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Influence of maternal food availability on offspring dispersal

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Abstract Prenatal effects caused by the maternal environment during gestation are known to contribute to the phenotype of the offspring. Whether they have some adaptive value is currently under debate. We experimentally tested the existence of such a maternal effect (food availability during gestation) on dispersal of offspring in the common lizard (*Lacerta vivipara*). Pregnant females were captured and kept in the laboratory until parturition. During this period, females were offered two rates of food delivery. After parturition, we released mothers and offspring at the mother's capture point. Dispersal of young was significantly affected by the mother's nutrition. To our knowledge, this is the first evidence of a prenatal effect on dispersal. Offspring of well fed mothers dispersed at a higher rate than those of less well fed mothers. As current hypotheses clearly predict the opposite result, our evidence calls for their reassessment. Dispersers are not always the least fit individuals or those coming from the poorest environments.

Key words Dispersal · Environmental fluctuations · Food availability · Prenatal effects · Reptile

Introduction

Prenatal effects caused by the maternal environment during gestation are known to contribute to the phenotype of the offspring (Herrenkohl 1979; Newman 1988; Kirkpatrick and Lande 1989; Bernardo 1991; Kaplan 1992). The study of maternal contributions has recently become an important issue in evolutionary biology (Falconer 1989; Kirkpatrick and Lande 1989;

Bernardo 1991; Schluter and Gustafsson 1993) because (i) maternal environment can contribute to offspring fitness (Bernardo 1991), and (ii) maternal control of the characteristics of the progeny may be adaptive if mothers can use cues about future environmental quality (Bernardo 1991). Notwithstanding their importance, the effects of maternal factors are unknown for most traits (Schluter and Gustafsson 1993).

Demonstrating the existence of such phenomena for dispersal may have profound consequences for the study of the evolution of this trait. Hanski et al. (1991) have emphasised that "experimental studies on possible maternal effects on natal dispersal are urgently needed, even if a pioneering study by Ims (1990) on *Clethrionomys rufocanus* failed to demonstrate such an effect". Depending on environmental conditions, offspring could indeed adopt the best dispersal strategy with no cost of assessing their environment after birth (cost in energy, time, predation, competitive interactions, etc.). This process could take place when mothers are able to use cues about their environment, and when the environment is sufficiently predictable. Its evolution would then depend on the factors driving the evolution of dispersal.

Three ultimate factors are generally thought to drive the evolution of dispersal: intraspecific competition, inbreeding and habitat quality (Johnson and Gaines 1990; MacDonald and Smith 1990). For each of these factors, dispersal has potential benefits and costs. If dispersal is advantageous to avoid locally intense competition (Shields 1987; Krebs 1992; Stenseth and Lidicker 1992) or to reduce competition among related individuals (Morris 1982; Anderson 1989), it may generate competitive costs due to the loss of familiarity with the local environment (Shields 1987; Anderson 1989; Pärt 1990), and notably with the social environment (Shields 1987; McShea 1990). Likewise, if dispersal helps to avoid the cost of inbreeding by decreasing the chance of mating with a genetically related partner (Greenwood 1980; Stenseth and

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Lidicker 1992), it may prevent local adaptation by breaking combinations of coadapted genes (Shields 1987; Anderson 1989; Stenseth and Lidicker 1992). Lastly, if dispersal is beneficial when potential settlement sites are better than the site of origin (Horn 1983; Stenseth and Lidicker 1992), it will be costly to disperse when potential settlement sites are of poorer quality, or when the habitats encountered during the transient phase are unfavourable (Lidicker 1975; Stenseth 1983). In parallel with these three pay-offs, movements during dispersal can increase the risk of predation or energy requirements (Stenseth 1983; Shields 1987).

