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

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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.

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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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STATEMENT OF CO-AUTHORSHIP

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.

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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*.

GENERAL INTRODUCTION

Picture: forest reflection in the Steamers Waterhole

The merger of wetland and terrestrial ecology

A wetland is traditionally described as an ecosystem that has arisen where hydric conditions force biota to adapt to periodic or prolonged inundation by water (Keddy 2002). Though definitions of wetlands vary in their details, most tend to follow a similar theme and focus on biotic and abiotic interactions within the boundaries of the aquatic habitat, which is typically delineated from surrounding terrestrial areas by soil and vegetation characteristics that mark the waterline (Cowardin et al. 1979, Buhlmann et al. 2001, Grant 2005). Defining the wetland from the standpoint of its water and how that water influences biota is simple and intuitive. The boundary between aquatic and terrestrial habitats is easy to decipher and the biota inhabiting these two habitat types are usually very distinct from one another in their morphology, physiology and ecology (Bentley and Schmidt-Nielsen 1966, Schmidt-Nielsen 1972, Gillis and Blob 2001). Such divisions give scientists a logical framework within which to narrow down potentially broad questions into more specialized inquiries. For instance, a researcher interested in identifying the biotic and abiotic factors regulating fish populations in a lake would more likely find answers by first collecting data on aquatic invertebrate prey and water temperatures than they would from leaf-litter invertebrates and soil moisture in the nearby forest. While these divisions can provide a useful starting point from which to launch scientific inquiry, they can also erect arbitrary boundaries.

Taking a broader view, a wetland is not a single entity, but rather a part of a much larger landscape comprised of other wetlands and terrestrial habitats, as well as their associated biota. Wetlands may appear to be isolated from one another on the surface, but sub-surface flows of groundwater or occasional above-surface flooding can connect them and provide a vector for water and material transfers, as well as movements of biota. As a result, water level manipulations, flow alterations, pollution, or biota in one area of the wetland system can eventually affect the hydrology, quality and population and community dynamics in other connected water bodies (Suso and Llamas 1993, Barendregt et al. 1995, Snodgrass et al. 1996, Chimney and Goforth 2001, Amezaga et al. 2002).

Aquatic systems can also be linked with adjacent terrestrial habitats. For instance, terrestrial habitats directly provide important structure and substrate to their aquatic counterparts in the form of woody debris and other organic matter (Minshall 1967, Bilby and Ward 1991), sediment from runoff (Allan et al. 1997), bank and shoreline stabilization from roots (Gregory et al. 1991) and can indirectly influence solar radiation and water temperature by the provision of shade by the canopy (Barton et al. 1995). Terrestrial habitats also provide energy and nutrients to aquatic systems with substantial consequences to the aquatic food web

(Fisher and Likens 1973, Spencer et al. 2003, McLeod and Wing 2007), but these transfers run in the opposite direction as well. Sediment and nutrients can be deposited from the wetland into nearby terrestrial areas during flooding or via the activities of animals (Ballinger and Lake 2006, Crait and Ben-David 2007). For example, forest trees near salmon spawning streams derive a substantial amount of essential nutrients such as nitrogen and carbon from fish (Ben-David et al. 1998). This transfer is in large part mediated by bears that congregate to forage on the fish and then deposit the nutrients into the forest in the form of partially-eaten salmon carcasses, urine and faeces (Hilderbrand et al. 1999). Fertilization of the forest with salmon-borne nutrients increases tree growth rates, which in turn provides more structure, canopy and nutrient and sediment filtering services to then enhance the quality of stream spawning habitats for the salmon (Herfield and Naiman 2001). An understanding of how such feedback loops can operate across habitat borders is going a long way towards breaking down the traditional boundaries between distinct "aquatic" and "terrestrial" ecosystems.

Despite these and other advances in our understanding of inter-ecosystem links, there are still major gaps in our knowledge. Perhaps the greatest misunderstanding or knowledge gap is in the ecology of wetland animals that also rely on terrestrial habitats. I am not referring here to ecotonal animals that occupy the interface between aquatic and terrestrial habitats, but rather to species that must meet critical needs by fully engaging in both of these distinct habitats at some time during their life or seasonal cycles. Ecological studies of these animals have understandably been traditionally focussed on their interactions with aquatic habitats, with a much less detailed emphasis on potentially important interactions with the terrestrial environment. This is not to suggest that terrestrial habitat use by aquatic animals has gone unrecognized in its contribution to a species' overall ecology. In fact, several recent reviews have compiled examples of terrestrial habitat use in various wetland-associated vertebrates (Sayer and Davenport 1991, Semlitsch 1998, Semlitsch and Bodie 2003, Gibbons 2003, Bodie 2001) and some invertebrates (Foster and Soluk 2006, Welch and Eversole 2006). These reviews and the individual studies within them typically do not go beyond a general description of the terrestrial behaviours observed, but there are exceptions. The role of terrestrial ecology in the overall biology of wetland-associated animals is perhaps best understood in aquatic-breeding amphibians (Berven 1990, Feder and Burggren 1992, Duellman and Trueb 1986, Pechmann 1995, Chazal and Neiwiarowski 1998, Taylor et al. 2006, Rothermel and Semlitsch 2002). Through these studies and others, the physiology and behaviour of amphibians within the terrestrial environment has been examined within the context of population regulation and community dynamics (op. cit.), increasing our knowledge beyond simple descriptions of habitat associations and leading towards a more

holistic understanding of amphibian ecology. However, it is safe to say that the ecology of aquatic and semi-aquatic species in the wetland has received far more attention than terrestrial behaviours even for amphibians (Semlitsch 1998, Scott et al. 2006). For most other semi-aquatic animals, emphasis is typically placed on one aspect of terrestrial habitat use (e.g., nesting biology of aquatic reptiles; see below) if any, when in fact there may be several additional terrestrial activities. What results is an imbalance in what is thought to contribute to a species overall ecology. This disconnect between terrestrial ecology and the factors contributing to population regulation in aquatic animals is perhaps most evident in the management of wetlands and associated wildlife (Semlitsch 1998, Semlitsch and Bodie 2003, Gibbons 2003, Roe et al. 2006).

Terrestrial ecology is defined here as the interaction of aquatic biota with their terrestrial environment, including all aspects of their seasonal and life cycles undertaken in terrestrial habitats, even if such activities occur only occasionally or for short durations of time. Aquatic animals directly interact with terrestrial habitats for reliance on its resources (e.g., food) or structural attributes (e.g., shelter sites) and as a medium through which they must travel when moving between wetlands. Whether the behaviour involves residing within or just moving through the terrestrial environment, aquatic animals will have to contend with several challenges when out of the water.   Species, populations and individuals will differ in the specifics of these interactions based on biological limitations that constrain behaviour or habitat characteristics that influence their motivation to behave in a particular manner. Understanding the unique challenges that aquatic animals face when out of the water as well as the behavioural and physiological mechanisms that they employ to address these challenges defines not only their terrestrial ecology, but also leads to a more holistic understanding of their overall biology.

Terrestrial ecology of freshwater turtles

The majority of turtle species inhabit either lentic (nonflowing) or lotic (flowing) freshwater habitats (Burke et al. 2000). Associations of freshwater turtles with their aquatic habitats are unquestionably important, but few (if any) carry out all essential behaviours or parts of their life cycle completely within the wetland. All species require some degree of terrestrial exposure during egg incubation and embryonic development, but some achieve this by never leaving the delineated wetland. For instance, *Chelodina rugosa* in the seasonal wet-dry tropics of Australia can lay eggs in shallow water, but development does not occur until the nest environment dries (Kennett et al. 1998, Fordham et al. 2006a). Other species inhabiting

extensive swamps in Papua New Guinea can nest on floating mats of vegetation (Georges et al. 2006). Both of these strategies allow turtles to remain within the wetland environment to nest, relieving them of the challenges encountered in terrestrial habitats.

The vast majority of freshwater turtles must nest terrestrially, which requires overland migrations by the female and a period of incubation and (at times) delayed emergence from the nest by hatchlings, followed by overland travel back to the wetland. The nesting biology of freshwater turtles is the most intensively studied aspect of their terrestrial ecology. The behaviour and physiology of females during nesting (Congdon et al. 1983, 1987, Congdon and Gatten 1989, Iverson 1990, Wilson et al. 1999, Spencer 2002) has been well explored. The influence of abiotic and biotic factors on the development and physiology of embryos and hatchlings in the nest (Packard et al. 1985, 1987, Janzen 1994, Costanzo et al. 1995, Spencer and Thompson 2005), as well as hatchlings during the period of travel to the wetland (Janzen 1993, Butler and Graham 1995, Janzen et al. 2000, Finkler 2001) have also been the subject of intensive observational and experimental investigations in the field and laboratory. These findings are typically examined in the context of individual fitness and the evolution of behavioural and physiological mechanisms that allow aquatic turtles to meet the many challenges of the terrestrial environment. As a result, studies of terrestrial ecology associated with nesting have contributed greatly to our knowledge of the overall biology of freshwater turtles.

Many species of freshwater turtles use the terrestrial environment not just to nest, but also for several additional behaviours. Some species such as the wood turtle (*Clemmys insculpta*) use the wetland for overwintering, courtship and nocturnal retreats, but most foraging and other activities are conducted in terrestrial habitats (Kaufmann 1992, Ernst et al. 1994). In other aquatic and semi-aquatic species, terrestrial habitats are used for extended periods of refuge during overwintering and aestivation, sometimes requiring periods of several months or more out of water (Bennett et al. 1970, Wygoda 1979, Burbidge 1981, Stott 1987, Buhlmann 1995, Burke et al. 1995, Graham 1995, Morales-Verdeja and Vogt 1997, Litzgus and Brooks 2000, Buhlmann and Gibbons 2001, Joyal et al. 2001, Milam and Melvin 2001, Ligon and Stone 2003). This list of examples is certainly not exhaustive, but instead reflects a set of representative studies for several species where terrestrial behaviour was of primary interest to the researchers. Observations of terrestrially inactive turtles are often anecdotal and not the primary focus of the investigators and as a result the documentation of such behaviour is buried within a broader autecological paper or only reported in a small research note (e.g., Teska 1976, Chessman 1983). Also, while there appear to be species that regularly engage in terrestrial aestivation and hibernation throughout their range (several

Kinosternon spp., *Emydoidea blandingii*, *Clemmys guttata*, *Pseudemydura umbrina*; op. cit.), some species typically considered to be highly aquatic can engage in extended terrestrial activity in particular situations. For instance, Buhlmann and Gibbons (2001) documented long-term terrestrial inactivity in common snapping turtles (*Chelydra serpentina*) and musk turtles (*Sternotherus odoratus*) inhabiting a seasonally fluctuating wetland in South Carolina, whereas this behaviour is not typical of these species in permanently flooded lakes and rivers in other parts of their range (Obbard and Brooks 1981, Mitchell 1988, Ernst et al. 1994). Thus, our understanding of the propensity for freshwater turtles to aestivate and overwinter on land should improve with more detailed studies in different habitat types and across the range of the species in question.

Freshwater turtles may also venture overland when travelling between wetlands. Reasons for turtle movement include dispersal, exploitation of seasonal resources, reproduction, escape from deteriorating conditions, or other enigmatic reasons (Gibbons 1986, Gibbons et al. 1990) and these generally apply to turtles inhabiting freshwater systems. Movements between wetlands have traditionally been considered as emigration between two demographically distinct populations (op. cit.), but this view has recently been challenged for species that move more regularly (Joyal et al. 2001, Bowne et al. 2006, Chelazzi et al. 2006). Instead, it is proposed that the turtles occupying a group of wetlands be considered the smallest demographic unit of a patchy population (op. cit., Harrison 1991). This approach is appealing because it emphasizes the potential importance of inter-wetland movements both at the level of the individual (i.e., the smallest unit of a population) and the metapopulation (i.e., a group of populations; Harrison 1991). Viewing inter-wetland movements as emigration events constrains its causes to only dispersal or evacuation of a deteriorating wetland, when in fact such movements may occur much more regularly as a part of the individual's strategy for meeting resource requirements in particular contexts. Also, just as terrestrial aestivation and overwintering behaviour can vary between populations in different habitat types across a species range, movements between wetlands can also be highly variable among different populations (e.g., painted turtles [*Chrysemys picta*]; Scribner et al. 1993, Bowne et al. 2006, Mitchell 1988, Rowe 2003). Many inter-wetland movements have likely escaped notice if the study is carried out in just a single wetland, landscape type, or region, further de-emphasizing the functional significance of this potentially important behaviour. However, it is unclear how many wetlands, or what size area, should be considered as collectively harbouring a single population.

The eastern long-necked turtle (*Chelodina longicollis*) inhabits nearly the full range of freshwater habitat types across a broad area in southeast Australia (Fig. 1.1). The aquatic

Figure 1.1. Range map for the eastern long-necked turtle (*Chelodina longicollis*) and the location of the study site, Booderee National Park, off the south coast of New South Wales, Australia.

ecology of this carnivorous turtle has been well explored (Chessman 1984a, 1988a, 1988b, Parmenter 1976, Georges et al. 1986, Kennett and Georges 1990). However, *C. longicollis* uses terrestrial habitats during several behaviours including nesting, aestivation, overwintering and movements between wetlands (Chessman 1978, 1983, 1984b, Stott 1987, Parmenter 1976, Kennett and Georges 1990). The abilities of *C. longicollis* to navigate while moving through terrestrial habitats (Graham et al. 1996) and the physiological mechanisms employed to resist water loss during terrestrial exposure (Rogers 1966, Chessman 1984b) have been studied in the most detail. However, the physiological studies were carried out in the laboratory, where natural behaviours were undoubtedly compromised and the turtles were removed from both the real challenges they face and opportunities available to capitalize upon when in terrestrial habitats on their own accord. Several observers have collectively documented inter-wetland movements and use of terrestrial refuges in *C. longicollis*, but most aspects of their terrestrial ecology remain unknown, particularly with respect to non-nesting activities. For instance, how frequently do individuals enter terrestrial habitats, what distances do they travel terrestrially and what duration of time is occupied by the various terrestrial behaviours? What are the proximal cues and ultimate (evolutionary) factors that instigate or drive terrestrial behaviour? Does terrestrial behaviour vary among individuals according to sex, size, or maturity status, or according to habitat type, landscape structure, season, or year? What are the consequences of terrestrial behaviour for other aspects of the turtle's biology, including movement and spatial ecology, water and energy balance, thermal biology, growth, reproduction, survival and ultimately individual fitness (i.e., lifetime reproductive success)? Are there tradeoffs between the different terrestrial behaviours, or between terrestrial and aquatic behaviour? Finally, how does terrestrial behaviour influence our concept of the population or metapopulation and the management of these demographic units across the landscape? Because *C. longicollis* uses terrestrial habitats for several reasons, this species provides a rich opportunity to examine the terrestrial ecology of a nominally aquatic animal.

The Study System

In order to capture the various terrestrial behaviours of *C. longicollis*, we elected to conduct the study in a relatively pristine and highly heterogeneous landscape. The freshwater wetlands of Booderee National Park, located on the Bherwerre Peninsula of Jervis Bay, offer such a system (Fig. 1.1). Booderee is jointly managed by the Wreck Bay Aboriginal

Figure 1.2. Select permanent wetlands and adjacent forest of Booderee National Park. Steamers 2 (top left), Blacks Waterhole (top right), Claypits (middle left), Lake McKenzie (middle right), Lake Windermere (bottom left), and a typical woodland (bottom right).

Figure 1.3. Select temporary wetlands of Booderee National Park. Emily's Swamp (top left), Steamers 1 (top right), South Blacks (middle left), South Blacks 2 (middle right), Ryan's Swamp (bottom left), and Northwest Steamers Creek (bottom right).

Community Council and the Department of the Environment and Water Resources under the Commonwealth of Australia. Booderee has a rich variety of wetlands, ranging from the large, permanent dune lakes McKenzie and Windermere to several smaller, shallow and temporary wetlands that vary in their flooding duration (Figs. 1.2 and 1.3). As it is a national park, these wetlands are imbedded within a terrestrial landscape that is relatively undisturbed by human infrastructure. Most of the park is forested or heathland, with only a few paved roads and three small settlements (Jervis Bay Village, Wreck Bay and a Naval Airstrip). More detailed aspects of the study system are described in the relevant chapters that follow.

Thesis Aims and Structure

The broad aim of this thesis is to provide a detailed examination of the terrestrial ecology of *C. longicollis*. This specifically involves 1) describing terrestrial aestivation and overland movement behaviours, 2) identifying the factors driving terrestriality as well as the functional significance of these behaviours, 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. As the study progressed, it became apparent that turtle behaviour was highly variable and that serious management issues needed to be addressed in park management strategies. Consequently, the thesis began to follow two parallel and overarching aims, one of which was to examine trade-offs between the various terrestrial behaviours and the other to identify and address management issues relating to the terrestrial ecology of turtles in the park. A set of specific objectives are introduced below in the following outline of thesis structure.

In chapter two, I provide a description of terrestrial habitat use by following the activities of several turtles using radio-telemetry. Particular emphasis is placed on the non-nesting behaviours of aestivation and movements between wetlands. The primary objectives are to first test whether *C. longicollis* confines movements to within the boundaries of a single wetland. If not, how many wetlands does a typical individual use, how frequently do they move between wetlands or to terrestrial refuge sites, what proportion of their time is spent terrestrially and how far from the wetland do they travel? Following from this, a final objective was to examine reasons why turtles may leave the wetland and whether males and females differ in these movement and habitat use behaviours. The results are presented in the context of the terrestrial ecology of other species of freshwater reptiles and how detailed knowledge for a single species or collective knowledge for a group of similar species can

influence how we define and manage wetland systems from the perspective of the associated wildlife communities.

In chapter three, using radio-telemetry and capture-mark-recapture, I identify variation in behaviour with respect to terrestrial aestivation and inter-wetland movements in *C. longicollis*. The primary objective is to determine what proximal or ultimate mechanisms are responsible for maintaining this variation both across the landscape and within a group of individuals occupying a single drying wetland. The concept of behavioural trade-offs and associated fitness consequences in the face of stochastic environmental fluctuations is presented in a behavioural model.

In chapter four, using radio-telemetry and a terrestrial drift fence, I examine movements, spatial ecology and terrestrial activity in *C. longicollis* and determine what factors underlie variation in these behaviours. The objective is to test whether extrinsic factors (e.g., environmental cues, habitat and landscape structure) are responsible for variation in these behaviours, or whether intrinsic attributes of the individual (e.g., sex, body size and maturity) are stronger drivers of behaviour. Emphasis is placed on how temporary wetlands influence terrestrial behaviour and the importance of interpreting proximal drivers of behaviour in the context of their ultimate underpinnings.

In chapter five, I examine aspects of physiology and thermal biology of *C. longicollis* free-ranging in terrestrial habitats by using the doubly-labelled water (DLW) technique and miniature temperature loggers. My first objective is to test the utility of the DLW for examining energy and water relations of freshwater reptiles during terrestrial behaviours. Additional objectives following from this are to quantify the energy and water costs of terrestrial aestivation and overland travel and to determine whether energy or water constrains the duration an individual can remain in terrestrial aestivation or the distance it can travel between wetlands. Finally, the estimates for energy and water relations are tested against the behavioural trade-off model presented in Chapter 2. I emphasize the importance of establishing these critical but missing links between terrestrial behaviour and associated physiological consequences in nominally aquatic animals in the field.

In chapter six, I report on findings from an extensive capture-mark-recapture study in all wetlands in the park. The primary objectives are to estimate an overall rate of inter-wetland movement, to re-examine factors driving the flows of turtles across the landscape over a period of several years using different techniques and to provide the critical data that should underpin how this turtle population should be defined. This is done by using network analysis and multi-stratum models that calculate movement probabilities between wetland pairs corrected for variation in survivorship and capture probability. These results are

discussed in the context of biotic wetland connectivity and how the park could remedy management policies that conflict with these natural flows across the landscape.

Chapter seven draws the conclusions from each proceeding chapter into a synthesized commentary on the terrestrial ecology of freshwater turtles. Recommendations for future research that should provide a richer perspective on the overall biology and conservation of *C. longicollis* in wetland and terrestrial ecosystems are presented.

Except for chapters one and seven, this thesis is written as a series of papers prepared for publication in peer-reviewed scientific journals. Each chapter is unaltered from how it appears in the journal, or as it was submitted. As a result, the chapters may differ slightly in their formatting, spelling and grammar and occasionally overlap in content. The research is my own, but as with any rigorous investigation, I benefited from the valuable contributions of several colleagues in various phases of this work. In particular, my supervisor Arthur Georges was instrumental in developing ideas, raising funds and analysing and interpreting the results in every chapter. Alicia Brinton contributed countless hours of assistance in the field and Brian Green provided expertise on the doubly-labelled water method. Co-authors are listed on the title page for each chapter in the reference to the publication. Others that contributed to this work are listed in the acknowledgements.

HETEROGENEOUS WETLAND COMPLEXES, BUFFER ZONES, AND TRAVEL CORRIDORS: LANDSCAPE MANAGEMENT FOR FRESHWATER REPTILES

Picture: *Chelodina longicollis* near Blacks Waterhole

Abstract

While the importance of nearby terrestrial habitats is gaining recognition in contemporary wetland management strategies, it is rarely recognized that different wetlands are often diverse in their functions of meeting the annual or life-cycle requirements of many species, and that migration between these wetlands is also critical. Using radio-telemetry, we examined terrestrial habitat use and movements of 53 eastern long-necked turtles (*Chelodina longicollis*) in an area of southeast Australia characterized by spatially diverse and temporally variable wetlands. Male and female *C. longicollis* exhibited a high degree of dependence on terrestrial habitat, the majority (95%) of individuals using sites within 370 m of the wetland. Turtles also associated with more than one wetland, using permanent lakes during droughts and moving en masse to nearby temporary wetlands after flooding. Turtles used 2.4 ± 0.1 (range = 1–5) wetlands separated by 427 ± 62 (range = 40–1470) m and moved between these wetlands 2.6 ± 0.3 (range = 0–12) times over the course of a year. A literature review revealed that several species of reptiles from diverse taxonomic groups move between wetlands separated by a mean minimum and maximum distance of 499-1518 m. A high proportion of studies attributed movements to seasonal migrations (55%) and periodic drought (37%). In such cases we argue that the different wetlands offer complimentary resources and that managing wetlands as isolated units, even with generous terrestrial buffer zones, would not likely conserve core habitats needed to maintain local abundance or persistence of populations over the long term. Core management units should instead reflect heterogeneous groups of wetlands together with terrestrial buffer zones and travel corridors between wetlands.

Introduction

Wetland losses and declines in associated faunal communities worldwide (Dahl, 1990; Richter et al., 1997; Finlayson and Rea, 1999) challenge conservation biologists with developing biologically relevant management actions that will prevent further endangerment of wetland communities and provide a framework for their recovery. Contemporary management strategies include establishing wetland reserves (e.g., Ramsar Convention), identifying and protecting keystone wetlands for particular taxa (e.g., North American Waterfowl Management Plan, U.S. Fish and Wildlife Service, 1986), and replacing wetlands lost through land development (e.g., mitigation banking, National Research Council, 2001). Because terrestrial habitats surrounding wetlands play an integral role in regulating microclimate and inputs of nutrients, sediments, and pollutants, it is generally recognized (though not always practiced) that managing a terrestrial buffer zone within 30–60 m of the wetland is vital to maintaining wetland quality (Semlitsch and Bodie, 2003). While the above strategies may adequately conserve the quality of selected wetlands, they have been criticized as focussing too narrowly on the wetland as an individual patch and de-emphasizing the functional linkages of the wetland with other wetlands and the wider landscape (Amezaga et al., 2002).

Criticism of the wetlands-as-patches approach to management derives primarily from an understanding that ecological processes regulating wildlife populations often depend on both patch quality and the structure of the wider landscape. For instance, Semlitsch and Bodie (2003) review the literature on habitat use in semi-aquatic amphibians and reptiles and suggest that core terrestrial zones should extend up to 289 m beyond the delineated wetland boundary to maintain terrestrial resources used by species for critical life-history functions, and an additional 50 m should be added to provide a buffer against edge effects. While Semlitsch and Bodie (2003) make important advances by expanding upon the focus of wetland management to include terrestrial habitats used by wildlife beyond the narrow strip immediately surrounding the wetland, their recommendations are still directed at individual wetlands as the management units, albeit larger and more comprehensive units. Such a strategy neglects the importance of other wetlands in the landscape and the quality of travel routes between them.

Where wetlands in a region are spatially diverse or temporally variable, wildlife may require the use of several different wetlands during a season or lifetime (Haig et al., 1997; Joyal et al., 2001; Naugle et al., 2001; Roe et al., 2003, 2004). For these species and those that interact as metapopulations, where dispersal between wetlands is vital for maintaining regional

population stability (Harrison, 1991), characteristics such as the availability, proximity, quality, and heterogeneity of other wetlands in the landscape and the facility with which individuals can travel among them (landscape connectivity) are all likely to influence demographic processes (Gibbs, 2000; Marsh and Trenham, 2001). These are fundamental concepts in landscape and wildlife ecology (Dunning et al., 1992; Taylor et al., 1993) that have not been sufficiently conveyed across disciplines (e.g., to wetlands scientists and policy makers; Cushman, 2006). Consequently, it comes as no surprise that land managers rarely consider landscape context when making decisions regarding management of aquatic wildlife.

Our aim was to determine whether management that considers wetlands as individual units, either as isolated aquatic patches or in conjunction with terrestrial buffer zones, would be sufficient for the freshwater turtle *Chelodina longicollis* in southeastern Australia. Specifically, we examine details of terrestrial habitat use around wetlands as well as movements by individuals among different types of wetlands. As previous studies have described several types of freshwater wetlands that differ widely between one another and over time according to temporal variation in rainfall at our study site (Georges et al., 1986; Kennett and Georges, 1990; Norris et al., 1993), we hypothesized that turtles of both sexes would associate with more than one wetland to meet annual needs. Furthermore, to bridge the gap between wildlife ecology and environmental management practices and policy, we summarize the literature on inter-wetland movements for wetland reptiles to assess the incidence of this behavior, its functions, and the spatial scales over which individuals typically travel. Such information for a broad range of wetland reptiles is needed to determine biologically relevant management strategies.

Methods

Study site

We studied turtles from September 2004 to March 2006 in Booderee National Park, a 7000 ha reserve located within the Commonwealth Territory of Jervis Bay in southeast Australia (150°43' E, 35°09'S). Kennett and Georges (1990) and Norris et al. (1993) provide a detailed description of the study site. The site is characterized by a mosaic of freshwater habitats including several permanent dune lakes, a network of permanent and ephemeral streams, and a number of temporary swamps of various hydroperiods (duration of surface water presence). Hereafter, we refer to all aquatic habitats as wetlands, and each wetland was defined as either permanent or

temporary based on whether it was observed to have dried during the course of our study or from examination of recent aerial photographs. Typical wetland plant species at our site include *Baumea articulata*, *Eleocharis sphacelata*, *Leptospermum juniperinum*, and *Schoenus brevifolius*. These wetlands occur within forests dominated by *Eucalyptus pilularis*, *E. gummifera, E. botryoides, E. paniculate, E. sclerophylla, Banksia serrata, B. integrifolia, Melaleuca linariifolia*, and heath scrubland dominated by *Allocasuarina distyla*, *B. ericifolia*, *Hakea teretifolia*, *Sprengelia incarnata*. The geology consists of sandstone covered by varying depths of sand.

We used digitized maps describing the distribution of terrestrial and aquatic habitats in the study area adapted from those of N. Taws (in litt.). Wetlands were classified as either permanent or temporary (as described above), and all non-aquatic habitats were collapsed into a single category and classified as terrestrial. We refined the mapping of some wetlands based on our assessment of wetland/terrestrial boundaries, and added other small wetlands (0.10 ha, representing the smallest habitat patch size on our maps) not easily identified from aerial photographs. Because many wetlands have fluctuating water levels, we defined the wetland edge as the interface of the temporarily flooded zone and terrestrial habitat. All habitat edges were drawn from aerial photographs and ground-truthed with a GPS unit (GPS III Plus, Garmin Corp., Olathe, Kansas) with an error of 1–7 m.

Data collection

We captured turtles using baited crab traps or by hand from eight different wetlands from three sets of wetland complexes (Lake McKenzie, Ryan's Swamp, and surrounding wetlands; Blacks Waterhole and surrounding wetlands; and Steamers Waterholes). We fitted 53 adult turtles (32 F, 21 M) with radio-transmitters (Sirtrack Ltd, Havelock North, New Zealand) mounted on aluminium plates and secured to the carapace with bolts or plastic ties through holes drilled in the rear marginal scutes. Initial plastron length and mass of females was 158.3 ± 1.7 mm (mean ± SE) and 691 ± 22 g, and for males 140.5 ± 5.7 mm and 512 ± 15 g. Transmitters ranged from 2.5 to 6.1% of the turtle's body mass.

We located turtles three to four days per week from September to March (active season) during each year of the study, and once per month from April to August (inactive season). At each location, we determined the coordinate position using GPS units held directly above the

turtle or from estimated distance and bearing measurements to known points (e.g., triangulation) when the turtle could not be closely approached. We then plotted location coordinates on habitat maps using ArcView GIS 3.1 (Environmental Systems Research Institute Inc., 1992). We also classified each location as being in either a terrestrial habitat or wetland. We calculated the proportion of locations in terrestrial habitats, terrestrial duration (the number of consecutive days spent in terrestrial habitats without returning to water), the number of movements to terrestrial refuge sites (defined as a movement away from a wetland where a turtle remained for at least five days before returning to the wetland), and the mean and maximum distance from terrestrial locations to the nearest wetland for each turtle. We also noted wetland type (either permanent or temporary) for each location, and measured straight-line distance to the nearest wetland edge for terrestrial locations. We quantified the total number of wetlands visited, the number of times movements between wetlands occurred (hereafter referred to as inter-wetland movements), and overland distances travelled between wetlands for each turtle. Wetlands were only considered distinct if they were isolated from each other by terrestrial habitat. We measured distances between wetlands and between terrestrial locations and the nearest wetland using the Nearest Features extension for Arc View GIS.

Statistical analyses

Although the main focus of this investigation is to determine the frequency and spatial scale of terrestrial habitat use and movements among different types of wetlands for *C. longicollis*, we nevertheless examined whether the sexes differed in their movements and behavior. We performed all statistical analyses with SPSS Version 11.5 (1999). Where appropriate, we examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, data were transformed to approximate normal distributions or equal variances. We used non-parametric tests when both raw and transformed data deviated significantly from normal distributions or equality of variances. Statistical significance was accepted at the $\alpha = 0.05$ level.

To determine if the sexes differed in the number of wetlands used, frequency of inter-wetland movements, number of temporary wetlands used, proportion of locations in terrestrial habitats, or the number of movements to terrestrial refuge sites, we used Mann-Whitney U tests. Additionally, we examined whether density of wetlands within a buffer radius of 1470 m (the longest inter-wetland movement observed in this study; see results) of the wetland of original

capture influenced the number of wetlands used or the number of inter-wetland movements using linear regression. We used analysis of variance (ANOVA) to examine whether the sexes differed in overland distances travelled between wetlands. To examine differences between the sexes in terrestrial duration and mean and maximum distances from terrestrial refuge sites to the nearest wetland, we used MANOVA. All distance variables, terrestrial duration, and number of wetlands used were $\log_{10}$-transformed prior to analyses, and number of inter-wetland movements was square root-transformed.

