colder

conditions (fig. 4). When mothers originated from dry sites, offspring dispersal was more frequent for mothers with humid conditions of gestation (fig.5 for males in 1997 and females in 1996). Humidity during gestation did not affect offspring dispersal when mothers came from humid sites (fig. 5).

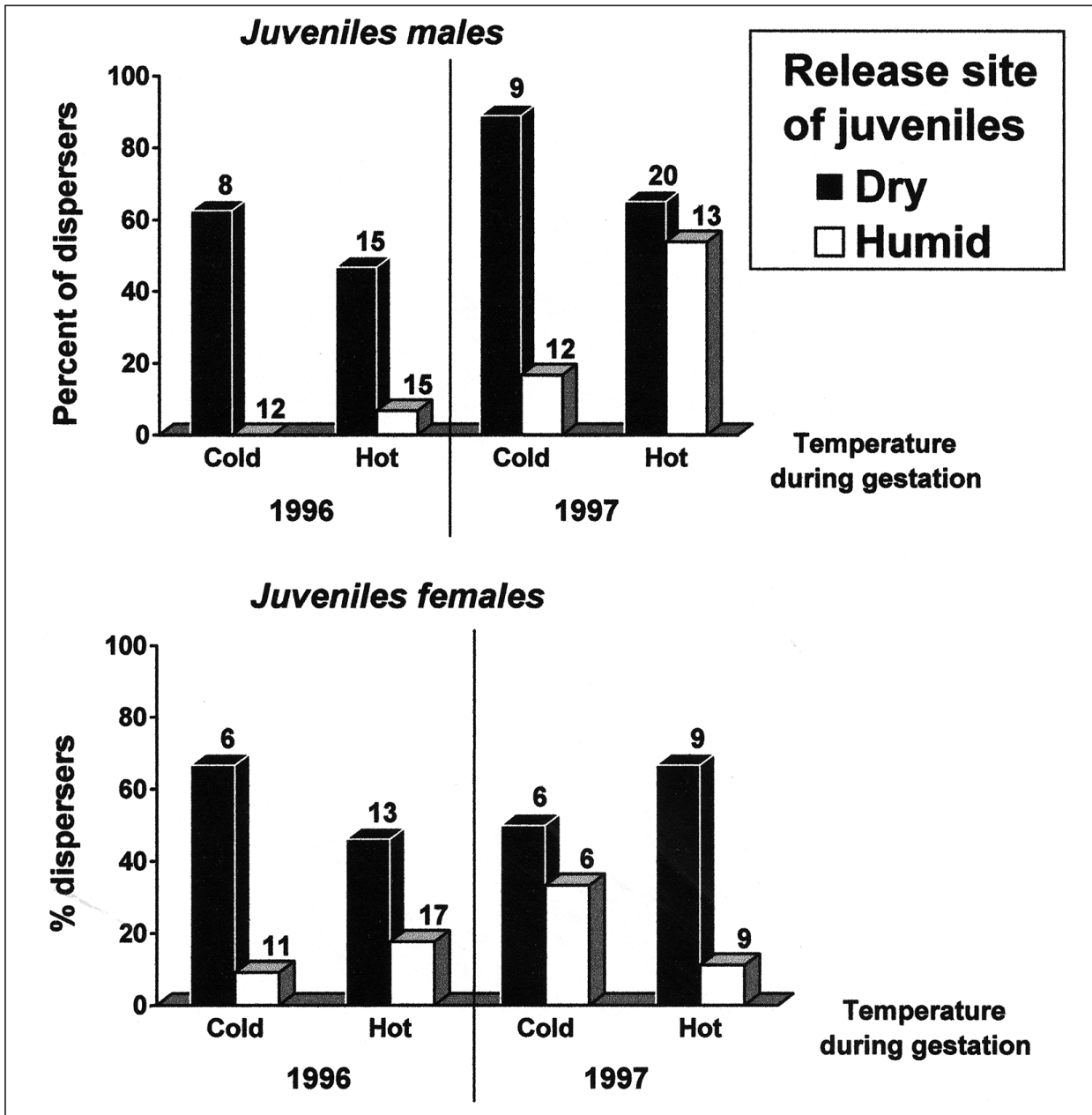


Fig. 4: Interaction between the release habitat of offspring and the temperature during gestation for offspring dispersal in 1996 and 1997. Sample sizes above bars.