Costs and benefits associated with dispersal should differ among individuals, depending on their environment, past history and/or genotype. This is supported by differences between philopatric and dispersing individuals (Swingland 1983; Clobert et al. 1988; MacDonald and Smith 1990; McCleery and Clobert 1990; Hanski et al. 1991). Although the nature of intraspecific differences is still largely unknown, dispersers are generally considered as less good competitors than philopatrics (Murray 1967; Dhondt and Hublé 1968; Dobson 1982; Waser 1985; Anderson 1989; Brandt 1992) or as coming from unfavourable environmental conditions (Horn 1983; Lidicker and Stenseth 1992). As recently shown by Ferrer (1993), dispersers do not seem to be always the least fit individuals: the well-nourished young of imperial eagles (*Aquila adalberti*) moved further than those that were less well nourished. Because it was obtained within a descriptive framework, this feeding effect could result from a confounding factor that both influenced feeding and dispersal. As underlined by Schluter and Gustafsson (1993) for maternal effects, the test of a specific factor in a descriptive study requires measurement of all the factors that affect the offspring trait under consideration, and it is "an immensely complicated task". Experiments provide a more tractable alternative (Schluter and Gustafsson 1993). In this paper, we report an experimental test of: (i) the existence of a prenatal effect on dispersal; and (ii) the influence of food availability on dispersal. The species used, the common lizard (*Lacerta vivipara*), was particularly interesting because its dispersal is known to be influenced by intraspecific competition (Massot 1992a, b; Massot et al. 1992, 1994b; Clobert et al. 1994), and its maternal environment affects the phenotype of the offspring (Sorci et al. 1994).

Materials and methods

The species

The small, live bearing lacertid lizard *L. vivipara* [50–70 mm snout-vent length, (SVL)] inhabits humid habitats such as peatbog and heathland. Males emerge from hibernation in late March or April,

followed by yearlings and adult females in early May. Mating takes place immediately after female emergence. Parturition usually starts in mid July and lasts for 2–3 weeks. On average 5 (range 1–12) shell-less eggs are laid and hatch as soon as laid. After laying, females leave their offspring (no parental care) and make far-ranging movements in search of food (Heulin 1984). At this time no interactions between mother and offspring seem to occur (observations in semi-natural enclosures: Lecomte, unpublished data). The activity season ends in late September and juveniles are the last to enter hibernation. A more detailed description of the life history can be found in Pilorge (1987).

Study site

The data on juvenile dispersal were collected on a population in southern France (Mont Lozère, 44°30'N, 3°45'E). The study area is a 4300 m² moor. It is mainly covered with grass and heath patches, but its physical heterogeneity is enhanced by trees and rocks scattered across the area. Lizard density is high with up to 1000 adults and yearlings ha⁻¹. The site is surrounded by less favourable habitats showing lower densities. The dispersal rate between the study area and less favourable habitats was less than 12% during the studied period (Clobert et al. 1994).

Experimental protocol

Ninety-four pregnant females were removed from the population (34 in 1990 and 60 in 1991) and maintained in a laboratory until they gave birth. The rearing period corresponded to their 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 for 6 h per day. During the rearing period, we manipulated the maternal environment. Females were offered two rates of food delivery: one larva of *Pyralis farinalis* per week, or one every 2 weeks. The choice of feeding rates was based on the assumption that the average mass of the food items provided (average live weight \pm SD, 0.189 \pm 0.051 g, $n = 30$; average dry weight \pm SD, 0.075 \pm 0.025 g, $n = 30$) was in the range of the natural food consumption of pregnant females. At birth, offspring were individually marked by toe-clipping and their sex was identified by counting ventral scales (Lecomte et al. 1992). They were then released at the capture point of their mother. As females are very sedentary during pregnancy (Bauwens and Thoen 1981), we chose the release point of offspring to match their birth site. Movements of offspring were inferred from their last recapture point at least 10 days after their release time (i.e. after the main phase of juvenile dispersal; Massot 1992a, b). Monitoring of offspring was accomplished by hand capture, and continued until the end of their second activity season when they were still immature. A grid composed of sticks placed every 3 m allowed us to measure distances covered, by comparing the coordinates of the release point with those of the last recapture point.