Results

Individual turtles were radio-tracked for 336 ± 23 (mean ± SE) consecutive days throughout which we obtained 79 ± 4 locations per individual. Individuals used terrestrial habitats extensively for periods of extended refuge, but males and females did not differ significantly in any aspect of terrestrial habitat use examined (Table 2.1, Fig. 2.1). Ninety-one percent of males and 75% of females used terrestrial habitats at some point during the study, and individuals that did so used terrestrial habitats for 28 ± 4% (range = 1–99%) of their locations where they stayed for 64 ± 14 (range = 1–480) consecutive days without returning to wetlands. The majority of terrestrial locations were in forests where individuals were either completely buried under detritus and sand or with a small portion of the carapace exposed. Although we did not locate turtles every day, estimates of terrestrial duration are likely accurate given that in most cases there was rarely any indication that individuals moved from terrestrial refuge sites, and terrestrial habitat use was mostly associated with wetland drying (i.e., turtles would have to travel to distant wetlands and back in a short time). Turtles travelled 99 ± 13 (range = 6–505) m from the nearest wetland, with 95% of terrestrial locations within 375 m of the nearest wetland (Fig. 2.2).

Most individuals maintained an association with several temporary ponds or streams, in addition to a permanent dune lake (Table 2.2, Fig. 2.1). However, males and females did not differ significantly in any aspect of wetland movements examined (Table 2.2). Seventy-six percent of males and 81% of females maintained an association with more than one wetland, with individuals using 2.4 ± 0.1 (range = 1–5) different wetlands, moving between these wetlands 2.6 ± 0.3 (range = 0–12) times, and travelling 427 ± 62 (range = 40–1470) m overland between wetlands. Wetland density surrounding the eight different wetlands where turtles were originally captured ranged from 1.29–2.45 wetlands / km^2, but had no influence on the number of wetlands used ($R^2 = 0.001$, $P = 0.789$) or number of inter-wetland movements ($R^2 = 0.005$, $P = 0.615$).

Table 2.1. Terrestrial habitat use by a freshwater turtle, *Chelodina longicollis*, in Booderee National Park, Australia.

Variable	female		male		test statistic	p
	mean ± SE	range	mean ± SE	range		
Terrestrial locations (%)	22 ± 5	0–99	24 ± 6	0–73	-0.563	0.574
Movements to terrestrial refuge (n)	0.84 ± 0.20	0–3	1.33 ± 0.30	0–4	-1.269	0.204
Terrestrial duration (days)	70 ± 22	1–480	55 ± 17	1–229	1.527	0.223
Mean distance to nearest wetland (m)	116 ± 20	20–390	77 ± 16	6–223	1.527	0.223
Max distance to nearest wetland (m)	208 ± 34	27–505	147 ± 36	6–457	1.527	0.223

See methods for statistical analyses used.

Table 2.2. Wetland use by a freshwater turtle, *Chelodina longicollis*, in Booderee National Park, Australia.

Variable	female		male		test statistic	p
	mean ± SE	range	mean ± SE	range		
Wetlands used (n)	2.3 ± 0.2	1–4	2.4 ± 0.3	1–5	-0.190	0.849
Inter-wetland movements (n)	2.6 ± 0.4	0–9	2.7 ± 0.6	0–12	-0.259	0.796
Inter-wetland movement distance (m)	388 ± 76	40–1147	489 ± 107	70–1470	1.222	0.276
Temporary wetlands used (n)	1.5 ± 0.1	0–3	1.9 ± 0.2	1–4	-1.026	0.305

See methods for statistical analyses used.
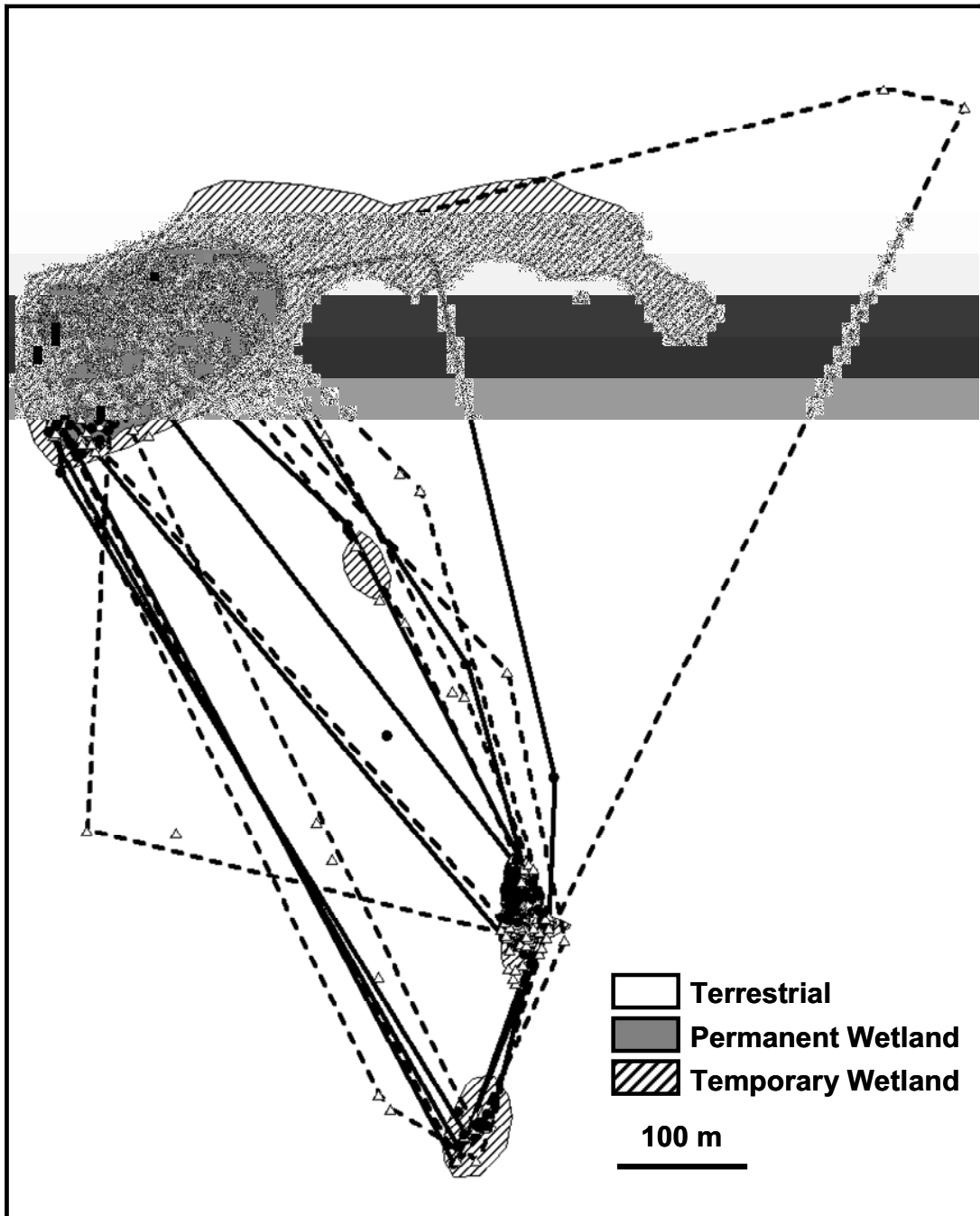
Figure 2.1. Locations and minimum convex polygons for *Chelodina longicollis* males (circles and solid lines) and females (triangles and dashed lines) studied by radio-telemetry at a wetland complex in Booderee National Park, Australia. Note that we show the movements of individuals at only one of three wetland complexes (Blacks Waterhole and surrounding wetlands), but patterns of movement among wetlands were similar at the other sites.
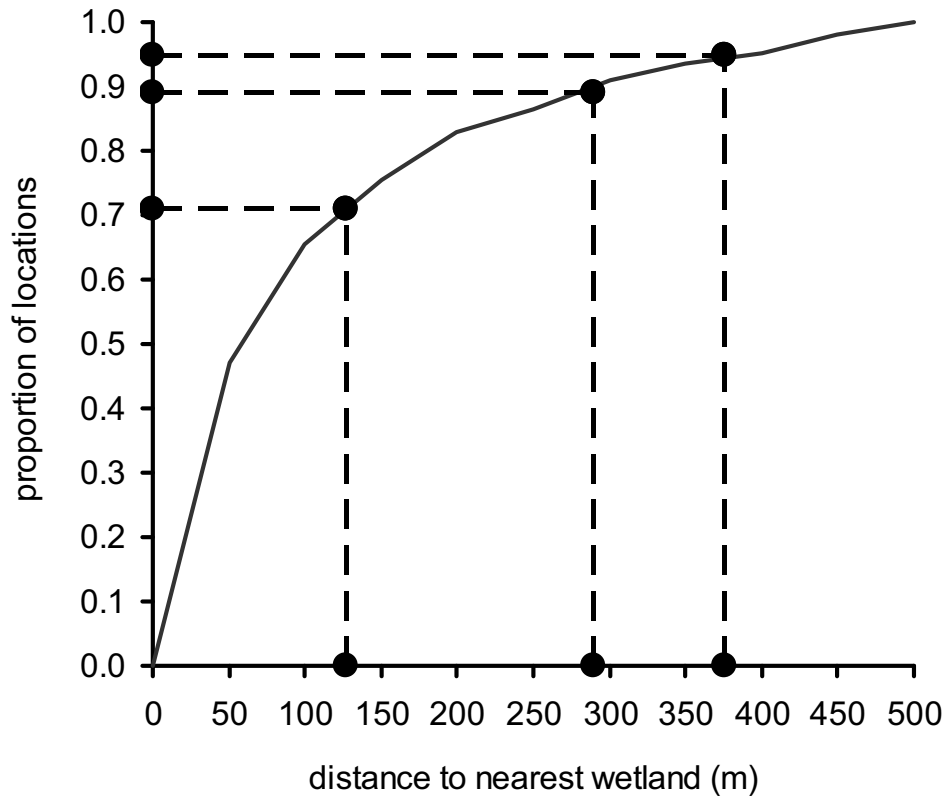
Figure 2.2. Proportion of terrestrial locations within various distances of the nearest wetland edge for *Chelodina longicollis*. The vertical and horizontal dashed lines represent the proportion of locations that would be included in the minimum (127 m) and maximum (289 m) terrestrial buffer zones recommended by Semlitsch and Bodie (2003) for reptiles. For reference, the distance that would include 95% of terrestrial locations is also indicated.

Discussion

Our study demonstrates that both male and female *C. longicollis* used terrestrial habitats far from wetlands for extended durations and maintained associations with several wetlands of different types over the course of a year, even when wetlands are widely dispersed. Terrestrial habitats were important sites of refuge and groups of wetlands, not individual wetlands, should be considered together as harbouring local populations. Consequently, management schemes directed at wetlands as individual units with only narrow terrestrial buffer zones would not adequately capture the mosaic of habitats used by this species.

The inclusion of wide terrestrial buffer zones in wetland management recommended by many researchers (reviewed in Semlitsch and Bodie, 2003) denotes an important shift in focus from wetlands as isolated patches to a more inclusive definition of what constitutes core habitat for wetland wildlife. Although the 127–289 m terrestrial core zones recommended by Semlitsch and Bodie (2003) for reptiles should not be considered canonical, such a zone would nevertheless encompass a large proportion (71–89%) of terrestrial habitats used by the *C. longicollis* population in this study (Fig. 2.2). For inclusion of 95% of *C. longicollis* terrestrial habitats, a considerably larger 375 m zone would be required (Fig. 2.2). That nearly every turtle used terrestrial habitats where they remained for extended durations indicates terrestrial habitat use served important functions including temporary refuge when wetlands dried, nesting, and overwintering. However, while managing wetlands and adjacent terrestrial buffer zones as a single habitat unit may succeed for animals that remain philopatric to a single wetland, the habitat requirements of species that maintain associations with more than one wetland would continue to be neglected.

Chelodina longicollis associates with several wetlands over the course of a year, but movements between wetlands are not specific to this species. Our literature review revealed that 19 species of turtles, 5 species of snakes, and 1 species of crocodilian from 18 U.S. states and 7 countries maintain associations with more than one body of water, sometimes making frequent trips between wetlands (Table 2.3). Reptiles using more than one wetland typically travel among two or three wetlands (full range = 2–9) separated by a mean minimum and maximum distance of 499 to 1518 m (full range 10–8500 m; Table 2.3). It could be argued that individuals may move between wetlands simply because several wetlands are available in some areas and populations could subsist in high abundance even when confined to using only a single wetland. While this may be true in some cases, the majority (55%) of studies documenting inter-wetland movements

Table 2.3. Summary of inter-wetland movements for wetland reptiles.

Species, location (n)	wetlands used	movement frequency	distance travelled	sex	data source, reasons for movement, and methods
Turtles					
Apalone Ferox, Florida (13)	2	---	50–2100	---	Aresco, 2005a[1,b,c]
Chelodina longicollis, Australia (25)	2	---	800–2500	M,F	Kennett and Georges, 1990[1,2,b]
Australia (11)	2	---	193–789	M,F	Stott, 1987[c,d]
Australia (53)	1–5 (2.4)	0–12 (2.6)	62–1470 (427)	M,F	This study[1,2,3,a]
Chelydra serpentina, Canada (2)	2	---	500	F	Obbard and Brooks, 1980[4,b]
South Carolina (1)	2	---	10	M	Gibbons, 1970[b,c]
Chrysemes picta bellii, Nebraska (12)	2	---	2100	---	McAuliffe, 1978[2,3,b]
Iowa (4)	2	---	---	---	Christiansen and Bickham, 1989[1,b]
C. p. marginata, Michigan (6)	1–2	---	125	M,F	Rowe, 2003[a]
Michigan (600)	2	---	550–1200	M,F	Scribner et al., 1993[b,c]
C. p. picta, Virginia (259)	1–2	0–2	230–3300	M,F	Bowne et al., 2006[1,a,b]
Clemmys guttata, Maine (16)	1–4 (2.3)	---	110–1150 (311)	F	Joyal et al., 2001[3,4,a,b]
Massachusetts (9)	2–3	2	120	M,F	Graham, 1995[2,3,a]
Massachusetts (26)	1–3	---	20–550	M,F	Milam and Melvin, 2001[2,3,a]
Connecticut (8)	2	---	250	M,F	Perillo, 1997[2,3,a]
C. muhlenbergii, Virginia (31)	1–2	0–4	200–530	M, F	Carter et al., 2000[a]
Deirochelys reticularia, Virginia (5)	1–9	---	250–600	M,F	Buhlmann, 1995[2,4,a]
South Carolina (3)	2	---	10	M	Gibbons, 1970[b,c]

South Carolina (7)	2	---	515–8500	M,F	Buhlmann and Gibbons, 2001[1,3,4,b,c]
Emydoidea blandingii, Maine (12)	1–6 (2.8)	---	90–2050 (680)	M,F	Joyal et al. 2001,[4,a,b]
Minnesota (25)	1–6	0–5 (1.6)	77–2900 (533)	M,F	Piepgras and Lang, 2000[3,4,a]
Illinois (23)	2	---	170–1400	M,F	Rowe and Moll, 1991[4,a,b]
Emys orbicularis, Italy (7)	1–2	0–2	600	F	Rovero and Chelazzi, 1996[4,a]
Italy (---)	2	---	200	---	Lebberoni and Chelazzi, 1991[2,b]
Germany (4)	1–3	0–3	200–600	F	Schneeweiss and Steinhauer, 1998[4,a]
Graptemys flavimaculata, Mississippi (26)	1–2	---	100	F	Jones, 1996[2,4,a]
Kinosternon baurii, Florida (15)	2	---	35–50	M,F	Wygoda, 1979[3,b,c,d]
K. flavescens, Oklahoma (1)	2	---	610	---	Mahmoud, 1969[3,b]
K. leucostomum, Belize (6)	2	---	200	---	Moll, 1990[3,b]
K. scorpioides, Belize (3)	2	---	200	---	Moll, 1990[3,b]
K. sonoriense, New Mexico (2)	2	---	1500	---	Ligon and Stone, 2003[b]
K. subrubrum, Florida (7)	2	---	50–2100	---	Aresco, 2005a[1,b,c]
South Carolina (1)	2	---	10	M	Gibbons, 1970[b,c]
South Carolina (1)	2	---	440–515	M,F	Buhlmann and Gibbons, 2001[1,3,4,b,c]
Pseudemydura umbrina, Australia (---)	2	---	500	---	Burbidge, 1981[3,a]
Pseudemys floridana, Florida (236)	2	---	50–2100	---	Aresco, 2005a[1,b,c]
South Carolina (5)	2	---	3000	M,F	Buhlmann and Gibbons, 2001[1,3,4,b,c]
Trachemys scripta, South Carolina (2)	2	---	10	M	Gibbons, 1970[b,c]
South Carolina (14)	2	---	3000–5500	M,F	Buhlmann and Gibbons, 2001[1,3,4,b,c]
South Carolina (11)	2	---	400	---	Gibbons et al., 1983[1,b,c]

South Carolina (178)	2	---	200–6000	M,F	Gibbons et al., 1990 [1,3,4,b,c]
Mississippi (39)	2	---	600–1100	M,F	Parker, 1984 [2,4,b]
Florida (119)	2	---	50–2100	---	Aresco, 2005a [1,b,c]
Snakes					
Liasis fuscus, Australia (25)	2	0–2	2000–5000	M,F	Madsen and Shine, 1996 [2,3,a]
Nerodia sipedon, Ohio/Michigan (13)	1–4 (2.1)	0–13 (2.8)	17–331 (97)	M,F	Roe et al., 2003 ,2004 [3,4,a]
N. erythrogaster neglecta, Ohio/Michigan (15)	1–7 (4.1)	0–45 (9.1)	15–1013 (143)	M,F	Roe et al., 2003, 2004 [2,3,a]
Thamnophis elegans, California (4)	2	--	1400–3000	---	Kephart, 1981 [b]
Thamnophis sirtalis, California (2)	2	---	1700	---	Kephart, 1981 [b]
Crocodilians					
Caiman crocodilus, Venezuela (20)	2	---	35–1050	---	Gorzula, 1978 [3,b]

The number of wetlands used, frequency of movement between wetlands, and straight-line overland distances moved by individuals are reported as either single values or ranges and (means) where available.

Movements to other wetlands were considered to have occurred only if individuals were observed in two or more different wetlands, and if wetlands were separated by terrestrial habitats. These distinctions exclude documented immigration / emigration where either the source or destination wetlands were unknown, and movements that exclusively followed aquatic connections (i.e., streams, canals).

Numbered footnotes: [1] movements associated with periodic drought, [2] foraging, [3] seasonal migrations (e.g., between active season and overwintering sites, areas that seasonally flood and dry), [4] reproduction (mating, nesting, parturition)

Lettered footnotes: [a] radio-telemetry, [b] aquatuic captures of marked individuals, [c] terrestrial drift fence, [d] spool-tracking

in reptiles attribute such movements to seasonal migrations (e.g., between active season and overwintering sites, wetlands that seasonally flood and dry), 42% note reproduction (mating, nesting, parturition), 37% specify movements from drying wetlands due to periodic drought, and 32% attribute movements to exploitation of alternate foraging sites (Table 2.3). We conclude that movements between wetlands allow individuals of several species to carry out many essential behaviors and such movements would likely continue even if long distances must be traversed.

We found that *C. longicollis* continued to move among groups of wetlands with similar frequency in areas representing a gradient from low to high wetland density (1.29–2.45 wetlands / km^2). Although wetland densities spanned only a small range at our site, the continued movements among wetlands where wetlands were most widely dispersed (up to 1470 m) suggests that movements between wetlands are not a simple artefact of the availability of nearby wetlands, but instead that migration served an important function. Previous studies demonstrate that *C. longicollis* in temporary wetlands exploit abundant prey resources in the absence of competitors, grow faster, and have substantially higher reproductive output than when in permanent lakes, but individuals must ultimately migrate back to the less productive permanent lakes to withstand extended dry periods (Kennett and Georges, 1990). Because the lakes at our site are low in productivity, invertebrate and vertebrate food resources, and have established populations of competitors typical of permanent waterbodies, should the turtles be confined to the permanent lakes alone, the regional population would likely decline as the lakes alone can only support low densities of carnivorous turtles (Kennett and Georges, 1990; Norris et al., 1993). Evidence for such declines comes from Kennett and Georges (1990) observations of many emaciated turtles in the lakes after a long drought when temporary wetlands did not flood, and our observation of high mortality (105 individuals over 17 months) in one permanent lake during a period of low rainfall when many turtles had left the dry temporary wetlands to return to the lake. Alternatively, if the turtles are confined to using only the temporary wetlands, the population would not persist following extended drought as individuals cannot remain in terrestrial habitats indefinitely without returning to water (Chessman, 1978). Thus, the combination of several permanent and temporary wetlands is a key landscape element contributing to regional carrying capacity, but this dynamic depends on the availability of both types of wetlands and the ability of turtles to migrate between them. For animals that migrate between wetlands to meet seasonal requirements or for those that must occasionally disperse to other wetlands to escape periodic environmental perturbations (e.g., extended drought), we argue that different wetlands offer

complimentary (i.e., non-substitutable) resources. In such cases, not only must groups of wetlands comprise the relevant population units for management (Haig et al., 1997; Joyal et al., 2001; Naugle et al., 2001; Roe et al., 2003), but managers should also maintain wetland complexes reflecting the different types of naturally-occurring wetlands in the region.

Together with maintenance of heterogeneous wetland complexes, landscape connectivity (the degree to which a habitat facilitates or impedes movement; Taylor et al., 1993), should be considered in wetland management. Maintaining terrestrial landscapes for connectivity may be a fundamentally different proposition than managing habitats immediately adjacent to wetlands (i.e., as a terrestrial buffer zone), as the quality of terrestrial habitat required for successful long-distance travel may be different that than required for other behaviors. Wetland reptiles seek very specific microclimate and structural conditions in terrestrial habitats for overwintering (Kingsbury and Coppola, 1999; Roe et al., 2003), aestivation (Morales-Verdeja and Vogt, 1997; Buhlmann and Gibbons, 2001), and nesting (Spencer and Thompson, 2003), all of which typically occur within 289 m of wetlands (Semlitsch and Bodie, 2003). In these areas, stringent restrictions on particular land use practices such as residential development, agriculture, and forestry would likely be necessary. Where wetlands are spatially clustered, terrestrial buffer zones may also include habitats used for travel between wetlands, but when wetlands are dispersed across greater distances, much of the habitat used for inter-wetland movements would be excluded (Fig. 2.3). Landscape management practices aimed at maintaining overland travel beyond the buffer zone areas may only require that habitats outside these zones remain permeable and offer safe passage for wildlife. For instance, roads are an example of a widespread terrestrial landscape modification that disrupts landscape connectivity, either as a behavioral barrier or as a mortality sink when roads bisect travel routes between wetlands (Dodd et al., 2004; Aresco, 2005), even on reserves designated for aquatic wildlife conservation (Bernardino and Dalrymple, 1992; Ashley and Robinson, 1996). Sources of mortality and movement barriers for wildlife along terrestrial travel routes could be identified and modified to mitigate their effects (e.g., fences and culverts; Dodd et al., 2004; Aresco, 2005), while still allowing for other land uses in these areas. Such a stratified approach to management, where zones of allowable land use are set by their likely impact on animals when using these zones, may be an effective way to strike a balance between the competing goals of wildlife conservation and land use (deMaynadier and Hunter, 1995; Semlitsch and Bodie, 2003; Fig. 2.3).
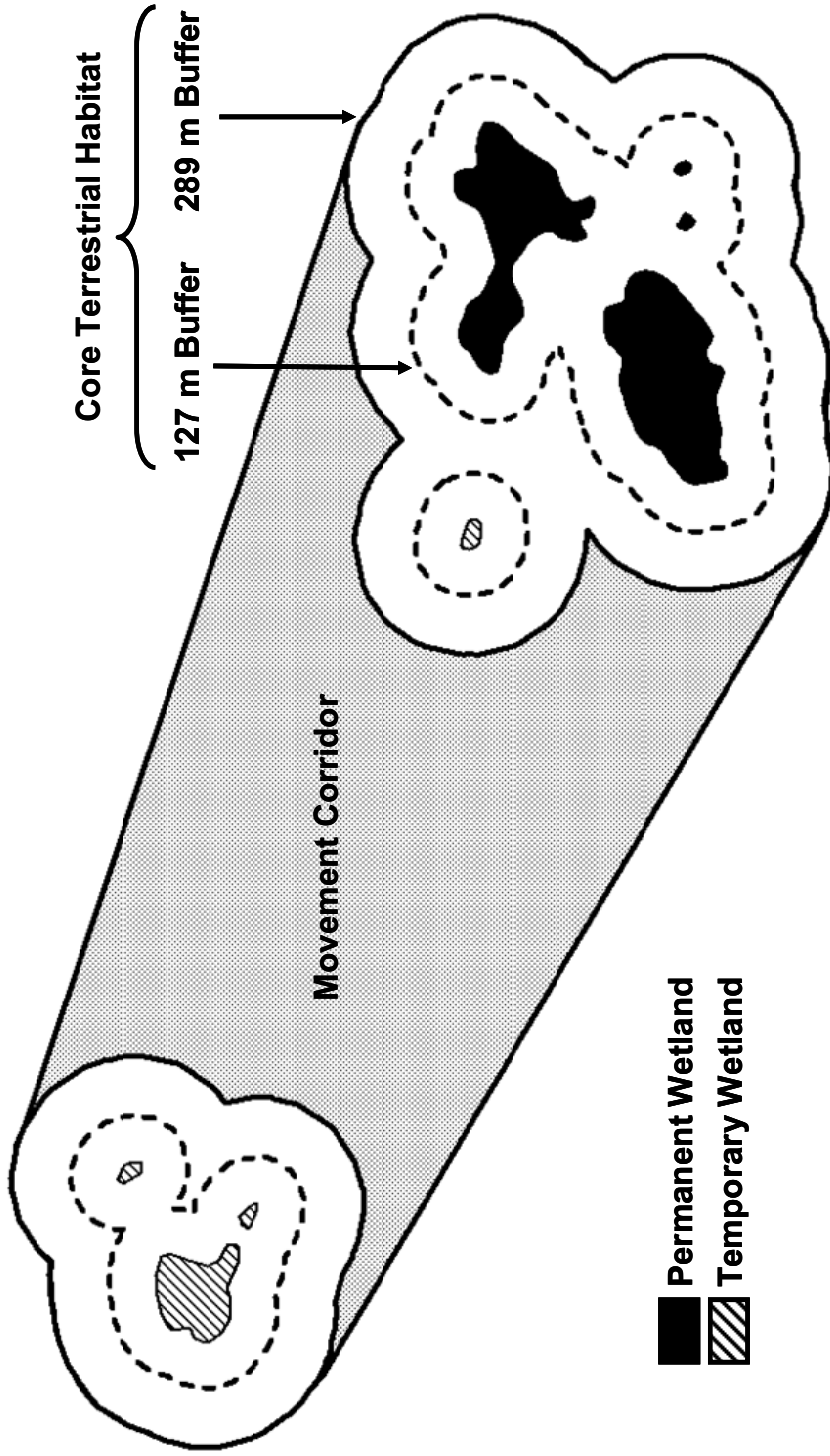
Figure 2.3. A stratified approach to landscape management for wetlands that considers heterogeneous groups of wetlands as the management units, along with buffer zones of 127 to 289 m to protect terrestrial habitat areas as recommended by Semlitsch and Bodie (2003), plus a broader terrestrial movement corridor where barriers to movement and sources of mortality are identified and mitigated while still allowing for sustainable land uses in this area.

Conservation and Management Implications

Reptile populations have been severely impacted by landscape changes, and while commonly lumped together with amphibians as "herpetofauna", reptiles have their own set of unique characteristics that warrant their consideration apart from amphibians in management decisions (Gibbons et al., 2000). Most amphibians are characterized as being philopatric to a single wetland and nearby terrestrial habitat (with the exception of juvenile dispersal; Marsh and Trenham, 2000), but our study demonstrates that many species of reptiles, including *C. longicollis*, may also move widely about the landscape maintaining associations with several types of wetlands to meet their life-cycle or seasonal requirements. Thus, it is not surprising that landscape characteristics such as forest cover, availability of other wetlands, and road density have all been identified as significant predictors of species persistence and local abundance for wetland reptiles at distances ranging from 250 to 2000 m from focal wetlands (Findlay and Houlahan, 1997; Joyal et al., 2001; Ficetola et al., 2004; Marchand and Litvaitis, 2004; Attum et al., *In press*).

Managing landscapes for high quality wetlands and large core terrestrial habitats adjacent to wetlands is an important step in a landscape approach to wetland management (Semlitsch and Bodie, 2003), but we argue that two additional measures, (1) maintaining the natural heterogeneity of wetland complexes and (2) provision of permeable travel corridors among wetlands, would ultimately strengthen the success of conservation strategies for wetland reptiles. At our site a terrestrial core protection zone extending 425 m from wetlands would encompass 95% of terrestrial habitat used by *C. longicollis* as well as a buffer from edge effects. We also identified several important overland movement corridors, and this information was used in addressing the impact of roads on turtle migration in the park, and in designing a predator-exclusion fence (surrounding a lake) for the European red fox (*Vulpes vulpes*) that remained permeable to turtles travelling between wetlands (N. Dexter pers. com.). In the absence of species- or site-specific information, management can be guided by all-encompassing mean minimum and maximum values of habitat requirements derived from what is currently known for the taxon in question (e.g., for reptiles: Semlitsch and Bodie, 2003; this study). Ultimately, conservation planning should extend beyond localized groups of wetlands and surrounding terrestrial habitats to consider connectivity among groups of wetland complexes to allow for inter-population movements that maintain the long-term regional viability of populations via dispersal (Semlitsch and Bodie, 2003; Cushman, 2006). As wetland landscapes continue to

become less dense and more homogeneous (Bedford, 1999; Brock et al., 1999; Gibbs, 2000), and as habitats between wetlands become increasingly fragmented and inimical, changing from an individual wetland to a landscape approach to managing wetland biodiversity should be of great concern to conservationists.

MAINTENANCE OF VARIABLE RESPONSES FOR COPING WITH WETLAND DRYING IN FRESHWATER TURTLES

Pictures: *Chelodina longicollis* travelling between wetlands (top), and buried in the leaf litter during terrestrial aestivation (bottom)

Abstract

Aquatic animals inhabiting temporary wetlands must respond to habitat drying either by aestivating or moving to other wetlands. Using radio-telemetry and capture-mark-recapture, we examined factors influencing the decisions made by individuals in a population of freshwater turtles (*Chelodina longicollis*) in response to wetland drying in southeastern Australia. Turtles exhibited both behaviors, either remaining quiescent in terrestrial habitats for variable lengths of time (terrestrial aestivation) or moving to other wetlands. Both the proportion of individuals that aestivated terrestrially and the time individuals spent in terrestrial habitats increased with decreasing wetland hydroperiod and increasing distance to the nearest permanent wetland, suggesting behavioral decisions are conditional or state-dependent (i.e., plastic) and influenced by local and landscape factors. Variation in the strategy or tactic chosen also increased with increasing isolation from other wetlands, suggesting that individuals differentially weigh the costs and benefits of residing terrestrially versus those of long-distance movement; movement to other wetlands was the near universal strategy chosen when only a short distance must be travelled to permanent wetlands. 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, but movement to permanent wetlands is more successful, or least costly, during dry periods due to survival and body condition benefits. This shifting balance may maintain diversity in response of turtles to the spatial and temporal pattern in wetland quality if their response is in part genetically determined.