■ DISCUSSION

Juvenile dispersal appeared family-dependent in the common lizard. Sources of differences among families were due to environmental influences at different ontogenic levels. Indeed, we found postnatal, short-term prenatal, and possibly long-term prenatal effects. Moreover, we showed interactions between effects of different ontogenic levels. The determinants of natal dispersal were also partly sex- and year-dependent.

We found a resemblance of dispersal beha-

viour among siblings. This was also shown in another lizard (*Sceloporus occidentalis*, Massot et al. in prep.), and several times in studies on mammals and birds (see Massot et al., 1994). The determinism of dispersal at the family level seems therefore a widespread feature in vertebrates. To understand the evolutionary significance of such a family effect, it is important to examine the various sources of siblings similarities.

We found two postnatal influences on juve-

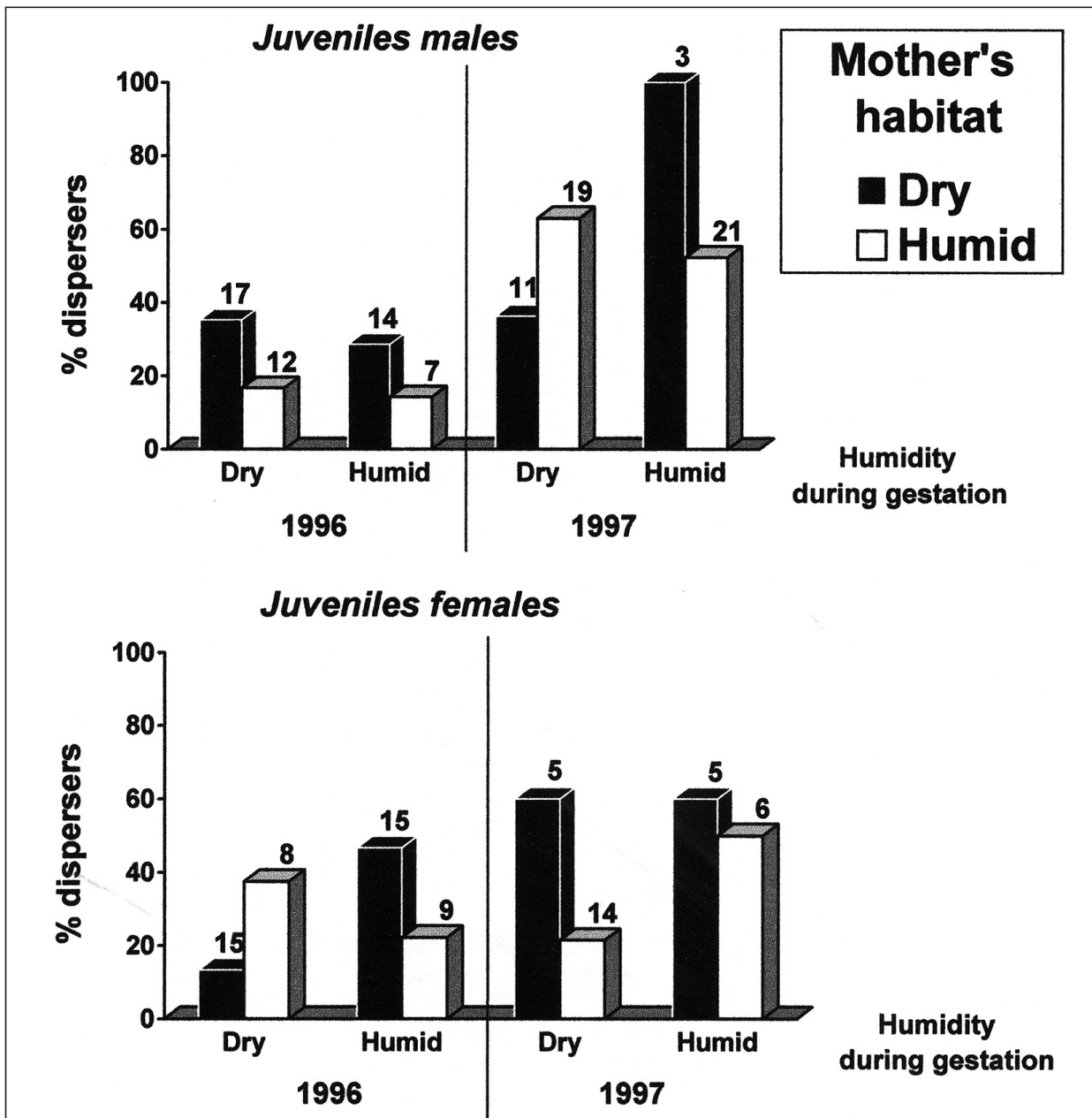


Fig. 5: Interaction between the mother's habitat and the humidity during gestation for offspring dispersal in 1996 and 1997. Sample sizes above bars.