We defined dispersal as a change in position over a distance between the birth site and the last recapture point exceeding the upper 95% confidence limit of the home range diameter, i.e. 30 m. We defined an offspring as philopatric when it moved less than the average home range diameter, i.e. 20 m. Offspring that moved distances between these two values were excluded from the analyses. This definition of dispersal seems to be consistent, since the individuals defined as dispersers were never observed to return to their natal site: of 20 offspring recaptured after a dispersal event, none was later found at a distance from the natal site less than a mean home range diameter. Movements that we called dispersal do not correspond to exploratory movements or movements of individuals having large home ranges.

Data analysis

Analyses of dispersal raise a difficulty because siblings cannot a priori be assumed as independent statistical units (Massot et al. 1994a). In our study, siblings showed resemblance in their dispersal behaviour (Massot 1992b; Clobert et al. 1994). Therefore, we could not use all offspring indiscriminately in the analyses. The small number of offspring recaptured per family prevented us from using nested analysis (offspring nested within litters). The discrete nature of the variable prevented using a mean value per family. Using only one randomly selected young per family would have wasted part of the information. For these reasons, we used numerical resampling techniques (Efron 1982; Massot et al. 1994a). The first step consisted in drawing at random one offspring per family and per sex to insure independence of data points. The influence of maternal food availability on offspring dispersal was then tested (log-likelihood ratio tests) on this subsample by a log linear analysis with sex, year and maternal feeding rate as factors (SPSS/PC + statistical package, Norusis 1986). We recorded the level of significance associated with each effect. We repeated this procedure (test on a random drawing of one offspring per family and sex) to produce a distribution of the probability of the statistics (i.e. distribution of significance levels). The distribution was characterized by the 95% confidence interval defined by the 2.5th and 97.5th percentiles of the distribution. We did 500 iterations (values of confidence limits stabilized after 150 resamplings).

Results

Maternal feeding and offspring characteristics

Dispersal may be related to offspring characteristics, which themselves could have been modified by the maternal feeding rate. We first verified that maternal feeding did not alter morphometric traits and growth rate of offspring, which are thought to integrate a large part of the individual phenotype (Peters 1983; Begon et al. 1990). Morphometric traits measured at birth were SVL, body mass and body mass corrected for SVL (corpulence). We carried out analyses on the mean values per litter and per sex because of resemblance among siblings. Maternal feeding did not affect SVL (feeding: $F_{1,149} < 0.01$ $P = 0.955$, feeding * sex: $F_{1,149} = 0.14$ $P = 0.706$, feeding * year: $F_{1,149} = 0.22$ $P = 0.640$, feeding * sex * year: $F_{1,149} = 0.56$ $P = 0.457$, ANOVA) and body mass (feeding: $F_{1,149} = 1.14$ $P = 0.288$, feeding * sex: $F_{1,149} = 0.04$ $P = 0.843$, feeding * year: $F_{1,149} = 0.28$ $P = 0.600$, feeding * sex * year: $F_{1,149} = 0.29$ $P = 0.590$, ANOVA). No feeding effect was found for corpulence (stepwise ANCOVA with body mass as dependent variable and SVL as covariate) (feeding: $F_{1,153} = 0.84$ $P = 0.360$, feeding * sex: $F_{1,148} = 0.83$ $P = 0.364$, feeding * year: $F_{1,147} = 0.40$ $P = 0.528$, feeding * SVL: $F_{1,149} = 1.16$ $P = 0.284$, feeding * sex * year: $F_{1,142} = 0.05$ $P = 0.824$, feeding * sex * SVL: $F_{1,145} = 1.76$ $P = 0.187$, feeding * year * SVL: $F_{1,143} = 0.01$ $P = 0.921$, feeding * sex * year * SVL: $F_{1,141} = 0.99$ $P = 0.320$). We also found no feeding effect on growth rate of offspring (feeding: $F_{1,22} = 0.64$ $P = 0.433$, feeding * sex: $F_{1,22} = 1.14$ $P = 0.297$, feeding * year: $F_{1,22} = 1.35$ $P = 0.257$, no test on feeding * sex * year due to empty cells,