Introduction

Organisms in landscapes characterized by spatial and temporal variability have evolved morphological, physiological, and behavioral life-history traits that allow for both survival and production (growth and reproduction) despite stochastic fluctuations in habitat extent or patch quality. Movement among habitats or patches (i.e., migration) is one behavior used by several taxonomic groups in variable environments (Alerstam et al. 2003), but residency within the variable habitat or patch is also widespread, often requiring periodic aestivation or dormant life stages (Christian et al. 1996, Cáceres and Tessier 2003). In many species, however, a decision to migrate or reside is not obligate, as variation in the behavioral response within a species or population can exist. Such a scenario has been described as a "facultative" or "partial" response (Terrill and Able 1988).

Several proximate and ultimate factors are thought to maintain variable responses within a population. Variable responses may exist between individuals that differ in age, sex, body size, experience, or dominance position (Swingland 1983), or alternate responses may be frequency-dependent, where the tactic chosen by an individual is based on the behavior of others (Lundberg 1987). In the above scenarios, intraspecific competition during resource scarcity is thought to ultimately maintain the variation, but the average fitness payoffs of the strategies or tactics may or may not be equal (Dominey 1984). It is also possible that variation is due to genetic differences among individuals irrespective of other asymmetries (Alerstam and Henderström 1998, Pulido et al. 1996), or phenotypic plasticity, where behavioral or life-history decisions are influenced by the individual's environment or physiological state (Semlitsch et al. 1990, Houston and McNamara 1992). Questions pertaining to variable responses in fluctuating environments, specifically whether to move between patches or remain and cope with environmental extremes, have been examined primarily in species with well-known, long, or conspicuous migrations (e.g., birds, insects, large mammals), but the same or other factors are likely at work in shaping the responses of animals using landscapes on smaller spatial scales, where habitats are also patchy and temporally variable.

Freshwater wetland systems can be highly variable environments. Wetlands are patchy in space, and the environment can differ widely among different wetlands or within a given wetland over time (Euliss et al. 2004), especially in temporary wetlands (i.e., wetlands that periodically dry; Kennett and Georges 1990, Bauder 2005). Consequently, the opportunity to move between wetlands and the associated costs vary both spatially and temporally. Animals from diverse

taxonomic groups eventually face the common challenge of wetland drying by either residing or moving to other wetlands, and both strategies or tactics typically exist within many groups (e.g., amphibians: Denoël et al. 2005; fish: Sayer and Davenport 1991; invertebrates: Cáceres and Tessier 2003, Hall et al. 2004; reptiles: Gibbons et al. 1983, Christiansen and Bickham 1989). Given that each response reflects complex attributes of behavior, physiology, and life history (*op cit.*), and because the response of related individuals at any one point in space and time is a product of their shared evolutionary history, when variation exists within the population in response to wetland drying, it raises the question of what factors maintain the variable responses.

Freshwater turtles are capable of terrestrial movement between wetlands (Graham et al. 1996, Gibbons et al. 1990), and by virtue of their low metabolic rates, ability to store water, and capacity for additional physiological adjustments to conserve energy and water, turtles are also well suited to remain dormant for extended periods (i.e., aestivate) and await re-flooding (Kennett and Christian 1994, Peterson and Stone 2000, Ligon and Peterson 2002). Differences in propensity to reside or move to other wetlands have been reported among species of freshwater turtles at a common locality (Gibbons et al. 1983, Christiansen and Bickham 1989) and even among populations of a single species (Ligon and Peterson 2002). Examples of variation among individuals within a single population of freshwater turtles are less common (but see Gibbons et al. 1990), and to our knowledge no studies have examined factors that explain the existence of variable strategies or tactics within a population in the context of wetland drying. Here, we examine intrapopulational variation in terrestrial residency and inter-wetland movements and associated fitness costs and benefits of each behavior in a carnivorous freshwater turtle, *Chelodina longicollis*. Because the typical *C. longicollis* at our study site maintains associations with several wetlands and terrestrial habitats during a single year (Roe and Georges 2007), we define a population as the individuals occupying a localized group of wetlands instead of each wetland as harboring a demographically distinct sub-population. Animals that demonstrate such vagility are perhaps best defined as comprising "patchy populations" (Harrison 1991), and such a classification has been recently adopted to describe the dynamic population structure of similarly mobile freshwater turtles (Joyal et al. 2001, Bowne et al. 2006). By examining variation within a population, we aim to identify factors shaping behavioral variation in freshwater reptiles while limiting, as much as possible, potentially confounding phylogenetic differences among individuals.

Methods

Study site

Turtles were studied from September 2004 to March 2006 in Booderee National Park, a 7000 ha reserve located within the Commonwealth Territory of Jervis Bay in southeastern Australia ($150^{o}43$' E, $35^{o}09$'S). Detailed descriptions of the study site are given by Kennett and Georges (1990) and Roe and Georges (2007). The site is characterized by forested terrestrial habitats and a mosaic of freshwater wetlands including several permanent dune lakes and a number of temporary swamps of various hydroperiods (duration of surface water presence; Fig. 3.1). Wetlands were continuously monitored for surface water presence from September to March of each year, corresponding to the turtle's activity season (Kennett and Georges 1990). Hydroperiod scores were calculated for each wetland by dividing the number of days surface water was present by the number of days monitored. Wetlands that remained continually flooded (hydroperiod score of 1.0) were classified as permanent, while wetlands that were known to have dried were classified as temporary. Temporary wetlands with a hydroperiod score between 0.5–0.9 were classified as intermediate, while those with a hydroperiod < 0.5 were classified as ephemeral.

Turtle capture

Turtles were captured using baited crab traps or by hand from wetlands distributed across the site. At each capture, we measured straight-line carapace length (CL) and plastron length (PL) to the nearest 0.1 mm using vernier callipers, and the mass of each turtle to the nearest gram. Turtles with CL < 145 mm were classed as juveniles, and for those with CL > 145 mm, we determined sex by examining the plastron curvature (see Kennett and Georges 1990). Each turtle was marked with a unique code by notching the marginal scutes of the carapace before release.

Radio-telemetry

Sixty adult turtles (39 F, 21 M) were fitted with radio-transmitters (Sirtrack Ltd, Havelock North, New Zealand) mounted on aluminium plates and secured to the carapace with bolts or plastic ties through holes drilled in the rear marginal scutes. In order to capture variation resulting from the

heterogeneity of wetlands at the study site, we studied individuals originally captured in eight different wetlands from two general regions of the site using radio-telemetry (18 turtles from wetlands in the northwest [Ryan's Swamp, Lake McKenzie, Windermere and Claypits area] and 42 from wetlands in the southeast [Blacks Waterhole and Steamers Waterholes area]; Fig. 3.1). All wetlands were within an area enclosed by a circle with a 2.6 km radius, a distance that *C. longicollis* is capable of traversing between wetlands (Kennett and Georges 1990, JHR unpubl. data). Initial carapace length and mass of males ranged from 162.9–193.5 mm and 410–653 g, while females ranged from 171.0–218.9 mm and 510–1004 g. Transmitters ranged from 2.5–6.1% of the turtle's body mass.

Turtles were located three to four days per week from September to March (active season) during each year of the study, and once per month from April to August (inactive season). At each location, we determined the coordinate position using GPS units (GPS III Plus, Garmin Corp., Olathe, Kansas) or from distance and bearing measurements to known locations. Coordinate positions determined by GPS units had an error of 1–7 m. Location coordinates were then plotted on habitat maps using ArcView GIS 3.1 (Environmental Systems Research Institute Inc. 1992). We classified each location as being in either a terrestrial habitat or wetland, and calculated two measures of terrestrial behavior for each individual: 1) proportion of locations in terrestrial habitats, and 2) terrestrial duration (the number of consecutive days spent in terrestrial habitats without returning to water). We also calculated two scores for each turtle to reflect 1) mean hydroperiod score of all wetlands used by the turtle throughout the radio-tracking period, and 2) straight-line distance to the nearest permanent wetland from the most distant temporary wetland used by the turtle. Distances between the closest edges of wetlands were estimated using the Nearest Features extension for Arc View GIS.

Growth and body condition

We conducted a capture-mark-recapture study using the capture techniques described above. We assessed growth patterns and changes in body condition of recaptured individuals. In this study, we only report on growth and body condition of recaptured turtles from two permanent lakes (Lakes McKenzie and Windermere) and one temporary swamp (Ryan's swamp) in order to facilitate comparisons with Kennett and Georges (1990). Growth was measured as the change in CL and PL between captures, and growth rates were calculated by dividing change in shell length by the fraction of the approximately six month growing season (15 September–15 March) elapsed

between initial and final captures. We only included individuals in the analyses if the period between captures spanned at least half of a growing season, and only if both captures were in the same wetland. Individuals were assumed to have grown appreciably only if the growth increment exceeded the accuracy of measurements ($\pm$ 0.5 mm); where the growth increment was < 0.5 mm, individuals were considered not to have grown appreciably and were omitted from analyses of growth rate. The proportion of individuals that grew appreciably was also determined for each wetland. All calculations and analyses of growth were done in accordance with that of Kennett and Georges (1990) to enable direct comparisons between studies.

Data analysis

Statistical analyses were performed with SAS Version 8.2 (1999). Where appropriate, we examined the assumptions of homogeneity of variances and normality. When data failed to meet assumptions, data were transformed to approximate normal distributions or equal variances. Statistical significance was accepted at the $\alpha \leq 0.05$ level except when stated otherwise.

To investigate factors influencing variation in terrestrial behavior among individuals, we used linear and quadratic multiple regression analyses. As previous investigations detected no differences between sexes in terrestrial habitat use or movement (Roe and Georges 2007), males and females were included together in our analyses. Additionally, individuals in both the northwest and southeast regions of the site were grouped together in analyses even though turtles do not regularly move between these regions, though movements among wetlands within both regions are frequent (Roe and Georges 2007). Due to the proximity of these regions to one another and the similarity in movement and habitat use behaviors of turtles in these regions, the regions were grouped to increase sample size and power of our analyses. We assessed how four independent variables (maximum distance between temporary and permanent wetlands, mean hydroperiod score, turtle size [PL], and condition index [mass adjusted for PL, calculated as g mm^{-b}, where b is the scaling exponent from a regression of $\log_{10}$ body mass (g) on log10 PL (mm); Peterson and Stone 2000]) influenced each of four dependent variables reflecting terrestrial habitat use (proportion of terrestrial locations, maximum terrestrial duration, variation in proportion of terrestrial locations, and variation in maximum terrestrial duration). The Dunn-Sidak method was applied to this family of multiple regressions to constrain the experiment-wide Type I error to 0.05 (Quinn & Keough 2002). The α level for statistical significance for each test

was $\alpha \leq 0.013$. Proportion of terrestrial locations was arcsin-square root transformed, and we added a value of one to terrestrial duration before $\log_{10}$-transformation to accommodate zero values. Variation in terrestrial habitat use was assessed by grouping individuals into 100 m distance and 0.1 hydroperiod score classes and calculating the standard deviation for each variable within each class. Variation was only assessed for classes with at least two individuals. Each dependent variable was examined against all independent variables together in separate analyses. Because we detected variance inequalities for the relationship between proportion of terrestrial locations and distance to permanent wetlands (see results), we used a weighted regression with distance$^{-1.2}$ as the weighted variable. For multiple regression, we dropped terms with a P-value < 0.10, then used multiple or simple regression models to re-assess relationships between the dependent and the remaining independent variables at the $\alpha \leq 0.013$ level. We compared survival of radio-tracked turtles that migrated to and remained in permanent wetlands following wetland drying to those that remained at temporary wetlands with Fisher's exact tests.

Growth and body condition of adults and juveniles were examined in three wetlands (Lakes McKenzie, Windermere, and Ryan's Swamp). The proportion of individuals (juveniles and adults separate) showing appreciable growth was compared between wetlands with a series of Fisher's exact tests, and growth rates were compared between wetlands using ANCOVA, with wetland as the independent variable, $\log_{10}$ carapace growth rate as the dependent variable, and initial CL the covariate. To examine changes in body condition for all turtles (juveniles and adults combined), we examined the relationship between mass (dependent variable) and PL (covariate) between initial and final captures of individuals using repeated measures ANCOVAs with compound symmetry covariance structure (PROC MIXED Model, SAS, vers. 8.2, SAS Institute, 1999). This analysis assumes an animal in good condition would have a greater mass than an animal of the same PL in poor condition.

Results

Terrestrial behavior and survival

Terrestrial behavior was highly variable among individuals (Figs. 3.1 and 3.2), with proportion of terrestrial locations ranging from 0–99%, and maximum terrestrial duration ranging from 0–480 days. Because hydroperiod score and distance from temporary to the nearest permanent wetland
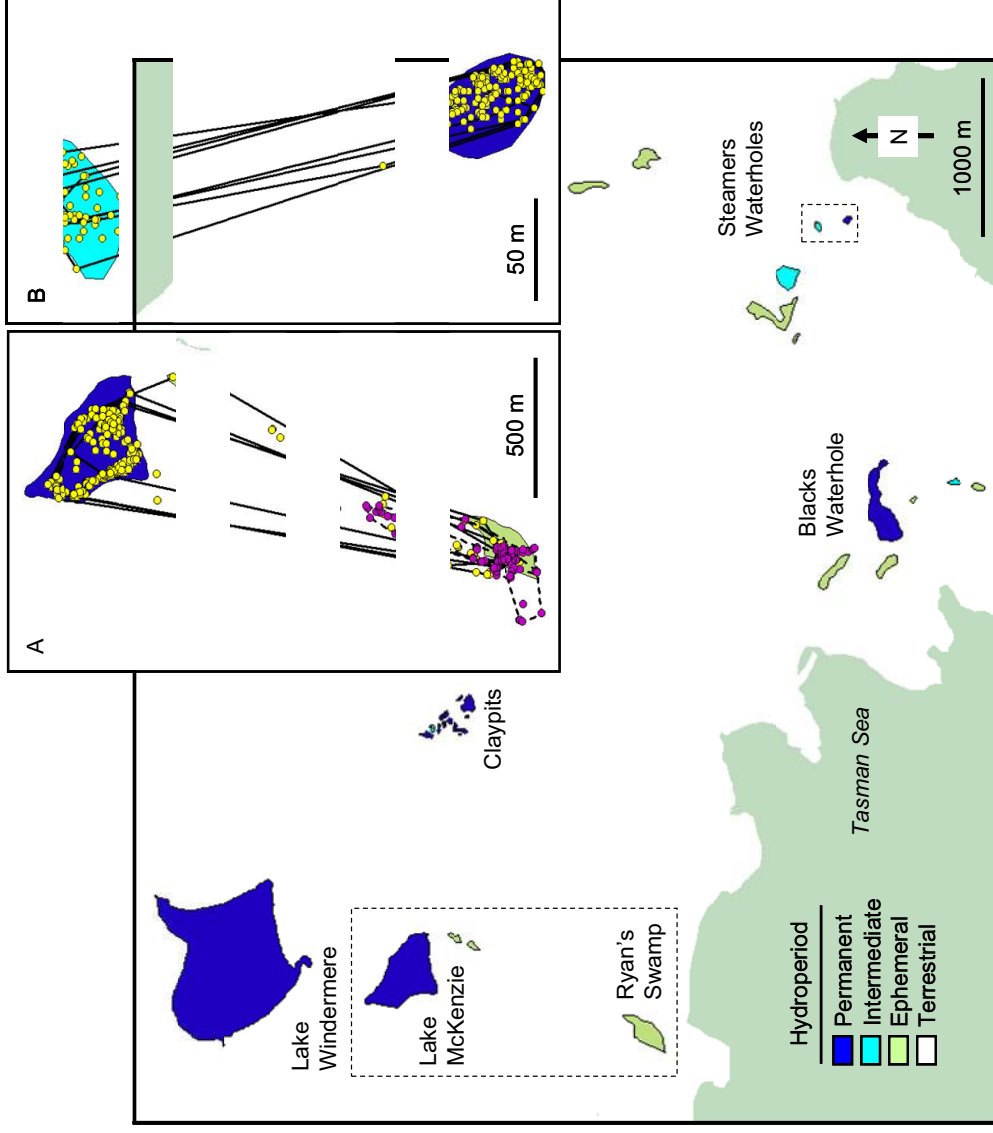
Figure 3.1. Map of wetlands in Booderee National Park. The insets show radio-locations and minimum convex polygons for *Chelodina longicollis* individuals that moved to a permanent lake (yellow circles and solid lines) or resided terrestrially near the temporary wetland (purple circles and dashed lines) in two sub-regions of the study: A) Lake McKenzie and Ryan's Swamp, and B) Steamers Waterholes. Detailed locations and movements could not be shown for all 60 turtles without obscuring the map. Note the difference in scale between insets and between insets and the larger map.
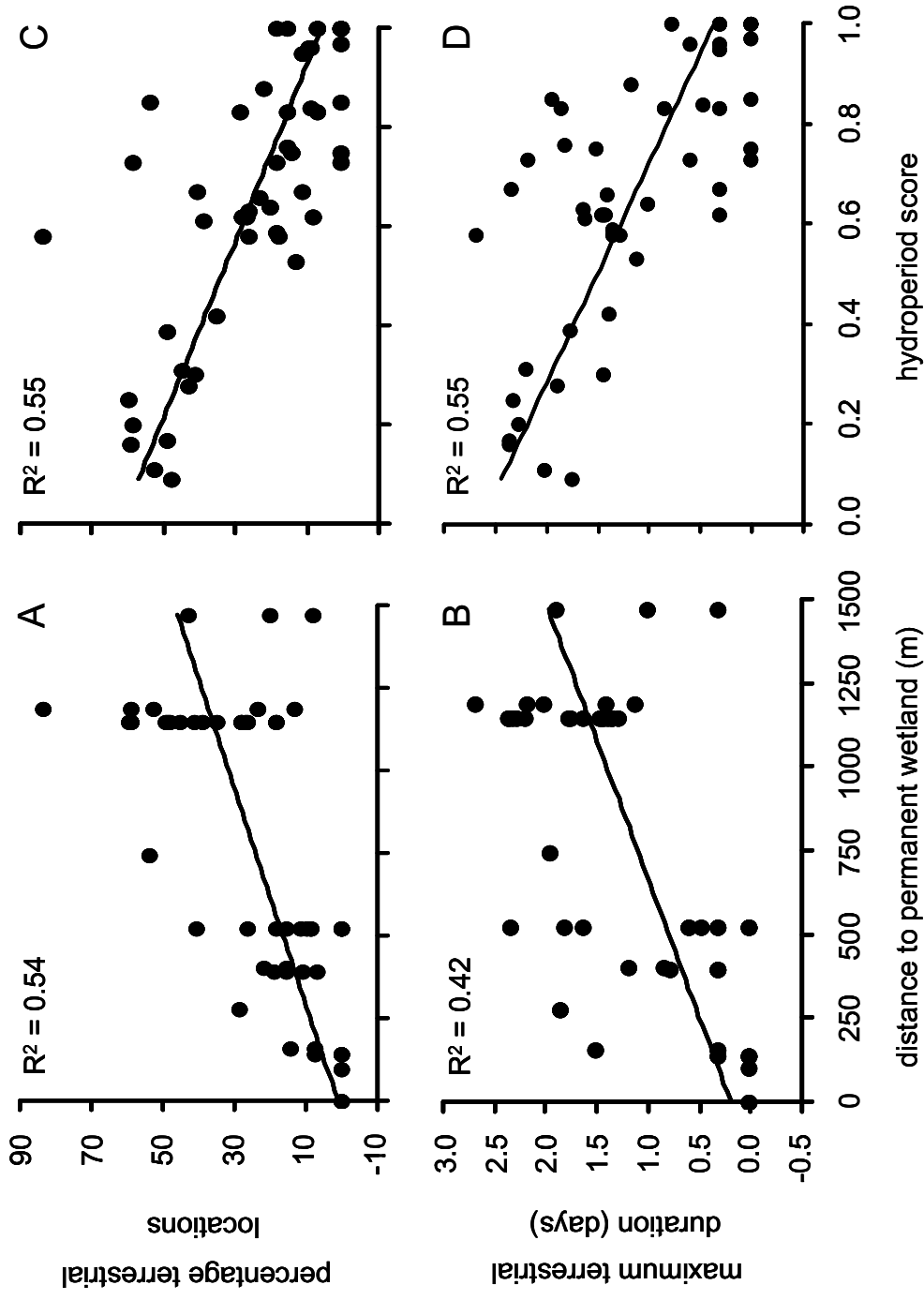
Figure 3.2. Relationships between terrestrial behavior, distance from temporary wetlands to the nearest permanent wetland (A, B), and wetland hydroperiod (C, D) in *Chelodina longicollis*. Percentage of terrestrial locations was arcsin-square root transformed, and we added a value of one to terrestrial duration before $\log_{10}$-transformation prior to analyses. Hydroperiod score is the proportion of time that surface water was present in the wetland, with a score of 1 reflecting wetlands that remained continually flooded, and a score of 0 wetlands that never flooded.

were significantly correlated ($r^2 = 0.59$; $F_{1,52} = 72.61$, $P < 0.001$), we ran two separate regression analyses to avoid complications of collinearity of independent variables, in addition to step-wise regression with both variables included in the model. This co-linearity is likely an artefact of the spatial arrangements of wetlands within the watersheds at our site; the more permanent wetlands tended to be lower in the catchments and thus functioned as collector pools, while those higher in the catchments (i.e., farther from the permanent collector pools) drained and dried more quickly.

The proportion of terrestrial locations increased linearly with increasing distance between temporary and permanent wetlands ($r^2 = 0.54$; $F_{1,52} = 57.63$, $P < 0.001$; Fig. 3.2) and was due to both an increase in terrestrial duration ($r^2 = 0.42$; $F_{1,52} = 37.18$, $P < 0.001$; Fig. 3.2), and an increase in the proportion of turtles residing at temporary wetlands ($r^2 = 0.74$, $F_{1,6} = 14.32$, $P = 0.013$). At the two extremes, 100% of turtles using temporary and permanent wetlands separated by < 100 m moved to permanent wetlands, but at a distance of 1400–1500 m 67% of turtles resided in or near the temporary wetland following wetland drying. Proportions of terrestrial locations and terrestrial duration also increased linearly with decreasing hydroperiod ($r^2 > 0.55$; $F_{1,52} > 62.64$, $P < 0.001$; Fig. 3.2). Both distance and hydroperiod ($P < 0.006$) were significant predictors of proportion terrestrial locations in a step-wise regression, but hydroperiod ($P < 0.001$) and not distance ($P = 0.185$) was significant for terrestrial duration. Neither turtle size nor body condition were significant predictors of terrestriality in any model ($P > 0.067$).

The analysis of variation in terrestrial habitat use (measured as the STDV within each class) included 51 individuals representing seven distance classes spanning the entire range of distances between permanent and temporary wetlands (0–100 m to 1400–1500 m), and 51 individuals representing eight hydroperiod classes spanning nearly the full range of wetland hydroperiod scores (0.1–0.2 to 0.9–1.0). Variation in proportion of terrestrial locations increased linearly with increasing distance between temporary and permanent wetlands ($r^2 = 0.90$; $F_{1,6} > 47.22$, $P = 0.001$; Fig. 3.3), but no relationship was found between variance in terrestrial duration and distance between wetlands ($P = 0.095$). Hydroperiod score was not a significant predictor of variance in either aspect of terrestrial behavior examined ($P > 0.385$).

Survival of radio-tracked turtles that moved to or remained within permanent wetlands (82%) was higher than those that remained at temporary wetlands (55%) following wetland drying ($P = 0.038$). Of the ten individuals (7 F, 3 M; 162.9–215.5 mm CL) that died while residing at temporary wetlands, one was depredated by an eagle (*Aquila audax* or *Haliaeetus leucogaster*), one was hit by a vehicle along a service track, while the other eight eventually
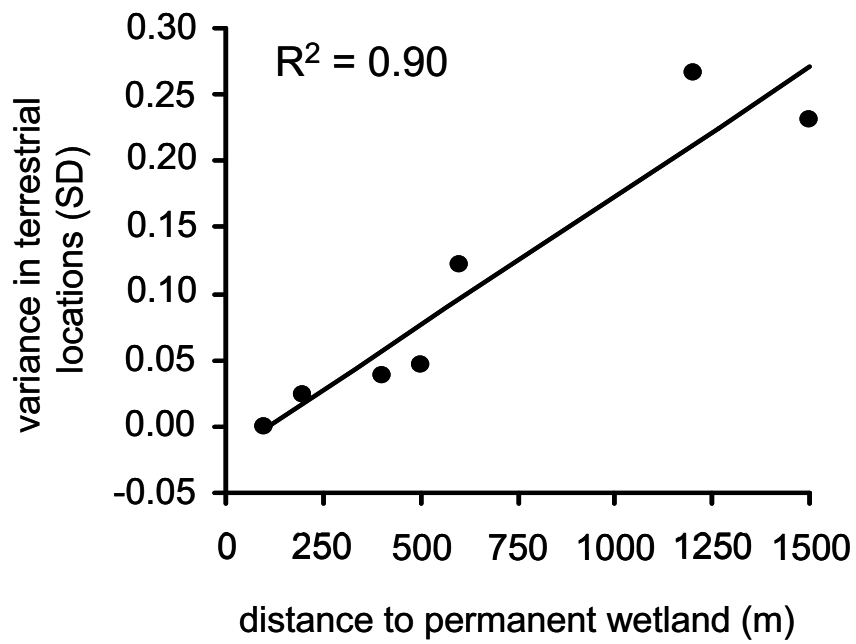
Figure 3.3. Relationship between variance in *Chelodina longicollis* terrestrial behavior (measured as the standard deviation [SD] in proportion of terrestrial locations for each distance class) and distance between temporary and permanent wetlands.

Figure 3.3. Relationship between variance in *Chelodina longicollis* terrestrial behavior (measured as the standard deviation [SD] in proportion of terrestrial locations for each distance class) and distance between temporary and permanent wetlands.

failed to bury in the substrate and were visibly emaciated prior to death. These observations suggest death from starvation and/or dehydration, but blood properties and body composition were not monitored and thus cause of death could not be confirmed (Peterson and Stone 2000). Of the seven individuals (4 F, 3 M; 168.0–206.0 mm CL) that died while moving back to or remaining within permanent wetlands, three were predated by eagles and the cause of death was undetermined for the other four. No sex or body size differences were detected among those that died in residency at temporary wetlands ($P > 0.296$) nor for those that moved to or remained within permanent wetlands ($P > 0.511$).

Growth and body condition

Two-hundred seventy turtles (217 adults, 53 juveniles) from the Lake McKenzie, Windermere, and Ryan's Swamp complex were recaptured in their wetland of original capture. The proportion of juveniles and adults showing appreciable growth did not differ among wetlands ($P > 0.103$; Table 3.1). Average adult growth rates did not differ among wetlands (Table 3.1), but after correcting for body size, the ANCOVA detected an interaction between CL and wetland for adult growth rate (CL: $F_{1,53} = 0.02$, $P = 0.891$; wetland: $F_{2,53} = 6.12$, $P = 0.004$; CL × wetland: $F_{2,53} = 5.98$, $P = 0.005$). Growth rates of Lake Windermere adult turtles decreased with increasing body size (n = 24, $R^2 = 0.50$) and increased with increasing body size in Ryan's Swamp (n = 3, $R^2 = 0.97$), but rates did not differ significantly among body sizes in Lake McKenzie (n = 32, $R^2 = 0.08$). The relationship between juvenile growth rate and size also varied between wetlands (CL: $F_{1,20} = 0.23$, $P = 0.635$; wetland: $F_{1,20} = 5.48$, $P = 0.030$; CL × wetland: $F_{1,20} = 5.69$, $P = 0.027$). Juvenile growth rate decreased with increasing size in Lake McKenzie (n = 16, 96.4–143.0 mm CL; $R^2 = 0.46$), but did not vary with size in Lake Windermere (n = 8, 129.6–144.7 mm CL; $R^2 = 0.35$), most likely an artefact of the relatively narrow size range. Because no juveniles in Ryan's Swamp grew appreciably, this wetland was excluded from this analysis. Although only four juveniles were recaptured in Ryan's Swamp, these individuals represented a wide size range (89.6–144.9 mm CL), which should have allowed for detection of any growing individuals had growth occurred.

Changes in body condition differed among wetlands. Turtles in Lake McKenzie increased body condition by 1.1% regardless of size ($\log_{10}$ PL: $F_{1,150} = 5305.26$, $P < 0.001$; condition: $F_{1,150} = 6.37$, $P = 0.013$), whereas turtles in Ryan's Swamp decreased body condition by 7.7% regardless of size ($\log_{10}$ PL: $F_{1,20} = 3367.50$, $P < 0.001$; condition: $F_{1,20} = 22.25$, $P <$

Table 3.1. Growth of adult (A) and juvenile (J) *Chelodina longicollis* from two permanent lakes and a temporary swamp.

wetland	recaptures (n)		% growing		carapace growth rate (mm / yr, mean ± SE [range])*	
	A	J	A	J	A	J
Lake McKenzie	119	34	29.4	47.1	1.04 ± 0.13 [0.11–3.21]	1.47 ± 0.37 [0.53–5.27]
Lake Windermere	80	15	28.8	53.3	1.09 ± 0.17 [0.25–3.38]	1.34 ± 0.31 [0.66–3.25]
Ryan's swamp	18	4	16.7	0.0	0.89 ± 0.05 [0.81–0.98]	0.00 [0.00–0.00]

* Because growth rates were size-dependent in some cases, we present both mean ± SE and range

0.001). In Lake Windermere, there was an interaction between body size and body condition change, but body condition change ranged between -2.0% and + 0.8% ($\log_{10}$ PL: $F_{1,94} = 3322.72$, $P < 0.001$; condition: $F_{1,94} = 6.10$, $P = 0.015$; $\log_{10}$PL × condition: $F_{1,94} = 5.84$, $P = 0.018$).

Discussion

The *C. longicollis* population exhibited a high degree of variation in terrestriality, reflecting alternate strategies or tactics of individuals in response to wetland drying. Some turtles immediately move to permanent wetlands while others reside terrestrially near temporary wetlands for various lengths of time. Both wetland hydroperiod and proximity to other more permanent waterbodies accounted for some of the behavioral variation, but variance still existed among individuals occupying the same wetlands. That such variation in response to wetland drying exists among individuals in the same population (i.e., using the same set of wetlands) suggests individuals may differentially weigh the benefits of one strategy or tactic against the costs of the other, and raises the question as to what ultimately maintains this behavioral variation.

Both movements to other wetlands and residency within or near dry wetlands to await more favorable conditions have potential costs and benefits. Costs of residing within the dry wetland or in nearby terrestrial habitats include depletion of energy and water stores (Ligon and Peterson 2002) or death from exposure to extreme conditions should the wetland remain dry for long periods (Christiansen and Bickham 1989, Bodie and Semlitsch 2000a). However, if the wetland soon re-floods, individuals in close proximity would maximize foraging opportunities by being first to take advantage of the bloom of aquatic productivity typical of recently-flooded wetlands (Brinson et al. 1981), even for short duration flooding events, without incurring the high costs of terrestrial movement. Costs of movement to other wetlands include increased mortality risk from predators (Spencer and Thompson 2005) and roads (Aresco 2005), energy expenditure (Stockard and Gatten 1983), time, and the potential cost of lost foraging opportunities if the wetlands they evacuated soon re-flood. However, should temporary wetlands remain dry, movement to the low productivity permanent lakes (Georges et al. 1986, Kennett and Georges 1990) would allow for at least some continued foraging elsewhere and avoidance of the costs of remaining at temporary wetlands. It becomes apparent that the relative costs and benefits of residing or moving to other wetlands would be contingent upon whether temporary wetlands quickly re-flood or remain dry for extended periods.

