The relative influence of density and kinship on dispersal in the common lizard

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We experimentally investigated the relative role of kinship and density on juvenile dispersal in the common lizard. A few days after birth, juveniles were introduced into seminatural enclosures, where they experienced different social environments: in the first experiment we varied the density of unrelated adults (males or females) within the enclosure (0, 1, or 2 adults), and in the second experiment, we varied the level of kinship and familiarity between juveniles and adults. Each enclosure was connected to a second enclosure by small holes which allowed only juveniles to move between enclosures. Juvenile movements were monitored during 14 days after birth, as juvenile dispersal is mainly completed within 10 days after birth under natural conditions. Most juveniles did not return to the first enclosure. Sex had no effect on juvenile dispersal. Adult density and kinship with adults both affected dispersal. Adult female density increased juvenile dispersal whatever the level of kinship and familiarity with the females. Dispersers had better body condition than nondispersers at high female density, and this difference was significantly greater when the mother and the familiar female were present in the enclosure. Furthermore, body condition of mothers and familiar females was positively correlated with juvenile dispersal, whereas there was no such correlation in the case of unfamiliar and unrelated females. These results strongly suggest that adult female density is a major factor promoting dispersal in this species and that both intraspecific and kin competition motivate dispersal. *Key words:* common lizard, dispersal, intraspecific competition, kin competition, *Lacerta vivipara*. *[Behav Ecol 9:500–507 (1998)]*

Social interactions may promote dispersal in three ways (Clobert et al., 1994; Johnson and Gaines, 1990): competition for resources that are spatially and temporally variable (McPeek and Holt, 1992); competition among kin, which will favor the dispersal of a fraction of the family (Comins et al., 1980), and inbreeding avoidance (Shields, 1983). Any of the three factors alone may favor the evolution of dispersal (Johnson and Gaines, 1990) despite the dispersal costs, but they may also act together, and their joint action may be the rule rather than the exception (Clobert et al., 1994; Dobson and Jones, 1985). Testing the relative importance of the three factors is not easy because they have many predictions in common (Lambin, 1994), and experiments are required to segregate their effects (Johnson and Gaines, 1990; Shields, 1987). One way to separate them is to experimentally control both the level of density and the level of kinship. For example, juvenile dispersal caused by intraspecific competition is expected to be enhanced whatever the degree of relatedness between adults and juveniles in species where dispersal mainly occurs at the juvenile stage. In contrast, juvenile dispersal arising from kin competition is expected to occur only when juveniles are related to the resident. In the former case, juveniles of both sexes or of the same sex as the resident adult are expected to disperse, while only the opposite sex of the resident adult is expected to disperse if juvenile dispersal is driven by inbreeding avoidance (Greenwood, 1980; Lambin, 1994; Wolff, 1992).

Only a few studies have attempted to separate the role of kin and intraspecific competition (Lambin, 1994; Wolff, 1993). These studies showed that the removal of a parent led

to philopatry of the opposite-sex offspring, suggesting that juveniles mostly disperse to avoid inbreeding (Brody and Armitage, 1985; Hölzenbein and Marchinton, 1992; Jacquot and Vessey, 1995; Lambin, 1994; Wolff, 1992). However, in many of these studies, density is not kept constant (Brody and Armitage, 1985; Hölzenbein and Marchinton, 1992; Wolff, 1992). Furthermore, all the studied species are mammals, and most of them are taxonomically closely related (Hölzenbein and Marchinton, 1992; Jacquot and Vessey, 1995; Lambin, 1994; Wolff, 1993). These species also have strong sex-biased dispersal in the wild, which has classically been explained by the inbreeding avoidance hypothesis (Bollinger et al., 1993; Greenwood, 1980; Shields, 1983, 1987). In species showing a less pronounced sex-biased dispersal, theoretical models of dispersal predict that kin competition is likely to play a more important role than inbreeding avoidance (Motro, 1991). Moreover, inbreeding avoidance does not necessarily require dispersal because mating with kin can also be avoided through kin discrimination (Barnard and Fitzsimons, 1988; Bateson, 1983; Waldman et al., 1992).

