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Stress and Body Condition as Prenatal and Postnatal Determinants of Dispersal in the Common Lizard (*Lacerta vivipara*)

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Dispersal is a complex phenomenon affected by multiple factors. Among the factors that influence dispersal in the common lizard (*Lacerta vivipara*), poor maternal body condition and stress are known to decrease dispersal propensity of juveniles. But the effect of individual factors on dispersal could change when several of them act concurrently or at different developmental stages. Prenatal factors can affect clutch and/or juvenile characteristics that later affect dispersal. Postnatal influences are mainly exerted on juvenile dispersal behavior. We investigated the role of body condition and stress on dispersal at a prenatal and a postnatal stage. Stress was mimicked by experimentally increasing corticosterone levels in pregnant females and recently born juveniles. We considered (1) the influence of maternal body condition and prenatal corticosterone treatment on clutch, juvenile characteristics and on dispersal behavior and (2) the influence of juvenile body condition and postnatal corticosterone treatment on juvenile dispersal behavior. There was an interaction between maternal condition and prenatal corticosterone treatment on juvenile dispersal. Dispersal decreased with maternal corticosterone increase only in juveniles from the more corpulent females, while it increased with juvenile body condition. Good maternal body condition affected clutch and juvenile characteristics favoring dispersal, while elevation of corticosterone level (stress) exerted the opposite effect. Juvenile body condition favored dispersal, while there was no effect of postnatal corticosterone treatment on juvenile dispersal propensity.

***Key Words: body condition; corticosterone; dispersal; Lacerta vivipara;* prenatal and postnatal effects.**

A large body of literature focuses on why and under what circumstances an animal leaves its natal site or its previous breeding place (Swingland, 1983; Clobert *et al.*, 1994, 2001). Although ultimate causes for the dispersal (habitat deterioration, avoidance of inbreeding, competition) have been well studied, particularly in mammals (Chepko-Sade and Halpin, 1987), determinants of dispersal remain poorly understood and, at the best, are known to involve a complex set of interactions, as dispersal seems to be affected by multiple factors (Schroeder and Boag, 1988; Lidicker and Stenseth, 1992). Moreover, different ontogenetic stages make the organism more sensitive to different dispersal cues, and thus determinants of dispersal can act at different stages in the life cycle. For example, dispersal in recently born juveniles has been shown to depend on maternal condition (Ims, 1990; Ims and Hjermann, 2001), while dispersal in mature individuals benefits from both increased access to unrelated mate and decreased intrasexual competition (Dobson and Jones, 1985).

Individual differences in dispersal ability can be achieved through differences in morphology, physiology, or behavior. Prenatal factors can affect clutch and/or juvenile characteristics that later affect dispersal. Therefore, prenatal mechanisms allow for maternal control of the dispersal propensity in the offspring. There is good evidence that females can manipulate the phenotypes of their offspring (Bernardo, 1991; Liu *et al.*, 1997, Mousseau and Fox, 1998).

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In mammals, females can control the sex ratio of the progenity (Clutton-Brock and Iason, 1986; Charnov, 1982). Female lizards control the paternity of their offspring by selective use of sperm (Olsson *et al.,* 1996) and control juvenile phenotypes via nest-site selection (Shine and Harlow, 1996). Maternal effects on dispersal propensity are especially well known from aphids. Aphid mothers fed on poor food, or kept under crowded conditions, give birth to winged daughters (Dixon, 1985). More generally, in temporally predictable environments, an adaptive maternal control of offspring dispersal behavior is expected to promote offspring fitness (Bernado, 1991; Massot and Clobert, 1995). Differences in dispersal ability can also be induced during the postnatal stage, sometimes shortly after birth (Falconer, 1989; Ferrer, 1993). For example, habitat characteristics, such as humidity and temperature, have been shown to influence dispersal after birth (Lorenzon *et al.,* 2001).