nile dispersal. In the 1991 experiment, a postnatal factor influenced the dispersal of offspring males: males dispersed in higher proportion in the good habitat with respect to the habitat of lesser quality. Such a postnatal effect was not observed in offspring females. The two habitats used in the study differed in their physical structure as well as in their population density. In an attempt to separate these two components, Léna et al. (1998) did an experi-

ment where local conditions differed only in the density of conspecifics. They observed that dispersal of both juveniles males and females increased with adult female density. Although density could explain the higher proportion of dispersing males in the good quality habitat, the absence of habitat effect for females could indicate the effect of another factor. This was shown by the study in 1996/1997 where the effect of the postnatal site was modulated by

the temperature during gestation.

The prenatal environment due to conditions experienced by the mother during (short-term effects) or before gestation (long-term effects) can produce a resemblance of dispersal behaviour among siblings. Here, we reported the influence of three short-term prenatal effects, i.e. the effects of feeding, temperature and humidity during gestation. These three responses clearly show the influence of prenatal conditions on dispersal in the common lizard. For the effect of maternal feeding, we found opposite responses between years. The same factor could therefore have opposite effects depending on the value of other factors. Such a multideterminism of dispersal was explicitly shown by the interactions between determinants of dispersal in 1996/1997. Moreover, we could have interactions between effects at different time scales as suggested by the marginally significant interaction between long- and short-term maternal feeding effects (fig. 3). The mother's habitat effect in 1996/1997 could correspond to a long-term prenatal effect or genetic effect.

Therefore, offspring dispersal of the common lizard responded in a complex way. This is also further substantiated by a variability of responses among years, between sexes, and with regard to environmental quality. The variability among years occurred in the short-term maternal feeding response, and in the interactions between determinants of dispersal. The variability between sexes was revealed by the postnatal effect only in offspring males in the 1991 experiment, and by the interactions between determinants of dispersal which were observed in different years for males and females. Concerning the variability of responses with regard to environmental quality, offspring dispersal was more frequent with bad as well as good environmental conditions. Dispersal frequency was increased by bad

conditions for the maternal feeding in 1992 (fig.2), the release site effect in 1996/1997 (fig.4), and for a high parasite load of mothers during gestation (Sorci et al., 1994). Conversely, dispersal frequency was decreased by bad conditions for the maternal feeding in 1990 and 1991 (fig.2), the dry prenatal conditions for mothers which came from dry habitats in 1996/1997 (fig.5), and also for mothers manipulated with a stress hormone (corticosterone) during their gestation (Meylan et al., this volume). The response to corticosterone could notably be related to the influence of humidity. Indeed, corticosterone seems involved in the regulation of water flows in the common lizard (Dauphin-Villemant and Xavier, 1986).

Several future prospects emerge from this study on the common lizard. First, we will have to confirm or invalidate the trend of a long-term prenatal effect by an analysis on more years. Second, the phenotypic plasticity of dispersal we found did not exclude the possibility that dispersal is under a genetic control. We plan to test such a genetic control of dispersal with breeding experiments in controlled environmental conditions. Finally, we will have to question the adaptive nature of differences among individuals related to dispersal. Here, we plan to analyse offspring survival rates (the main fitness component in the common lizard) with regard to dispersal and environmental conditions.

ACKNOWLEDGEMENTS: We are grateful to L. SEITZ and two anonymous referees who provided valuable comments on the manuscript. We thank all the people who helped collecting the data, and the "Office National des Forêts" and the "Parc National des Cévennes" for providing very good conditions to work in the field. Our study was realised in agreement with the "Parc National des Cévennes". The CNRS and the French "Ministère de l'Environnement" (grant 94186) supported this study.

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