In this experimental study, we investigated the respective role of kin and intraspecific competition in juvenile dispersal in the common lizard (*Lacerta vivipara*). We chose this species because (1) immigration and emigration are known to be important parameters in population regulation (Massot et al., 1992) and are likely to be related to the surrounding level of competition, as indicated by the influence of adult density (Clobert et al., 1994); (2) field studies showed that natal dispersal occurs mainly at the juvenile stage and is mainly completed within 10 days after birth (Clobert et al., 1994; Massot, 1992a,b); (3) natal dispersal is only slightly sex-biased, in particular with respect to the level of parasitism encountered by the mother during gestation (Clobert et al., 1994; Sorci et al., 1994); (4) the mother's high prospect of survival increases juvenile dispersal, as revealed by the influence of the feeding rate during pregnancy (Massot and Clobert, 1995) and the
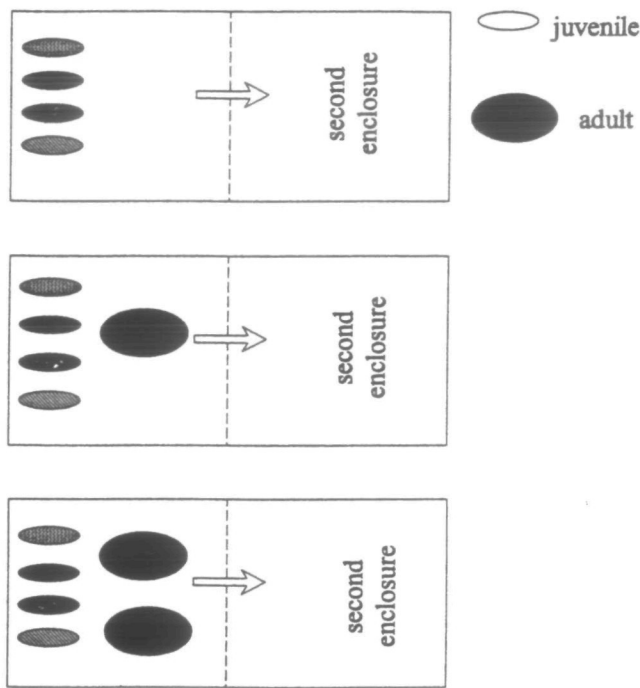
Figure 1
Experimental design used in experiment 1 to test adult density influence. Siblings are represented by the same fill patterns. Adults of the same sex were used in each set of experiments.

age of the mother (Ronce et al., 1998); and (5) juveniles recognize their mother even if they are reared apart from their mothers from birth (Léna and de Fraipont, 1998). From these results, we hypothesized that high densities of adult females increase juvenile dispersal whatever the level of kinship with these females, but that the survival prospect of a female only affects the dispersal of its offspring as predicted by theory (Hamilton and May, 1977; Ronce et al., 1998). The aim of this work was therefore to experimentally investigate the effect of adult densities on juvenile dispersal and to analyze how the adult body condition influences dispersal with respect to kinship, as this characteristic is correlated with the survival prospect of adult females in the common lizard (Sorci et al., 1996). A second goal was to examine the relative importance of prenatal and postnatal contacts with the female in establishing the response toward kinship. Indeed, Léna and de Fraipont (1998) showed that postnatal contacts are not needed for juveniles to recognize their mother and that the prenatal environment rather than genetic determinism is likely to be the main factor. We therefore hypothesized that contacts with the mother are the cues used to assess the maternal survival prospect and that prenatal contacts with the mother may be sufficient to achieve this. We therefore placed juveniles in the presence of their true but unfamiliar mother (i.e., we separated offspring from mothers just after birth) and of a foster mother (i.e., an unrelated female kept close to the juveniles during the 3 days after birth) to create the high level of kinship. This design allowed us to examine and possibly segregate the effects of the body condition of the true but unfamiliar mother from the body condition of the foster mother on offspring dispersal.

METHODS

Species and study site

Lacerta vivipara is a small (50–70 mm snout–vent length; SVL), ovoviviparous, lacertid lizard inhabiting peatbogs and heathlands. Mating occurs in late May, immediately after the female's emergence. Laying begins 2 months later, and females lay on average five eggs which hatch soon after laying. Neonates (20 mm SVL) are independent from the mother immediately after hatching. Field studies over a large temporal scale (>10 years) showed that dispersal from the birth site mainly occurs at the juvenile stage and is mainly completed 10 days after birth (Clobert et al., 1994; Massot, 1992a,b). More details on the species can be found in Pilorge et al. (1987) and Clobert et al. (1994).

At the beginning of July 1991 and 1992, we removed 32 pregnant females from a population situated at the Mont Lozère (1420 m), in southern France (44°30′ N, 3°45′ E). These females were used for experiment 1. In July 1995, we collected an additional 36 females from the same population and used them for experiment 2. Females were maintained in the laboratory until laying, housed in individual terraria (18 × 12 × 12 cm) with food and water ad libitum, and exposed to a heating light 6 h per day. After the experiments, mothers and offspring were released back into their population of origin. Body mass and SVL of juveniles and females were measured after laying. We determined juvenile gender by counting ventral scales, with less than 5% of mis-sexing (Lecomte et al., 1992).

