ULLER, T. 2004. SEX ALLOCATION AND MATERNAL EFFECTS IN LIZARDS

ABSTRACT

An adult organism is the product of genes, and pre- and postnatal environmental influences, including maternal effects. Understanding the relevance importance of these different factors and their interaction is a major goal of evolutionary biology. Maternal effects occur when the phenotype of the mother, or the environment she experiences, influence the phenotype of her offspring. Maternal hormone profile can shape offspring phenotype in both egg-laying and live-bearing animals, via steroid allocation to the yolk or the developing fetus, but the potential adaptive value of this is unknown. Experimental manipulation of prenatal testosterone exposure in the live-bearing common lizard, *Lacerta vivipara,* increased growth after birth, which may have beneficial effects on age at maturity or fecundity. However, offspring experiencing high levels of testosterone in utero were more susceptible to ectoparasites. Not only androgens can shape offspring development. Under stressful conditions, maternal production of glucocorticoids increases, with potential consequences for offspring brain development. In the common lizard, exposure to corticosterone before birth made offspring less risk-prone in their behaviour. If maternal stress is indicative of an unsafe environment, this could be an adaptive mechanism whereby females can increase offspring survival.

In viviparous animals, offspring can influence each other via hormonal diffusion between fetuses. The exposure to sex-specific steroids in utero is likely to be a function of the relative number of males and females in the clutch. Prenatal sex ratio is therefore predicted to correlate with degree of masculinization/feminization in viviparous animals, but this hypothesis has been little explored. In *L. vivipara,* prenatal sex ratio influenced sexual dimorphism at parturition. A long-term study of a natural population further showed that such effects have important and long-lasting fitness consequences by influencing, e.g., age at maturity and fecundity. Although there were negative effects of opposite-sexed siblings, maternal fitness may not be compromised if negative effects on the underrepresented sex are counteracted by positive effects on the overrepresented sex. Alternatively, offspring from clutches of different sex ratios could represent different points along a trade-off function, e.g., between age at maturity and fecundity.

Whenever expected fitness returns from sons and daughters differ, sex allocation theory predicts that females should invest more in the sex with highest return. Theoretical modelling of sex-specific sex ratio effects on offspring fitness (as found in live-bearing animals) suggests that this can either select for skewed sex ratios, or constrain sex ratio evolution. Furthermore, the presence of sex chromosomes can select for skewed sex ratios in relation to parental genetic quality, because deleterious alleles on the sex chromosomes will have higher penetrance in the heterogametic sex. Thus, the fitness return from the heterozygous sex is likely to parallel, or surpass, that of the homogametic sex only under high paternal genetic quality (an extension of Haldane's rule). In sand lizards, *L. agilis,* females are the heterogametic sex (females ZW, males WW). Clutches with more males showed higher hatchability and fewer malformations than female-biased clutches. In accordance with predictions from sex allocation theory, females skewed their sex ratio towards females when mating with males of high genetic quality, both in the laboratory and in a natural population.