Hormones, especially corticosterone, have recurrently been proposed as a mechanism for the species to modify its dispersal propensity (Wingfield, 1994; Silverin, 1997; Dufty and Belthoff, 2001). It has been shown that corticosterone can influence dispersal at a postnatal stage (increasing dispersal) or at a prenatal stage (decreasing dispersal; de Fraipont *et al.,* 2000; Meylan *et al.,* submitted for publication; Silverin, 1997) and that the effect of corticosterone is modulated by the individual's condition (Silverin, 1998).

Therefore, corticosterone seems to be involved in the dispersal process, but its action at different stages of ontogeny in a given species, and the possible interactions with the individual body condition, remain poorly studied. In this work, we considered the common lizard (*Lacerta vivipara*) as a model system for investigating such effects on dispersal. Natal dispersal occurs mainly at the juvenile stage in the common lizard. In this species, maternal condition, in particular the level of food delivered to the mother (Massot and Clobert, 1995), the age of the mother (Ronce *et al.,* 1998), and the experimental increase of corticosterone levels in pregnant females influence offspring dispersal (Meylan *et al.,* submitted for publication). On the other hand, juvenile dispersal takes place within 10 days after birth, when postnatal factors, such as density of individuals in the natal site and/or habitat characteristics, influence dispersal (Massot and Clobert, 2000; Lorenzon *et al.,* 2001).

We investigated the role of body condition and corticosterone level increase on dispersal at a prenatal and a postnatal stage, considering (1) the influence of maternal body condition and prenatal on clutch and juvenile characteristics and on dispersal behavior and (2) the influence of juvenile body condition and postnatal corticosterone treatment on juvenile dispersal behavior.

MATERIALS AND METHODS

The Species

The common lizard (*L. vivipara*) is a small Lacertidae (snout–vent length up to 55 mm) that is found throughout Europe and Asia. This viviparous species lives in peat bogs and heath (a substrate covered by *Callune vulgaris*). The study was conducted at Mont-Lozère (Massif Central, in southeastern France), where males emerge from hibernation in mid April, followed by yearlings, and females emerge in mid May. Mating takes place as soon as females emerge from hibernation. Embryos are only surrounded by a thin membrane which is 9 μm thick (Heulin, 1991). A primitive chorioallantoic placenta allows respiratory and hydric exchanges between mother and embryos during pregnancy (Panigel, 1956). Parturition occurs after 2 months of gestation, when youngs are fully formed. Females lay a clutch, on average, of five soft-shelled eggs and offspring hatch within 1 h of oviposition. The youngs (snout–vent length up to 18 mm) are independent of their mother immediately after birth. Dispersal occurs mainly at the juvenile stage. Juvenile dispersal starts about 4 days after birth and is almost completed after 15 days (Massot, 1992).

We captured 100 pregnant females at the end of June 1999 and kept them in a laboratory until parturition (usually at the beginning of August). Individuals of *L. vivipara* were captured by hand at the field site. We walked at the field site, and individuals were spotted in the vegetation and blocked by hand on the soil, taken, and introduced into a terrarium. The authors wanted to attest the adherence to the *National Institutes of Health Guide for the Care and Use of Laboratory Animals.* Females occupied individual terraria ($18 \times 12 \times 12$ cm) where thermoregulation was facilitated through incandescent illumination 6 h a day. They were offered water *ad libitum* and *Pyralis* larvae once a day. One week after giving birth, mothers were released to the area of capture. At the end of the study the juveniles were released to the area of capture of females. We noted size (snout–vent length, mm), mass (mg), and corpulence (mass divided by snout–vent length) of mothers (just after the capture and after parturition) and offspring (just after birth).

Hormonal Treatment

Prenatal and postnatal stress was mimicked by increasing corticosterone levels in pregnant females and in newly born juveniles. We used a method that elevated plasma corticosterone levels without exposing the control animals to the stress of surgery. Circulating levels of corticosterone were manipulated using a noninvasive method for sustained elevation of steroid hormone levels in reptiles, similar to that described by Knapp and Moore (1997). Corticosterone was delivered transdermally to the lizards by using a mixture of the steroid hormone and sesame oil. Because *L. vivipara* is very similar in size and weight to the species used by Knapp and Moore (1997; tree lizards, *Urosaurus ornatus*), we used the same corticosterone concentration. We diluted corticosterone (Sigma C2505) in commercial sesame oil (3 μg of corticosterone / 1 μl of sesame oil).