General design

We established 12 experimental testing devices, 3 in spring 1991 and 9 in spring 1995. The testing devices were placed outside, near the population from which the lizards were caught. Each device consisted of two enclosures (1.5 × 1.5 m). The habitat in each enclosure was standardized and contained the most important elements of the natural habitat (heath, rock, and grass). We did not provide supplemented food because (1) small insects and spiders, which are mostly predated by juvenile lizards (Avery, 1966), were quite abundant inside and outside the enclosures during the entire study period, (2) lizards were placed in the enclosures only for a short time, and (3) the prey size distributions of adults and juveniles do not overlap (Avery, 1966). Direct (i.e., immediate) competition for food between the two age categories is therefore unlikely. The two enclosures were connected by small holes (4.5 mm diam), which only allowed the passage of juveniles. The enclosures were thoroughly rinsed with water between the two experiments to remove odors. Adults were placed in one enclosure (the starting enclosure) the day before juvenile introduction; the second enclosure was empty. Each treatment was randomly assigned to a testing device, and the starting enclosure was chosen randomly.

Experiment 1

The goal of experiment 1 was to test if the density of unfamiliar and nonkin adults of both sexes influenced juvenile dispersal. A complementary goal was to verify that the timing of dispersal (age at dispersal) was the same as in natural conditions.

We performed two set of experiments, one to test the effect of female density, and the other to test the effect of male density. The experimental design was the same for each set of experiments. Three different treatments were staged in three testing devices with respect to density of unrelated and unfamiliar adults (0, 1, and 2, respectively). One sibling was introduced in each experimental treatment; three siblings per family were thus used in each set of experiments. Four families simultaneously experienced the same set of conditions, so that we were able to assess the effect of adult density independently from the effect of sibship (Figure 1). Families of dif-
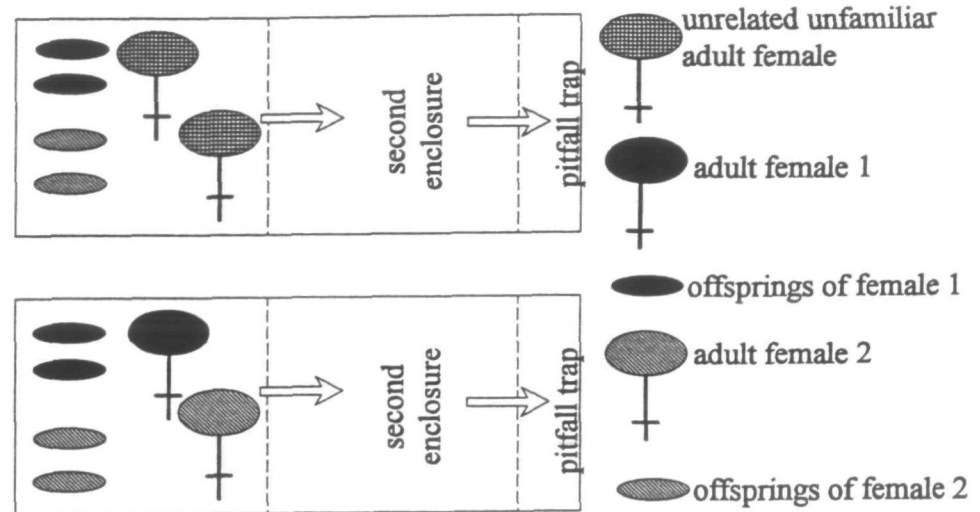
Figure 2
Experimental design used in experiment 2 to test kinship influence on dispersal. Female 1 is the foster mother of offsprings of female 2, and female 2 is the foster mother of offsprings of female 1. The experimental treatment with no adult is not presented in the figure.

ferent ages were used (range = 2–11 days; mean ± SD = 6.5 ± 2.5 days) to study age at dispersal. Each set of experiments lasted 3 days in order to have enough replicates over the same breeding season. Each enclosure of each testing device was observed during 15 min, four times per day, and the position of each juvenile was recorded. We randomly assigned the order in which enclosures were observed at each time. This design allowed us to monitor juvenile movements and to know the age at which they attempted to move to the other half of the experimental testing device. Each set of experiments was replicated four times. Then we used a total of 16 families to test the effect of female density and a total of 16 families to test the effect of male density.

Experiment 2

In experiment 2, we aimed to test the effect of kinship with adult females on juvenile dispersal. Juvenile dispersal was demonstrated to be influenced by prenatal and postnatal effect (Clobert et al., 1994; Massot and Clobert, 1995). Therefore we also wanted to test whether dispersal arising from competition with kin also had a pre- or postnatal component.

Offspring were isolated from their mother immediately after birth (within 1 h) to avoid postnatal contact with the mother before the dispersal experiment. Just after birth, offspring in natural conditions are not in close contact with any females other than their own mother (Léna et al., personal observations). Offspring were then housed during 3 days with another female in a terrarium (18 × 12 × 12 cm). This level of familiarity before dispersal can naturally only be achieved by the mother through postnatal contact with her offspring. We therefore called the familiar unrelated female a foster mother. All juveniles thus had a true but unfamiliar mother (no contact after birth) and a foster mother (the familiar, unrelated female).

