Optimizing reproduction in the Tasmanian echidna *Tachyglossus aculeatus setosus*: the influence of an obligatory hibernation period and intense sexual conflict

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

University of Tasmania
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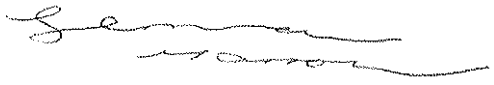

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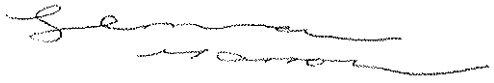

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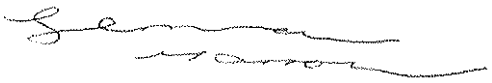

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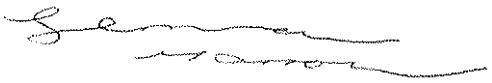
The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.



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Statement of Publication and Co-authorship

The following people and institutions contributed to the publication of the work undertaken as part of this thesis:

Paper 1:
Cool Sex? Hibernation and reproduction overlap in the echidna. *PLoS ONE*
Located in chapter 2
Candidate (50%), author 1 (Stewart Nicol) (50%)

Details of authors roles:
Author 1 contributed to the concept and planning of the study and data collection.

Paper 2:
Maternal Care in the Tasmanian echidna (*Tachyglossus aculeatus setosus*). *Australian Journal of Zoology*
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Candidate (70%), author 1 (Stewart Nicol) (30%)

Details of authors roles:
Author 1 contributed to the planning of this study and assisted with data analysis

We the undersigned agree with the above stated "proportion of work undertaken" for the above published peer-reviewed manuscripts contributing to this thesis:

Signed: _____ _____

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Date: 5 September 2013

The following people contributed to the research undertaken as part of this thesis

Stewart Nicol (School of Zoology, University of Tasmania) contributed to the concept and planning of the study, provided assistance with statistical analysis as well as constructive criticism of data analysis and interpretation of results and chapter drafts.

Susan Jones (School of Zoology, University of Tasmania) provided guidance on data collection, supervised radioimmunoassay work, provided constructive criticism of data analysis and interpretation of results and chapter drafts.

Rachel Harris (School of Zoology, University of Tasmania) assisted with data collection in the field.

Sean Muir (Hobart Private Hospital, Tasmania) provided field assistance and took the first ultrasound of an egg *in utero* (featured in chapter 2).

This thesis is based on field data collected by me in the period of January 2008 to December 2010, but also includes some data collected by me in 2007 as well as data collected as part of a long time project on echidna reproductive biology. Data I collected in 2007 is included in chapter 2 *Cool sex? Hibernation and reproduction overlap in the echidna* and chapter 5 *Maternal care in the Tasmanian echidna*. Data from 2007 in chapter 2 *Cool sex? Hibernation and reproduction overlap in the echidna* includes two observations previously reported in my honours thesis (Morrow 2007). A small number of additional data collected by other researchers is included in chapter 2 *Cool Sex? Hibernation and reproduction overlap in the echidna*, Chapter 3 *Reproductive tactics of the Tasmanian echidna* and Chapter 5 *Maternal care in the Tasmanian echidna*.

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Abstract

The echidna is a solitary, seasonally breeding monotreme mammal with a mating system characterized by high levels of intra-male competition for access to receptive females. Throughout Australia the breeding season follows a period of inactivity which ranges from shallow bouts of torpor to prolonged deep hibernation. In this thesis I investigated how the Tasmanian echidna optimizes its reproduction around an obligatory hibernation period and in the presence of intense sexual conflict.

The bradymetabolic (slowing of metabolism) effect of hibernation was exploited by both sexes to optimize their reproduction. I found that testes recrudescence (defined as an increase in testes volume and density) was initiated prior to males entering hibernation, a strategy not seen in any other hibernating mammal. This strategy can be linked to the low energy and density diet and requirement to hibernate to maximise energy-savings, and to the large relative size of echidna testes reflecting a mating system with intense levels of intra-male competition. It took approximately two months at euthermic body temperatures from the initiation of recrudescence in December for echidna testes to reach 75% of peak size. Therefore if testes recrudescence did not occur prior to entering hibernation, hibernation would be restricted to a one and a half month period to allow mating in June.

Male echidnas initiated mating activity by locating hibernating females and entering their hibernacula. This strategy was common in my study population and males that remained with a female in her hibernaculum for 13 hours or more gained a copulation opportunity. However, all females that mated or were disturbed by males prior to July 27 re-entered hibernation. This indicates that mating often occurred earlier than optimal for female reproductive success. Many of the females that re-entered hibernation after mating were pregnant. Pregnant females entered hibernation only in early pregnancy: hibernation extended the gestation period and hence allowed females to delay egg-laying. Females timed their reproduction so that they emerged from their 37 day period of nursery burrow confinement as ecosystem productivity increased. Hibernation therefore allows successful reproduction in a population where there is asynchronous timing of optimal mating between males and females.

This thesis explores the influence of hibernation on sexual conflict, demonstrates the numerous interactions that can occur between hibernation and reproduction and shows that the bradymetabolic property of hibernation is exploited by both male and female echidnas to optimize reproductive fitness.

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