To control for the possibility that the transdermal patch itself might affect corticosterone levels (Knapp and Moore, 1997), we applied the hormone solution to the backs of all females daily, using a pipette (see below). The high concentration of lipids in lizard skin (Mason, 1992) enables lipophilic molecules, such as steroid hormones, to cross the skin readily. We did not remove blood from pregnant *L. vivipara* because this increases both the mortality rate of the females and the rate of abortion (Massot and Smith, unpublished data). However, we verified that our technique increased plasma corticosterone to levels similar to those obtained by Knapp and Moore (1997) by measuring corticosterone in blood taken from two additional groups of pregnant *L. vivipara* females. One group received the same corticosterone treatment as that in the present study, and the other group received the same sesame oil treatment (Meylan and Dufty, in preparation). Radioimmunoassays have shown that circulating corticosterone levels in pregnant females have been increased by corticosterone treatment (281.9 $\pm$ 46 ng / ml in corticosterone-treated females versus 18.18 $\pm$ 10 ng / ml in placebo-treated females; 21.64 $\pm$ 4.52 ng / ml as the range of corticosterone values in a population of untreated lizards). Randomly chosen pregnant females (N = 50) were given 4.5 μl of the hormone solution dorsally, every day until parturition (27 days on average), while control females (N = 50) received the same amount of sesame oil. A similar procedure was used with juveniles. In every family, half of the offspring were given 0.5 μl of the hormone mixture (N = 203), while the other half received the same amount of sesame oil placebo (N = 195). Individual juveniles were treated during their first 3 days of life.

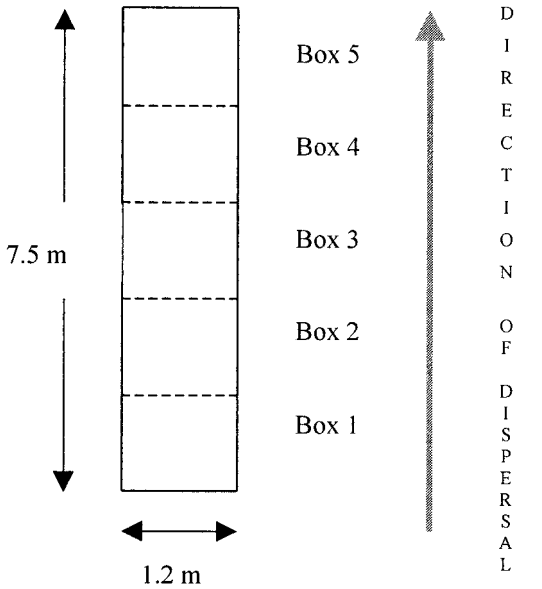

FIG. 1. Experimental runway used to discriminate between philopatrics (never leave Box 1) and dispersers (leave Box 1 through the wholes and are found at Box 2 to Box 5) in juveniles of the common lizard.

Dispersal Behavior

Given the difficulty of following natal dispersal of young in natural populations, we followed a surrogate procedure to investigate dispersal without releasing juveniles into their natal population. Natal dispersal occurs almost exclusively within 10 days of birth in *L. vivipara* (Clobert *et al.*, 1994; Massot and Clobert, 1995). Juvenile dispersal was studied through an experimental design involving experimental runways (N = 20; 7.5 $\times$ 1.2 m in length, Fig. 1), each consisting of five boxes connected by small holes allowing displacement of juveniles along the structure but not of adults (see Léna *et al.*, 1998; de Fraipont *et al.*, 2000; Meylan *et al.*, submitted for publication, for a similar approach). The habitat in each box was standardized, with most important elements of the natural habitat (soil, heath, rock, and wood). We offered water *ad libitum* in all the boxes. Four days after parturition, a family (mother and offspring) was introduced at one end of the runway (no dispersal has previously been observed prior to this age, Léna *et al.*, 1998), and 5 days later, the location of juveniles in the experimental setup was recorded. Juveniles found in the initial box, where the