At introduction in the starting enclosure, juveniles were faced with one of three experimental treatments (Figure 2): the enclosure contained no adult female, the enclosure contained two unrelated, unfamiliar females, or the enclosure contained the true but unfamiliar mother and the foster mother. The first treatment was replicated 12 times, the second 10 times, and the third 11 times. Four juveniles (two offsprings per family) were introduced in each experimental treatment. In most cases, each family experienced two different treatments (n = 30 families). However, six families experienced only one treatment because their clutch size was too small for a complete set of experiments.

Juveniles were introduced in the starting enclosure when they were 4 days old. Because we added more testing devices in experiment 2, more time was needed to remove individuals from all the testing devices. We therefore added an extra day so that each experiment lasted 4 days.

We slightly modified the device of experiment 1. We made small holes in the external side of the second enclosure, and juveniles were collected in a pitfall trap placed along the external side (Figure 2). Thus, juveniles that attempted to leave the second enclosure were categorized as individuals attempting longer dispersal movement. We checked the pitfall traps three times per day (1100 h, 1300 h, and 1700 h). At the end of each experiment, the connection was closed and animals were removed from the testing device. We recorded the number of juveniles in the second enclosure at the end of the experiment as well as those that left the second enclosure during the experiment.

Data analysis

Siblings of the common lizard tend to disperse with the same propensity and in the same direction (Clobert et al., 1994; Massot and Clobert, 1995; Massot et al., 1994). For this reason, sibship (family) was introduced in all statistical models as a categorical covariate for testing the effects on dispersal of juvenile characteristics, adult density, and kinship. However, this was not required when testing the effect of adult characteristics because, in this case, we could use the dispersal rate per litter within each treatment as the dependent variable. We used ANOVA to analyze factors influencing the timing of dispersal. We used generalized linear models to test for factors influencing the probability to disperse because this approach allowed us to perform logistic regression modeling with both nominal and continuous variables (procedure GENMOD; SAS Institute, 1990b). We first fit a model with all interaction terms. We then dropped all nonsignificant terms and finally kept the model where all terms explained a significant part of the variation (backward selection). GENMOD has a maximum likelihood-based approach. In each model, the statistical significance (LRS_{df}) of each term can be evaluated using a likelihood ratio test (McCullagh and Nelder, 1989; SAS Institute, 1990b). We used a nonsequential procedure because we did not want our tests to depend on the ordering of the introduction of the variables into the model. Juveniles participating in the same trial may influence the behavior of each other. Therefore, juveniles of the same replicate may resemble each other more than juveniles in other replicates. This will

Table 1

Effect of sibship, juvenile gender, and adult density on the probability to disperse in experiment 1

Effect of	Density of adult females				Density of adult males			
	n	df	LRS	p	n	df	LRS	p
Sibship	42	15	32.28	.005	45	15	29.59	.013
Adult density	42	1	5.82	.016	45	1	4.21	.040
Juvenile gender	42	1	0.59	.444	45	1	0.10	.753
Juvenile gender × adult density	42	1	0.01	.923	45	1	0.43	.509

cause the data to be overdispersed. We therefore examined the parameter describing the statistical dispersion ($C^{\wedge}$ = deviance value/degree of freedom) to control for the validity of the final model as recommended by McCullagh and Nelder (1989), and we corrected the value of the LRS_{df} when necessary (LRS_{df} corrected = $LRS_{df}/C^{\wedge}$, $C^{\wedge}$, the variance inflation factor).

We estimated body condition by taking the residual score of the linear regression of body weight on SVL. All analyses were done using SAS software (SAS Institute, 1990a).

RESULTS

Experiment 1

Among the 96 juveniles that were used for this experiment, 44 of them dispersed, and 9 were never recaptured.

Timing of dispersal

The age of juveniles at the onset of the experiment did not affect the proportion of dispersers at the end of the experiment (n = 87; age effect corrected for sibship: LRS_1 = 0.68, p = .41). The time at dispersion from introduction in the enclosure, however, was negatively related to the age at the onset of the experiment (ANOVA, n = 44, time effect corrected for sibship: F = 6.23, p = .022). Juveniles older than 7 days at the onset of the experiment mostly dispersed within the first day of the experiment (16 out of 26; time at dispersion: mean ± SD = 0.57 ± 0.80 days). Younger individuals mostly dispersed when they were 6 days-old (n = 18; age at dispersion: mean = 6.16 ± 1.43 days; time at dispersion: mean = 1 ± 0.84 days). As in the field (Clobert et al., 1994; Massot, 1992a,b; Massot and Clobert, 1995), most juvenile dispersal took place within 10 days after birth.

Influence of adult male and female density

Siblings dispersed at similar rates (sibship effect), regardless of density treatment and adult gender (Table 1). Juvenile gender did not influence dispersal whatever the densities and the gender of the adults (Table 1). Both adult male density and adult female density influenced dispersal (Table 1). High female densities increased dispersal rate, whereas high male densities decreased dispersal rate (Figure 3).

