THE TERRESTRIAL ECOLOGY OF A FRESHWATER TURTLE, *CHELODINA LONGICOLLIS*, IN BOODEREE NATIONAL PARK, AUSTRALIA

By

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STATEMENT OF ORIGINALITY

This thesis is my original work and has not been submitted, in whole or in part, for a degree at this or any other university. Nor does it contain, to the best of my knowledge and belief, any material published or written by another person, except as acknowledged in the footnotes, quotations or references.

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STATEMENT OF CONTRIBUTION

Because this thesis is written as a series of chapters prepared for publication in peer-reviewed journals, several people other than myself contributed to the work, and they deserve acknowledgement. These include:

- Arthur Georges (Institute for Applied Ecology, University of Canberra), who as my primary supervisor provided his guidance and wisdom in all phases of the work, and was also instrumental in fund raising
- Brian Green (Institute for Applied Ecology, University of Canberra), who provided his technical expertise and advice in the design, implementation, sample analyses, and interpretation in doubly-labelled water
- Alicia Brinton (my wife), who willingly spent her time tramping around, paddling through, and snorkelling in the waterholes of Booderee National Park

These people are included as authors in the following chapters as well as the associated publications, in the order of their contribution to the work. However, despite the collaborative nature of this thesis, the work within is my own, and I received no additional assistance other than that which is stated above.

I as primary supervisor, agree with the above stated proportion of work undertaken for each of the published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Prof Arthur Georges

December 2007

ACKNOWLEDGMENTS

I have always looked forward to acknowledging the contributions of others at the beginning of a work instead of at the end. A project of any magnitude reflects the collective contributions and support from several people and organizations. A doctoral thesis is certainly no exception. Recognizing those that helped to complete this process should not come as an afterthought, but should be at the forefront for the reader to encounter before they are skipping every second line and only looking at the pictures by the end.

I would first like to thank Alicia Brinton, who willingly uprooted herself from friends, family and career to travel to Australia with me and help me pursue a long-time dream of studying Australian reptiles. She snorkelled her way through reedy and at times cold wetlands filled with eels, battled the winds of Lake Windermere in the canoe, filled bait bags with smelly meat and soggy bread, marked and measured turtles until her hands and back ached, swatted flies, pulled funnel webs out of pitfalls by the hundreds, sidestepped red-bellied black snakes and generally put up with my absence of attentiveness throughout various stages of our time here in Australia. I could not have done any of this without her support and understanding. I would also like to thank Tasman, whom I looked forward to coming home every afternoon and weekend to play with.

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ABSTRACT

Most studies of wetlands tend to focus on the biotic and abiotic interactions within the aquatic habitat. Though wetlands and associated biota may appear to be somewhat isolated from the influence of the wider landscape, wetland habitats are critically linked with adjacent terrestrial habitats and other wetlands through the two-way flows of energy and nutrients and provision of structure. While an understanding of these inter-habitat linkages is breaking down the perceived boundaries between "aquatic" and "terrestrial" ecosystems, there is more limited knowledge on the ecology of wetland animals that must meet critical needs in both aquatic and terrestrial habitats at some time during their life or seasonal cycles. Here, I examine the terrestrial ecology of a freshwater turtle, the eastern long-necked turtle (*Chelodina longicollis*) in the temporally dynamic and heterogeneous landscape of Booderee national park in south-east Australia by 1) providing a description of terrestrial behaviours, 2) identifying the factors driving terrestrial behaviour and its functional significance, 3) examining factors that may limit or constrain terrestrial behaviour and 4) demonstrating how various terrestrial behaviours can factor prominently in the overall biology of a nominally aquatic animal.

Chelodina longicollis used terrestrial habitats for reasons other than nesting, including aestivation and movements between wetlands. Radio-telemetry of 60 turtles revealed that nearly 25 % of all locations were in terrestrial habitats up to 505 m from the wetland, where turtles remained for extended periods (up to 480 consecutive days) buried under sand and leaf litter in the forest. Individuals also maintained an association with a permanent lake and at least one temporary wetland within 1470 m, though some inter-wetland dispersal movements were much longer (5248 m). As a result of their associations with several wetlands and terrestrial aestivation sites, *C. longicollis* traversed large areas and long distances (13.8 ± 2.8 ha home range, 2608 ± 305 m moved), indicating that this species is highly vagile. In fact, a three-year capture-mark-recapture study conducted in 25 wetlands revealed that 33% of the population moved overland between wetlands. After scaling this rate to the number of generations elapsed during the study, *C. longicollis* moved between discrete water bodies at a rate of 88–132% per generation. This rate is not only high for freshwater turtles, but is among the highest rates of inter-patch movement for any vertebrate or invertebrate.

Chelodina longicollis demonstrated an impressive capacity for individual variation in nearly every aspect of its behaviour examined. Most of the variation in space use, movements, terrestrial aestivation and activity could be attributed to extrinsic local and landscape factors, seasonal influences and rainfall, whereas intrinsic attributes of the individual such as sex, body size, body condition and maturity status were less important.