mother was present, were considered "residents." Juveniles that left that initial box and were found in other boxes were considered "dispersers" (see Léna *et al.*, 1998; de Fraipont *et al.*, 2000, for more details). In nature, juvenile can disperse distances that exceed 50 m (Clobert *et al.*, 1994; Massot and Clobert, 1995). So, in previous studies with a similar design (Léna *et al.*, 1998; de Fraipont *et al.*, 2000; Meylan *et al.*, submitted for publication) we verified that the movement of juveniles between boxes was not simply a random process (e.g., exploration or passive diffusion). In some species (plants and insects), dispersal can be achieved by a diffusion process (Colas *et al.*, 1997). To check this, we recorded the position of each juvenile three times a day during the experiment (0900, 1200, and 1500 h, e.g., during the animals' rest and active phases). First, we observed the majority of dispersing individuals going to the second or third box. Second, most movements occurred in the 2 first days. Furthermore, very few juveniles returned to a previously visited box and none returned to the release box. As previously found (Léna *et al.*, 1998) in a different experimental design, these movements appear to be definitive and not random, two characteristics of natal dispersal. Our dispersal pattern does not follow a diffusion process. The timing and the rate of dispersal as well as the magnitude of the family effect are the same that those observed under natural conditions (Clobert *et al.*, 1994; Lecomte and Clobert, 1996; Léna *et al.*, 1998). In this experimental design, as observed in nature, individuals coming from the same mother have a similar tendency to disperse. This is not consistent with a simple passive diffusion process. Furthermore, disperser in natural populations had characteristics similar to those of juveniles observed to colonize the nonmaternal boxes (Massot and Clobert, 1995; Léna *et al.*, 1998; Ronce *et al.*, 1998). For example, juveniles called dispersers in this design were in a better body condition (higher corpulence) than those called "philopatrics." And we have found the same factors influencing juvenile dispersal behavior as those found in nature. Léna *et al.* (2000) have found in nature that juvenile dispersal is related to an aversion toward maternal cues at birth. In this dispersal design, we found the same result, i.e., that the juvenile dispersal rate was dependent on its sensitivity to the mother's odor; dispersing individuals avoided the maternal odor in one experiment designed to investigate the reaction of a juvenile to the odor of its mother (de Fraipont *et al.*, 2000).

Statistical Analysis

Data analysis involving siblings raises a statistical difficulty. Siblings cannot be assumed to be independent statistical units (Massot *et al.*, 1994). After verifying the normality of the continuous dependent variables (snout–vent length, mass, corpulence), we used the procedure GLM of SAS Institute (SAS, 1992). For the analysis of juveniles, the female effect was nested within the treatment effect. We then performed a nested analysis of variance or covariance.

For dependent variables that are percentage measurements (dispersal rate), we used the GENMOD procedure of SAS Institute. We corrected for overdispersion of data, induced by the non-independence among siblings, by using the DSCALE option of the GENMOD procedure (Massot and Clobert, 2000). Prenatal and postnatal effects were introduced as factor effects. In both cases, we used type III sum of squares (nonsequential decomposition). We started with a general model including all the potential effects and their interactions. We then dropped the nonsignificant effects, starting with the most complex interaction terms. Only the results of the final model are reported.

RESULTS

We first examined the effect of prenatal factors (maternal condition and prenatal corticosterone treatment) on clutch and juvenile characteristics and checked the effect of these phenotypic characteristics on dispersal. Then we examined the effect of postnatal factors (juvenile condition and postnatal corticosterone treatment) on juvenile dispersal behavior.