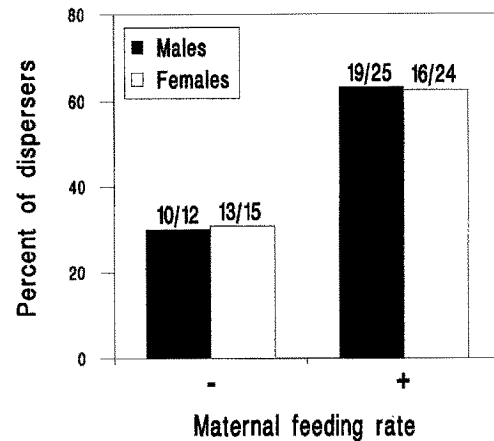


Fig. 1 Effect of maternal feeding rate on offspring dispersal. The percentages of dispersers are medians of the distributions from 500 resamplings of a single individual per sex and family. The sample sizes are given above the bars (average sample sizes from resamplings/total sample sizes)

ANOVA on change in SVL during the first month of life divided by the time interval separating recapture from birth).

Maternal feeding and offspring dispersal

To test the effect of maternal feeding rates on offspring dispersal, we used the resampling technique described in Materials and methods. Maternal food availability significantly influenced offspring dispersal: 95% of the tests of a feeding effect fell between $P = 0.004$ and $P = 0.044$. Offspring of well fed mothers dispersed at a higher rate than those of less well fed mothers (Fig. 1). This maternal effect did not differ between sexes and years (95% confidence intervals of P values for feeding * sex: 0.540–1.000, feeding * year: 0.218–1.000, feeding * sex * year: 0.179–0.527).

Discussion

Offspring of well fed mothers dispersed more frequently than those of less well fed mothers. There was no difference according to sex, and this was repeatable over years. The experiment seems to mimic the natural situation, since previous studies have shown that offspring dispersal is weak in bad years and in poor habitats (Clobert et al. 1994), which are likely to be associated with reduced maternal feeding.

Interpretation of the experiment

Maternal feeding is known to modify offspring phenotype in *L. vivipara*. The sprint speed at birth of male offspring has been shown to be influenced by maternal

feeding rate in interaction with body size (Sorci and Clobert submitted). Sprint speed was positively correlated to body size in males coming from well fed mothers while this correlation was absent in males coming from less well fed mothers. As the offspring sprint speed is related to offspring dispersal (Sorci et al. 1994), the maternal effect on male dispersal could have been a by-product of the maternal effect on sprint speed. This interpretation, however, does not seem to hold because no difference in body size was revealed between dispersers and philopatric individuals (Massot 1992b). Also, the maternal effect on female dispersal, which is similar to that on male dispersal, would be left unexplained. Moreover, we found no effect of maternal feeding on morphometry and growth rate of offspring. It follows that no obvious change in offspring characteristics induced by the experiment seems to explain the observed difference in dispersal.

The effect of maternal feeding on offspring dispersal could result from behavioural manipulation of offspring by their mother. Well fed mothers could have forced their young to disperse. Such behavioural manipulation is often proposed in small mammals, although a recent review (Wolff 1994) has shown evidence that young small mammals disperse voluntarily rather than as a result of maternal aggression. This hypothesis is still less likely for our species (a reptile), which shows a less evolved sociality when compared with small mammals. Moreover, common lizard females leave their offspring at laying to wander in search of food (Heulin 1984), and a behavioural study in semi-natural enclosures has shown no aggressive interactions between adult females and juveniles (13 experiments; Lecomte unpublished data).

