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Natalia Atkins

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Parental effects in two species of viviparous lizards: *Niveoscincus microlepidotus* and *N. ocellatus*



by

Natalia Atkins BSc. (Hons)

Submitted in fulfillment of the requirements for the Degree of
Doctor of Philosophy, School of Zoology, University of
Tasmania
(June, 2007)

Declaration

This thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution, and to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text of the thesis.

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This thesis contains the following published papers:

Chapter 2: **Atkins, N, Swain R, Jones SM. 2007a.** Are babies better in autumn or spring? The consequences of extending gestation in a biennially reproducing viviparous lizard. *Journal of Experimental Zoology* **307A**: 397-405.

Chapter 3: **Atkins N, Swain R, Jones SM. 2006.** Does date of birth or a capacity for facultative placentotrophy influence offspring quality in a viviparous skink, *Niveoscincus microlepidotus*? *Australian Journal of Zoology* **54**: 369-374.

Chapter 4: **Atkins N, Swain R, Wapstra E, Jones SM. 2007b.** Late stage deferral of parturition in the viviparous lizard *Niveoscincus ocellatus* (Gray 1845): implication for offspring quality and survival. *Biological Journal of the Linnean Society* **90**: 735-746.

Chapter 5: **Atkins N, Jones SM, Guillette Jr. LJ. 2006.** Timing of parturition in two species of viviparous lizard: influence of beta-adrenergic stimulation and temperature upon uterine responses to arginine vasotocin (AVT). *Journal of Comparative Physiology B* **176**: 783-792.

Appendix 1: **Atkins N, Wapstra E. 2004.** Successful treatment of a mite infestation in gravid spotted snow skinks (*Niveoscincus ocellatus*). *Herpetofauna* **34**: 66-69.

Abstract

This thesis focuses on maternal contributions to offspring fitness in viviparous lizards. Although parental effects may include both pre- and postpartum components, the majority of squamate reptile species exhibit no parental care: parental effects on offspring fitness can, therefore, be imposed only until the time of oviposition or parturition.

In viviparous reptiles, offspring are retained *in utero* for the entire duration of embryogenesis, but in most species the majority of embryonic nutrition is supplied through the yolk with a small contribution by a simple placenta. In some reptilian species, viviparity has evolved further, resulting in a diverse range of placental arrangements and a complete spectrum of embryonic nutritional modes being displayed across a wide range of taxa. It has been suggested that facultative placentotrophy (the ability to supplement an adequate yolk supply) allows the introduction of flexibility into the timing of parturition by providing embryos with additional energy stores to utilise if parturition is delayed. My study species were two closely related viviparous lizards found in Tasmania, Australia. Previously, embryonic nutrition has been shown to be predominantly placentotrophic in *Niveoscincus ocellatus*; I have now determined that embryonic nutrition is predominantly lecithotrophic in *N. microlepidotus*, and that females may utilise facultative placentotrophy only in some years.

My thesis investigated the major hypothesis that deferral of parturition after completion of embryonic development is a key strategy employed by females of viviparous lizards to maximise offspring fitness. The three interlinked papers on this theme that I have included in my thesis support my hypothesis. In *N. ocellatus*, deferring parturition in response to cold conditions had no effect on offspring

phenotype at birth, dispersal distance or survivorship of offspring after release; however, there was a significant negative effect on offspring growth measured after release, which has profound implications for age and size at maturity. I found that females from a high elevation population were less able to defer birth under “long” periods (three weeks) of cold conditions than females of a low elevation population. I attribute the reduced ability of females from the high elevation population to defer parturition to selection for preventing births too close to winter.

However, in the biennially reproducing *N. microlepidotus*, my results have identified that the naturally protracted deferral of parturition from autumn until spring represents a trade-off between offspring quality and offspring size. Finer scale variation in the timing of parturition also influences neonatal characteristics: I have shown that there is an effect of date of birth on several key offspring characteristics at birth in *N. microlepidotus*. Experimental manipulations of the maternal environment demonstrated that females are able to defer birth for an additional four weeks at the end of gestation, but with no significant effect on offspring characteristics.

How is the timing of parturition determined if fully developed embryos may be held *in utero* for significant periods of time? I discovered that in *N. microlepidotus* the uteri are equally responsive to hormonal stimulation (arginine vasotocin (AVT) and prostaglandin ($\text{PGF}_{2\alpha}$) in autumn and spring. In both *N. microlepidotus* and *N. ocellatus*, females are more responsive to AVT than to $\text{PGF}_{2\alpha}$, and the response to AVT is decreased, but not prevented, by β -adrenergic stimulation. In *N. ocellatus*, temperature modulates the response to AVT *in vivo*, with the time to parturition increasing as temperature decreases. In these viviparous

species, then, the endocrine cascade leading to parturition is modulated by the β -adrenergic system.

The final component of the thesis investigated male reproductive success in a population of *N. ocellatus*. I determined the paternity of 65% of the offspring; the results demonstrate that the species has a high level (93%) of multiple paternity within litters, with females having access to many males. While female size is correlated with litter size, I was unable to identify any factors that determine male reproductive success. In addition, the size of the father within a litter had no effect on offspring characteristics at birth, and no measured parental characteristics were determinants of offspring survival.

This thesis has demonstrated that females of viviparous lizards exhibit a suite of characteristics that enable them to manipulate offspring characteristics through the control of the timing of parturition. This provides new evidence to support Shine's "Maternal Manipulation Hypothesis".

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