Prenatal Factors: Maternal Condition and Prenatal Corticosterone Treatment Effects on Clutch Characteristics

Clutch size (here the number of neonates alive) was significantly influenced by both maternal condition (ANOVA with corpulence, $F = 36.28$, $P < 0.0001$, $n = 99$; ANOVA with size, $F = 9.47$, $P = 0.0027$, $n = 99$) and corticosterone treatment of pregnant females ($F = 7.62$, $P = 0.0069$, $n = 99$). Date of parturition was significantly affected by body condition of pregnant females and by the maternal hormonal treatment. Corpulent and large females gave birth earlier (ANOVA with corpulence, $F = 9.59$, $P = 0.0026$, $n = 99$; ANOVA with size, $F = 16.1$, $P = 0.0001$, $n = 99$). Corticosterone-treated females gave birth later than

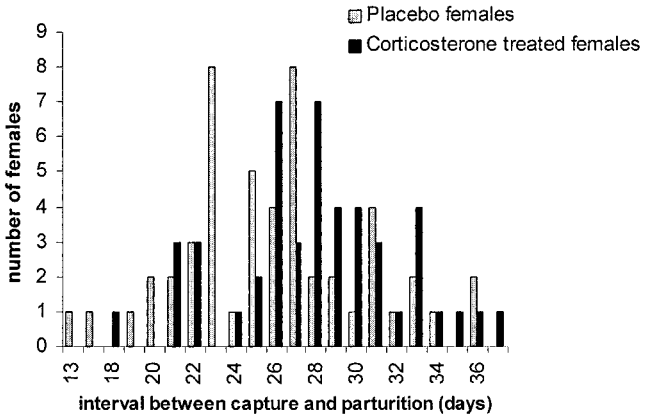

FIG. 2. Days elapsed between capture and parturition for placebo (gray bars) and corticosterone-treated (black bars) females. Corticosterone-treated females gave birth later than placebo females (F = 6.28, P = 0.014).

placebo females (F = 6.28, P = 0.014, n = 99, Fig. 2). Moreover, female treatment affected the number of dead neonates, with treated mothers giving more dead neonates than placebo females (F = 7.62, P = 0.0069, n = 99; 1.708 dead neonates versus 0.72). Maternal hormonal treatment also reduced the corpulence of neonate juveniles (n = 99, F = 8.16, P = 0.0054, 78.5 mg/cm versus 84.4 mg/cm). Hatching date had a significant negative effect on dispersal (χ^2_1 = 4.02, P = 0.0451, n = 256).

Prenatal Factors: Maternal Condition and Prenatal Corticosterone Treatment Effects on Dispersal

Maternal size increased dispersal (ANOVA with size, F = 8.16, P = 0.0054, n = 99). There was a significant interaction between mother's corpulence and maternal hormonal treatment on the propensity of juvenile to disperse (n = 149, χ^2_1 = 8.63 P = 0.0033). In those females below the average corpulence, maternal hormonal treatment did not affect the likelihood of juveniles to disperse (n = 83, χ^2_1 = 3.14 P = 0.08). In contrast, in those females above the average corpulence, maternal hormonal treatment decreased juvenile propensity to disperse (χ^2_1 = 5.61 P = 0.018, n = 66, Fig. 3).

Postnatal Factors: Juvenile Condition and Postnatal Corticosterone Treatment Effects on Dispersal

Juvenile corpulence was positively related to dispersal propensity (n = 256, χ^2_1 = 3.64 P = 0.05). Corticosterone treatment on juveniles had no effect on dispersal behavior (n = 164, χ^2_1 = 0.01 P = 0.905).

DISCUSSION

Prenatal factors, such as maternal body condition and prenatal corticosterone treatment, influenced both juvenile phenotype and juvenile dispersal. Postnatal factors such as juvenile condition influenced dispersal, while the increase in corticosterone on juveniles had no effect on juvenile propensity to disperse.