The significant opposite effect of the adult gender on juvenile dispersal was further confirmed by comparing dispersal rate of juveniles experiencing high male density to those experiencing high female density (n = 31; adult sex effect: LRS_1 = 5.67, p = .02).

Experiment 2

Among the 132 juveniles participating in the experiments, 77 dispersed. The dispersal rate in each treatment was 48% in
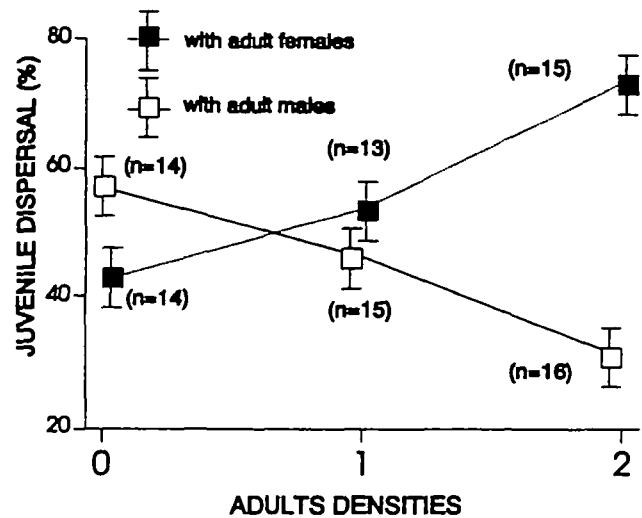

Figure 3

Effect of adult males and females on juvenile dispersal. Adult density represents the number of adults introduced in the starting enclosure. Juvenile dispersal is the percentage of dispersers within each density treatment. Sample sizes are given in parentheses. Bars represent standard errors.

the absence of adult females, 68% in the presence of unrelated unfamiliar females, and 61% in the presence of the true and the foster mothers.

Influence of sibship and female density

As in experiment 1, sibship and female density significantly influenced juvenile departure from the starting enclosure (Table 2). As in experiment 1, juvenile sex did not influence dispersal, regardless of female density (Table 2). Both sibship and density remained significant only when the juveniles that left the second enclosure were classified as dispersers (n = 108; family effect: LRS_{35} = 71.99, p = .0002; density effect: LRS_1 = 5.20, p = .0226). Moreover, female density did not influence the number of enclosures (i.e., one or two) that the dispersers traveled through (n = 77, LRS_1 = 1.09, p > .10). Therefore, any juvenile leaving the starting enclosure could safely be considered a disperser.

Influence of the true and the foster mothers on juvenile dispersal

We first verified that offspring morphometric traits (mean values per litter) were not significantly correlated with morphometric traits of their mothers (n = 35; body mass: F = 0.26, p = .61; SVL: F = 2.84, p = .10; body condition: F = 0.33, p = .57). The effect of offspring morphometry was thus unlikely to result from the effect of maternal morphometry. Because juvenile body lengths were homogeneous, weight and body condition of juveniles are strongly correlated (n = 130, F =

Table 2

Effect of sibship, juvenile gender, and female density on the probability to disperse in experiment 2

Effect of	n	df	LRS	p
Sibship	132	35	64.71	.002
Female density	132	1	5.78	.016
Juvenile gender	98	1	0.34	.559
Juvenile gender × female density	98	1	0.42	.519

Table 3

Effect of juvenile characteristics on the probability to disperse according to the status of the adult females (true and foster mothers versus unfamiliar, unrelated females)

Effect of	n	df	LRS	p
Female status	84	1	0.19	.659
Juvenile body condition	84	1	5.70	.017
Juvenile body condition × female status	84	1	6.33	.012
Juvenile gender	66	1	1.67	.196
Juvenile gender × female status	66	1	0.63	.420

The effects of explanatory variables were statistically controlled for sibship effect (sibship effect: $n = 84$, $LRS_{34} = 53.36$, $p = .014$).

1916.32, $p = .0001$, coefficient of correlation $= .94$). We use only body condition hereafter.

The presence of the true and the foster mothers did not affect the number or the sex of the juveniles that dispersed when compared to the presence of the two unfamiliar, unrelated females (Table 3).

The mean body condition of dispersers (i.e., corrected for sibship effect) was significantly higher than that of nondispersers in the presence of adult females, whatever their status (Table 3). This was not the case when adult females were absent ($n = 46$, $LRS_1 = 0.08$, $p = .77$). Furthermore, the difference in mean body condition between dispersers and nondispersers was significantly greater when the true and the foster mothers were present than when the unfamiliar and unrelated females were present (Table 3).