First evidence of a prenatal maternal effect on dispersal

Prenatal effects caused by the maternal environment during gestation are known to contribute to offspring phenotype through morphology (Herrenkohl 1979; Brody and Lawlor 1984; Bernado 1991; Kaplan 1992), physiology (Ims 1990) and behaviour (Vom Saal 1984; Rau 1985). To our knowledge (see Hanski et al. 1991), this study reports the first evidence of a prenatal maternal factor influencing dispersal. Only one other study has investigated the influence of a prenatal factor on dispersal (Ims 1990), and this failed to demonstrate its existence. If we extend our interest to factors acting during the period of parental care (i.e. when young are still dependent on their parents), our result can be further compared with two other studies (Ferrer 1993 in imperial eagles; Wong and Bondrup-Nielsen 1993 in meadow voles). These studies also found a feeding effect on dispersal of young. Ferrer found that better-nourished young dispersed more frequently. This result is similar to our maternal feeding effect. However,

Wong and Bondrup-Nielsen (1993) obtained the opposite result. Besides working with different species, the studies differed in the type of data collected (observational vs experimental) and the time when food acted in the life cycle (postnatal vs prenatal). This may explain the disparity in the response of dispersal to early feeding environment.

The sensitivity to maternal environment could be an adaptive trait since it may serve as a cue to modify offspring characteristics in accordance with their future environment (Bernado 1991). Depending on the quality of their future environment, offspring could disperse or not without the associated cost of exploration of their birth site. As poor or deteriorating environmental conditions are thought to enhance dispersal (Horn 1983; Stenseth and Lidicker 1992), offspring of less well fed mothers were expected to disperse at a higher rate than those of well fed mothers. A similar prediction would have been made by a less adaptationist scenario. Dispersers are generally assumed to be less good competitors than philopatric individuals (Murray 1967; Dhondt and Hublé 1968; Dobson 1982; Waser 1985; Anderson 1989; Brandt 1992). If offspring quality was affected by maternal feeding, offspring of less well fed mothers could be thought of as being of poor quality. Therefore, these offspring would have been predicted to lose in competition against those of well fed mothers, and then forced to leave their natal area. Both theories therefore lead to the prediction that offspring of well fed mothers should be philopatric while offspring of less well fed mothers should disperse. This prediction is negated by our results.

Why did dispersers come from mothers experiencing better feeding conditions?

Good environmental quality during an early life stage may result later in life in enhanced competitive ability, and in turn decrease costs associated with dispersal. This explanation, advocated by Ferrer (1993), cannot explain why individuals disperse when they are good competitors or when environmental quality is good. According to Ferrer, only the existence of an important selective advantage to those individuals that disperse could explain it. We can think of, at least, one alternative hypothesis.

Classical theories on dispersal widely assume that poor environmental conditions enhance dispersal. This assumption follows from assuming that potential dispersers monitor their environment at a local scale, and that their environment is stable. Moving out of a good natal area will then result in being in a poorer environment and, without an important selective advantage of dispersal (such as inbreeding avoidance or avoidance of competition among related individuals), philopatry will therefore be a better strategy. The alternative hypothesis considers that temporal variations in

environmental conditions on a local scale are negatively autocorrelated. In this case, dispersal from a good local environment can be an adaptive strategy since an individual staying at home will later on be subjected to poorer environmental conditions. The opposite will hold for offspring produced in poor environments, which will benefit from being philopatric, since their future environment will turn to the better. Negative temporal autocorrelation of local environmental conditions could, for example, arise from competition on a local scale. In an environment that fluctuates randomly on a local scale, individuals living in a good environment at one time will have a higher probability of survival during the following unit of time, with, as a consequence, an increased amount of competition in the next time step.

Conclusion

Offspring of common lizards coming from well fed mothers dispersed more frequently than those from less well fed mothers. Our study provides the first evidence of a prenatal effect on dispersal and reinforces the recent result of Ferrer (1993): dispersers are not always the least fit individuals or the individuals coming from the poorest environments. This unexpected result could be explained by a selective advantage to dispersal or by a negative temporal autocorrelation in the environment on the local scale. We cannot discriminate between these two alternatives because the effects of dispersal and maternal food availability on offspring fitness are unknown. Future work will be devoted to the study of these effects and of environmental fluctuations that are crucial to understanding the positive relationship between maternal feeding and dispersal.

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