In our study, terrestrial aestivation (defined here as terrestrial inactivity during dry periods, Gregory 1982) was a facultative behavior dependent in part on both local (wetland hydroperiod) and landscape (distance between wetlands) factors, but not attributes of the turtles themselves such as size, sex, or the body condition index. The negative relationship between terrestrial habitat use and wetland hydroperiod is likely a result of individuals maximizing resource acquisition in wetlands for as long as flooded conditions permit, as most freshwater turtles, including *C. longicollis*, rarely if ever feed on land (JHR, unpubl. data). That more individuals declined to move to permanent wetlands by remaining terrestrial for longer times when temporary and permanent wetlands were farther apart is perhaps reflective of the perceived high costs and risks of long distance overland movement. When only short distances must be travelled, the costs of round trip migration between temporary and permanent wetlands would be low relative to the potentially high costs of residing at dry wetlands (e.g., depletion of energy stores, death), but for turtles using more distant temporary wetlands (up to 1.5 km in this study), the high costs and risks of a round trip journey (e.g., energy expenditure, predation) may be incentive to delay or forego a trek altogether and await the return of flooding. That the relationship between terrestriality and both local and landscape habitat variables have nonzero slopes suggests that terrestriality is in part a behaviorally plastic response (sensu Stearns 1989), and that competition for resources and the behavior of others (i.e., a frequency-dependent decision) was less of a factor in explaining the chosen strategy or tactic. If individuals were simply behaving based on the choices already made by others, we would expect to see a similar distribution of behaviors among individuals at temporary wetlands regardless of wetland isolation or hydroperiod, which was not the case. We also found little evidence for synchrony of movements from drying wetlands among individuals at a particular wetland, beyond that which can be attributed to rainfall (JHR, unpubl. data). This observation suggests individuals are not directly following one another in their behavioral decisions.

Even though some *C. longicollis* survived extended terrestrial aestivation (up to 480 consecutive days) while awaiting re-flooding, a large proportion (45%; irrespective of adult size or sex) died, compared to lower mortality rates (18%) of those that moved to permanent wetlands. In light of these extreme consequences, the existence of any behavioral variation in response to wetland drying is at first puzzling. To provide additional insight on potential causes of this variation, we examined historical patterns of a critical environmental factor. Annual rainfall has fluctuated widely and unpredictably, with years of high rainfall as much as 4.3 fold above years of low at our site (Fig. 3.4). Although we do not know the complete history of

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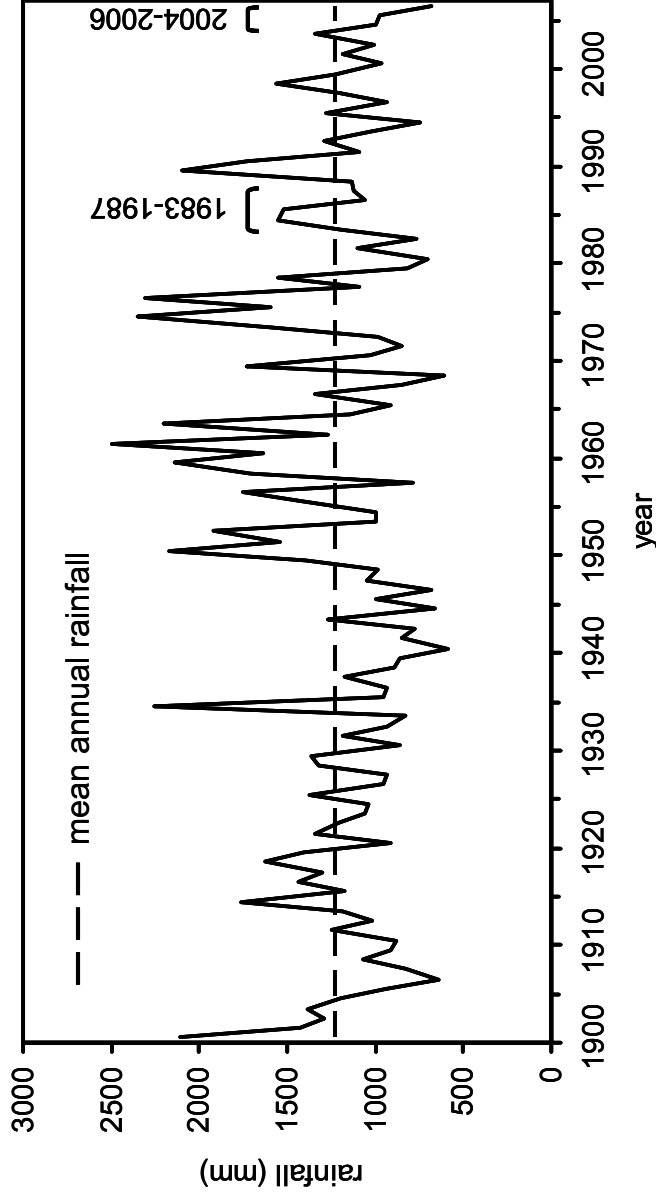
Figure 3.4. Historic annual rainfall variation at the Point Perpendicular weather station (Australian Bureau of Meteorology) located approximately 13 km northwest of our study site. As our study encompassed only three months of 2006 (January–March), we projected annual rainfall for this year by multiplying total rainfall during this period by four. The periods during which our study (2004–2006) and Kennett and Georges' (1990) study were conducted are indicated.

flooding and drying patterns of temporary wetlands at our site, the limited data we have come from observations at Ryan's Swamp from 1983–1987 (a relatively wet period; 1288 mm / yr), and again from 2004–2006 (a relatively dry period; 886 mm / yr; Fig 3.4). During the wet period, the swamp fluctuated between depths of 0.8–1.5 m but was never observed to completely dry, and during the dry period it was dry for 82% of the active seasons (September–March), with a maximum hydroperiod of only 30 days and depth of 0.22 m. The observations during these two periods, together with evidence from other studies demonstrating a strong correlation between annual precipitation and wetland hydroperiod (Bauder 2005) suggest that temporary wetlands at our site have historically flooded and dried in a pattern reflective of the unpredictable precipitation. We then asked the question of whether this environmental variability also translates into variation in the costs and benefits to turtles moving to permanent wetlands or residing at temporary wetlands once wetlands dry.

Indeed, several life history traits and condition indices with fitness consequences differed markedly between turtles in temporary and permanent wetlands, but the higher quality habitat shifted between wet and dry periods. During the wet period, body condition, juvenile and adult growth, as well as reproductive output were considerably higher in the temporary wetland than in the nearby permanent lakes, reflecting the higher productivity of temporary wetlands at this time (Kennett and Georges 1990). In contrast, during the dry period, turtle body condition declined by nearly 8% between recaptures in the temporary wetland compared to relatively little change (-2% to + 1%) in the permanent lakes, and adult and juvenile growth rates were similarly low in both permanent and temporary wetlands (Table 3.1). We hypothesize that the large production benefits offered in temporary wetlands over permanent lakes during wet periods (Kennett and Georges 1990) weighed against the potential costs of long-distance overland movement would select for maximization of time in or near these distant temporary wetlands (residency) even throughout short duration or near-drying events. During dry periods, when temporary wetlands no longer offer production benefits, the survival and body condition payoffs in permanent lakes would select for movements to the lakes at this time. During extended periods of extremes such as multi-year droughts or continuous wet (1979-1982 or 1958-1964, respectively; Fig. 3.4), persistent fitness payoffs of one response over another would likely lead towards fixation of a behavior, but due to the historic unpredictability of rainfall, individuals would not have reliable information on which to anticipate the best response for the immediate future. Under this scenario both behaviors could coexist as is predicted by Giesel (1976), as a propensity to escape wetland drying in space (move to other wetlands) or in time (aestivate) becomes a bet-hedging

strategy maintained by in part genetic variation. Underlying genetic variability could theoretically reflect a dichotomous polymorphism or a continuum of heritable environmental switch points or thresholds that differ among individuals (Lack 1968, Lundberg 1987). Although the different responses have clear fitness consequences, before giving weight to the role of genetics in explaining the ultimate maintenance of variable responses observed here, we would need to demonstrate that the turtles' responses are also in part genetically determined (i.e., heritable). It is plausible that behavioral decisions are influenced by other factors that we could not examine such as age, experience, hatching site, or more robust measures of body condition that measure lipid stores.

Conclusions

We provide an example of intrapopulation diversity on a small spatial scale in the behavioral response to wetland drying for a freshwater reptile, and are the first to examine factors contributing to such variability in the field. These findings, together with recent laboratory studies (Peterson and Stone 2000, Ligon and Peterson 2002), demonstrate substantial behavioral and physiological variation in response to simulated and real drying conditions among individuals within a population of freshwater turtles. Moreover, both our field study and other laboratory studies (*op cit*.) link substantial fitness consequences with terrestrial aestivation and movement to other wetlands in turtles, indicating that aspects of behavior in oscillating environments, such as habitat choice, are subject to natural selection.

We identify three factors likely to be instrumental in shaping the behavioral response of freshwater reptiles inhabiting wetlands that periodically dry: 1) wetland hydroperiod, 2) the perceived cost of travel, and 3) predictability of environmental variation (Fig. 3.5). Where temporary wetlands are isolated from other waterbodies by long distances or other barriers that may increase risk, and where flooding duration is short, we expect the proportion of residential individuals in a population to increase relative to regions where wetlands are more spatially clustered and permanently flooded. We hypothesize that in areas characterized by stochastic environmental variation (e.g., precipitation) where wetlands flood and dry erratically, behavioral variation in response to wetland drying may be maintained, though the ratio of individuals exhibiting a particular strategy or tactic will vary to reflect the relative success of that strategy or tactic over others during recent environmental conditions. We demonstrate that a holistic understanding of behavioral variation must consider several factors simultaneously, and that
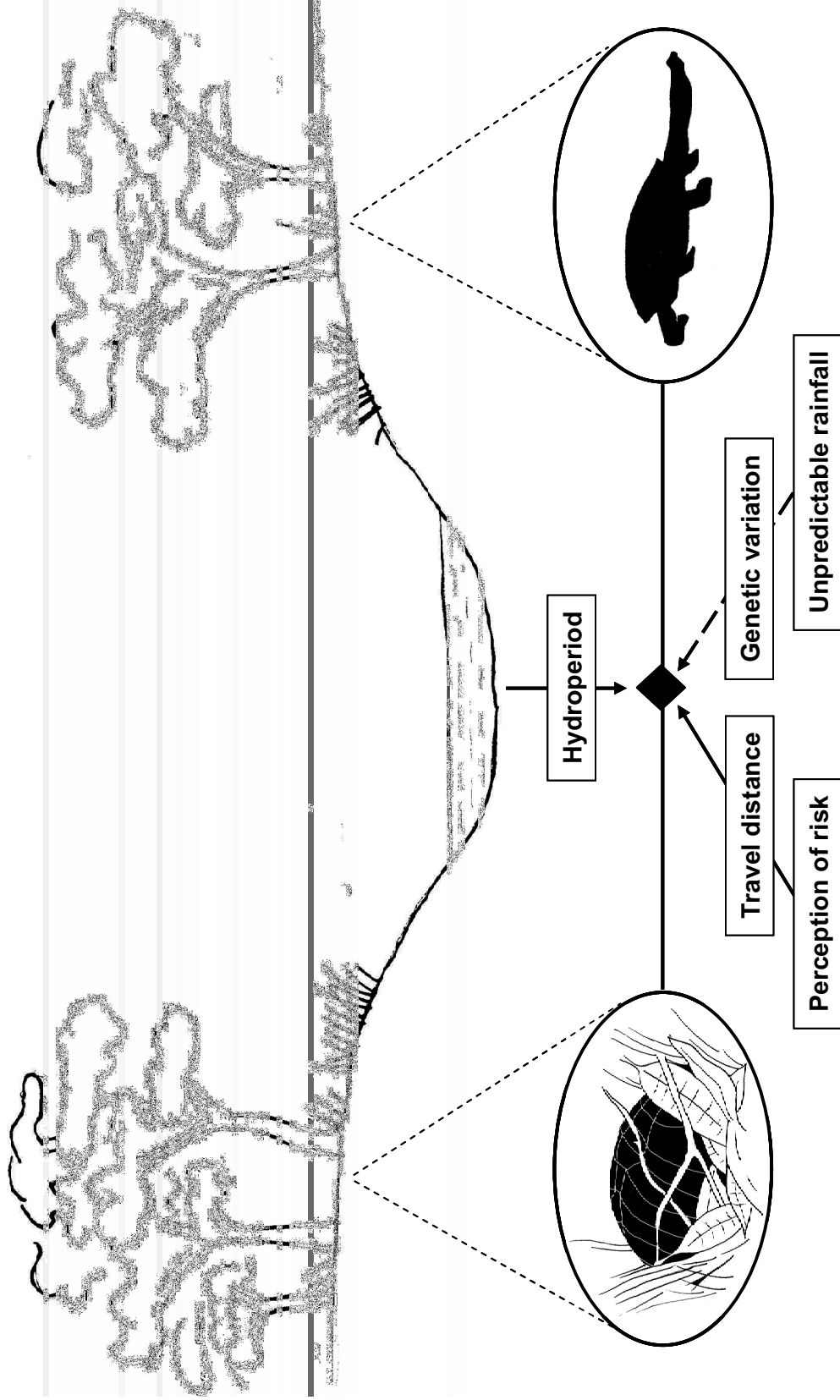
Figure 3.5. Factors influencing the decision to aestivate, how long to aestivate, or whether to move to permanent wetlands for the freshwater turtle *Chelodina longicollis*. The dashed arrow represents an hypothesized link, but other factors may also contribute.

long-term or repeat studies of a single population may be necessary to capture the wide variability of environmental conditions that have shaped a population's behavior over time.

TERRESTRIAL ACTIVITY, MOVEMENTS, AND SPATIAL ECOLOGY OF AN AUSTRALIAN FRESHWATER TURTLE, *CHELODINA LONGICOLLIS*, IN A TEMPORALLY DYNAMIC WETLAND SYSTEM

Picture: Ryan's Swamp when flooded (top) and dry (bottom)

Abstract

Animal movements, use of space, activity patterns, and habitat use are in part determined by proximal factors such as the landscapes they occupy, seasonal or environmental cues, and individual attributes such as sex and body size. Using radio-telemetry and a drift fence, we examined the contribution of these factors to variation in movements, use of space, and terrestrial activity in a freshwater turtle, *Chelodina longicollis* (Testudines: Chelidae), in south-east Australia. Movements and use of space depended strongly on landscape attributes, while sex and body size were less important. Movements and use of space also varied seasonally and were partly correlated with rainfall. The high overall vagility of turtles, irrespective of sex and adult body size (13.8 ± 2.8 SE ha home range, 2608 ± 305 m total distance moved, 757 ± 76 m range length), probably reflects a common need to be mobile in a landscape characterized by fluctuating resources in temporary wetlands. Use of temporary wetlands also drives *C. longicollis* into terrestrial habitats for movements between wetlands and extended refuge. Timing of inter-wetland movements was associated with rainfall, but most notably for immature individuals and for those moving towards temporary wetlands. Movements of adults, evacuation of the drying wetland, and periods of extended refuge (i.e., aestivation) were less dependent upon rainfall if at all. We conclude that movements about and use of the landscape by *C. longicollis* are under the strong influence of several interacting factors such as patch configuration, seasonal and environmental cues, and in part, body size. We argue that such behaviours are also ultimately under selection from the costs and benefits of these behaviours in the context of fluctuating resources.

Introduction

Information on animal movements, use of space, and activity patterns is critical for understanding their life history and conservation because attributes such as home range size, movement rates, and timing of movements in part determine fitness costs and benefits (Swingland & Greenwood 1983). Traversing large areas incurs costs of energy, predation risk, and time (Huey & Pianka 1981), and may also increase the number and quality of resources available that could then be translated into higher survivorship, growth, and reproductive success. For instance, migratory animals and wide-ranging foragers cover long distances to capitalize on seasonally variable resources not available to more sedentary individuals (Schoener 1971; Alerstam *et al*. 2003; Roe *et al*. 2004), but often do so at a high relative cost (Swingland & Lessells 1979; Sillett & Holmes 2002). The ratio of costs to benefits can depend on sex and body size (Pough 1978; Swingland & Lessells 1979), which can lead to variable movement strategies among individuals. Overall movement and space use patterns are thus likely to be shaped by both the proximal intrinsic (i.e., individual) and evolutionary (i.e., fitness costs and benefits) drivers of these behaviours.

An animal's movement, activity, and space use patterns can also depend on extrinsic factors. On a proximate and / or ultimate level, the spatial and temporal distribution of resource patches and the intervening matrix can directly or indirectly influence patterns of movement and space use (Schoener 1971; Huey & Pianka 1981; Ricketts 2001). When resources are patchy and widely distributed within a matrix of less suitable habitat, animals must traverse long distances and large areas, and tend to undertake such activity to coincide with conditions that maximize the probability of a successful outcome. Wetland landscapes present a system that is well suited for examinations of extrinsic drivers of behaviour. Wetlands are patchily distributed within terrestrial habitat, yet wetlands (especially temporary wetlands that occasionally or regularly dry) may vary in quality and so provide gradients in resource quality through space and time. This in turn affords a potential incentive to move and find a more suitable patch (Sayer & Davenport 1991; Roe & Georges 2007). When moving overland, animals adapted to aquatic habitats must contend with mechanical, physiological, and other challenges (Bentley & Schmidt-Nielsen 1966; Schmidt-Nielsen 1972; Wilbur 1975; Gillis & Blob 2001) that can restrict terrestrial activity to conditions that minimize costs (i.e., water loss, heat stress, predation risk) and that maximize ease of travel and the likelihood of finding another suitable site (Gasith & Sidis 1985; Bowne & White 2004). However, the extrinsic proximal cues that influence movement cannot be interpreted in isolation from intrinsic factors. For instance, terrestrial activity may be constrained to

occur during moist conditions (an extrinsic factor) in small but not large individuals (an intrinsic factor) owing to their different surface area to volume ratios, water storage capacity, and rates of water loss (Gans *et al*. 1968; Finkler 2001).

In this paper, we examine the movements, spatial ecology, and timing of terrestrial activity in the eastern long-necked turtle, *Chelodina longicollis* (Testudines: Chelidae), occupying a system of temporary wetlands and permanent lakes in south-east Australia. Previous studies have described the extent to which *C. longicollis* moves overland among wetlands, between wetlands and terrestrial refuge sites for aestivation (Stott 1987; Kennett & Georges 1990), and hypothesized how these behaviours may be ultimately influenced by long-term natural stochastic variation in rainfall (Roe & Georges 2008) or by anthropogenic modifications to their habitat (Roe & Georges 2007). Here, we used radio-telemetry and a terrestrial drift fence to examine the contribution of several natural proximal drivers to their behaviour. Specifically, we assess how intrinsic demographic, as well as a suite of extrinsic seasonal, environmental, local habitat, and landscape factors influence movement rates, space use, and timing of terrestrial activity. By examining several proximate factors simultaneously in the context of their ultimate (evolutionary) underpinnings, we argue that a more holistic understanding of a species' ecology can emerge.

Methods

Study site

We studied turtles from September 2004 to March 2006 in Booderee National Park (hereafter, Booderee), a 7000 ha reserve within the Commonwealth Territory of Jervis Bay in south-east Australia (150°43' E, 35°09'S). Georges *et al*. (1986), Kennett and Georges (1990), and Roe and Georges (2007, 2008) provide detailed descriptions and maps of the site. *Chelodina longicollis* is the only species of turtle in Booderee. A variety of freshwater wetlands ranging in size from 0.1 to 54 ha occur in the park, including permanent dune lakes, a network of permanent and ephemeral streams, and several temporary swamps that vary in hydroperiod (duration of surface water flooding). We classified all aquatic habitats as wetlands, and each wetland was defined as either permanent or temporary based on whether it was observed to have dried during the course of our study or from examination aerial photographs taken between 2001-2003. Wetlands occur within forested habitats in the park. The mapping and composition of typical plant communities are summarized in Roe and Georges (2007).

Radio-telemetry

Turtles were captured using traps or by hand from eight different wetlands in Booderee. We fitted 60 adult turtles with radio-transmitters (Sirtrack Ltd, Havelock North, New Zealand) mounted on aluminium plates and attached to the carapace with bolts or plastic ties through holes drilled in the rear marginal scutes. However, seven turtles in the vicinity of dry temporary wetlands died of starvation, dehydration, or were killed by sea eagles relatively early in the study (< 65 days of initiation of radio-tracking, Roe & Georges 2008) and thus were not included in our analyses of movement and spatial variables. The initial plastron length and mass (mean ± SD) of the remaining 53 turtles was 158.3 ± 9.7 mm and 691 ± 125 g for 32 females, and 140.5 ± 7.6 mm and 512 ± 68 g for 21 males. Transmitters ranged from 2.5 to 6.1% of turtle body mass.

Turtles were located three to four days per week from September to March (active season) during each year of the study, and once per month from April to August (inactive season). At each location, their coordinate position was taken by GPS (GPS III Plus, Garmin Corp., Olathe, Kansas; estimated error of 1–7 m) held directly above the turtle or from distance and bearing measurements to known points when the turtle could not be closely approached. Locations were plotted on habitat maps using ArcView GIS 3.1 (Environmental Systems Research Institute Inc., 1992).

Several variables were used to describe the movements and use of space for each turtle. Given the debate over whether minimum convex polygon (MCP) or kernel density techniques are more appropriate for describing use of space (Row and Blouin-Demers 2006, Nilsen *et al*. in press), we use both methods to estimate the size of total area use (hereafter, home range), while only the kernel methods were used to define intensively-used areas (hereafter, activity centres). For kernel density analysis, we used the fixed kernel method and the least squares cross validation method to select a bandwidth for the smoothing parameter, *h*, and used the 95 and 50% isopleths to estimate the size of home range and activity centres, respectively. Linear range length, defined as the straight-line distance between the two most widely spaced locations, was also determined. Total distance moved was estimated as the sum of the straight-line distances between sequential locations; this distance was then broken into movements in water and on land. Movement rates (m/day), space use, as well as the frequency with which individuals used terrestrial habitats for aestivation and movements between wetlands were also determined on a monthly basis. We calculated two variables to represent the wetland landscape used by each turtle, 1) an index of the distances between wetlands (hereafter, inter-wetland distance), calculated as the mean Euclidian distance

between the edges of all wetlands used by the individual, and 2) the mean surface area of all wetlands used by the individual. Distances and areas were calculated with the Nearest Neighbor, Animal Movements, and XTools extensions for ArcView GIS.

Drift fence

We constructed a terrestrial drift fence and pitfall array perpendicular to the axis of travel along a known turtle movement corridor approximately midway between a 0.2 ha temporary wetland (South Blacks) and a 4.5 ha permanent lake (Blacks Waterhole) separated by 400 m. The fence was constructed from polythene dampcourse (70 m long, 0.38 m high) buried several cm into the ground and held erect by wooden stakes. We buried seven sets of paired 20 L buckets, one on each side of the fence at 12 m intervals, allowing us to determine the turtle's direction of travel. Pitfalls were open from 6 September 2005 to 29 March 2006 and checked once daily. We measured straight-line carapace length (CL) and plastron length (PL) of each turtle to the nearest 0.1 mm using vernier callipers, and the mass to the nearest gram using a pesola spring balance. Individuals with CL < 145 mm were classed as juveniles, and for those with CL > 145 mm, we determined sex by examining the plastron curvature. Sub-adult females between 145–165 mm CL, though not sexually mature, can be distinguished from mature males in this size range (Kennett & Georges 1990). Thus, in this paper we group sub-adult and mature females together in all analyses as "females". Each turtle was then marked with a unique code by notching the marginal scutes of the carapace and immediately released on the opposite side of the fence from its point of capture.

Environmental variables

We assessed relative prey abundance in six wetlands from October 2005 through February 2006. Wetlands were systematically chosen to represent three temporary and three permanent wetlands used by turtles. Only vertebrate and invertebrate animals were sampled, as *C. longicollis* is an obligate carnivore that primarily forages on aquatic insects, anuran larvae and eggs, and fish (Chessman 1984a; Georges *et al*. 1986). Prey were collected from the littoral zone by sweeping a 34 cm × 28 cm dipnet (500 μm mesh) around available structure (e.g., macrophytes, rocks, debris) and by agitating the sediment. Three time-constrained (30 sec) sweeps were conducted at each wetland on a monthly basis. Specimens were immediately sorted in the field while alive. Invertebrates were preserved in 90% ethanol and later identified to order, counted, and weighed in the laboratory, while larval anurans were weighed

in situ and returned to the wetland alive. Potential prey items were referenced against previous studies (*op. cit.*) and were included only if recorded as an item in *C. longicollis* diet.

Daily rainfall and air temperature recordings were collected from the ranger depot in Booderee, a centralized location within 5 km of all study wetlands. We also recorded maximum and minimum daily shaded air temperature at the drift fence. Water levels were monitored from depth gauges every second day at each wetland.

Statistical analyses

We performed statistical analyses with SPSS (1999) and SAS (1999). Where appropriate, we examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, data were transformed to approximate normal distributions or equal variances. We used non-parametric tests when both raw and transformed data deviated significantly from assumptions. Statistical significance was accepted at the $\alpha \leq 0.05$ level except where stated otherwise. The Dunn-Sidak method was applied to multiple related comparisons to constrain the experiment-wide Type I error to 0.05. Values are reported as mean $\pm$ SE unless otherwise stated.

To examine differences in movement and area use estimates, we used a multivariate analysis of variance (MANOVA) with total movement distance, MCP, range length, and activity centre size as dependent variables, and sex as the independent variable. The 95% kernel density estimate was not included in this MANOVA due to its similarity with the MCP (see results). Relationships between an individual's movements and use of space (total movement distance, range length, home range, and activity center size), and five predictor variables (inter-wetland distance, wetland size, number of wetlands used, plastron length, number of days radio-tracked) were then investigated using a series of multiple regressions. Each estimate of movement and space use (dependent variables) was individually regressed against all predictor variables in a multiple backwards stepwise regression. All dependent and independent variables were $\log_{10}$-transformed prior to analysis. The Dunn-Sidak adjusted α level for statistical significance for this group of tests was $\alpha \leq 0.01$.

Monthly patterns of movement and space use were examined using repeated measures MANOVA, with $\log_{10}$ movement rate (m/day) and $\log_{10}$ range length as the response variables, month and month $\times$ sex as the within-subjects factors, and sex as the between-subjects factor. To determine if either the frequency of inter-wetland movements or overall proportion of locations in terrestrial habitats differed among months we used a series of Friedman tests for each sex separately. In the above analyses, each year was examined

separately, and only individuals radio-tracked during all active season months within the year were included. To examine if monthly variation in movements and habitat use were related to environmental variables, we used a series of multiple backwards stepwise regressions with monthly rainfall and mean air temperature as predictor variables, and $\log_{10}$ movement rate, $\log_{10}$ range length, inter-wetland movement frequency, and overall proportion of terrestrial habitat use as the dependent variables. Frequency of inter-wetland movements and proportion of terrestrial habitat use were arcsin square-root transformed prior to the regression analysis. The Dunn-Sidak adjusted α level for statistical significance for this group of tests was α ≤ 0.004.

We used the drift fence captures to examine relationships between terrestrial movements and environmental variables. First, we investigated coarse patterns of inter-wetland movements by using multiple backwards stepwise regressions to examine whether the number of turtles captured per month (response variable) was related to either rainfall or temperature (predictor variables). We then examined terrestrial activity on a fine temporal scale by assessing relationships between the number of turtles captured per day (response variable) and daily maximum shaded air temperature and rainfall (predictor variables) using Poisson regression (PROC GENMOD, SAS 1999). Captures were organized into five groups that were then used as the response variables in the model; 1) total number of turtles captured, 2) number of adult turtles captured, 3) number of immature turtles captured, 4) number of turtles moving from the permanent to the temporary wetland, and 5) number of turtles moving from the temporary to the permanent wetland. This model was run with an identity link and with the scale parameter equal to the deviance to correct for overdispersion, with type III sum of squares being calculated. The Dunn-Sidak adjusted α level for statistical significance for this group of tests was α ≤ 0.007.

Results

Movement and space use

Females were radio-tracked for an average of 342 ± 176 (SD) consecutive days during which 77 ± 34 (SD) locations were recorded per individual, while males were radio-tracked for an average of 327 ± 148 (SD) days throughout which 81 ± 29 (SD) locations were recorded per individual. Turtles exhibited high variation in total movement distance and space use, with some moving as little as 252 m and using home ranges as small as 0.1 ha, while others traversed total distances up to 13,127 m and had home ranges as large as 90.4 ha (Table 4.1).

Table 4.1. Movement and space use estimates (mean ± 1SE) for 21 male and 32 female *Chelodina longicollis* in Booderee National Park, Australia.

	male	female	combined	range
MCP (ha)	13.7 ± 4.2	10.1 ± 2.4	11.5 ± 2.2	0.1 – 78.5
95% KD (ha)	13.2 ± 3.7	14.2 ± 4.0	13.8 ± 2.8	0.1 – 90.4
50% KD (ha)	2.7 ± 0.7	2.6 ± 0.7	2.6 ± 0.5	0.01 – 14.90
RL (m)	829 ± 127	710 ± 94	757 ± 76	45 – 1945
total movement (m)	2677 ± 433	2562 ± 423	2608 ± 305	252 – 13,127
terrestrial movement (m)	1189 ± 196	1066 ± 127	1115 ± 108	0 – 3942

Note: abbreviations are MCP (minimum convex polygon), KD (kernel density), RL (range length).

However, in no case did variability in movement and space use measures reflect sex differences (MANOVA: Wilks' Λ = 0.97, $F_{4,48}$ = 0.42, P = 0.792; Table 4.1), and the MCP and 95% kernel density methods yielded similar home range estimates (Table 4.1). A considerable proportion of total movement distance was through terrestrial habitat (males: 47.2 ± 5.1 %, females 46.0 ± 4.7 %; Table 4.1).

Variation in movement and space use was most strongly influenced by attributes of the wetland landscape (Table 4.2). The inter-wetland distance and wetland size indices explained significant amounts of the variance for every estimate of movement and space use examined. Other factors that contributed significantly to variation in at least one of the models were the number of wetlands used, body size, and the length of the radio-tracking period. Together these factors explained between 61–86% of variation in movement and space use estimates (Table 4.2). Relationships between predictor and response variables were linear and positive, with the exception of a quadratic relationship between inter-wetland distance and MCP home range size (Table 4.2).