Turtles increased movement distance and home range size in regions where inter-wetland distances were farther and with increasing wetland size. Individuals spent more time in terrestrial habitats with decreasing wetland hydroperiod and increasing distance to the nearest permanent lake. Overland movements between wetlands were correlated with rainfall, but the directionality of these movements and the frequency with which they occurred varied according to the prevalent rainfall patterns; movements were to permanent lakes during drought, but turtles returned to temporary wetlands *en masse* upon the return of heavy rainfall. However, deteriorating conditions in drying wetlands forced turtles to move even in the absence of rainfall. Captures at a terrestrial drift fence revealed that immature turtles as small as 72.3 mm plastron length may move overland between wetlands with similar frequency as larger adults. Taken together, these results suggest that *C. longicollis* behaviour is in part conditional or state-dependent (i.e., plastic) and shaped by the spatiotemporal variation and heterogeneity of the landscape.

Perhaps the most surprising aspect of individual variation was the alternate responses to wetland drying. Turtles either aestivated in terrestrial habitats (for variable lengths of time), or moved to other wetlands. Movement to other wetlands was the near universal strategy when only a short distance from permanent lakes, but the proportion of individuals that aestivated terrestrially increased with distance to the nearest permanent lake. When long distances must be travelled, both behaviours were employed by turtles in the same wetland, suggesting that individuals differentially weigh the costs and benefits of residing terrestrially versus those of long-distance movement. I propose that diversity in response to wetland drying in the population is maintained by stochastic fluctuations in resource quality. The quality of temporary wetlands relative to permanent wetlands at our study site varies considerably and unpredictably with annual rainfall and with it the cost-benefit ratio of each strategy or tactic. Residency in or near temporary wetlands is more successful during wet periods due to production benefits (high growth, reproduction and increased body condition), but movement to permanent wetlands is more successful, or least costly, during dry periods due to the fitness benefits of increased survival and body condition.

I used the doubly-labelled water (DLW) method to provide the first estimates of water and energy costs of aestivation and overland movement for any freshwater turtle behaving naturally in the field. *Chelodina longicollis* remained hydrated while terrestrial with water flux rates (14.3–19.3 ml kg^{-1} d^{-1}) on par with those of strictly terrestrial turtles, but field metabolic rate during aestivation (20.0–24.6 kJ kg^{-1} d^{-1}) did not indicate substantial physiological specializations in metabolism during aestivation. Energy reserves, but not water, are predicted to limit survival in aestivation to an estimated 49–261 days, which is in

close agreement with the durations of natural aestivation. The energy costs of overland movement were 46–99 kJ $(kg\ d)^{-1}$, or 1.6–1.7 times more expensive than aestivation. When a wetland dries, a turtle that foregoes movement to other wetlands can free sufficient energy to fuel up to 134 days in aestivation. The increasing value of this energy "trade-off" with travel distance fits our behavioural observations of variance in response to wetland drying.

Taken together, this evidence indicates that terrestrial habitats provide more than just organic and structural inputs and filtering services and that nearby wetlands are important for reasons other than potential sources of occasional colonists to a population. Terrestrial habitats are used for aestivation in response to wetland drying and different wetlands are diverse in their functions of meeting the annual or life-cycle requirements of *C. longicollis* in temporally dynamic wetland systems. As overland movements between these various habitat types are in response to spatiotemporal variation in habitat quality and associated shifts in the fitness gradient between them, I suggest that terrestrial and different aquatic habitats in Booderee offer complementary resources contributing to regional carrying capacity and population persistence of the turtle population. Thus, important ecological processes regulating *C. longicollis* in a focal wetland should not be viewed as operating independently of other nearby wetlands and their adjacent terrestrial habitats. Collectively, these findings highlight the complex and dynamic associations between a population of freshwater turtles and the wider terrestrial and aquatic landscape, demonstrating that turtle populations and the factors that impact them can extend well beyond the boundaries of a focal wetland.

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List of publications associated with this thesis:

Roe JH**,** Georges A (2007) Heterogeneous Wetland Complexes, Buffer Zones, and Travel Corridors: Landscape Management for Freshwater Reptiles. *Biological Conservation* 135, 67-76.

Roe JH, Georges A (2008) Maintenance of variable responses for coping with wetland drying in freshwater turtles. *Ecology* 89, 485-494.

Roe JH, and Georges A (in press) Terrestrial activity, movements, and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis*, in a temporally dynamic wetland system. *Austral Ecology*. Accepted pending revision.

Roe JH, Georges A, Green B (in press) Energy and water flux during terrestrial aestivation and overland movement in a freshwater turtle. *Physiological and Biochemical Zoology*.

Roe JH, (in press) *Chelodina longicollis* (Eastern Long-necked Turtle). Drinking Behavior. Herpetoligical Review.

Roe JH, Brinton AC, Georges A (in review) Temporal and spatial variation in landscape connectivity for an Australian freshwater turtle in a temporally dynamic wetland system. *Ecological Applications*.