Influence of adult female characteristics
Because of the significant family effect, we computed the proportion of dispersers per litter within each treatment. We examined the influence of female characteristics, either by including the traits of the two females separately into the model, or by averaging their characteristics. The body condition of unrelated and unfamiliar females did not significantly influence juvenile dispersal (female body condition effect: $n = 18$, $LRS_1 = 1.94$, $p = .16$).

The average body condition of the true and of the foster mothers was significantly related to dispersal when these females were present in the enclosure (in presence of these females: $n = 22$, $LRS_1 = 9.56$, $p = .002$). Offspring did not modify their dispersal rate according to the true or foster mother phenotype when these females were absent or when they were replaced by unrelated and unfamiliar females (in absence of female: $n = 24$, $LRS_1 = 1.71$, $p = .19$; in presence of unrelated unfamiliar females: $n = 20$, $LRS_1 = 0.98$, $p = .32$). A higher average body condition of the females significantly increased juvenile dispersal (Table 4). Both the true and the foster mother significantly contributed to this effect (Table 4, Figure 4). Moreover, a positive interaction between the body condition of the true mother and the body condition of the foster mother significantly influenced offspring dispersal (Table 4).

DISCUSSION

In our experiments, dispersal was unaffected by the sex of the juveniles, regardless of adult density and kinship. Both adult density and kinship influenced offspring movements. Male density reduced juvenile dispersal, while female density enhanced dispersal. At high female density, dispersers had a better body condition than nondispersers. Although the average rate of dispersal was not influenced by female status, the body condition of dispersers in the presence of the true but unfa-

Table 4

Effect of the body condition of the true mother and of the foster mother on juvenile dispersal

Body condition effect of	n	df	LRS	p
True mother	22	1	5.51	.019
Foster mother	22	1	7.07	.008
True mother × foster mother	22	1	4.70	.030

Juvenile dispersal is the dispersal rate per litter.

miliar mother and the foster mother was greater when compared to those that dispersed in the presence of unfamiliar and unrelated females. Better body conditions of both the true and the foster mothers increased dispersal rate. These results strongly suggest that dispersal is driven by the presence of females and is motivated equally by intraspecific and kin competition. However, the body condition of dispersing juvenile was found to vary according to the level of kinship with the adult females.

Relevance of the experiment

Natal dispersal is usually defined as the movement from the birth site to the first breeding place, and individuals are classified as dispersers if this movement exceeds the diameter of an average adult home range (Bekoff, 1977; Johnson and Gaines, 1990; Lidicker and Stenseth, 1992; Murray, 1967; Waser, 1985; Waser and Jones, 1983). In our experiments, we assumed that the departure from an enclosure, which was much
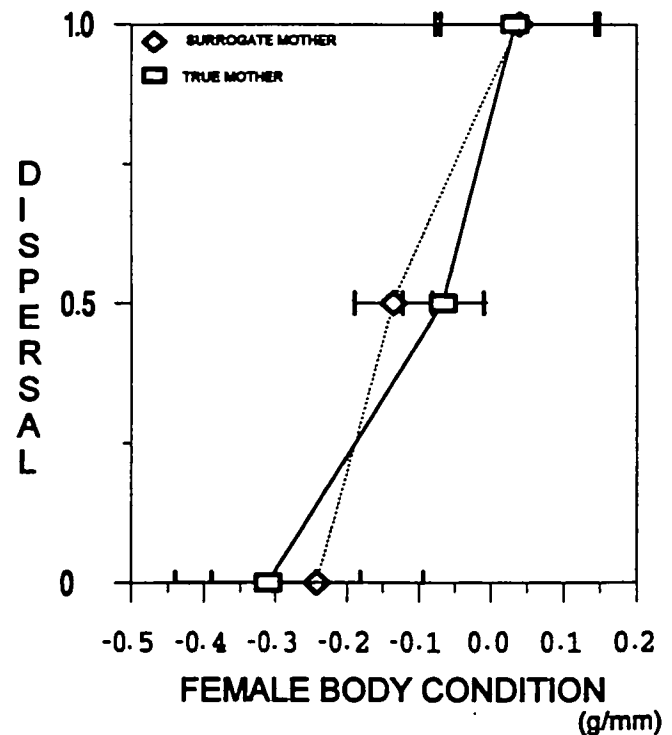

FEMALE BODY CONDITION
(g/mm)

Figure 4
Influence of body condition of the true and the foster (surrogate) mothers on juvenile dispersal. Juvenile dispersal is the percentage of dispersers per litter. Body condition is the residual value of the regression of body mass on log(body length) (expressed as g/mm). Bars represent standard errors. This relationship was obtained only when these females were present in the starting enclosure (see text).