Seasonal patterns

Twenty-two (10 M, 12 F) and 20 (9 M, 11 F) turtles were radio-tracked through the entire active season in the first and second years, respectively. Monthly movement rates and range lengths varied among months similarly for males and females in the first year (month: Wilks' Λ = 0.32, $F_{10,198}$ = 15.36, P < 0.001, month × sex: Wilks' Λ = 0.91, $F_{10,198}$ = 0.929, P = 0.508), but in the second year there was an interaction between month and sex (month: Wilks' Λ = 0.66, $F_{12,214}$ = 4.05, P < 0.001, month × sex: Wilks' Λ = 0.76, $F_{12,214}$ = 2.60, P = 0.003). Movements and range length were generally highest in spring and early summer of both years and declined in late summer and early autumn, with the exception of female range length in year two, which did not vary among months (Fig. 4.1). However, in no case did the sexes differ in monthly movements or range length (P > 0.217). Monthly movement rate was positively correlated with rainfall (r^2 = 0.62, P = 0.002), but monthly range length was not correlated with either rainfall or temperature (P = 0.186). Owing to the high positive correlation between range length and home range size (MCP: r^2 = 0.91, kernel density 95%: r^2 = 0.78), the monthly trends in linear space use are likely to provide an accurate reflection of monthly variation in area use as well.

Inter-wetland movement frequency and proportion of locations in terrestrial habitats did not differ significantly among months for males in either year after applying the Dunn-Sidak adjustment to α (X^2 < 14.43, P > 0.025). Females only exhibited significant monthly

Table 4.2. Relationships between movement and area use estimates (dependent variables) and independent variables found to be significant for *Chelodina longicollis*.

dependent variable[a]	independent variables[b]	coefficient	df	F	R^2	P
MCP (ha)	wetland size	0.598	4,48	72.6	0.86	< 0.001
	number of wetlands	1.840				
	inter-wetland distance	–0.629				
	inter-wetland distance^2	0.284				
	constant	–0.256				
95% KD (ha)	inter-wetland distance	0.413	2,50	38.6	0.61	< 0.001
	wetland size	0.804				
	constant	–0.300				
50% KD (ha)	inter-wetland distance	0.463	2,50	46.9	0.65	< 0.001
	wetland size	0.793				
	constant	–1.132				
RL (m)	inter-wetland distance	0.185	4,48	41.5	0.78	< 0.001
	wetland size	0.367				
	plastron length	2.026				
	number of wetlands	0.525				
	constant	–2.245				
total movement (m)	inter-wetland distance	0.233	3,49	59.4	0.78	< 0.001
	wetland size	0.192				
	days radio-tracked	0.226				
	constant	2.255				

[a] abbreviations are MCP (minimum convex polygon), KD (kernel density), RL (range length).

[b] independent variables are listed in order of their overall contribution to the model.
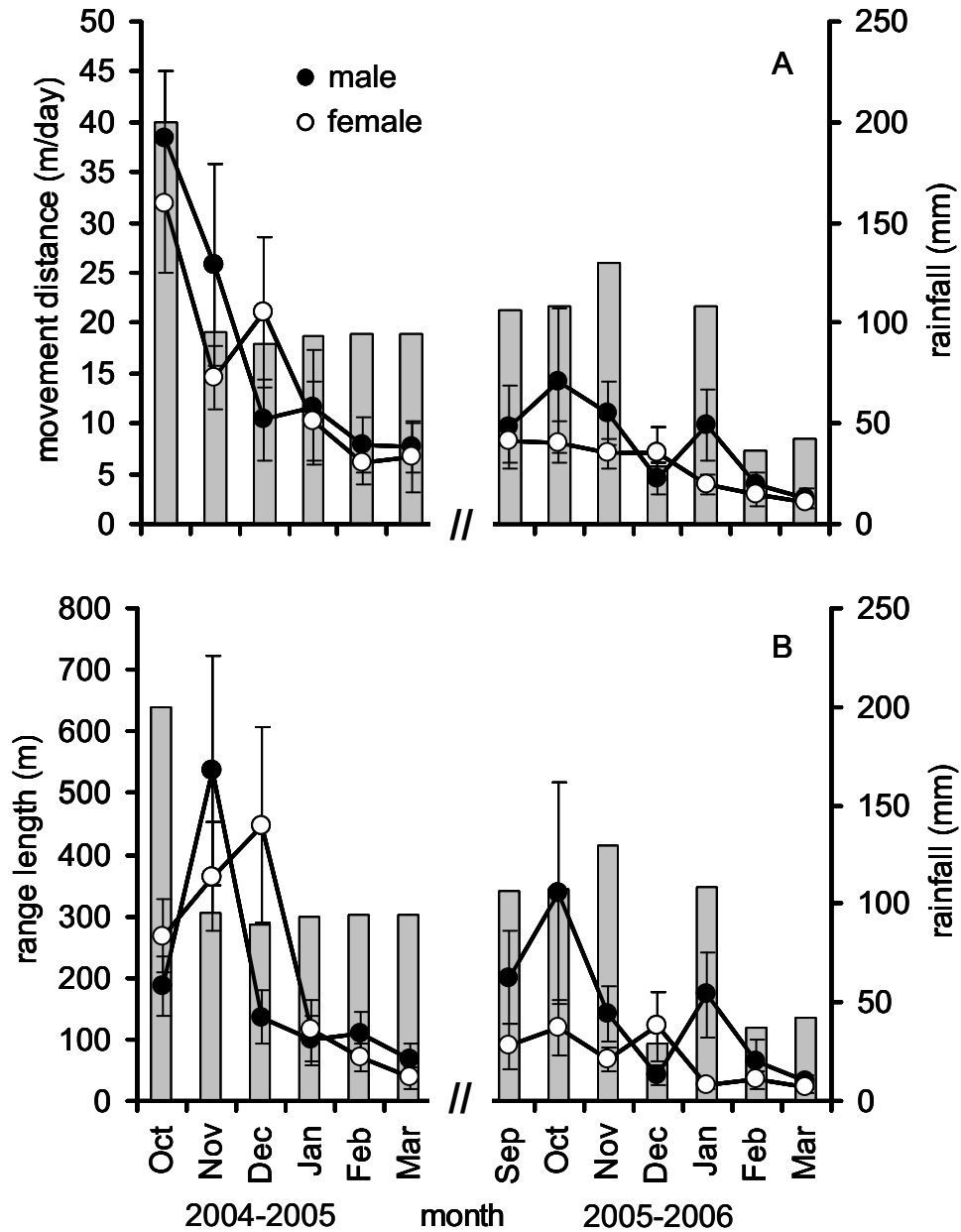
Figure 4.1. Relationships between monthly rainfall (bars) and A) movement distance, and B) range length for *Chelodina longicollis* studied with radio-telemetry during the active season. Movement variables are mean ± 1SE.
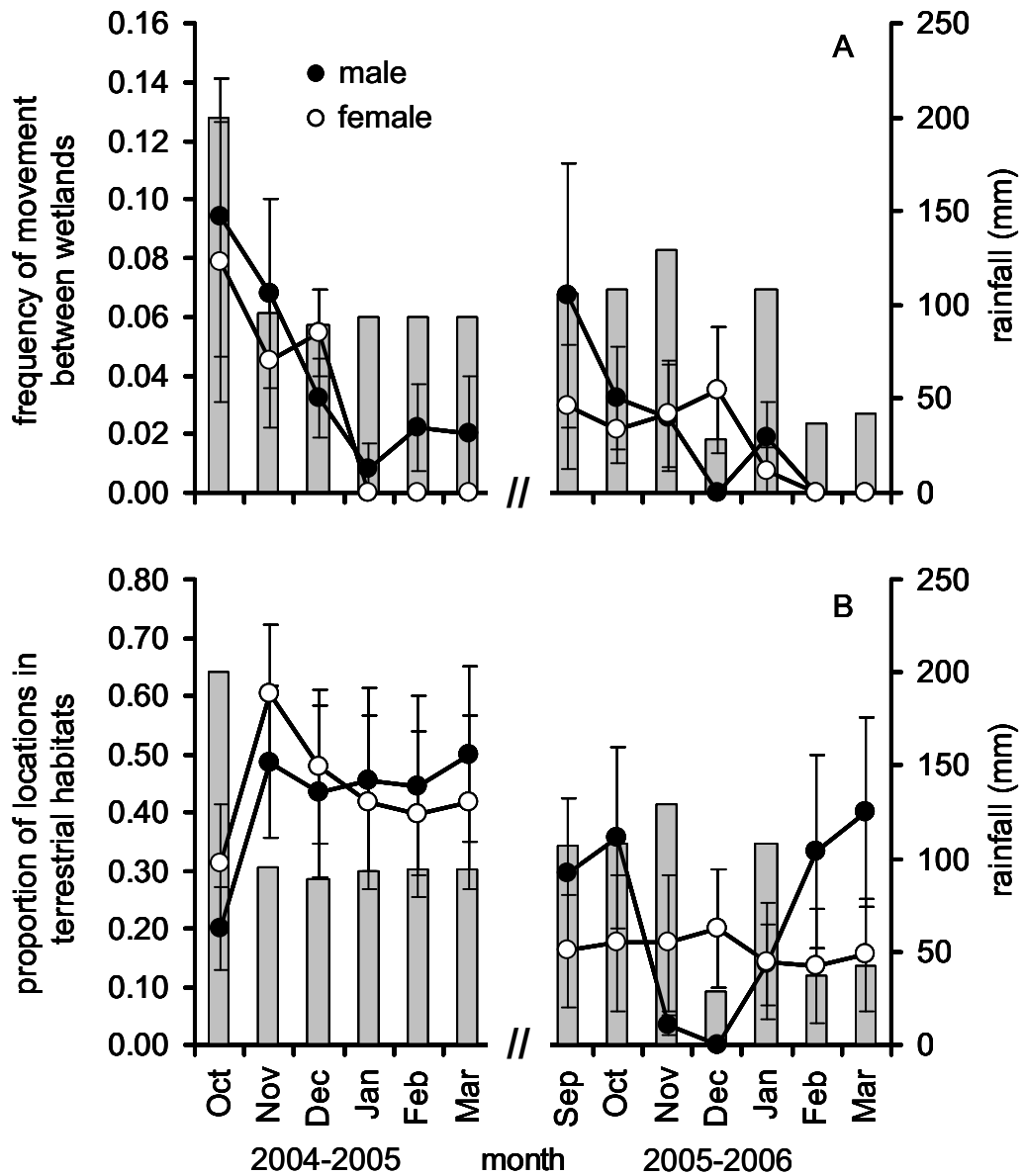
Figure 4.2. Relationships between monthly rainfall (bars) and use of terrestrial habitats for A) overland movement between wetlands, and B) overall terrestrial habitat use for *Chelodina longicollis* studied with radio-telemetry during the active season. The independent variable is the proportion of locations in each month where a movement between wetlands or terrestrial habitat use was observed. Habitat use variables are mean ± 1SE.

variation in inter-wetland movement frequency during the first year when movements were more frequent in spring and early summer ($X^2 = 19.07$, $P = 0.002$), but did not vary in overall terrestrial habitat use in either year ($X^2 > 5.00$, $P > 0.416$; Fig. 4.2). Monthly inter-wetland movement frequency was positively correlated with rainfall ($r^2 = 0.50$, $P = 0.007$) but not temperature, but after applying the Dunn-Sidak adjustment to α neither environmental variable was a significant predictor of movement frequency. The monthly proportion of locations in terrestrial habitats was not correlated with either rainfall or temperature ($P = 0.949$).

Drift fence

A total of 178 turtles were captured moving overland at the drift fence, with the majority (70%) moving from the temporary wetland to the permanent lake (Fig. 4.3). Coarse patterns of monthly movement were not related to rainfall or temperature ($P > 0.231$ in all cases, Fig. 4.3), but daily movements were significantly related to rainfall (Table 4.3). The number of turtles captured per day increased with rainfall, but the strength of the relationship, assessed from F-values and r^2 analogues, differed between groups. The strongest relationships with rainfall were for movements from permanent to temporary wetlands and for movements of immature turtles (r^2 of 0.31–0.34; Table 4.3), whereas movements from temporary to permanent wetlands and movements of adult turtles were only weakly related to rainfall (r^2 of 0.06–0.08; Table 4.3).

Prey and water variability

All invertebrates and tadpoles captured in our sweeps were included in the diet of *C. longicollis*. However, we captured no small fish despite their presence in one of the permanent wetlands (Fig. 4.4 E, J. Roe personal observation). Although not designed for statistical comparisons, our sampling of relative prey abundance and water levels demonstrates large absolute changes in prey abundance among months in all three temporary wetlands (maximum changes of between 7.9–27.5 g / sample; Fig. 4.4 A–C), and in one case complete absence when the wetland dried (Fig. 4.4 A). In permanent wetlands, there were generally smaller absolute changes in prey availability among months (maximum changes of between 1.1–9.1 g / sample; Fig. 4.4 D–F), and no times of complete absence of prey. Likewise, water levels changed more dramatically in temporary wetlands (62–100 % loss of
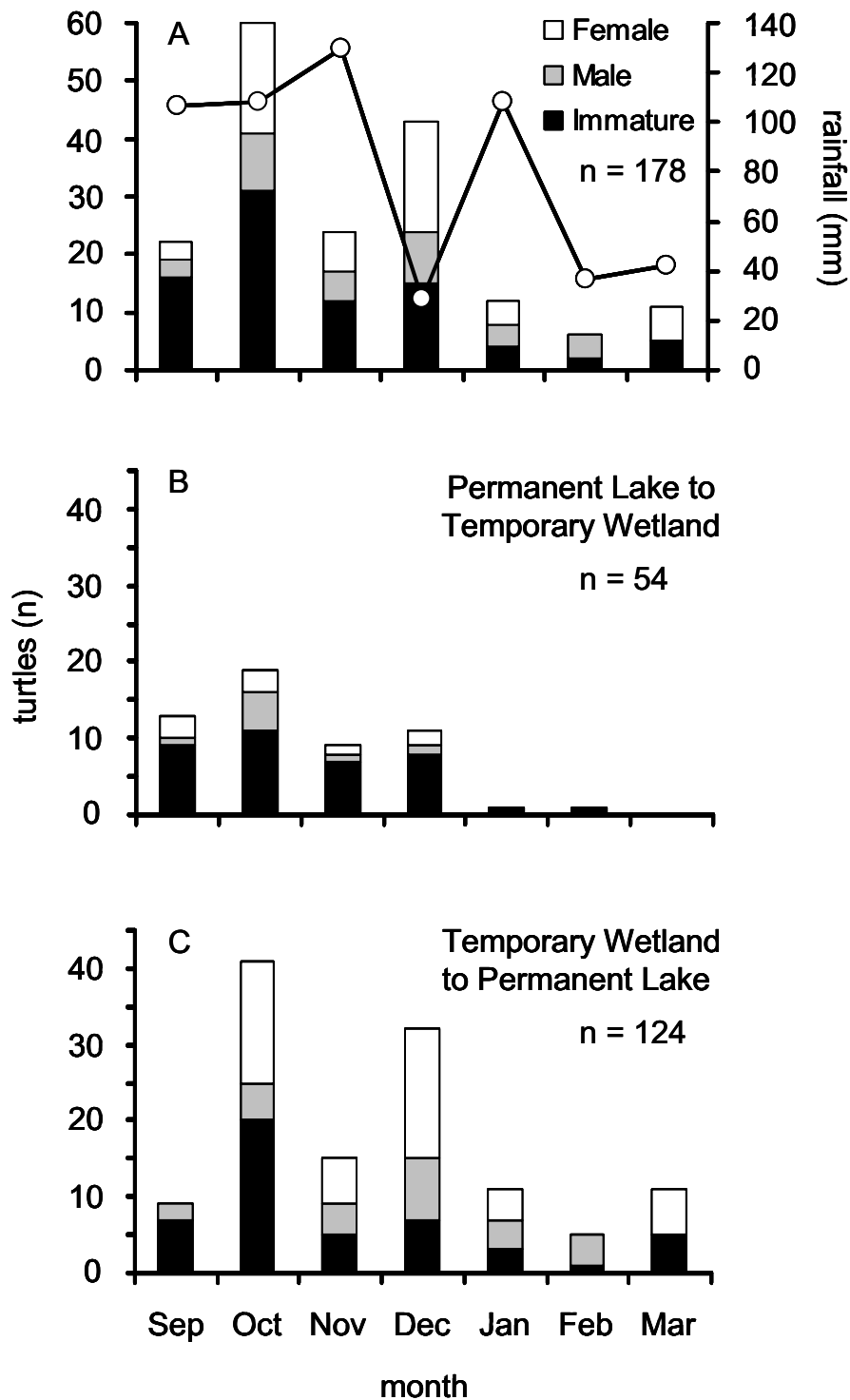
Figure 4.3. Relationship between monthly rainfall (circles) and number of turtles captured along a drift fence while moving overland between two wetlands for A) all individuals, B) individuals moving from the permanent lake to the temporary wetland only, and C) individuals moving from the temporary wetland to the permanent lake only.

Table 4.3. Summary of regression statistics demonstrating the relationships between rainfall, temperature, and the number of *Chelodina longicollis* captured at the terrestrial drift fence.

group	variable	$F_{1, 194}$	*P*	R^2 **
all turtles	rainfall	52.07	< 0.001*	0.21
	temperature	1.49	0.223	
adult turtles only	rainfall	9.56	0.002*	0.06
	temperature	5.11	0.025	
immature turtles only	rainfall	90.51	< 0.001*	0.31
	temperature	0.25	0.616	
permanent to temporary wetland	rainfall	108.99	< 0.001*	0.34
	temperature	0.66	0.419	
temporary to permanent wetland	rainfall	15.54	< 0.001*	0.08
	temperature	4.01	0.047	

Note: Relationships were examined using Poisson regression (PROC GENMOD, SAS 1999).

* indicates variables that were significant after adjusting alpha for multiple comparisons.

** a single R^2 value is reported for the multiple regression of rainfall and temperature for each group.
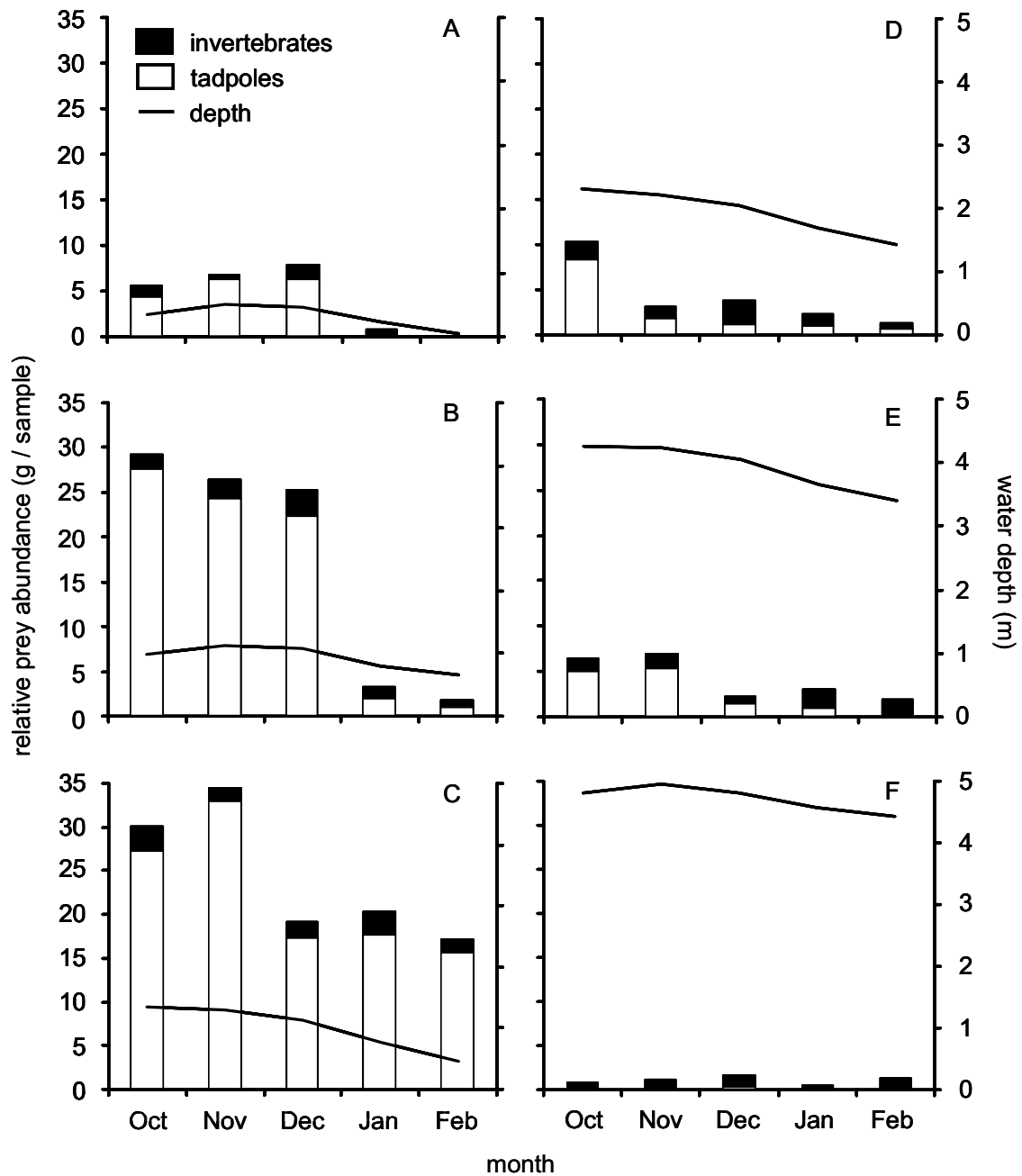
Figure 4.4. Monthly variation in relative prey abundance (primary axes) and water depth (secondary axes) in temporary wetlands (A–C) and permanent lakes (D–F). Values for tadpole and invertebrate abundance represent mean wet mass for the three time-constrained sweeps. No small fish were recorded in the prey sampling, though they occur in one of the permanent wetlands, Blacks Waterhole (E).

maximum water level; Fig. 4.4 A–C) than in permanent wetlands (18–51 % loss of maximum water level; Fig. 4.4 D–F).

Discussion

Our large sample size of turtles from several wetlands allowed us to simultaneously examine how numerous proximal intrinsic and extrinsic factors influence movement and space use in *C. longicollis* across a heterogeneous landscape. Movements and space use largely reflected variation in the habitat and landscape used by the individual, and to some extent season and rainfall, while body size and sex were less important. Timing of terrestrial activity was also dependent upon season and rainfall, but the degree of dependence on rainfall varied according to the specific behaviour exhibited, the context of the behaviour in relation to wetland flooding and drying, and turtle maturity (or size). However, the proximal factors that influence turtle behaviour at our site must be examined in the context of their ultimate underpinnings.

Movements and space use

Numerous proximal intrinsic factors such as sex, maturity, and body size (Morreale *et al*. 1984; Schubauer *et al*. 1990; Doody *et al*. 2002; Litzgus & Mousseau 2004), as well as extrinsic attributes of the environment including weather, season, and wetland size, configuration, and biotic productivity (Plummer *et al*. 1997; Piepgras & Lang 2000; Milam & Melvin 2001) determine the movements and space use of freshwater turtles. Sex and body size did not strongly influence movements or use of space in *C. longicollis*, even on a seasonal basis. The lack of a body size effect may in part stem from our exclusion of immature animals from radio-telemetry, but our sample nevertheless included nearly the complete size range of adults from the population. Seasonal differences in movement and space use patterns between sexes, typical of many freshwater turtles, are often attributed to the "reproductive strategies hypothesis" of Morreale *et al*. (1984), which predicts males should become more active and traverse longer distances at times of peak breeding activity to increase encounters with females, and females should increase activity during peak nesting activity in search of the most suitable nesting sites (Morreale *et al*. 1984). Breeding occurs soon after spring emergence in September–October in *C. longicollis*, while nesting occurs from October–December (Parmenter 1976; J. Roe, personal observation), but the sexes did not differ significantly in behaviour at these times or any other (Table 4.1; Fig. 4.1). Females

did not nest far from wetlands (e.g., < 30 m, J. Roe unpublished data), nor did we observe long-distance migrations to distant wetlands for the specific purpose of nesting. Both of these observations suggest potential reasons why females may not have travelled farther than males during the nesting season, but why don't the sexes differ at any other time of the year, especially in the breeding season?

The influence of extrinsic landscape characteristics and weather cues may outweigh other competing intrinsic factors also thought to be influencing behaviour in *C. longicollis*. Rainfall was an important proximal cue driving some aspects of movement in *C. longicollis*, a conclusion consistent with several studies of wetland animals (Wygoda 1979; Donaldson & Echternacht 2005; Todd & Winne 2006). Structural attributes of the landscape also influenced turtles' overall patterns of movement and space use (Table 4.2). That turtles traversed larger areas and longer distances with increasing inter-wetland distance seems like an obvious conclusion, but this finding raises the question of why most turtles continued to travel between wetlands, even in the face of increasing costs and risks associated with this behaviour. Temporal and spatial oscillations in water and prey availability associated with flood-dry cycles (Fig. 4.4) could be a proximal cause for movement among distant wetlands, as such variation presents opportunities for movement to recently flooded wetlands, as well as forcing evacuation from drying wetlands. The use of fluctuating resources can also influence the evolution of movement and space use patterns in animals (Schoener 1971; Huey & Pianka 1981). Several species of reptiles using temporary wetlands traverse large areas as they travel between patches to meet annual or life-cycle requirements, examples of which include turtles (Mahmoud 1969; Buhlmann 1995; Piepgras & Lang 2000; Milam & Melvin 2001), snakes (Shine & Lambeck 1985, Madsen & Shine 1996; Roe *et al*. 2004), and crocodilians (Gorzula 1978). Such movements allow individuals to capitalize on fitness benefits of improved foraging, increased growth, and greater reproductive output in flooded temporary wetlands (Chessman 1984a; Kennett & Georges 1990), but an ability to move also allows individuals to benefit from improved survival and body condition in the permanent wetlands when others have dried (Roe & Georges 2008). However, vagility in response to resource fluctuations is not the only successful strategy employed by aquatic reptiles. Aestivation is a more sedentary alternative taken by several species inhabiting temporary wetlands (Kennett & Christian 1994, Christian *et al*. 1996., Willson *et al*. 2006), including *C. longicollis* in particular contexts (Roe & Georges 2007, 2008). The occurrence of both strategies or tactics in *C. longicollis* is reflected in their high variability in movements and space use (Table 4.1).

Terrestrial habitat use

The two behaviours requiring the most extensive use of terrestrial habitats in this *C. longicollis* population were overland travel between wetlands and aestivation (Roe & Georges 2007), which accounted for nearly half of overall estimated movement distances and substantial amounts of time (Table 4.1, Fig. 4.2 B). We expected timing of terrestrial activity to correlate with extrinsic weather variables or intrinsic attributes that reduce thermal and hydration stress (e.g., body size, maturity status), but temperature was a poor predictor of timing in terrestrial habitats, and the influence of rainfall and body size (or maturity) was neither strong nor consistent. Instead, the timing of terrestrial habitat use and factors instigating terrestrial activity are complex in *C. longicollis*, perhaps reflecting the variety of reasons for using terrestrial habitats as well as the variable costs and benefits among individuals for these diverse behaviours.

The poor connection between rainfall and periods of extended terrestrial occupancy in *C. longicollis* may be in part owing to specific adaptations of this species to terrestriality. *Chelodina longicollis* has several water conserving abilities including the capacity to store and reabsorb water from the cloacal bladder, adjust uric acid excretions, limit cutaneous water loss, and may also conserve water by burying in the soil and debris (Rogers 1966; Chessman 1978; 1983; 1984b). Such a capacity for extended occupancy out of water characterizes several freshwater reptiles inhabiting temporary wetlands (Seidel & Reynolds 1980; Kennett & Christian 1994; Christial *et al*. 1996; Ligon & Peterson 2002; Roe *et al*. 2003), which suggests the frequent exposure to terrestrial conditions in these habitats has led to the evolution of water conserving abilities, whether for the purpose of terrestrial movement or aestivation. However, even given the suite of adaptations for terrestrial activity, Chessman (1978; 1984b) predicted that *C. longicollis* would not survive more than a few months out of water. That some individual *C. longicollis* can remain terrestrial 13–16 months in natural situations (Stott 1987; Roe & Georges 2007) challenges this prediction. Studies of water and energy relations of turtles free-ranging in terrestrial habitats would provide valuable insight into physiological constraints on their terrestrial activities.

The use of terrestrial habitats for movements between wetlands was more closely associated with rainfall than was terrestrial aestivation, though relationships with rainfall for inter-wetland movements were not particularly strong or consistent. A closer association with rainfall for inter-wetland movements may be due to a higher risk of desiccation associated with this behaviour. Increased body surface exposure, activity levels, and respiration rates are positively associated with evaporative water loss in reptiles (Gans *et al*. 1968; Seidel 1978; Wygoda & Chmura 1990), all of which would be higher during long overland movements

between wetlands than for aestivation. For instance, movements between wetlands are on average 4.5 times longer than movements to aestivation sites in this population (Roe & Georges 2007). Both juveniles and adults move between wetlands (Fig. 4.3), but terrestrial movements of juveniles were more closely associated with rainfall than for adults (Table 4.3), which is likely to reflect size-specific costs associated with surface area to volume ratios and water storage capacity (Finkler 2001). However, only a low proportion of the variance in movement timing was explained by rainfall for any group, including juveniles, indicating that inter-wetland movements are not constrained to coincide with rainfall, and that other factors may at times instigate movements between wetlands.

Wetland reptiles move between waterbodies for several reasons including dispersal, seasonal movements to and from overwintering sites, for reproduction, opportunistic movements to exploit recent flooding, and to escape deteriorating conditions such as wetland drying (reviewed in Roe & Georges 2007). Our drift fence sampling provided a detailed examination of the biotic and abiotic factors that instigate movements between a temporary wetland experiencing dramatic resource fluctuations and a more stable permanent lake (Fig. 4.4 B, E). The majority of movements were from the temporary wetland to the permanent lake, possibly reflecting overall resource declines in the drying temporary wetland. More interestingly, however, was that movements from the temporary wetland were less correlated with rainfall than were movements towards the temporary wetland (Table 4.3). A case in point is December, a period when the majority (75%) of captures were of turtles leaving the temporary wetland. During this period, we recorded the second highest number of terrestrial captures, but also the lowest rainfall and greatest monthly decrease in both prey availability (-87%) and water level (-32%) at the temporary wetland (Figs. 4.3 and 4.4). Deteriorating conditions in drying wetlands can have severe consequences for turtles that fail to evacuate (Bodie & Semlitsch 2000a; Buhlmann & Gibbons 2001; Fordham *et al.* 2006b), and when these additional fitness pressures are added to the equation, forced terrestrial movement in search of more suitable sites will be likely to occur even if conditions for overland travel are sub-optimal. When moving from permanent to temporary wetlands, turtles would be afforded the luxury of time to await the most suitable conditions for overland travel while in a relatively stable wetland, perhaps accounting for the higher correlation with rainfall for movements in this direction. Alternatively, overland movements during periods of high rainfall may be an evolved behaviour to ensure a higher likelihood of prolonged flooding at the destination site (Gasith & Sidis 1985), as movements to temporary wetlands that fail to fully flood would not provide the expected benefits. Both of the above explanations,

however, suggest that turtles tend to time terrestrial movements to temporary wetlands with rainfall to maximize chances of a successful outcome.

