OFFSPRING PHILOPATRY IS PROMOTED BY MOTHER STRESS IN THE COMMON LIZARD (*LACERTA VIVIPARA*)

MEYLAN S.[1], DE FRAIPONT M.[1,2], CLOBERT J.[1] AND JOHN-ALDER H.[3]

[1] *Laboratoire d'Ecologie, CNRS-UMR 7625, Université P.et M. Curie, Paris, FRANCE*
[2] *Laboratoire de Zoologie et des Sciences de l'environnement, Université de Reims Champagne Ardenne, FRANCE*
[3] *Rutgers University, Department Animal Sciences, New Brunswick, NJ, USA*

Abstract: Offspring natal dispersal as many other morphological, physiological or behavioural traits are influenced by the maternal environment during gestation. In these present study, we wanted to see if many environmental stressors result in an increase of the plasma corticosterone. An increase of this stress-related hormone in pregnant females may directly influence their offspring dispersal and behaviour. To do this, we captured many pregnant females *Lacerta vivipara* in one population of the Mont Lozère and kept them in individual terrarium until parturition. Two days after capture females were implanted with subcutaneously silastic implants which contained either corticosterone or physiological water. Raising the level of circulating corticosterone has modified both the behavior of the mother during pregnancy and the behaviour of the juveniles just after birth. Hormones-implanted females increased their activity rate of escape attemps than juveniles issued from non stressed mothers. This trend was reversed when the odour of the mother was present in the terrarium. Finally, we demonstrated that juveniles of stressed mother dispersed in lower number than juveniles of placebo mother.

Corticosterone appears therefore to be intimitately linked to natal dispersal in common lizard. This hormone seems to constitue the offspring cue to assess maternal condition, an indication of survival prospect. Offspring dispersal therefore appears, at least in part, to be motived by kin competition.

KEY WORDS: Dispersal, environmental stress, corticosterone, lizard.

Introduction

Phenotypic plasticity allows individuals to change their phenotype according to the environment in which they live. An important source of phenotypic plasticity occurs in offspring in response to the maternal environment, likely because this give a chance to the offspring to be preadapted to their future environment (Bernado 1991). Morphological, physiological or behavioural traits can be influenced by the maternal environment during gestation.

The social environment of the common lizard influences dispersal (Clobert *et. al.* 1994). The relationship between social factors and dispersal may depend on the prenatal environment. The maternal environment could modify offspring dispersal to better adapt them to their environment. In a high quality environment, there are two possibilities. First if the mother is in good condition, this indicates a high quality environment, the prenatal environment could be a signal to offspring to stay in an environment where food is easy to find. Secondly, a mother in good condition living in a high quality environment has good survival prospects and the likelihood that the mother and her offspring eventually compete is increased if the offspring remain in the natal environment. Thus, a good prenatal environment could be the signal to leave in order to avoid kin competition (Hamilton et. May 1977). Kin competition was shown to be important in shaping natal dispersal in the common lizard (Léna *et. al.* 1998, Ronce *et. al.* 1998).

By which mechanism could the maternal environment influence offspring dispersal? A mother sends messages to embryos by physiological processes one of which is maternal hormones. Stress related hormone such as corticosterone are commonly used as indicators of stress and are likely to act as mechanistic signals of stress in the maternal environment. Previous studies demonstrated that an environmental stressor such as a lack of food was likely to raise the level of plasma corticosterone in mother (Harvey *et. al.* 1984). It is quite likely that a change in the mothers, corticosterone level could be tranferred to her young. Another study demonstrated that corticosterone was implicated in dispersal behaviour of individuals (Wingfield 1994, Silverin 1997). Thus, the transfer of corticosterone from mother to young could modify the juvenile propensity to move after birth. In this study, we examined how an experimental increase in maternal plasma corticosterone increases the philopatry of their young.

Material and Methods

The species

The common lizard (*Lacerta vivipara*) is a small lacertidae that we can found across Europe and Asia. We study populations on the Mont Lozère (Massif central, South-east of France), where male emerge from hibernation in mid-april, followed by yearlings and females in mid-may. Mating takes place as soon as females emerge from hibernation. After two months of gestation, females lay a clutch of on average 5 soft-shelled eggs of which offspring hatch within one hour. Young (18mm SVL) have an independent life from their mother right from birth. Finally, individuals enter hibernation in mid to late september.