Prenatal Factors: Maternal Condition and Prenatal Corticosterone Treatment

We analyzed if mother's condition and prenatal corticosterone treatment could be driving dispersal by having an effect on clutch and juvenile characteristics. It is a common observation that dispersing and philopatric individuals often differ in their morphology, such as the presence or the absence of wings in some insects (MacKay and Wellington, 1977; Swingland, 1983), the pappus of a seed (Venable *et al.*, 1993), and the degree of fatness in the naked mole rats (O'Rian *et al.*, 1996). Animals with large energy reserves may better endure the transience stage from leaving home to establishing their own territory, especially where this is energetically costly. To what extent these dif-

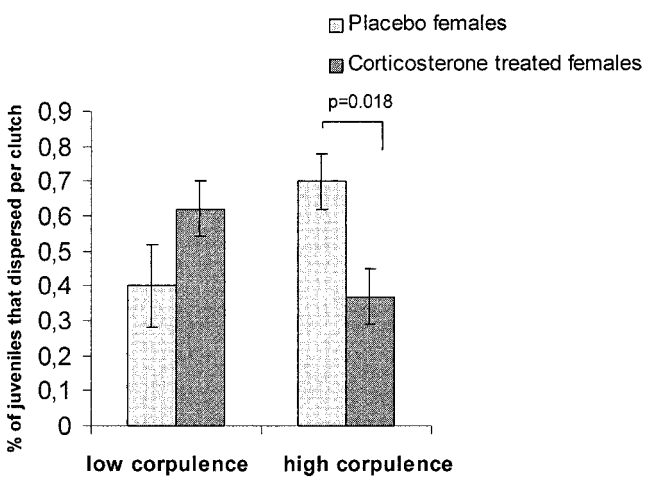

FIG. 3. Diagram showing the interaction between prenatal corticosterone increase and maternal corpulence on the percentage of juveniles that dispersed per clutch in the common lizard (n = 149, χ^2_1 = 8.63 P = 0.0033). For females with high corpulence, maternal hormonal treatment decreased juvenile propensity to disperse (χ^2_1 = 5.61 P = 0.018).

ferences are determined by long-term prenatal factors (like mother's corpulence) or by short-term prenatal factors (like maternal recent exposition to stress)? We found in earlier studies that maternal corticosterone elevation increased offspring philopatry, depending upon female size (Meylan *et al.*, submitted for publication). In the present study, prenatal corticosterone treatment also had an effect on dispersal but modulated, this time, by female corpulence. Dispersal decreased with maternal elevated corticosterone level only in juveniles from the more corpulent females, while it increased with juvenile body condition. Size and corpulence have been repeatedly found to be associated with individual quality (i.e., reproductive success; survival, Partridge and Farquhar, 1983; Jakob *et al.*, 1996; Lefranc and Bundgaard, 2000). However, in many cases, the extent to which size and corpulence are positively or negatively related to quality has been found to be condition dependent (Massot and Clobert, 2000). Size and corpulence do not exactly reflect the same kind of information and aren't sensitive to the same factors. While size of individuals may reflect their age and constitute a component of the body condition that integrate information of past years, corpulence, however, more likely reflects the condition of the individual at present. Depending on the environment and on the different selective factors acting, these two morphological variables may vary together or independently. This fact can explain the alternative role of maternal corpulence and maternal size that is observed in *L. vivipara*. They both affect juvenile dispersal, growth, and survival (Massot and Clobert, 2000; Lorenzon *et al.*, 2001). Short (corpulence)- and long (size)-term maternal effects might themselves represent different forces acting on juvenile dispersal behavior, such as intraspecific or kin competition.

The action of corticosterone is indeed known to be itself context dependent (Silverin, 1998). Silverin demonstrated that corticosterone implants stimulate natal dispersal in juvenile tits (*Parus montanus*) during winter flock formation, a time when birds normally leave their natal territories. However, similar implants given at the same time to adults or to juveniles after winter flocks have no effect. We hypothesize that corticosterone might be the mechanism by which environmental cues (internal or external) are transmitted to offspring, through corticosterone-mediated maternal effects on embryonic development. Only recently has it been determined that the hormonal milieu of developing embryos varies, both within and between clutches, and that this variation is of maternal origin. For example, Schwabl (1993) found that maternal testosterone is deposited in yolk during avian egg formation. Increased amounts of testosterone in eggs enhances nestling development, stimulates food begging, and increases aggressive behavior in the young (Schwabl, 1996, 1997).