Conclusions

Drawing from the wider literature, it should come as no surprise that the movements, spatial ecology, and activity patterns of *C. longicollis* were largely driven by extrinsic factors, as the behaviours of animals using fluctuating resources in heterogeneous landscapes are often shaped more by the spatiotemporal distribution of suitable patches and environmental cues than by other factors (Sinclair 1983, McIntyre & Wiens 1999, Schwarzkopf & Alford 2002), However, whereas inter-patch movement over large areas is a common response to seasonal or unpredictable resource variation in many animals (Swingland & Lessells 1979, Sinclair 1983, Alerstam *et al*. 2003), freshwater reptiles are generally considered to be less mobile in response to resource fluctuations (Madsen & Shine 1996), especially when terrestrial activity is required   We argue that the use of fluctuating resources in temporary wetlands imposes strong proximal and selection pressures on *C. longicollis*' patterns of movement, space use, as well as their terrestrial activity, and that these pressures extend to all members of the population, regardless of sex or body size. We concur with Gibbons (2003) that a high degree of mobility, terrestriality, as well as variability in these behaviours characterizes other freshwater reptiles in temporally dynamic systems. A large proportion of Australia's wetlands and associated biota are under the influence of flood-dry cycles, but the distribution of temporary wetlands, their hydrology, and thus the responses of dependent biota are being drastically altered, both directly from water management and indirectly from climate change (Brock *et al*.1999; Kingsford 2000; Roshier *et al*. 2001). Knowledge of the ecology of wildlife using these temporally dynamic habitats in Australia is limited, yet such information is needed to inform the effective management of wetland systems.

ENERGY AND WATER FLUX DURING TERRESTRIAL AESTIVATION AND OVERLAND MOVEMENT IN A FRESHWATER TURTLE

Pictures: Drawing a fluid sample from a turtle in the doubly-
labelled water study (top), and a turtle equipped with a miniature
temperature data logger (bottom).

Abstract

The doubly-labelled water (DLW) method for studying energy and water balance in field-active animals is not feasible for freshwater animals during aquatic activities, but several species of nominally aquatic reptiles leave wetlands for several critical and extended behaviors where they face challenges to their energy and water balance. Using DLW, we studied energy and water relations during terrestrial aestivation and movements in the eastern long-necked turtle (*Chelodina longicollis*), a species that inhabits temporary wetlands in southeastern Australia. Water efflux rates of 14.3–19.3 ml $(kg\ d)^{-1}$ during aestivation were largely offset by influx, indicating that turtles maintained water balance while terrestrial. Aestivation energy expenditure declined over time to 20.0–24.6 kJ $kg^{-1}\ d^{-1}$, but did not indicate substantial physiological specializations. Energy reserves are predicted to limit survival in aestivation to an estimated 49–261 days (depending upon body fat), which is in close agreement with observed bouts of aestivation in this population. The energy cost and water flux rates of overland movement ranged from 46–99 kJ $(kg\ d)^{-1}$ and 21.6–40.6 ml $(kg\ d)^{-1}$ for turtles moving 23–34 m d^{-1}. When a wetland dries, a turtle that forgoes 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 previous observations that more turtles aestivate when longer distances must be travelled to the nearest permanent lake, whereas emigration is nearly universal when only short distances must be traversed. We demonstrate that the DLW method can be applied to address questions on the behavioral ecology and physiology of freshwater turtles.

Introduction

Energy is a limiting resource that features prominently in the behavioral ecology and life history of ectotherms (Congdon et al. 1982; Congdon 1989). Ectotherms must balance a finite energy intake against expenditures for maintenance as well as discretionary production (growth, reproduction, and storage), all of which could influence overall fitness. When energy expenditure surpasses intake, an individual is in negative energy balance, and with the exception of storage, energy allocated to one function is typically unavailable for others. Owing to these trade-offs, individuals must not only weigh the benefits of expenditure against intake, but also respond in a way that results in the most optimum distribution of available energy among competing compartments. Individuals can exert some control over these energy allocations through their behavior. Some classic examples of energy trade-offs are for reproductive effort, where individuals may cease foraging and expend variable amounts of energy in parental care (Shine et al. 1997), attracting mates (Grafe 1996), defending territories (Grantner and Taborsky 1998), or migrating to breeding grounds (Kinnison et al. 2003).

Water is another resource that is vital for nearly all life-processes, but access to water can be limited in terrestrial environments. Water generally comprises 65-80% of an animal's body mass, but body water can fluctuate according to its availability in the environment and the individual's ability to physiologically or behaviourally regulate water balance through intake and loss. Physiological mechanisms to conserve water include metabolic depression (Guppy and Withers 1999), changes to skin permeability (Lillywhite 2006), and temporary storage of excretory wastes (Peterson 1996a). Behavoiral regulation can include habitat choice and altered activity levels (Christian et al. 1996; Ligon and Peterson 2002), drinking and eating (Peterson 1996b), posture (Wygoda and Chmura 1990), and storage (Jorgensen 1998). Individuals that most successfully manage their energy and water budgets through behavioral or other allocation responses are expected to have the highest fitness (i.e., lifetime reproductive success) and thus be favored by natural selection.

Studying animals in the field, where they are free to respond in ways that influence their survival, would provide the most useful information with which to address behavioral ecology and evolutionary questions. The development of the doubly-labelled water technique (DLW; Lifson and McClintock 1966) has revolutionized the study of energy and water relations in animals (Nagy et al. 1999; Butler et al. 2004). Reptiles have proven to be tractable for the DLW method, but studies of turtles are limited to three terrestrial species and two sea turtles (Nagy and Medica 1986; Peterson 1996b; Henen 1997; Penick 2002; Wallace et al. 2005; Jodice et al. 2006; Clusella Trullas et al. 2006). The overall bias against turtles is

puzzling, for most can be easily tracked and recaptured, and their ecology and life history has been otherwise well documented within a theoretical framework of energy and water that could be greatly advanced by field studies (Congdon et al. 1982; Mautz 1982; Minnich 1982; Congdon 1989). The bias against freshwater turtles stems from the intractability of the DLW method during aquatic activities (Booth 2002), but several critical aspects of their ecology occur in terrestrial habitats. For instance, nearly all freshwater turtles must leave the water to nest, and several make occasional or regular and extensive use of terrestrial habitats to move between wetlands, to overwinter, or to aestivate (Semlitsch and Bodie 2003; Roe and Georges 2007). Terrestrial habitats feature perhaps most prominently in the ecology of turtles inhabiting temporary wetlands (Buhlmann and Gibbons 2001; Roe and Georges 2008).

The eastern long-necked turtle (*Chelodina longicollis*) inhabits both permanent and temporary wetlands and uses terrestrial habitats extensively for aestivation and movements between wetlands (Roe and Georges 2007). The typical pattern of movement involves travelling from nutrient-poor permanent lakes to several highly productive temporary wetlands upon flooding, and then back to the lakes when the wetlands dry (Kennett and Georges 1990; Roe and Georges 2007). However, there is considerable behavioral variation among individuals in response to wetland drying, as some immediately move to other wetlands while others aestivate. We hypothesized that such behaviors are influenced by a weighing of the expected costs, risks, and benefits of overland movement versus those of aestivation in the context of unpredictably fluctuating flood-dry cycles (Roe and Georges 2008). Energy and water costs are likely to factor into turtles' responses, but we currently have very little knowledge of these costs for freshwater turtles in the field.

Here, we measure energy use and water flux in a freshwater turtle (*C. longicollis*) during terrestrial behaviors using the DLW technique. We assess whether water or energy constrains the duration that individuals can survive in terrestrial aestivation. We also estimate the energy and water flux rates associated with overland movements. These determinations allow us to compare the physiological costs of terrestrial aestivation to those of movements between wetlands, and ultimately arrive at a better understanding of the consequences of behavioral trade-offs in *C. longicollis* and perhaps other freshwater turtles.

Material and Methods

Study site

Field work was conducted in Booderee National Park (hereafter, Booderee), a 7000 ha reserve located within the Commonwealth Territory of Jervis Bay on the southeast coast of Australia (150°43' E, 35°09'S). The site is characterized by several permanent dune lakes and a network of temporary wetlands within a matrix of forests and heath scrubland. Booderee has a temperate maritime climate with a long-term average annual rainfall of approximately 1100-1200 mm spread evenly throughout the year, with each month typically receiving > 80 mm, though the timing and intensity of rainfall can be highly variable. Summers are warm and winters mild, with average minimum and maximum temperatures of 18–24 °C in January, and 9–15 °C in July. Relative humidity typically exceeds 69% throughout the year. Climate statistics were obtained from the Australian Bureau of Meteorology. A more detailed description of the site can be found in Kennett and Georges (1990) and Roe and Georges (2007; 2008).

Doubly-labelled water study design

We studied the terrestrial movements, behavior, temperature, energy use, and water flux of two groups of turtles. The first group comprised seven individuals (4 males and 3 females) that were, of their own accord, inactive under leaf litter in the forest adjacent to two temporary wetlands that had been dry for 43 and 65 days. Five of these animals were part of an ongoing radio-telemetry study (Roe and Georges 2007; 2008), and the other two were captured by searching under debris near the tagged turtles. These turtles were considered to be aestivating, and we refer to them as the "aestivation group" hereafter. The initial mid-line carapace length (CL) and mass of these turtles averaged 189.9 mm (range = 168.0–216.0 mm) and 612 g (range = 401–931 g).

The second group of turtles comprised 12 individuals (3 males and 9 females) captured from a nearby wetland. After capture, this group was kept at the University of Canberra field station for two days before being translocated to a terrestrial site approximately 4.5 km from the capture wetland. The release site was an extensive area of continuous forest and heathland in undulating dunes, very closely resembling the terrestrial landscape and vegetation that turtles travelled through when moving between wetlands. By taking turtles to a distant and unfamiliar site, we aimed to take advantage of the turtle's ability to orientate

itself and eventually initiate searching or homing behavior to return to wetlands (Graham et al. 1996), but without allowing a quick return to water. This group of turtles in simulated overland movement is referred to as the "translocated group" hereafter. The initial CL and mass of these turtles averaged 170.8 mm (range = 152.4–188.6 mm) and 482 g (range = 357–645 g).

Turtles in both groups were fitted with radio-transmitters (Sirtrack Ltd, Havelock North, New Zealand) according to protocols in Roe and Georges (2007). We also attached temperature dataloggers (Thermochron iButton; Dallas Semi-conductor, Dallas, TX) to the carapace to approximate body temperatures. Dataloggers were sealed using a fast-drying black rubber coating (Plasti Dip International, Blaine, MN) in a method identical to Grayson and Dorcas (2004). Dataloggers were programmed to record temperature at one hour intervals simultaneously for all turtles. None of the equipment impeded the movement of the hind legs, and averaged a combined 5% of turtle body mass (range = 3.0–7.8 %). In the forest near each of the two temporary wetlands and the translocation site, we measured environmental temperatures at a location central to that used by the turtles. Dataloggers were either buried under the leaf litter and sand or hung from a branch 1.5 m above the ground under dense canopy. Rain gauges were also placed in open areas at the three sites and checked daily.

Turtles were located every second day using a hand-held receiver and antenna. We estimated the percentage of the turtle's carapace that was visible (hereafter, cover index) and determined their coordinate position using GPS units (GPS III Plus, Garmin Corp., Olathe, Kansas; error of 1–7 m) or by distance and bearings from previous locations. We then plotted locations on habitat maps using ArcView GIS 3.1 (Environmental Systems Research Institute Inc., 1992). We estimated movement distance along a straight-line path between sequential locations. This estimate is not likely to significantly overestimate actual movement distance, as *C. longicollis* typically travels in nearly linear paths with minimal sinuosity when moving overland (Stott 1987, Graham et al 1996). Immediately following the final body water determinations (see below), we examined whether they had recently fed by flushing their stomachs (Georges et al. 1986).

Field metabolic and water flux rate measurements

We estimated field metabolic rate (FMR) and rates of water influx and efflux using the DLW technique (Lifson and McClintock 1966; Nagy 1980), a method that has been previously validated in several species of reptiles with an estimated accuracy of ~11% (Nagy 1989). The

most precise estimates require that isotopes decline by approximately half of their starting enrichments without approaching too closely to background levels (Nagy 1980).

On 16–17 January 2006, we took an initial body fluid sample and then injected each turtle intraperitoneally with DLW containing 200 μl 37 MBq ^{3}H and 250 μl 95% atoms excess H_2 ^{18}O. After a 4–5 hr equilibration period in dry plastic bins in the laboratory (23–24°C), and in the field for aestivating turtles (22–26°C), a second body fluid sample was taken. It was previously determined that isotopes take 2.5 hours to come to equilibrium with body fluids at 22°C (Kilgour 1995). This period was adequate for isotope equilibration with body fluids in the translocated group, but not the aestivation group (see below). Following the equilibrium period and second fluid sample, each individual in the aestivation group was released exactly where they were captured, while the translocated group was released at their designated site.

We measured FMR and water flux over three periods. Turtles were recaptured and additional fluid samples drawn on 3–4 February 2006 (ending period 1), 21–22 February 2006 (ending period 2), and 11–12 March 2006 (ending period 3). Upon the first recapture in early February, we re-injected turtles with volumes and isotope activities of DLW identical to the first injection, took another fluid sample after a five hour equilibration period, and then released them. In late February, no re-injections were made, and at the final sampling in March turtles were reinjected with 100-200 μl ^{3}H and a final fluid sample was taken five hours later. Body fluid samples were drawn from a position anterior to the hind leg, typically in the vicinity of the bridge. This region quickly yielded an adequate volume of extra cellular fluid and blood. No leakage was observed at any injection, nor did any turtles void the contents of their bladder during handling. Prior to each fluid sample, turtles were brushed clean with a dry cloth and body mass was measured to the nearest gram. All fluid samples (0.5–1.0 mL) were stored in plastic O-ring vials and refrigerated (3°C) until analysis.

Isotope analyses

Water samples were extracted from body fluids by micro-distillation under vacuum. Standard solutions of ^{3}H and ^{18}O injectate were prepared in volumetric flasks and analysed along with the extracted water samples and the diluent used for the standard preparations. For tritium analysis, 20 μl sub-samples of extracted water were pipetted into 3 ml of scintillation cocktail (Ultima Gold) and counted for 10 minutes in a Packard LSC (Model 1600CA). Additional sub-samples of extracted water were sent to Metabolic Solutions (Nashua, NH) for ^{18}O analyses within eight months of sample collection in the field.

Calculations

Total body water (TBW) was estimated using the isotope dilution space technique (Nagy 1980), either as ^{18}O dilution for DLW injections or as ^{3}H dilution for singly-labelled water. TBW estimates from ^{3}H dilution were corrected by regression to reflect ^{18}O dilution because the use of ^{18}O yields more accurate estimates of TBW (Nagy 1980). For the 21–22 February sample when no re-injections were made, TBW values were interpolated assuming linear change in TBW between samplings.

Our method was originally designed to measure rates of CO_2 production and water flux with the traditional two-sample technique, where rates of isotope turnover are determined from measurements of isotope activity in an initial (equilibrium) and final fluid sample bracketing the sample period. We were alerted to the fact that equilibrium had not yet been reached in the initial samples in the aestivating turtles by their high TBW estimates (>100% as a percentage of body mass in several cases), whereas estimates in translocated turtles appeared to be in line with expectations for freshwater turtles (60–80%; Minnich 1982, Crawford 1994). For this reason, we employed the one-sample (or single-sample) technique for both groups, where the equilibrium isotope enrichment in the animal is predicted from the isotope dilution space calculation rearranged to solve for isotope enrichment (Nagy et al. 1984, Webster and Weathers 1989). This method yields estimates of energy and water flux with reasonable reliability (i.e., errors of 5–15%, *op cit*). TBW estimates from the translocated turtles (the group that reached equilibrium) were used to establish TBW as a percentage of body mass at each sampling. For aestivating turtles that had been out of water for 43–65 days, and were thus presumably more dehydrated, we used the percent body water established for the translocated turtles at the end of the 54-day study to estimate initial TBW for all sample periods. This assumption was supported by our observations that percentage body water in the translocated turtles (determined by the two-sample technique) initially declined in the first period, but then became relatively stable for the duration of the study (see results), a trend consistent with the that of Kilgour's (1995) study of the same population. We then assessed the accuracy of the isotope enrichments predicted by the single-sample technique by comparing them to the actual post-equilibrium measurements from the two-sample technique for the translocated turtles.

Rates of CO_2 production were calculated using equation (2) of Nagy (1980), and water efflux and influx rates were calculated using equations (4) and (6), respectively, of Nagy and Costa (1980). Net water movement was calculated as influx - efflux. We also calculated the

fractional turnover rates for ^{3}H (k_h) and ^{18}O (k_o) as in Lifson, Gordon, and McClintock (1955) to assess the k_o / k_h ratio. To convert VCO$_2$ to VO$_2$ and units of energy, we assumed turtles in both groups were fasting (see results) and utilizing either fat or mixed (fat:protein) energy stores. We used a thermal equivalent of 27.8 kJ L^{-1} CO$_2$ and an RQ of 0.71 for fat catabolism, and for a mixed metabolic substrate of fat and protein in equal proportions, 26.4 kJ L^{-1} CO$_2$ and an RQ of 0.75 (Gessaman and Nagy 1988). We assumed fat and protein yield 39.7 and 18.4 kJ g^{-1}, respectively, and metabolic water production from fat yields 1.07 ml H$_2$O g^{-1} and protein 0.50 ml H$_2$O g^{-1} (Shmidt-Nielsen 1964; Gessaman and Nagy 1988).

Supplementary observations

In order to determine if behavior of translocated turtles was similar to that of natural overland movement, we quantified the movement rates of 41 turtles studied by radio-telemetry that moved overland between wetlands (for details see Roe and Georges 2007). To compare temperatures of turtles aestivating terrestrially to those active in wetlands, we equipped five additional aquatically-active turtles with iButtons. To compare temperatures of aquatic and terrestrial turtles in spring and summer, we equipped 16 turtles with iButtons and placed iButtons in aquatic and terrestrial environments from Oct–Nov 2005.

Statistical analyses

We performed statistical analyses with SPSS Version 14.0 (1999) and SAS Version 8.2 (1999). Where appropriate, we examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, data were transformed to approximate normal distributions or equal variances. Statistical significance was accepted at the $\alpha \leq 0.05$ level except where stated otherwise. The Dunn-Sidak correction was applied to multiple related comparisons to constrain the experiment-wide Type I error to 0.05. All metabolic and water flux values are reported as mean ± SE for a group of individuals (Speakman 1997; Butler et al. 2004).

For comparisons of the various rate functions (CO$_2$ production, water influx and efflux) among animals of different body sizes, it is important to account for the effects of body mass. To do so, our first approach was to examine relationships between log$_{10}$ body mass and log$_{10}$ rate for each sample period using regression. However, relationships between body mass and whole body rate functions were weak and none were significant after applying the Dunn-Sidak adjustment ($R^2 < 0.25$, $P >> 0.008$ in all cases). Our inability to detect a

mass effect for whole-body rate functions is not completely unexpected, as small sample size, mass range, and behavioral variation among individuals often hides any underlying mass effects in field studies (Peterson 1996b). As a result, we used allometric relationships between FMR and water flux rates for reptiles in general because insufficient data for turtles alone exists (but see Jodice et al. 2006). The mass exponent for FMR in reptiles is 0.89 (Nagy et al. 1999), and for water flux in non-tropical habitats is 0.91 (Nagy 1982). We used mass-specific values for FMR and water flux rates in all analyses, calculated accordingly: $(FMR)/(body\ mass)^{0.89}$; $(water\ flux)/(body\ mass)^{0.91}$.

To determine if water influx and efflux rates (response variables) differed within any sample period, we used analysis of covariance (ANCOVA) with flux type and group (aestivation or translocated) as the independent variables, and mass as a covariate. To examine changes in body water over time, we used repeated measures ANCOVAs with sample period as the within-subjects factor and body mass as the covariate in a model with a compound symmetry covariance structure (PROC MIXED Model, SAS, vers. 8.2, SAS Institute, 1999). FMR and water efflux and influx rates (response variables) were also tested using the repeated measures ANCOVA described above, but with group (aestivation or translocated) as a between-subjects factor in the model. We then examined differences in rate functions calculated by the one- and two-sample techniques for the translocated turtles using ANOVAs. To assess whether shell temperature or movement rates (response variables) differed over the sample periods or between groups, we used a repeated measures ANOVAs with sample period as the within-subjects factor and group as the between-subjects factor. In the above analyses, FMR, water flux rates, body mass, and movement rates were log_{10}-transformed, while TBW (% body mass) was arcsin transformed.

The relationship between distance and duration of inter-wetland movements was examined using linear regression, with the distance between wetlands as the independent variable, and days in transit as the dependent variable. To determine if turtle shell temperatures (dependent variable) during terrestrial aestivation differed from those in wetlands in the two seasons (spring and summer), we used a two-way ANOVA with habitat, season, and their interaction as the independent variables.

Results

Doubly-labelled water

All translocated turtles and six of seven aestivating turtles were followed throughout monitoring, with none successfully returning to water. One aestivating turtle died between days 18–36 (61–79 days after wetland drying), presumably of natural causes, and was not included in analyses. Another aestivating individual began moving towards the nearest permanent lake. We retained this animal in the aestivating group for all statistical analyses, but in some cases we eliminate it when reporting energy and water flux rates characteristic of aestivating turtles.

Translocated and aestivating turtles differed behaviorally only with respect to movements. Translocated turtles moved longer distances than those in natural aestivation during the three sample periods (ANOVA; period: $F_{2,32} = 3.94$, $P = 0.030$; group: $F_{1,16} = 14.63$, $P = 0.001$; period $\times$ group: $F_{2,32} = 2.30$, $P = 0.127$; Table 5.1). Mean shell temperatures did not differ between groups or among periods ($P > 0.272$ for group, period, group $\times$ period; Table 5.1), and cover index was also similar (Table 5.1). Rainfall was highest in the first sample period and declined thereafter (Table 5.1). At the end of the study, stomachs were empty and the upper and lower surfaces of the mouth were joined by a thick mucous.

Percentage isotope declines dropped to a level insufficient to confidently interpret CO_2 and water flux in the aestivating turtles for the final two periods (Table 5.2). The k_o / k_h ratios were typically above 1.11, but fell to 1.09 in the translocated turtles for the final sample period (Table 5.2). Due to these potential limitations in the final sampling periods (Nagy 1980; Nagy and Costa 1980; Speakmann 1997), we used the initial period and a final one that incorporated periods two and three into a single final period. We were able to combine periods two and three because no isotope re-injections were made between them. In doing so, we ensured that isotopes had declined by at least 41–47%, and that k_o / k_h ratios remained $\geq$ 1.11. When we report results from periods two and three alone, we do so with the caution that estimates may be less precise.

Using the ^{18}O dilution space and the two-sample technique for translocated turtles, TBW estimates dropped from an initial $64.3 \pm 0.9\%$ of body mass to $62.6 \pm 0.8\%$ by the end of the first sample period, and finally falling to $62.2 \pm 2.0\%$ by the end of the study. TBW estimates determined by ^3H dilution were higher, dropping from 72.0% to 69.7%. However,

Table 5.1. Summary of behavior, temperature, and rainfall for *Chelodina longicollis* during terrestrial aestivation and movements following translocation.

	duration (days)	movement (m day^{-1})	cover index (% visible)	T shell (^{o}C)	rainfall (mm)
aestivation					
1	17.81	3.0 ± 1.5	13.7 ± 10.5	21.9 ± 0.2	25.3
2	17.96	3.5 ± 2.2	15.8 ± 12.8	21.7 ± 0.3	20.5
3	17.96	2.6 ± 1.7	21.5 ± 15.5	21.5 ± 0.3	0.3
2-3[a]	35.83	2.7 ± 1.9	18.7 ± 14.1	21.6 ± 0.2	10.4
translocated					
1	17.75	34.1 ± 6.0	20.2 ± 4.3	22.0 ± 0.2	37.4
2	17.97	35.2 ± 9.6	19.7 ± 5.9	21.9 ± 0.2	16.7
3	17.97	10.9 ± 2.6	7.7 ± 3.4	21.7 ± 0.3	0
2-3[a]	35.59	23.1 ± 6.0	13.7 ± 4.4	21.8 ± 0.2	8.4

[a] interval 2-3 reflects temperature and behavior through both of the final two periods

Values are either means or means ± SE

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Table 5.2. Summary of water flux and field metabolic rate (FMR) for *Chelodina longicollis* studied using doubly-labelled water during natural terrestrial aestivation and terrestrial movements after translocation.

	mass	water efflux	water influx	FMR	FMR[a]	^{3}H turnover	^{18}O turnover	k_o / k_h
	(g)	(ml kg^{-1}d^{-1})	(ml kg^{-1}d^{-1})	(ml CO$_2$ g^{-1}hr^{-1})	(ml O$_2$ g^{-1}hr^{-1})	(%)	(%)	
aestivation								
1	634 ± 60	19.3 ± 3.1	17.8 ± 2.7	0.095 ± 0.008	0.126 ± 0.010	41	47	1.23
2	620 ± 62	17.2 ± 2.2	16.2 ± 1.8	0.063 ± 0.007	0.084 ± 0.009	39	43	1.16
3	605 ± 68	13.1 ± 2.0	12.1 ± 1.6	0.039 ± 0.008	0.052 ± 0.011	31	32	1.11
2-3[b]	606 ± 65	15.3 ± 2.2	14.3 ± 1.8	0.043 ± 0.008	0.057 ± 0.011	57	61	1.11
translocated								
1	456 ± 23	40.6 ± 1.8	38.1 ± 1.7	0.148 ± 0.012	0.196 ± 0.016	68	72	1.15
2	447 ± 21	25.9 ± 0.9	25.5 ± 0.8	0.102 ± 0.007	0.136 ± 0.009	54	58	1.16
3	445 ± 21	17.7 ± 0.8	17.3 ± 0.8	0.040 ± 0.007	0.053 ± 0.009	42	44	1.09
2-3[b]	440 ± 21	22.0 ± 0.7	21.6 ± 0.6	0.072 ± 0.004	0.097 ± 0.006	73	77	1.13

[a] assuming an RQ of 0.75

[b] interval 2-3 reflects isotope declines through both of the final two periods

Values are either means or means ± SE

changes in TBW (% body mass) were not significant (ANCOVA; $F_{1,21} < 1.04$, $P > 0.370$ for mass and period), and water efflux was not statistically different from influx (ANOVA; $F_{1,31} < 1.08$, $P > 0.307$ for flux type and flux type × group). Even though water influx did not differ significantly from efflux, mean net water movement was consistently negative, dropping from an initial -2.56 to -0.36 ml kg^{-1} d^{-1} in the final period for the translocated group, and from -1.41 to -1.01 ml kg^{-1} d^{-1} in aestivators. Water efflux and influx were 1.5–2.1 times higher in translocated than aestivating turtles, declined in both groups from the first to second sampling periods, but the decline was much more pronounced in the translocated turtles (Tables 5.2 and 5.3). FMR also declined in both groups, but remained 1.6 to 1.7 times higher in translocated than aestivating turtles with the exception of period three, when FMR of translocated turtles was similar to aestivators (Tables 5.2 and 5.3; Fig. 5.1). Both mass-specific FMR and water flux rates declined with increasing body mass (Table 5.3).

Post-equilibrium ^{3}H enrichments predicted from the one-sample technique differed from two-sample determinations by an average of +0.3% (range = -4.2 to +7.0%) for the first period, and by -2.2% (range = -5.6 to +2.9%) for the second, while ^{18}O enrichments differed by an average of +0.5% (range = -3.7 to +10.7%) for the first period, and by -0.5% (range = -4.8 to +7.2%) for the second. These differences did not translate into significant variation between the one- and two-sample techniques for estimates of water efflux, influx, or FMR (water flux: $P > 0.206$; FMR: $P = 0.158$).

Supplementary observations

Movements of translocated turtles were relatively straight, with minimal sinuosity and typically in the direction of familiar wetlands (Fig. 5.2), and were drawn out over several days and interrupted by periods of extended inactivity buried in detritus. This behavior is similar to those undertaking overland movements during the course of their natural activities. Travel time for turtles moving between wetlands separated by an average of 427 m (range = 40–1470m, Roe and Georges 2007) was 15 ± 2.8 days (range = 1.5–44 days), increasing with distance according to the following equation: time (days) = 0.024 × distance (m) + 5.447 ($F_{1,39}$=12.85, $P = 0.001$, $R^2 = 0.25$). These turtles travelled at an average rate of 27.4 m day^{-1}, which is comparable to those of the translocated turtles (Table 5.1).