Individual collection and laborarory conditions

We captured 50 pregnant females from the field on 1st of July and kept them in the laboratory in individual terrarium until parturition (usually at the beginning of august). To facilitate the thermoregulatory activity, we maintained the mothers under incandescent illumination for 6 hours a day. We also gave them water ad libidum and offered them larvae of *Pyralis* once a day.

HORMONES IMPLANTATION

Two days after all females were brought to the laboratory, we started the implantation of corticosterone. Each female was cold-anestesized and the implant was subcutaneously delivered through a 5mm incision in the middle of the lateral side of the animal. 25 females received silastic implants of 6 mm length and 2mm of diamater, contained B cristalline. The total quantity of corticosterone in the implants was calculated to last 30 days, the average time that the pregnant females stayed in the laboratory until parturition. 25 females received silastic implants with physiological water to serve as control.

FEMALE BEHAVIOUR DURING GESTATION

The female behaviour was recorded three times a day at 9h30, 13h and 16h30. At each visit to the terrarium, we recorded whether the female was outside or within its shelter. We also recorded whether the females were motionless or active. An indication of the level of stress could also be given by the number of food items offered that each female accepted to consume.

JUVENILE BEHAVIOUR AT BIRTH

Four types of experiments were conducted just after birth.

The first experiment examined the reaction of juveniles towards the odour of their mother (n=90). Indeed the juvenile are attracted towards the odour of their mother and this behaviour has a prenatal determination (Léna *et. al.* 1998). We wanted to verify this point again, and to know if the corticosterone could be the mechanism by which this variation arose. To perform this experiment, we placed two shelters in a terrarium, one with no odour and one containing the odour of the mother. Before this, we placed the mother with a wet paper in a terrarium, 4 hours, to impregnate the paper by mother's odour and so we put the paper under the shelter. The juvenile was introducted in the terrarium the day of its birth at 4 p.m. At midnight, we recorder the position of the juvenile as follow : 1) either the juvenile was outside the two shelters or was inside one of the shelter, 2) if in a shelter, either the juvenile was in the shelter containing its mother's odour or in the shelter containing no odour.

The second experiment was designed to examine the reaction of the juvenile to an acute stressor (n=96). Each juvenile was placed at the centre of a terrarium with a shelter. The juvenile was left alone for 10 minutes. Then, an observer provided a stimulus by tapping with a stick on the tail. Three types of behaviours were recorded : 1) the juvenile did not react to the stimulus; 2) the juvenile reacted by running within the terrarium;
3) the juvenile ran directly to the shelter.

The third experiment aimed to study the reaction of the juvenile in a new situation (n=90). To do this experiment, we placed a juvenile in an empty terrarium topped by a video camera. After 10 minutes, the camera was set in motion for 10 minutes to record juvenile's behaviour. We introduced a paper impregnated with the odour of its mother and recorded again the juvenile behaviour for 10 minutes. We recorded the time spend in the different places in the terrarium (centre versus along the inner side) and the time spent walking. We also measured the time spent scratching the inner wall, interpreted as an active tentative to leave the terrarium.

The fourth experiment examined juvenile dispersal (n=90). The juvenile dispersal is difficult to study in natural populations, so we used an experimental design which allows us to study this behaviour. The experimental design was as follows : each experimental set is constituted of two boxes of 4m2 connected by small holes which allows the passage of the juveniles only. First, we introduced the mother one day late. The juveniles were introducted in the mother's box (see Lena *et. al.* 1998 for more details). After 6 days, we recorded the number of juveniles which were found in the box not containing the mother.

Statistical analysis

For continous variable (time spent, size, weigth), we used the procedure GLM of SAS Institute. When doing analysis at the juvenile level, the female effect has to be nested within the traitment effect, since juveniles of a same family cannot be considered as independent event. We then performed nested analysis of variance or covariance.

For percentage (dispersal rate, percentage of time spent), we used the procedure GENMOD of SAS Institute. This procedure performs logistic-linear regression analysis particularly suited for this type of dependent variable.

Results

During the time spent in the laboratory, corticosterone-implanted females did not take more food than placebo-implanted females (χ^2_1=0.19 p=0.66). Placebo-implanted females did stay more often hidden at all periods of the day than hormone-implanted females (morning χ^2_1=9.48 p<0.01, midday χ^2_1=11.5 p<0.01, end of the afternoon χ^2_1=6.08 p<0.05).