Body condition of females had an effect on hatching date, mothers in better condition giving birth earlier. Contrarily, corticosterone-treated females, even in good body condition, gave birth later. This fact could be interpreted as an accidental consequence of corticosterone or as effective plasticity. A retarded hatching in a stressful situation could be advantageous because embryos have more time for fetal growth. But a retarded hatching date could also be a by-product of the manipulated maternal condition. It is known the pregnant females have reduced locomotor performance and increased vulnerability to predation (Shine, 1980). Thus, our results probably show an accidental increase in gestation time due to corticosterone administration. Chronic stress (as induced by parasitism, for example) during pregnancy potentially constitutes an important maternal effect that can affect the phenotype of the offspring. In many species of reptiles, including *L. vivipara*, the production of corticosterone has been found to rise during pregnancy (Dauphin-Villemant *et al.*, 1990). Corticosterone is involved in regulation of body fluids (Bradshaw *et al.*, 1984), including transplacental water flow (Dauphin-Villemant and Xavier, 1986), and is therefore likely to have an important impact on embryonic development. The retardation in the parturition date that we observed in our study points to corticosterone influencing fetal growth. This has also been suggested by Pollard (1986) and Dauphin-Villemant (1986) for *L. vivipara*. In other studies with *L. vivipara* where corticosterone was applied to pregnant females (de Fraipont *et al.*, 2000, Meylan *et al.*, submitted for publication), those effects on development were not found. A reasonable interpretation of this is that many other factors may determine how glucocorticoids modulate physiology during development of the embryos.

Juvenile characteristics were not influenced of maternal condition but of prenatal corticosterone increase. Corticosterone-treated females gave birth to a higher number of dead neonates and to less corpulent juveniles than placebo females. In contrast, juvenile survival is not affected by the maternal corticosterone treatment (Meylan and Clobert, in preparation). Pollard (1984) and Dauphin-Villemant and Xavier (1986) also found a higher mortality at birth in juveniles issued from treated females. A higher mortality and a

decreased corpulence can also be a consequence of a retarded fetal growth promoted by maternal stress. The presence of dead neonates did not increase the corpulence of the siblings, suggesting that there was not an effective reallocation of embryonic resources. The condition of the mother during gestation is crucial for the right development of the embryos. The timing of parturition is dependent on a cascade of endocrine signals, and corticosterone constitutes a key to parturition (McMillen *et al.,* 1995).

Postnatal Factors: Juvenile Condition and Postnatal Corticosterone Treatment

Dispersing juveniles were in a better body condition than philopatrics. Dispersal is potentially energetically expensive, as dispersers are vulnerable to predation, may have difficulty finding food, and may encounter aggression from conspecifies as the former attempt to establish in new territories or groups (Gaines and McLanaghan, 1980; Van Vuren and Armitage, 1994). Thus, a robust physical condition may decrease the high risks associated with these movements, and the result found here may respond to this. Indeed, natural selection could favor animals that delay departure from natal areas until their energy reserves are adequate to support the potential demands of the dispersal movements (Nunes and Holekamp, 1996; Belthoff and Dufty, 1998; Nunes *et al.*, 1998).

Corticosterone increase in neonates did not influence juvenile dispersal. In birds, experimentally elevated corticosterone level has been demonstrated to increase the offspring dispersal propensity. In one oviparous reptile, corticosterone has also been demonstrated to increase locomotor activity (Belliure and Clobert, in preparation). Our ovoviviparous species is characterized by a lack of maternal care, a long gestation period, and a short postnatal period before the onset of dispersal. Therefore, a likely explanation for the absence of a corticosterone effect at the postnatal stage is the restricted window of time during which dispersal can be influenced postnatally. Dispersal takes place very early in life in this species, within 10 days of birth. Therefore, juveniles must assess natal environment quality very quickly. Consequently, prenatal acquisition of this information would be useful in making the appropriate decision and would avoid the cost of exploring the natal site (Massot and Clobert, 1995). However, other factors, such as crowding (Léna *et al.,* 1998) and habitat characteristics (humidity and temperature, Lorenzon *et al.,* 2001), have been shown experimentally to influence dispersal after birth.

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