Shell temperatures during terrestrial aestivation were lower than those of aquatically active turtles by 2.0°C and 2.5°C in spring and summer, and lower in spring than summer for turtles in both habitat types (ANOVA; habitat: $F_{1,23} = 20.00$, $P < 0.001$; season: $F_{1,23} = 36.16$, $P < 0.001$, habitat × season: $F_{1,23} = 0.33$, $P = 0.570$; Fig. 5.3). Shell temperatures matched the

Table 5.3. Results of repeated measures ANCOVA for the effects of body mass, sample period, and group (translocated and aestivating) on field metabolic and water flux rates for turtles studied with doubly-labelled water.

variable	df	F	P
water efflux			
$\log_{10}$ mass	1,15	10.95	0.005
period	1,15	136.97	< 0.001
group	1,16	11.56	0.004
period × group	1,15	26.77	< 0.001
water influx			
$\log_{10}$ mass	1,15	12.85	0.003
period	1,15	153.46	< 0.001
group	1,16	16.08	0.001
period × group	1,15	29.08	< 0.001
FMR (CO_2 production)			
$\log_{10}$ mass	1,15	9.35	0.008
period	1,15	45.96	< 0.001
group	1,16	4.62	0.047
period × group	1,15	0.69	0.418
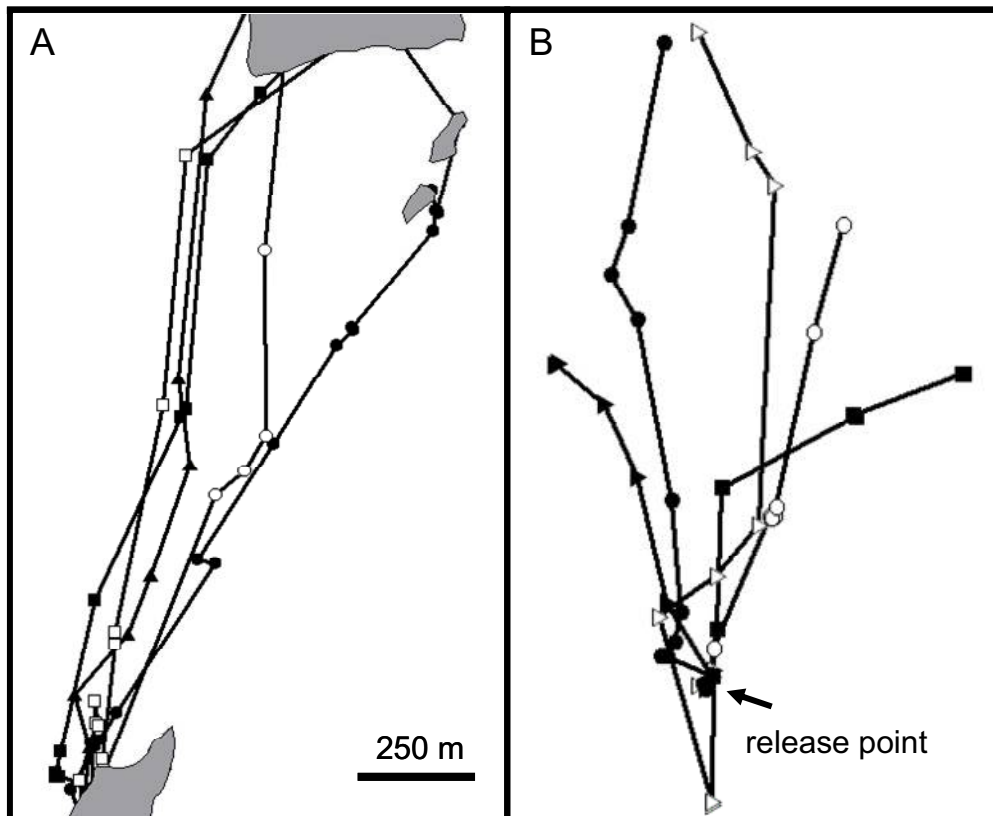
Figure 5.1. Similarity of terrestrial movements of turtles A) naturally travelling between wetlands and B) after translocation to stimulate movements back to the wetland. To avoid obscuring individual movement paths, not all individuals are shown.
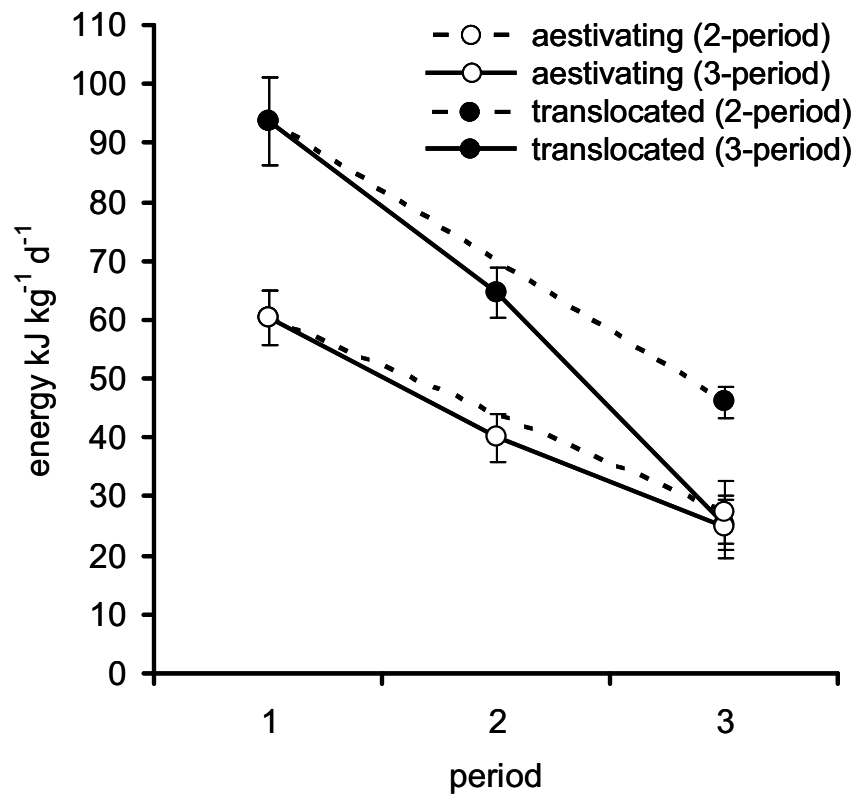
Figure 5.2. Field metabolic rates (FMR) for *Chelodina longicollis* naturally aestivating in terrestrial habitats (mass range = 469–910g) compared to those during overland movement after translocation to a site distant from water (mass range = 351–629g). A thermal equivalent of 26.6 J/L CO_2 was used to reflect the catabolism of protein and fat. We report FMRs for all three periods (3-period) and the initial and a final period (2-period) reflecting isotope declines through the final two periods combined.
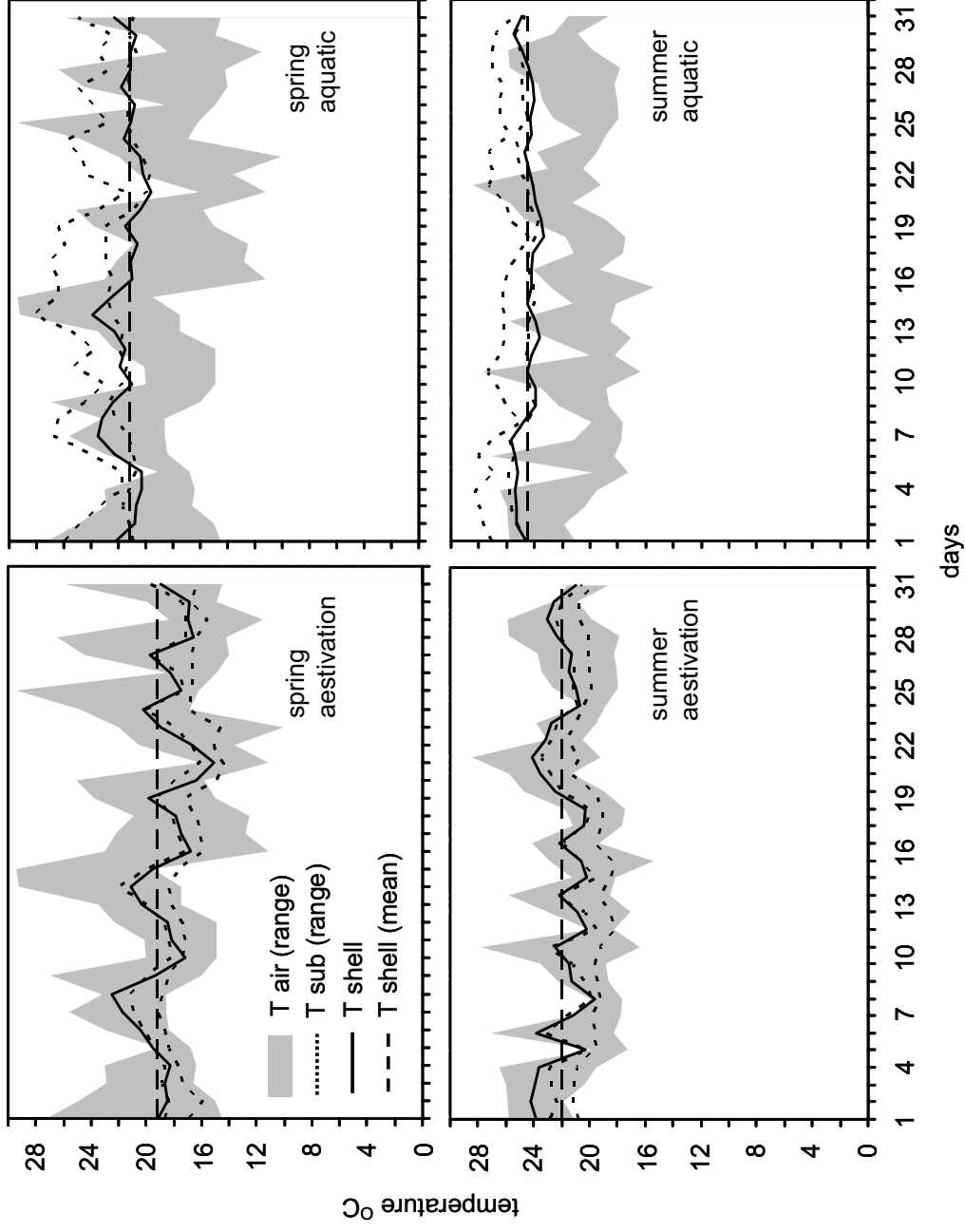
Figure 5.3. Environmental and shell temperature (T shell) variation for turtles terrestrially aestivating and aquatically active in spring (27 Oct – 26 Nov) and summer (27 Jan – 26 Feb). Substrate temperatures (Tsub) for terrestrial turtles reflect sand/detritus temperatures, and water temperature at 0.2 and 1.2 m depths for aquatic turtles. The horizontal dashed line is mean T shell through the sampling period.

surrounding substrates, generally tracking maximum detritus and minimum water temperatures while in terrestrial and aquatic habitats, respectively (Fig. 5.3).

Discussion

Rates of water flux and energy expenditure in *Chelodina longicollis* were consistent with other terrestrial turtles (Tables 5.2 and 5.4, Fig. 5.2), indicating that the DLW method can be successfully applied to freshwater turtles during terrestrial behaviors. Water flux and metabolic rates varied considerably between aestivating turtles and those moving overland, suggesting that these two behaviors have very different physiological consequences. Below, we explore these physiological consequences and limitations in the context of variable behaviors in response to wetland drying.

Terrestrial aestivation

When a turtle aestivates, survival depends on its ability to maintain water and osmotic balance and to support energy requirements until wetlands re-flood. Turtles can survive on minimal inputs of energy and water, and tolerate prolonged osmotic imbalances in body fluids (Peterson 1996a; Henen 1997; Peterson and Stone 2000; Ligon and Peterson 2002), while some nominally aquatic turtles can also forage on land to replenish energy stores (Scott 1976). For those that cannot feed while terrestrial, such as *C. longicollis*, water or energy will ultimately limit the duration they can survive out of water.

Aestivation is a behavioral strategy to reduce energy and water demands with or without accompanying physiological adjustments (Seidel 1978). The lower temperatures of aestivating turtles compared to those in wetlands (Fig. 5.3) would allow for some energy savings on top of lowered activity, but a physiological adjustment that could further reduce energy use during aestivation is metabolic depression. A reduction of 70–80% below standard metabolic rate (SMR) at high temperatures is typical of aestivating ectotherms (Guppy and Withers 1999), but depression to this extent in freshwater turtles has only been demonstrated in *Kinosternon flavescens* (Siedel 1978) and *Chelodina rugosa* (Kennett and Christian 1994), though such a capacity may be population specific (see Grigg et al. 1986; Peterson and Stone 2001; Ligon and Peterson 2002). We found little evidence that *C. longicollis* depresses metabolism to this extent after at least 97 days in aestivation (time since wetlands dried). The lowest FMR for aestivating *C. longicollis*, after excluding the individual

that became active, was 0.042–0.049 ml O_2 g^{-1} hr^{-1} and 20.0–23.4 kJ kg^{-1} d^{-1} (catabolism of protein and fat), or 0.047–0.055 ml O_2 g^{-1} hr^{-1} and 21.0–24.6 kJ kg^{-1} d^{-1} (catabolism of fat only). These values are more than 70% below predictions for reptiles of similar mass during their active seasons (Nagy et al. 1999), but similar to terrestrial tortoises during drought (Table 5.4; Peterson 1996a,b) and freshwater crocodiles in dry-season aestivation (Christian et al. 1996). Chessman (1978) estimated SMR for *C. longicollis* at 26°C to be 0.026 ml O_2 g^{-1} hr^{-1}, so a metabolic depression consistent with other ectotherms should have yielded metabolic rates in the range of 0.005–0.008 ml O_2 g^{-1} hr^{-1}. While it is possible that aestivating *C. longicollis* could gradually enter deeper states of torpor over time, as indicated by declining FMR throughout our study (Table 5.2, Fig. 5.2), we interpret such declines to be consistent with a more moderate degree of torpor with increasing starvation (Belkin 1965; Hailey and Loveridge 1997) rather than that associated with substantial metabolic specializations. This conclusion fits with the observations that aestivating *C. longicollis* remains partially active (Chessman 1983; Stott 1987; this study).

It is not surprising that *C. longicollis* did not feed in terrestrial habitats, as chelid turtles utilize a "strike, gape, and suck" method of prey capture that is not possible out of water (Parmenter 1976). Consequently, metabolic demands must be met by energy stores, the largest of which are primarily in the form of fat and protein in reptiles (Derickson 1976). To calculate the length of time that energy stores could last requires knowledge of the reserve amount and substrates catabolized. We were unable to directly determine either of these in our study animals, so we report an energy expenditure range based on catabolism of fat only and a mixed substrate of fat and protein in equal proportions (Crawford 1994). For reserve amounts, we used previous determinations of lipids in freshwater turtles, the most thorough of which was that of Congdon et al. (1982), where it was determined that *C. picta* was on average 3% lipid by weight, but some individuals were up to 9–10% lipid (Congdon et al. 1982). Other studies of lipids in small-to-medium sized freshwater turtles document a similar level of variability in lipid amounts (Belkin 1965; McPherson and Marion 1982; Crawford 1994; Kennett and Christian 1994), though one (*K. flavescens*) may have much higher reserves (Long 1985). Based on expenditures of 20.0–24.6 kJ kg^{-1} d^{-1}, a 500 g *C. longicollis* with 15–45 g (3–9%) of fat could survive for 49–261 days (Fig. 5.4). Survival times for any given initial fat reserve will likely be towards the higher end of this range, as turtles typically burn both protein and fat during long-term fasting (Crawford 1994; Henen1997). That TBW (% body mass) did not increase over time provides indirect evidence that *C. longicollis* catabolised both fat and protein.

Table 5.4. Water flux and field metabolic rates for free-ranging terrestrial turtles in mid- to late-summer.

species (sex)	mass (g)[a]	water flux[b]		field metabolic rate[b]		source
		ml d^{-1}	ml (kg d)$^{-1}$	kJ d^{-1}	kJ (kg d)$^{-1}$	
Gopherus agassizii (M,F)	900 (500 – 2200)	4 – 15	5 – 17	33 – 52^c	36 – 57^c	Nagy and Medica 1986
Gopherus agassizii (M)	3000 (2500 – 3500)	3 – 36	1 – 13	30 – 69	11 – 26	Peterson 1996a,b
Gopherus agassizii (F)	1500 (1350 – 1750)	NR	NR	42 – 49	29 – 34	Henen 1997
Gopherus polyphemus (M,F)	3400 (2500 – 4300)	31 – 93	11 – 30	77 – 188	34 – 62	Jodice et al. 2006
Terrapene carolina (M,F)	400 (383 – 426)	11	24	26^c	58^c	Penick et al. 2002

[a] mass is as an estimated mean value and reported range

[b] mass-specific water flux and metabolic rates were calculated as (water flux)/(body mass)$^{0.91}$ and (FMR)/(body mass)$^{0.89}$

[c] where FMR is reported as ml CO_2, we assume a thermal equivalent of 21.7 J ml^{-1} CO_2
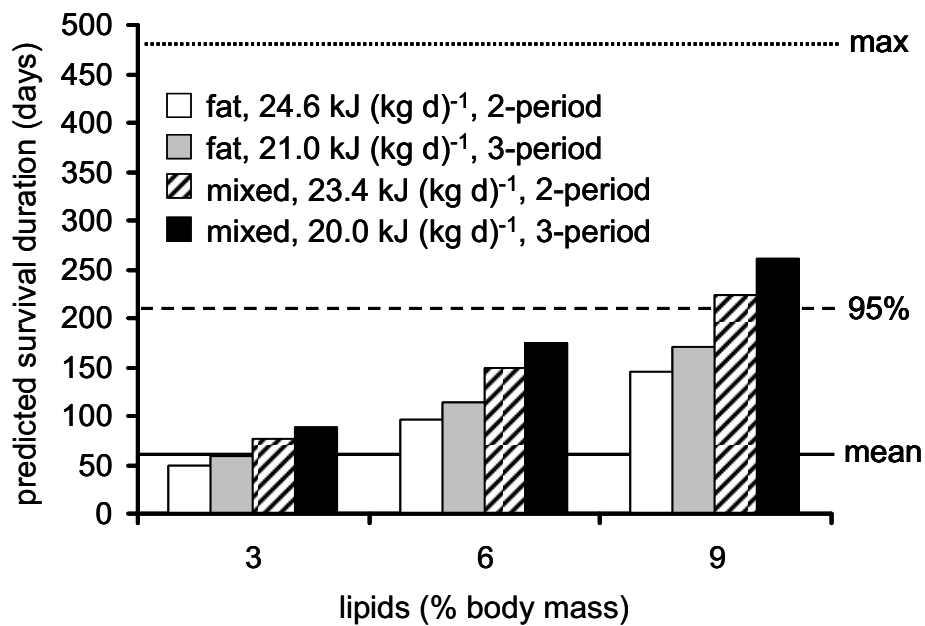
Figure 5.4. Range of predicted survival times (bars) for a 500 g turtle in terrestrial aestivation, assuming catabolism of fat only or protein and fat (mixed). Energy expenditures are the lowest mean FMRs measured at 21–22 $^{\circ}$C for aestivating turtles (469–908 g) estimated from division of sampling into either two or three sample periods (see Results for a detailed explanation). The horizontal lines are the mean, 95%, and maximum durations that turtles are known to aestivate at the study site (Roe and Georges 2007).

Chelodina longicollis is known for its ability to store and reabsorb water from the cloacal bladder, adjust uric acid excretions, and limit cutaneous water loss, all of which are adaptations to combat desiccation (Rogers 1966; Chessman 1984b). Our study is the first to examine *C. longicollis*' ability to maintain water balance in the field. Two lines of evidence suggest *C. longicollis* can maintain adequate levels of hydration during extended periods of terrestrial occupancy. First, TBW (% body mass) had not dropped significantly after 54 days terrestrial in the translocated turtles. This does not mean that water was not lost, but only that body water as a proportion of body mass remained relatively constant (i.e., Christian et al. 1996). Second, turtles in both groups took in water at rates to nearly offset efflux (Table 5.2). Fasting animals can take in water by drinking, absorption from the environment, utilizing water stores, or metabolic water production. Metabolic water only accounted for 4.2–9.6% of influx during any sample period (assuming both energy substrate scenarios), and water influx was beyond what turtles could have stored before leaving wetlands if they are capable of storing water outside of the body water pool. The majority of water intake must then be through pulmo-cutaneous exchange with environment and/or drinking. We observed several *C. longicollis* emerging from their terrestrial refuges and drinking from pooled water in the leaf litter during heavy rainfall (Roe, in press), and *C. longicollis* can "drink" when the cloaca is submerged in water (Chessman 1978). Although it has never been demonstrated in *C. longicollis*, contact with moist microhabitats may also allow for some water uptake through the skin or via respiration. Through a combination of behavioral and physiological means, *C. longicollis* aestivating in terrestrial habitats achieves rates of water flux on par with other strictly terrestrial turtles (Table 5.4).

Even though the changes in TBW over time and differences between water influx and efflux were not statistically significant, assuming (for arguments sake) that the consistently negative net water movements that we observed were biologically significant, *C. longicollis* would eventually reach lethal dehydration limits. Such limits are generally thought to occur at a loss of 30-35% of initial body mass from water in turtles (Seidel 1978; Mautz 1982; Peterson and Stone 2000; Ligon and Peterson 2002). After excluding the individual that became active, aestivating turtles lost water at a rate of -1.41 to -0.66 ml kg^{-1} d^{-1} during the first and final sampling periods. At these rates, a 500 g *C. longicollis* would have lost < 5% of its body mass from water after 54 days, and could survive 455 days in aestivation before reaching vital dehydration limits. As this survival time is considerably longer than that predicted for starvation (Fig. 5.4), it appears that depletion of energy reserves constrains the length of time *C. longicollis* can aestivate, a conclusion that is supported our observations of aestivation in this population (Fig. 5.4). A typical turtle aestivates for 64 days before dying or

moving back to water (Roe and Georges 2007), a duration consistent with our projections for turtles with 3% body fat (Fig. 5.4). Ninety-five percent of turtles aestivated for no longer than 216 days, a duration consistent with projections for turtles with 9% body fat (Fig. 5.4). The longest known aestivation was 480 days (Roe and Georges 2007), but this particular turtle was the only one that aestivated over an entire over-wintering and early spring period (June–November), when energy demands are expected to be substantially reduced due to low temperatures.

Several studies have examined how energy and/or water may limit survival in freshwater turtles, but responses are generally measured in turtles kept in confinement at constant temperature and humidity and deprived of food or water (or both) in the laboratory. *Sternotherus minor* survived for 164–270 days in water with no food (Belkin1965), a time very similar to our predictions and field observations for *C. longicollis* (Fig. 5.4). Several species of *Kinosternon* deprived of water reach critical dehydration limits within 25–80 days (Seidel 1978; Peterson and Stone 2000; Ligon and Peterson 2002), and based on measures of evaporative water loss, Chessman (1978; 1984b) proposed that *C. longicollis* could survive only a few months out of water in natural situations. While such laboratory studies are valuable for determining physiological capacities and tolerance limits, they are limited in their ability to mimic the complex conditions that turtles react to in the wild. We found no evidence that water loss had approached vital limits after several weeks in natural aestivation, which is due in large part to their ability to access water in terrestrial environments. Maintaining energy balance during terrestrial behavior is much more difficult, as individuals must rely solely on diminishing reserves that cannot be replenished without returning to wetlands.

Terrestrial movements

Much like studies of aestivation, the costs of terrestrial movement in aquatic animals are often measured under conditions that completely remove them from the challenges they face in natural environments. The only aerobic costs of terrestrial activity in freshwater turtles are derived from point estimates of respirometry while walking on level treadmills during short bouts of activity (Baudinette et al. 2000), stimulated to move by electric shock, (Stockard and Gatten 1983), or during spontaneous bouts of activity in metabolic chambers where actual activity level is difficult to quantify. In reality, animals must contend with soft substrates (e.g., leaf litter and sand), irregularities in slope, obstacles to traverse (e.g., rocks, woody debris), resistance from vegetation, and exposure to high temperatures, all of which could add

substantially to movement costs (van Marken Lichtenbelt et al. 1993). Movements may also require bouts of intense activity, where some energy demands are met anaerobically (Stockard and Gatten 1983; Congdon and Gatten 1989). Even though our measures were not taken from turtles moving overland during the course of their natural behaviors, our protocol simulated as closely as possible these natural movements.

Because the DLW technique measures the sum of all demands on metabolism and water over long periods of natural behaviour (i.e., costs of physical displacement, maintaining awareness and posture, circadian cycles, recovery from oxygen debt, and SMR), our measures provide the most ecologically relevant estimates yet reported for the energy expenditure and water flux of terrestrial movements for freshwater turtles. FMRs for translocated turtles moving 34 m d^{-1} were 94–99 kJ kg^{-1} d^{-1} (assuming both energy substrate scenarios), which are nearly identical to predictions for active reptiles of similar size (Nagy et al. 1999). Water influx and efflux rates of 38–41 ml kg^{-1} d^{-1} during this period were nearly double those predicted for other reptiles from arid and semi-arid regions, but in line with those from the tropics (Nagy 1982). FMR and water flux of turtles moving 23 m d^{-1} were 46–48 kJ kg^{-1} d^{-1} and 22 ml kg^{-1} d^{-1}, both of which are similar to active box turtles and gopher tortoises (Table 5.4; Penick et al. 2002; Jodice et al. 2006) and consistent with water flux for other non-tropical reptiles (Nagy 1982). However, as was the case for aestivation, overland movement must be supported by stored energy reserves that cannot be replenished until they return to water, but hydration levels can be more easily maintained.

Our estimates of the energy costs of terrestrial behaviors fill some important gaps in or knowledge of field energetics in *C. longicollis*. The only behavioral difference between translocated and aestivating turtles was the distances they moved (Table 5.1), so by comparing FMR between these groups, we estimate that movement is 1.6–1.7 × more energetically expensive than aestivation. This value is towards the lower end of the spectrum for other active reptiles (range = 1.1–5.1, mean = 2.6; Christian et al. 1997), but this is to be expected because our inactivity estimates based on FMR are higher than if we had used the more typical SMR (Neiwarowski and Waldshmidt 1992), and our activity estimates are of animals that are only sporadically active. Together with our equation relating movement time to distance, these estimates allow us to explore the energy consequences and trade-offs of aestivation and movement in the context of wetland flood-dry cycles (Table 5.5).

A 500 g turtle with 3–9% body fat would have 608–1787 kJ expendable energy assuming fat catabolism, or 889–2614 kJ assuming protein and fat catabolism. At a drying temporary wetland 1500 m from the nearest body of water, a turtle faces a movement cost of 672–705 kJ, which is 265–278 kJ more than aestivation costs over the same time frame. By

Table 5.5. Energy trade-offs between terrestrial aestivation and one- and two-way movements to other wetlands for a 500 g turtle[a].

travel distance[b] (m)	one-way movement					two-way movement				
	total energy[c] (kJ)	total time aestivating (days)	energy profit from trade-off[c] (kJ)	extra time in aestivation (days)		total energy[c] (kJ)	total time aestivating (days)	energy profit from trade-off[c] (kJ)	extra time in aestivation (days)	
50	109 – 114	11	43 – 45	4		218 – 228	22	86 – 90	8	
500	284 – 298	28	112 – 117	12		568 – 596	56	224 – 234	24	
1000	478 – 502	48	188 – 198	19		956 – 1004	96	376 – 396	38	
1500	672 – 705	67	265 – 278	26		1344 – 1410	134	530 – 556	52	

[a] a turtle of this size would have between 608–2614 kJ expendable energy assuming both energy substrate alternatives and 3–9% fat

[b] distances are representative of the range of required overland travel distances at the site (Roe and Georges 2007)

[c] energy values represent the range assuming catabolism of mixed substrates (fat and protein) or fat only

not moving, this energy could instead be used (i.e., a trade-off) to fuel the demands for an extra 26 days aestivation, allowing for a total of 67 days at the dry wetland to await re-flooding (Table 5.5). If the turtle is to make a two-way movement (i.e., to a permanent lake and back when the wetland re-floods), these costs and their equivalent days in aestivation gained in the trade-off would be doubled. Assuming all else is equal, should the temporary wetland re-flood at 134 days (4.5 months) after drying, both strategies would be energetically equivalent if a distance of 1500 m must be travelled. For earlier re-flooding, aestivation would be the more economic strategy, but if the wetland remains dry beyond this time, it would have been better to move to a permanent lake where at least some energy needs could be met before staging a return when temporary wetlands re-flood. Our model demonstrates that the energy costs of movement and potential gains in extended aestivation time in the trade-off will be high when long distances must be travelled, but will decrease with distance between wetlands (Table 5.5). When wetlands are only 50 m apart, turtles that forego movement would only gain eight additional days in aestivation, which is a short window of time to expect a wetland to re-flood. In this case, a trade-off may be of little value and movement to another wetland would almost always be more economical. This change in value of the trade-off with distance fits with our previous behavioral observations that more turtles aestivate and for more extended periods when longer distances must be travelled to the nearest permanent lake, whereas movement to other wetlands is the near universal response when only a short distance must be traversed (Roe and Georges 2008). We realize that other factors can influence behavior (e.g., predation risk and social interactions) and that our energy models are oversimplified by not including other energy allocations (e.g., reproduction; Congdon and Tinkle 1982). However, our aim was not to present an ecological energy budget, but only to explore the relative costs of energy and water for aestivation and terrestrial movement.

Future applications in freshwater turtles

Despite the commonly cited problems of the DLW technique for studying aquatic turtles, it has recently been used to examine the energetics of sea turtles (Wallace et al. 2005; Clusella Trullas et al. 2006), and here we demonstrate its utility for freshwater turtles during terrestrial behaviors. However, the DLW technique is not without some potentially serious drawbacks even for terrestrial studies of freshwater turtles. The high water flux rates and relatively low metabolism of *C. longicollis* during aestivation resulted in a low washout ratio of isotopically-labelled oxygen to hydrogen (k_o / k_h; Table 5.2). When this ratio falls below 1.1, estimates of

CO_2 production will lack sufficient precision, as any errors or deviations from assumptions will become more prominent (Speakman 1997). Because our ratios were never much above this critical minimum, and actually dropped below it during the third sample period in one group (Table 5.2), it is apparent that we were operating at the limits of the DLW technique. For turtles that substantially depress metabolism, this technique may not be useful. As turtles become increasingly inactive, future studies would benefit from longer equilibration periods than those determined in the laboratory on active animals, as well as longer sample intervals in the field.

We demonstrate how field measures of energy and water flux can greatly contribute to our understanding of animal behavior beyond that which can be achieved in laboratory studies alone. By examining the physiological limitations of aestivation and costs of overland movement, we were able to construct models that were remarkably consistent with observed behaviors of *C. longicollis* in response to wetland drying (Roe and Georges 2007; 2008). The physiological ecology of terrestrial activities is a largely unexplored frontier in freshwater turtle biology that promises to yield important insights into their behavioral ecology and evolution. Behavioral responses to wetland drying have been relatively well documented (Gibbons et al. 1983; Buhlmann and Gibbons 2000), but examining the underlying physiological responses to water and energy limitations under natural conditions could provide a richer understanding of species' range limits, habitat associations, and local adaptations (Peterson and Stone 2000; Ligon and Peterson 2002). There is often a high degree of variability in nesting among individuals and species, both in terms of the time spent in terrestrial habitats (Burke et al. 1994; de Solla and Fernie 2004) and migration distances (Congdon et al. 1983; 1987). These costs represent components of an individual's reproductive effort (Congdon and Gatten 1989), and should reflect a balancing of the benefits and costs of the behavior. Several turtles also undertake movements between wetlands in search of alternate resources and dispersal (Roe and Georges 2007), a behaviour that is particularly characteristic of males in several species (Morreale et al. 1984; Gibbons et al. 1990; Tuberville et al. 1996). Such movements are undertaken with expectations of gains in resource acquisition (i.e., multiple matings for males) that also have an associated cost. Long distance and extended terrestrial movement in the above contexts is typically assumed to exact a high cost on energy and water budgets, yet these costs have never been quantified in the field before now. Though our specific results may be of limited direct applicability to other systems, our framework and methods could help to address some of these and other unresolved issues in freshwater turtle ecology.

TEMPORAL AND SPATIAL VARIATION IN LANDSCAPE CONNECTIVITY FOR AN AUSTRALIAN FRESHWATER TURTLE IN A TEMPORALLY DYNAMIC WETLAND SYSTEM

Picture: captured turtles showing their unique marks (above),

and a turtle moving overland towards Ryan's swamp (bottom)

Abstract

Inter-wetland connectivity, defined here as the movement of biota among discrete water bodies, can have important population and community level consequences in aquatic systems. However, the details of aquatic animal movements across the landscape remain poorly understood, which is especially true of reptiles. We examined inter-wetland connectivity in a relatively pristine landscape in south-east Australia by monitoring the movements of freshwater turtles (*Chelodina longicollis*) via capture-mark-recapture. A high percentage (33%) of turtles moved between wetlands, but movement frequency and directionality between wetland pairs were highly variable across the landscape and over time. Permanent lakes were the major recipients of immigrants and hubs of regional connectivity during drought, but upon the return of rains and flooding, turtles moved back to temporary wetlands in large numbers. These movement patterns reflect turtle responses to changes in wetland quality and associated shifts in the fitness gradient between wetlands. Captures at a drift fence revealed that small and immature turtles move between wetlands with similar frequency to adults, a finding in opposition to that reached from wetland captures. We caution that measures of actual (or functional) connectivity can be biased by sampling methods, and must also be interpreted in the context of factors that motivate the movements of animals between patches. This requires some understanding of spatial and temporal variation in intra-patch processes (e.g., quality and extent) and the expected movement responses of animals (e.g., habitat selection), information that can potentially yield more important insight on animal movements than measures of landscape structural features alone.

Introduction

Connectivity is a measure of the degree to which the landscape impedes or facilitates movement among patches (Taylor et al. 1993), and is most accurately assessed from the observed movements of individuals (i.e., actual or functional connectivity; Calabrese and Fagan 2004). A detailed determination of inter-patch movement is critical for understanding population dynamics in any species, as such movements can be highly variable, ranging from the regular displacement of nearly all individuals from one patch to another (i.e., seasonal migrations) to the total or near-complete isolation of individuals within a single patch (Bowne and Bowers 2004). Moreover, inter-patch movements may vary in timing, frequency, and distance according to size, sex, age, motivation, and other individual differences. Without information on the appropriate spatial (i.e., landscape) and temporal scales over which these movements occur for all demographic groups, our perceptions of what constitutes a population and the processes that regulate them may be biased and misinformed, which can ultimately spawn inappropriate management strategies for their conservation.