Shelter with the mother's odour

Each juvenile was in an individual terrarium at the beginning of the night. The juvenile had the choice to spend the night in a shelter containing the odour of its mother, in a shelter containing no odour or stay out the shelter. The hormonal treatment of the mother had no effect on the choice of the juvenile to stay outside or to spend the night in a shelter (χ^2_1=1.79 p>0.05). But when we examined the effect of this treatment on the choice of the shelter with or without a mother's odour, we found that juveniles of corticosterone implanted female choose more often the shelter containing their mother's odour (43% versus 29%, p<0.01).

Acute stress

When placed with a predator-like stimulus, only 6 juveniles stayed motionless, so we analysed only the type of escape strategy (going to a refuge versus running in the terrarium). The results showed that juveniles of hormone-implanted females went in the refuge more often than juveniles from placebo-implanted females (55% versus 33%, χ^2_1=4.70 p<0.05).

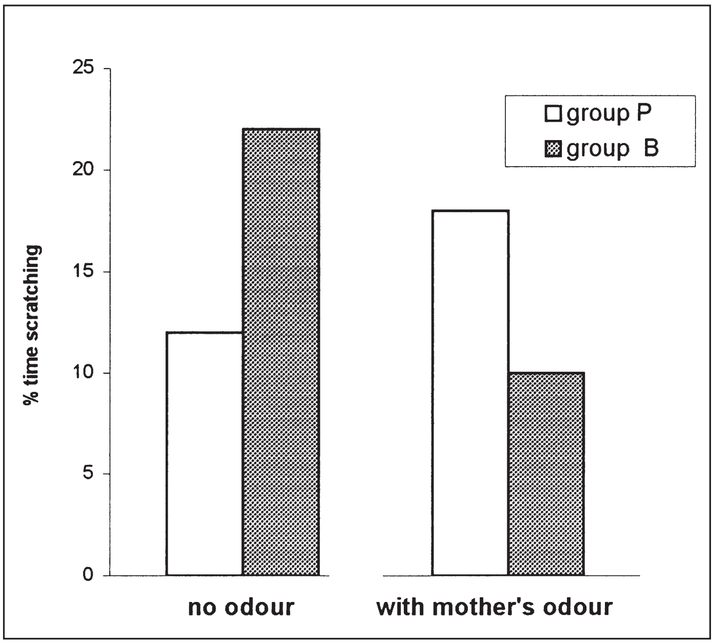

Fig. 1: percentage of juveniles time scratching the sides of the terrarium

Exploration and stress

In absence of the mother's odour, juvenile lizards spent 25% of their time scratching the sides of the terrarium. Juveniles issued from hormone-implanted females were more active than juveniles from placebo-implanted females. This trend was reversed when juveniles were in the presence of their mother's odour. In this case, juveniles from hormone-implanted females spent significantly less time to scractch the sides of the terrarium than juveniles from placebo-implanted females ($p<0.01$, Fig. 1).

Juvenile dispersal

Juveniles issued from hormones-implanted females dispersed in fewer numbers than juveniles from placebo-implanted females (13.9% versus 37%, $\chi^2_1=5.19$ $p<0.05$).

Discussion

Implantation of corticosterone modified the behaviour of pregnant females and the behaviour of their offspring. Corticosterone-implanted females were more active. When the offspring of corticosterone-implanted females were placed alone in an unfamiliar terrarium, they spent more time scratching the wall of the terrarium in the absence of maternal odour and less in the presence of the maternal odour. Similary, the number of offspring which chose to spend the night inside a shelter marked by maternal odour was higher for corticosterone implanted than for placebo-implanted mother. Dispersal rates were lower for offspring of corticosterone-implanted mothers when compared to placebo ones.

The level of plasma corticosterone is generally viewed as an integral component of stress response. As such, our use of silastic implants to experimentally supplement or replace endogenous corticosterone secretion mimics an animal's response to chronic, unpredictable stress. Chronic stress during the pregnancy potentially constitutes an important maternal effect that can affect the phenotype of the offspring. In many species of reptiles, including *Lacerta vivipara*, corticosterone production has been found to be particularly important during pregnancy (Leboulenger *et. al.* 1982, Wilson et.Wingfield 1992). Corticosterone is involved in the regulation of body fluids including trans-placental water flow and is therefore likely to have an important impact on embryonic development.