smaller than the diameter of an adult home range (average diameter = 20 m; Massot and Clobert, 1995), reflected dispersal. The observed movements could have been the result of exploration or of a passive diffusion process, not necessarily related to a motivation to disperse. However, several considerations lead us to believe that the observed movements are directly related to dispersal. Few juveniles returned to the starting enclosure (4 out of 87 juveniles in the first experiment). This would not have been expected if changing enclosures was related to exploration alone. Most juveniles significantly moved toward a third enclosure (moved longer distances) when a third enclosure was offered (53 individuals out of 77 in the second experiment, $\chi^2_1 = 10.92$, $p = .001$). This was not expected if these movements were the result of passive diffusion alone. Moreover, the number of days necessary to leave the starting enclosure depended solely on the age of the juvenile, not on the time spent in the enclosure. Offspring older than 8 days moved within the first day of the introduction, whereas younger juveniles started to move on average when they were 7 days old. This timing of dispersal is similar to that observed in natural conditions (Clobert et al., 1994; Massot, 1992a,b). In agreement with the field observations, we found a strong similarity of dispersal tendencies among siblings (i.e., a strong family effect; Clobert et al., 1994; Massot and Clobert, 1995). The similarities between the type of observed movements in the field and in the experimental units make us confident in interpreting juvenile departure from the starting enclosure as an attempt to disperse.

Dispersal and the avoidance of intraspecific competition

Sibling competition alone was not an important determinant of dispersive movements in the common lizard. High female densities increased juvenile dispersal in all experiments. Surprisingly, male densities had the opposite effect; higher male densities promoted juvenile philopatry.

In many species, higher adult densities are usually found to increase dispersal because of a higher level of intraspecific competition (Bengtsson et al., 1994; Christian, 1970; Lidicker, 1962, 1975; Morris, 1989; Nakajima and Kurihara, 1994; Partridge, 1978). In the common lizard, several studies suggest that populations with higher female densities show higher levels of intraspecific competition. Pilorge et al. (1987) reported a negative correlation between yearling survival and adult female density. Furthermore, Massot et al. (1992) showed that both juvenile survival and yearling growth rate decreased when adult densities increased (Massot, 1992a; Massot et al., 1992); the adult sex ratio is female-biased in these populations (Pilorge et al., 1987). It follows that the avoidance of intraspecific competition may well explain the dispersal pattern observed in the presence of adult females.

Why did male density have the opposite effect of female density? At first sight, it is doubtful that this effect is related to the mating system of this species because we did not observe a sex-biased juvenile dispersal in our experiments (there is only a slight male-biased dispersal at the population level in natural conditions; Clobert et al., 1994) as we should have expected if females were more territorial than males (Dobson, 1982; Greenwood, 1980). A high conspecific density could also be a good indicator of habitat quality, providing that competition does not entail high costs (Stamps, 1988, 1991). In the common lizard, males do not seem to compete with juveniles or yearlings (Lecomte et al., 1994). For instance, Pilorge et al. (1987) failed to find any negative relationship between yearling survival and male density. Consequently, juveniles could be attracted by a high male density either because males occupy better habitats than females or because males are less direct competitors compared to females. The first hypothesis is less likely because habitats selected by adult males apparently do not differ from those used by females (Heulin, 1985; Lecomte et al., 1994).

Two alternative hypotheses are usually proposed to explain the effect of competition on the evolution of dispersal. The first one assumes that inferior competitors are forced to disperse when there is an increase in competition at the natal site (Anderson, 1989; Brandt, 1992; Christian, 1970; Lidicker, 1975; Lidicker and Stenseth, 1992; Murray, 1967; Waser, 1985). In this case, the fitness of dispersers will be lower than the fitness of philopatric individuals. The alternative hypothesis posits that, when high densities deteriorate local conditions, better competitors will be more able to withstand the risks associated with dispersal (even if the cost to disperse is high; Lemel et al., 1997). Dispersers will also benefit from less crowded habitats. In this scenario, the fitness of dispersers will be equal to or even higher than the fitness of philopatric individuals (Bélichon et al., 1996).

In our experiments, a higher female density led juveniles with a higher body condition to disperse, and in this species, body condition is positively correlated to survival in adult females (Sorci et al., 1996). This strongly suggests that competition led the better juvenile competitors to leave the natal site and favors the view of dispersal as an adaptation to intraspecific competition. Indeed, juvenile dispersal seemed to be active and not caused directly by aggressive interactions with females (no aggressive interactions recorded in more than 100 h of observations). Juveniles were even observed to climb on females without provoking any aggressive behavior.

Dispersal and the avoidance of kin competition

Both offspring-and maternal morphology influenced dispersal. Dispersing juveniles were of better body condition in the presence of the unfamiliar and the foster mothers than in the presence of unrelated, unfamiliar females. Relatedness and intensified familiarity with females did not increase the overall dispersal propensity. However, offspring born to mothers of better than average body condition did disperse in higher proportion than those born to mothers in lower body condition, when the mother was present in the starting enclosure. The same relationship was found with the foster mother. No correlation was found between juvenile dispersal and female morphology when the latter was unfamiliar and unrelated. Body condition of adult females was measured after laying. This means that a female with a low body mass with respect to its body length invested more in reproduction than a female with a high body mass with respect to its body length. Indeed, female body condition is positively related to female survival (Sorci et al., 1996). In other words, juvenile dispersal increases with the survival prospect of the mother.

Intrasexual competition or inbreeding avoidance may enhance such a dispersal pattern if sex also affects dispersal. Sex-biased dispersal is a common phenomenon and is also reported in lizards, although both sexes tend to disperse in the studied species (Doughty et al., 1994; Olsson et al., 1996). In the common lizard, natal dispersal has also been found to be slightly sex biased (Clobert et al., 1994; Sorci et al., 1994), and Sorci et al. (1994) showed that maternal parasite load causes both a higher survival and a higher propensity to disperse in male offspring but causes the opposite effect in female offspring. Massot and Clobert (1995) showed that maternal feeding during pregnancy which does not produce a sex-biased survival in offspring increases the natal dispersal propensity in both sexes and concluded that intrasexual competition and the avoidance of inbreeding are not the main determinants of natal dispersal in the common lizard. The results of our study support this conclusion. In our design, intrasexual com-

petition should result in an increased dispersal of juvenile females, while inbreeding avoidance should result in an increase of juvenile male dispersal according with kinship with adults. If both were operating we should expect an increase in the total number of dispersal attempts. Neither the sex of the adult nor their relatedness to offspring significantly affected the sex of dispersers. However, this is not to say that gender does not influence dispersal in the common lizard, because it can become a main factor at the onset of the maturity (i.e., breeding dispersal). Because there is no immediate competition for food between juveniles and adults (Avery, 1966), the avoidance of future kin competition seems to be the most likely explanation for the positive relationship between juvenile dispersal rate and maternal body condition. Ronce et al. (1998) demonstrated that the risk of kin competition can theoretically play a major role in the evolution of natal dispersal according to the parental survival prospect, and they showed that their finding applies to the common lizard.

There is good evidence that juvenile dispersal is, at least in part, under parental control through maternal effects because it was possible to increase juvenile dispersal by increasing maternal feeding rate during gestation (Massot and Clobert, 1995). In our design, offspring dispersal was influenced by the survival prospect of an unfamiliar female placed in the enclosure only when the female was the mother. This suggests that kin discrimination based on prenatal cues is implicated in juvenile dispersal. As support for this, Léna and de Fraipont (1998) showed a juvenile preference for shelters containing maternal olfactory cues even when juveniles are reared apart from their mothers.

Kin-biased behavior may be a complex phenomenon. It may arise from familiarity rather than from kin discrimination per se (Barnard et al., 1991; Grafen, 1990; Waldman et al., 1988). Postnatal and/or prenatal imprinting may influence discriminatory behaviors (Fletcher, 1987; Holmes, 1995; Robinson and Smotherman, 1991; Waldman, 1988; Waldman et al., 1988). In our case, a postnatal component has to also be considered. In our design, a postnatal effect was generated by a close familiarity between an unrelated adult female and the juveniles just after birth. Could this close familiarity with an unrelated female happen in nature? Several reasons strongly suggest that this cannot be the case. In our experiments we housed juveniles with an unrelated female during 3 days. Such familiarity with an unrelated female is unlikely to occur in nature because juveniles and adults use different microhabitats and have their peak of activity at different hours (Lecomte et al., 1994; Léna et al., personal observations). In addition, even if juveniles encounter unrelated females before they disperse, these contacts are at best as important as those that juveniles experienced with the unrelated, unfamiliar females in our experimental enclosures. Close contact with the mother after birth is more likely. Females are not very active just after laying (Léna et al., personal observations) and therefore are likely to stay in close contact with their offspring. It may be that the familiarity with the mother (mainly during pregnancy) plays a major role in the response to maternal cues and in the decision to disperse. However, further experiments are needed to explore the role of close contact with the mother for juvenile dispersal and the relationship between the decision to disperse and the response to maternal cues.

CONCLUSION

Juvenile dispersal rate in the common lizard is positively related to female density. In our experimental design, juveniles that attempted to disperse were of better body condition than

those that did not. Dispersing juveniles are therefore not the weakest individuals, but most probably those that can afford the costs of dispersal. In our system, kin competition appears to be a special case of intraspecific competition. The knowledge of the mother's survival prospect through maternal effects, and therefore of the probability of future kin competition, may have selected juveniles to adjust their dispersal behavior accordingly, leaving when the mother's survival prospect is good, staying when it is not. This may explain both the fact that dispersal is family dependent and that kin competition did not increase the overall dispersal rate. The extent to which this is a female "manipulation" or a pure juvenile "decision" should be investigated by looking more closely at the issues of the parent–offspring conflict through the comparison of offspring and parent fitness gain.

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