In the present experiments, maternal corticosterone implantation influenced the behaviour of juveniles placed into an unfamiliar, potentially stressful environment. The offspring of stressed females exhibited a higher rate of escape attempts than offspring of unstressed females, and this effect was reversed in the presence of maternal odour. The familiarity of maternal odour apparently acted to counteract the stress of an unfamiliar environment. Offspring from corticosterone-implanted mother seemed always to adopt a strategy to minimize stress. Perhaps offspring exposed to prenatal stress have a diminished endocrine capacity to respond to postnatal stress as demonstrated in rats (Pollard 1984, Takahashi *et. al.* 1988).

The results of our experiments may have profound implications regarding exploratory movements and habitat selection in the wild. We demonstrated that maternal corticosterone implantation increase offspring philopatry. In *Lacerta vivipara*, dispersers are likely to be individuals who are the best able to tolerate the stress associated with exploration of a new environment. The ultimate cause seems to be linked to the avoidance of kin competition as this factor is an important force driving the evolution of dispersal in this species. It follows that poor maternal condition, indicated by chronic stress, would foretell a poor prospect of maternal survival and would thus promote philopatry in the offspring.

ACKNOWLEDGEMENTS: We are grateful to all the people who helped in collecting the data and to two anonymous reviewers who critically revised a previous draft of the paper. We also thank the "Parc National des Cévennes" and the "Office National des Forêts" for providing facilities during our field work. This researchhas been supported by the CNRS.

REFERENCES

• BERNARDO, J. (1991). Manipulating egg size to study maternal effects on offspring traits. Trends in Ecology and Evolution, 6:1-2.
• CLOBERT, J., MASSOT, M., LECOMTE, J., SORCI, G., DE FRAIPONT, M. AND R. BARBAULT. (1994). Determinants of dispersal behavior : the common lizard as a case study. In : Lizard ecology : historical and experimental perspectives, L.J. Vitt and E.R. Pianka, Eds, pp. 183-206. Princeton University Press, Princeton.
• HAMILTON, W.D. AND R.M. MAY (1977). Dispersal in stable habitats. Nature, 269:578-581.
• HARVEY, S., PHILLIPS, J.G., REES, A. AND T.R. HALL (1984). Stress and adrenal function. Journal of experimental Zoology, 232:633-645.
• LEBOULENGER, F., DELARUE, C., BELANGER, A., PERROTEAU, I., NETCHITAILO, P., LEROUX, P., JEGOU, S., TONON, M.C. AND H. VAUDRY (1982). Direct radioimmunoessays for plasma corticosterone and aldosterone in frogs. I. Validation of the methods and evidence for daily rythms in a natural environment. General and comparative Endocrinology, 46:521-532.
• LÉNA, J.P. AND M. DE FRAIPONT (1998). Kin discrimination in the common lizard. Behavioral Ecology and Sociobiology, 42:341-347.
• MASSOT, M. AND J. CLOBERT (1995). Influence of maternal food availability on offspring dispersal. Behavioral Ecology and Sociobiology, 37:413-418.
• POLLARD, I. (1984). Effects of stress administrated during pregnancy on reproductive capacity and subsequent development of the offspring of rats : prolonged effects on the litters of a second pregnancy. Journal of Endocrinology, 100:301-306.
• RONCE, O., CLOBERT, J. AND M. MASSOT (1998). Natal dispersal and senescence. Proceedings of the national Academy of Sciences USA (in press).
• SILVERIN, B. (1997). The stress response and autumn dispersal behaviour in willow tits. Animal Behaviour, 53:451-459.
• TAKAHASHI, L.K., KALIN, N.H., BARKDALE, C.M. AND J.A. VANDEN BURGT (1988). Stressor contrallability during pregnancy influences pituitary-adrenal hormone concentrations and analgesic responsiveness in offspring. Physiology and Behavior, 42:323-329.
• WILSON, B.S. AND J.C. WINGFIELD (1992). Correlation between female reproductive condition and plasma corticosterone in the lizard Uta stansburiana. Copeia, 1992(3):691-697.
• WINGFIELD, J.C. (1994). Corticosterone and alternate behavioral patterns in response to unpredictale events. Journal of ornithology, 135:488.