Due to the worldwide degradation and loss of wetland habitats and threats to associated faunal communities (Dahl 1990, Richter et al. 1997, Finlayson and Rea, 1999), there is an immediate need for more basic research on wetland systems that will provide for their effective management. One aspect of freshwater systems that has received much needed attention of late is biotic wetland connectivity, defined as the interactions of biota among water bodies across the landscape (Haig et al. 1997, Cushman 2006, Roe and Georges 2007). Wetlands do not have to be physically connected by water flows for their biota to move between them, but the patchy occurrence of "isolated" wetlands within a terrestrial matrix does superficially impose a spatially structured distribution of discrete aquatic populations and low degrees of movement between patches (Gibbons 2003). This distribution pattern is thought to characterize many aquatic species with limited dispersal abilities (Gibbs 2000, Semlitsch and Bodie 2003), and in this classical approach of wetlands as isolated patches, it may be safe to assume that population regulation would depend mostly on the quality of the focal wetland and a zone of nearby terrestrial habitat, while the regional stability of a group of populations (i.e., a metapopulation, Harrison 1991) would hinge upon occasional connectivity between patches (Marsh and Trenham 2001).

In some cases, inter-patch movements may function critically in both local and regional population regulation. For instance, high quality patches can serve as a source of immigrants to lower quality patches which are unable to support viable populations and are referred to as sinks (Pulliam 1988). Individuals can also require the use of several patches to

meet their life-cycle or seasonal requirements to obtain complimentary or supplementary resources (Dunning et al. 1992). In the above examples, movements among discrete resource patches are thought to support larger populations and allow for more stable regional persistence than would be possible in one patch alone (Pulliam 1988, Dunning et al. 1992). It follows that such patches should not be considered as harboring independent populations, as the processes that regulate them would ultimately depend upon not just the focal patch, but also the quality and heterogeneity of nearby patches as well as the ability of individuals to move between them. Details of these inter-patch movements, such as the spatial scales over which they occur, their timing, rates, functional significance, and directionality in response to habitat quality gradients may be just as important to determine as other biological characteristics (e.g., life history traits, demographics) upon which management plans are traditionally based.

Freshwater turtles are a group severely threatened by human modifications to wetlands (Burke et al. 2000), yet these threats often extend beyond the delineated wetland boundaries when turtles undertake essential terrestrial behaviors (Buhlmann and Gibbons 2001, Marchand and Litvaitis 2004, Steen and Gibbs 2004). Terrestrial movement across the landscape is arguably one of the least well understood aspects of turtle behavior, yet such information is critical for identifying and mitigating threatening processes for conservation and management. Our previous radio-telemetric studies of the eastern long-necked turtle (*Chelodina longicollis*) show that individuals use terrestrial habitats for both aestivation and movements between wetlands (Roe and Georges 2007, 2008), but due to logistical constraints associated with telemetry, these studies are limited in their ability to describe the flows of animals across a large area and over extended time frames, both of which are important for addressing landscape-level questions in long-lived animals such as turtles. To this end, we undertook an intensive capture-mark-recapture study of *C. longicollis* over three years and more sporadically over 25 years in a relatively pristine system of freshwater wetlands in Booderee National Park in southeastern Australia to provide several measures of actual (or functional) inter-wetland connectivity. First, we describe the spatial patterning of connections between wetlands via turtle movements and test whether particular wetlands are more connected than others using a network analysis (Rhodes et al., 2006). Second, we test whether wetlands differ in the relative proportions of immigrants they receive over time, and whether relative immigration varies between permanent and temporary wetlands. Third, we calculate movement probabilities between wetland pairs using multi-stratum models. We then compare the results from the capture-mark-recapture data to that collected at a drift fence

intercepting turtles moving overland between wetlands to assess whether sampling biases could lead to misinterpretations of movements for particular size and sex classes.

Methods

Study site

Turtles were studied in Booderee National Park, a 7000 ha reserve located within the Commonwealth Territory of Jervis Bay in south-east Australia (150°43' E, 35°09'S). Detailed descriptions of the study site are given by Kennett and Georges (1990), Norris et al. (1993) and Roe and Georges (2007, 2008). *Chelodina longicollis* is the only species of freshwater turtle occurring in the park, which is characterized by forested terrestrial habitats and a mosaic of freshwater wetlands ranging in size from 0.1 to 54 ha, the most distantly separated of which are 5.4 km apart (Fig. 6.1). Wetland habitats include several permanent dune lakes and a number of temporary swamps that vary in their duration of surface water presence (Roe and Georges 2008). Booderee is on a peninsula surrounded by the Tasman Sea and a brackish water lake (St. George's Basin) and inlet to the sea, with the nearest freshwater wetland on the mainland > 5 km away and opposite the basin. The region has a temperate maritime climate with a long-term average annual rainfall of approximately 1100 – 1200 mm spread evenly throughout the year (~100 mm / month), though the timing and intensity of rainfall can be highly variable (Australian Bureau of Meteorology). Distance between wetlands and wetland sizes (surface area) were measured using the Nearest Features and X-Tools extensions for Arc View GIS. Rainfall amounts were recorded daily at the Booderee ranger's depot, located within 5 km of all study wetlands.

Field data collection

We conducted a capture-mark-recapture study in 25 wetlands (14 temporary and 11 permanent), including all wetlands that were identifiable from aerial photographs or that were otherwise known to park rangers (Fig. 6.1). Wetlands were sampled for turtles using baited crab traps (80 cm × 60 cm × 25 cm, 3 cm mesh) and by hand. Hand capture techniques included snorkelling when wetlands were deep enough (water depth > 1 m), and wading, probing in vegetation, and netting in shallower wetlands until all accessible areas of the wetland had been covered. Samplings were divided into an equivalent spring (1 September – 31 December) and summer (1 January – 30 April) period in each of the three years of the

study from 2004–2007, excluding periods of typical inactivity (May-August; Kennett and Georges 1990). During each sample period, wetlands were typically trapped for one to two days and subject to a similar number of hand-capture sessions, the exceptions being when a wetland was too shallow to set traps or was completely dry, and at the Claypits where only traps were used due to poor visibility and accessibility. Captures from the various sampling methods were combined into a single encounter session. This resulted in six capture-mark-recapture sessions (two in each of the three years) in which capture techniques were standardized as much as possible. In addition to our standardized sampling regime, several of the wetlands had been sampled using similar techniques in twelve of the 21 years from 1983 to 2003 (Georges et al. 1986, Kennett and Georges 1990, Graham et al. 1996).

At each capture, we recorded the date and location of capture, whether the turtle was marked or unmarked, and its identification code. Each turtle was marked with a unique code by notching the marginal scutes and underlying bone of the carapace. Straight-line carapace length (CL) and plastron length (PL) were measured to the nearest 0.1 mm using vernier callipers. All turtles with CL < 145 mm were classed as juveniles, and for those with CL > 145 mm, we were able to determine sex by examining the plastron curvature (see Kennett and Georges 1990). Minimum size at maturity in males is 145 mm, and in females 165 mm (*op. cit*). All males > 145 mm and only females > 165 mm were classified as adults, while females between 145.0 – 164.9 mm were classed as subadults. Turtles were released at their capture locations typically within 24 hours.

In addition to the capture-mark-recapture protocol, we constructed a terrestrial drift fence and pitfall array perpendicular to the axis of travel along a known turtle movement corridor approximately midway between a temporary wetland (South Blacks) and a permanent lake (Blacks Waterhole) separated by 400 m. The fence was constructed from polythene dampcourse (70 m long, 0.38 m high) buried several cm into the ground and held erect by wooden stakes. We buried seven sets of paired 20 L buckets, one on each side of the fence at 12 m intervals. Pitfalls were open from 6 September 2005 to 29 March 2006, spanning nearly an entire active season, and were checked once daily. Turtles were processed in the same manner as wetland captures, then released on the opposite side of the fence.

Data handling and analyses

The percentage of recaptured individuals that moved between wetlands was calculated for males, females (including sub-adult and adult individuals), and immature turtles during each sample period and compared using logistic regression (PROC LOGISTIC Model, SAS, 1999).

To determine whether distance moved between wetlands differed among these three groups, we used a Kruskal-Wallis test (SPSS, 1999). We then examined whether turtle size influenced distance travelled by regressing log_{10}-transformed distance against plastron length in SPSS.

We assessed three measures of actual connectivity. First, we constructed a spatial network of wetlands (nodes) with links drawn to connect wetlands that turtles moved between. We then tested whether connections between wetlands were arranged as a random network, where the distribution of node degree (k, the number of links from a node) is expected to follow a Poisson distribution (Erdös and Rényi 1960), or as a scale-free network, where the number of nodes with k links decreases according to a power law (Barabási and Albert 1999) using non-linear regression in SPSS.

Second, we assessed connectivity for each wetland as the relative proportion of the total immigrant pool that a wetland received during each sampling period. This value was calculated as the number of individuals recaptured in wetland i (target wetland) that were known to have moved from other wetlands j_n (source wetlands) divided by the total number of individuals that transitioned between wetlands across the entire site (i.e., the immigrant pool) minus any emigrants from wetland i during the same period (Bowne et al. 2006). We examined whether permanent and temporary wetlands differed in the number of immigrants received during each sampling period using chi-squared tests. For each wetland type and sampling period combination, we also assessed whether individual wetlands differed in immigrant numbers using chi-squared tests. Significance values for this series of comparisons were lowered to $\alpha < 0.003$ using the Dunn-Sidak correction.

Third, we calculated survivorship (Φ), capture (p), and transition (ψ) probabilities using the program MARK version 4.2 (White and Burnham 1999). As a first step, we constructed capture histories for the McKenzie-Windermere and Blacks-Steamers wetland systems separately (due to the infrequency of movements between them, see Results and Fig. 6.1) and examined whether survival and capture probabilities varied over time or according to maturity status. The Claypits were excluded from this analysis owing to differential capture efforts. We started with a fully-saturated model with time dependence for two groups (adult and juvenile) and fitted a series of reduced-parameter models. Turtles that were removed from the population (trap deaths, subjects of manipulative studies) were accounted for as a negative number in the capture histories (Cooch and White 2004). Guided by the most well supported models for survival and capture probabilities, we then constructed candidate model sets examining time and wetland-dependence in transition probabilities using multi-stratum models (Arnason 1973, Brownie et al. 1993). Multi-stratum models were limited to adult

turtles in a core set of wetlands where the majority of captures took place and where sampling protocols were standardized as much as possible. These included B, SB, SB2, S1, and S2 in the Blacks-Steamers system and W, M, and R in the McKenzie-Windermere system.

Model selection was based on Akaike Information Criterion (AIC), with the most supported models having the lowest values. When multi-stratum models were overparameterized, movement probabilities that could not be estimated were fixed to zero to achieve model convergence (e.g., Spendelow et al. 1995). The most saturated model in a candidate model set was tested for its adequacy to describe the data using a goodness-of-fit (GOF) test. In the initial survival and capture analyses, GOF was tested using the bootstrap procedure with 500 simulations, and an overdispersion parameter, ĉ, was derived by dividing the model deviance by the mean of simulated deviances (Cooch and White 2004). In the multi-stratum models, GOF was tested in the program U-CARE (Pradel et al. 2003), and ĉ derived by dividing the χ^2 statistic by the degrees of freedom (Cooch and White 2004). Where there was evidence for overdispersion (ĉ > 1), we adjusted models with the derived ĉ to improve model fit and calculate a quasi-liklihood estimator, QAICc (Burnham and Anderson 1998). We used model averaging in reporting all values to account for model uncertainty.

Demographic comparisons of animals captured at the fence were limited to those captured in the nearby wetlands (B, IB, SB, and SB2). A series of chi-square tests were run using the PROC FREQ procedure in SAS to examine potential differences in the size frequency distributions among three groups, 1) turtles captured at the drift fence, 2) all turtles captured in the wetlands, and 3) only those captured in the wetlands that were known to have moved by examining their capture histories. Significance values for this series of comparisons were lowered to $\alpha < 0.016$ using the Dunn-Sidak correction.

Results

We recorded a total of 4250 captures of 2580 individuals (703 M, 907 F, 970 J) from 2004 – 2007. Of the 1057 turtles (331 M, 436 F, 290 J) that were recaptured, 33% (39% M, 37% F, 19% J) moved between wetlands. The proportion moving varied between periods and by group (M, F, J), as well as the interaction of these factors (period: $\chi^2 = 7.8$, df = 1, $P = 0.005$, group: $\chi^2 = 14.1$, df = 1, $P < 0.001$, time × group: $\chi^2 = 4.7$, df = 1, $P = 0.030$; Table 6.1). Turtles moved between wetlands separated by 16 – 1946 m, the distance increasing with turtle size ($r^2 = 0.03$, $P < 0.001$; Fig. 6.2). Mean distance moved was highest in males (700 ± 39 m), intermediate in females (589 ± 32 m), and lowest in juveniles (412 ± 49 m; Kruskal-

Table 6.1. Percentage of recaptured turtles that moved between wetlands over the five capture intervals from 2004 – 2007.

	percent moving per capture period *				
group	2	3	4	5	6
M	44.2	30.5	33.8	28.1	22.0
F	36.4	22.8	29.5	29.6	27.4
J	13.6	18.7	9.6	22.6	15.8

* No estimates could be derived from the initial capture session because the individual's prior location was unknown.
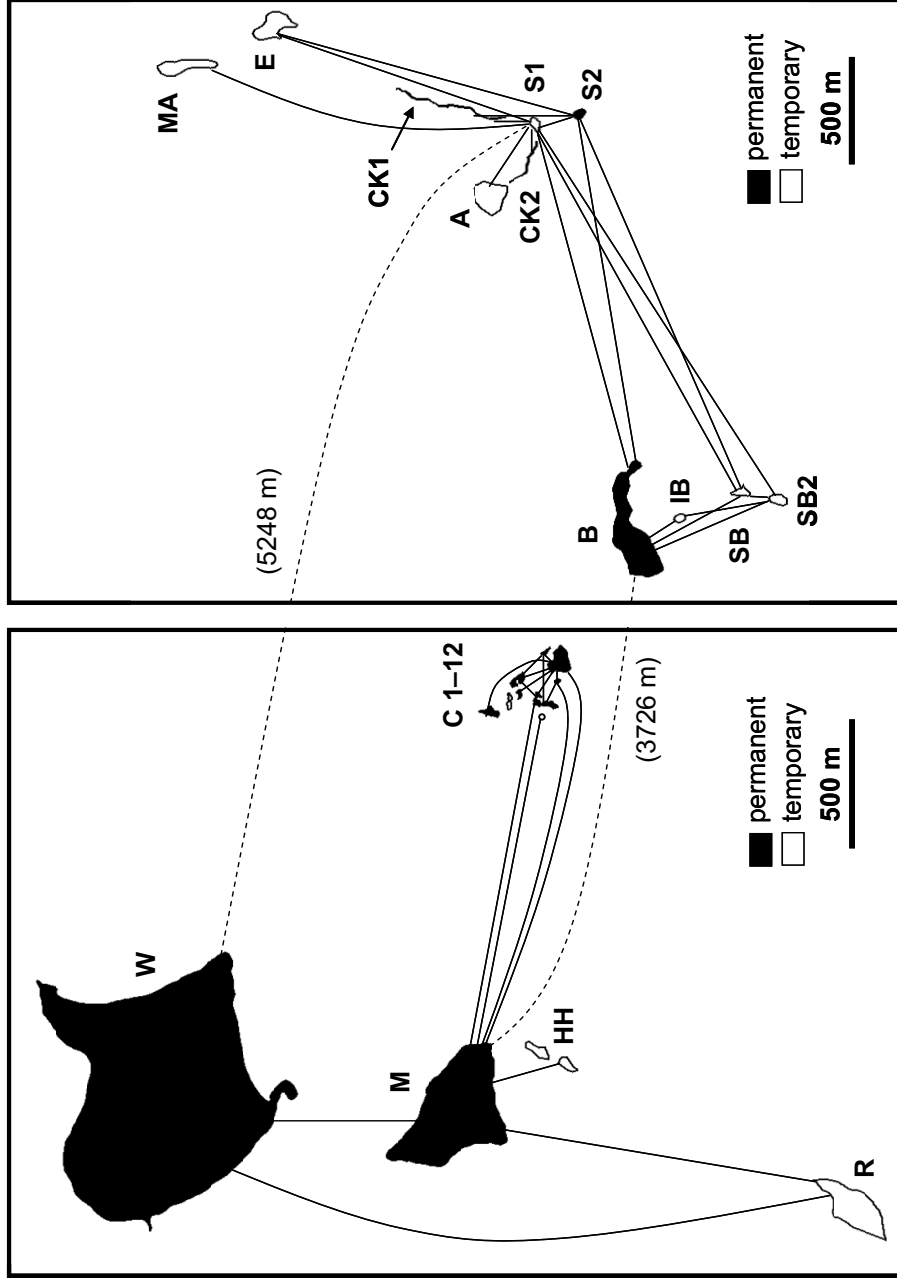
Figure 6.1. Network of connections between wetlands via turtle movements. The solid lines are movements detected during standardized sampling from 2004 to 2007, and the dashed lines are additional movements that were detected by examining the capture histories from the long-term data set (1983 and 2007). Note that the two boxed regions are depicted as being closer to one another than they actually are. Wetland identifications are as follows: W – Lake Windermere, M – Lake McKenzie, HH – Halfway Holes, R – Ryan's Swamp, C – Claypits 1-12, B – Blacks Waterhole, IB – Inter-Blacks, SB – South Blacks, SB2 – South Blacks 2, A – Alicia's Bog, S1 – Steamers 1, S2 – Steamers 2, E – Emily's Swamp, MA – Martha's Swamp, CK1 – Northwest Steamers Creek, and CK2 – North Steamers Creek.
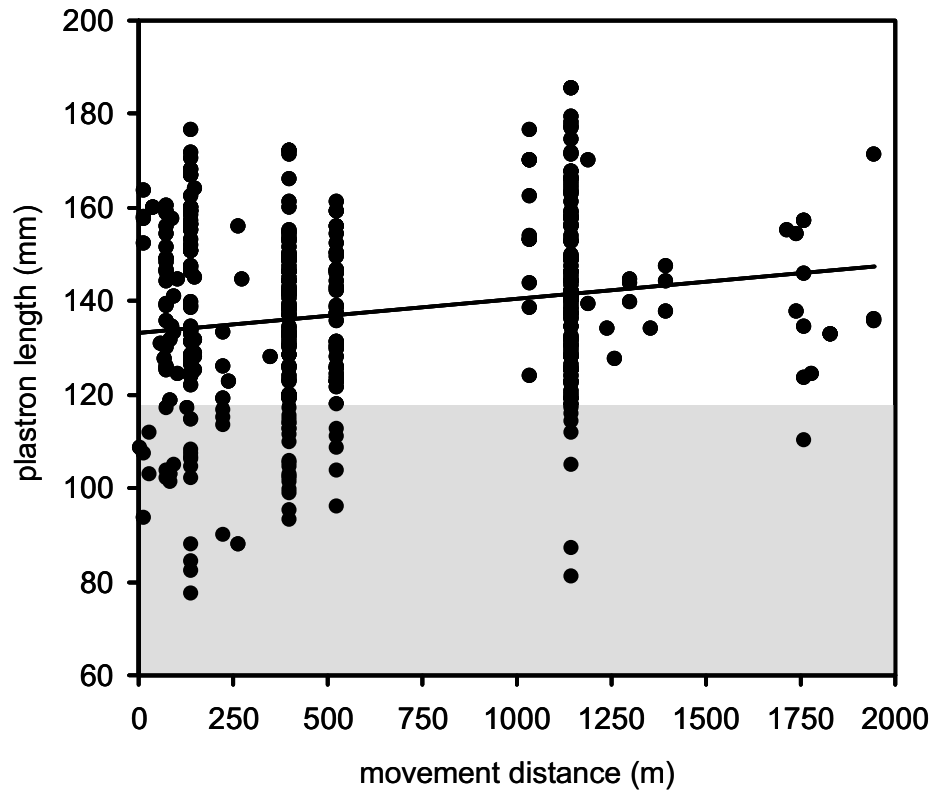
Figure 6.2. Relationship between turtle size and overland distance moved between wetlands for 442 movements. The unshaded region denotes adult males and both subadult and adult females, while the shaded area denotes immature individuals.

Wallis $\chi^2 = 14.08$, df $= 2$, $P = 0.001$).

The network analysis revealed a system with a wide spatial distribution and large number of connections between wetlands (Fig. 6.1). The distribution of k was best explained by the power relationship y $= 8.89x^{-0.885}$ ($r^2 = 0.90$, $P < 0.001$; Fig. 6.3). We identified two wetland systems within which movements were common, hereafter referred to as the McKenzie-Windermere and Blacks-Steamers systems (Fig. 6.1). Polygons that encompassed all connected wetlands within each system were 460 and 290 ha. Only two adult males were known to have moved between these systems (one in each direction), travelling distances of 5248 and 3726 m. Both were determined to have moved only by examining the long-term data set, with times between captures spanning 1985 – 2007 (22 years) and 1996 – 2005 (9 years).

Wetlands were not equal recipients of immigrants over time (Fig. 6.4). Permanent wetlands received a greater number of immigrants in periods 2 – 4 ($\chi^2 \geq 17.1$, df $= 1$, $P < 0.001$ in all cases), while temporary wetlands received a higher number in periods 5 and 6 ($\chi^2 \geq 12.3$, df $= 1$, $P < 0.001$ in both cases). Immigrant numbers were not equally distributed among permanent wetlands in periods 2 – 5 ($\chi^2 \geq 35.3$, df $= 4$, $P < 0.001$ in all cases), while the individual temporary wetlands differed in relative immigration in periods 5 and 6 ($\chi^2 \geq 26.7$, df $= 4$, $P < 0.001$ in both cases). The number of immigrants entering temporary wetlands increased with mean monthly rainfall amount ($r^2 = 0.83$, $P = 0.033$; Fig. 6.4).

In the Blacks-Steamers system, the model with the most support in the initial survival and capture analyses was for constant and equal survival between adults and juveniles, but where capture probability varied according to maturity status. There was only minimal support for survival differences between adults and juveniles and time-dependent capture probability (Table 6.2). Juvenile survivorship was 0.93 ± 0.04 and capture probability ranged from 0.14 to 0.22, while adult survivorship was 0.94 ± 0.02 and capture probability ranged from 0.40 to 0.42. On a per wetland basis, the multi-stratum models revealed that adult survival was lowest in Blacks Waterhole (0.90 ± 0.05), intermediate in Steamers 1 (0.94 ± 0.03), and highest in both South Blacks and Steamers 2 (0.99 ± 0.02). In the McKenzie-Windermere system, the best fit model was for constant and equal survival between adults and juveniles, and both group and time-dependence in capture probability. Again, there was only minimal support for survival variation between adults and juveniles (Table 6.2). Juvenile survivorship was 0.86 ± 0.07 and capture probability ranged from 0.13 to 0.30, while adult survivorship was 0.85 ± 0.03 and capture probability ranged from 0.18 to 0.43. Multi-stratum models identified no variation in adult survival among wetlands in the McKenzie-Windermere
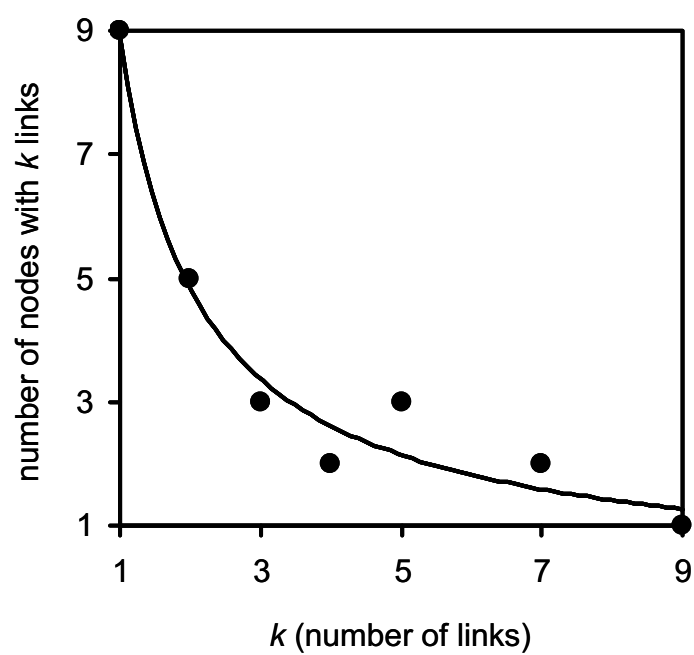
Figure 6.3. Power relationship demonstrating a scale-free network of wetland connectivity, where the number of wetlands with a high number of connections decays according to the equation $y = 8.89x^{-0.885}$ ($r^2 = 0.90$).
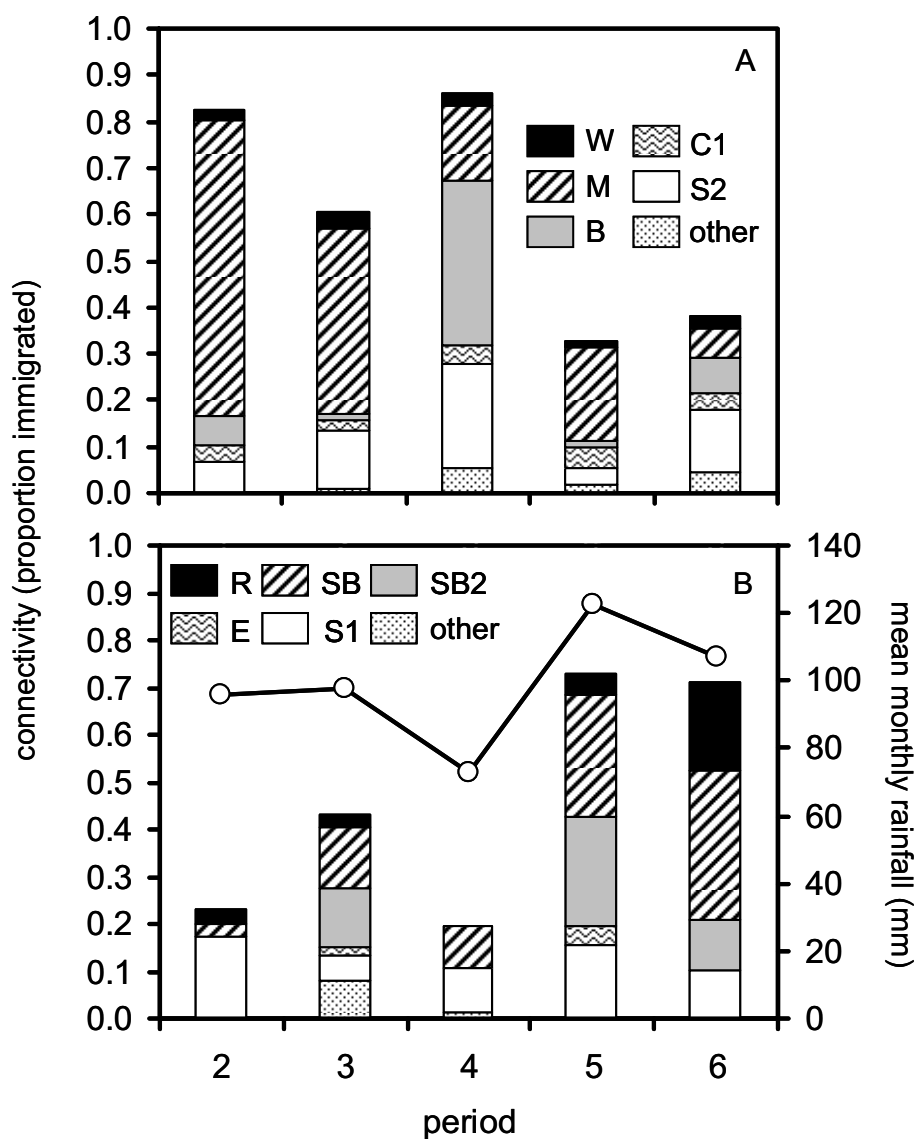
Figure 6.4. Relative proportion of immigrant turtles (bars) entering A) permanent and B) temporary wetlands during the five sampling intervals. Rainfall (open circles and solid lines) is also shown on the lower graph. Wetlands are arranged in order of decreasing size from top to bottom within each bar. Note that the keys for wetland identification are different on the two graphs. See Fig. 6.1 for full wetland identifications.

Table 6.2. Model selection for factors influencing survival (Φ), capture (p), and movement (ψ) probabilities for turtles in the Blacks-Steamers (B-S) and McKenzie-Windermere (M-W) wetland systems. Time (t) indicates sample interval, group (g) separates adult from juvenile, and wetland (w) designates the different strata.

site	model[a]	QAICc	Δ QAICc	model weight	parameters (n)	deviance
survivorship models (adults and juveniles)						
B-S	$\Phi(\cdot)p(g)$	2085.62	0.000	0.382	3	115.01
	$\Phi(\cdot)p(gt)$	2086.25	0.627	0.279	11	99.44
	$\Phi(g)p(g)$	2087.49	1.864	0.150	4	114.90
	$\Phi(g)p(gt)$	2087.91	2.286	0.122	12	99.05
M-W	$\Phi(\cdot)p(gt)$	1758.89	0.000	0.439	11	96.54
	$\Phi(g)p(gt)$	1759.99	1.101	0.254	12	95.62
	$\Phi(g)p(t)$	1760.53	1.645	0.193	7	106.27
	$\Phi(\cdot)p(t)$	1762.36	3.471	0.078	6	110.11
multi-stratum models (adults only)						
B-S	$\Phi(w)p(w)\psi(wt)$	2089.03	0.000	0.737	32	570.90
	$\Phi(\cdot)p(w)\psi(wt)$	2091.09	2.062	0.263	29	579.60
M-W	$\Phi(\cdot)p(wt)\psi(wt)$	2187.34	0.000	0.923	32	251.66
	$\Phi(w)p(t)\psi(wt)$	2192.78	5.438	0.061	23	275.77

[a] The overdispersion parameter, ĉ, in the survivorship models was 1.15 and 2.49 in the B-S and M-W systems, respectively. In the multi-stratum models, ĉ was 0.81 and 1.77 in the B-S and M-W systems, respectively.

system. Multi-stratum models indicated both wetland- and time-dependent variation in movement probability in each wetland system (Tables 6.2, 6.3, and 6.4).

Collectively, the group of turtles encountered moving overland at the drift fence was demographically similar to those captured in the nearby wetlands (Fig. 6.5A). The proportions of immature turtles from the drift fence and wetlands were 45% and 42%, respectively, and size frequency distributions did not differ significantly ($\chi^2 = 11.1$, df $= 16$, $P = 0.803$). The smallest individual moving overland at the drift fence was 72.3 mm PL. In contrast, only 15% of movers detected via capture-mark-recapture were immature, and this is reflected in the significant bias towards larger individuals in the size frequency distribution compared to both the entire wetland and drift fence samples ($\chi^2 \geq 50.4$, df $= 16$, $P < 0.001$ in both cases; Fig. 6.5B). The smallest turtle detected to have moved between wetlands by the capture-mark-recapture method in the region of the drift fence was 93.2 mm PL.

Discussion

The movement models and analyses described in this paper represent one of the most detailed studies of wetland connectivity for any freshwater reptile. Movement rate estimates adjusted for survival and capture probabilities are rare in studies of turtle movements (but see Tucker et al. 2001, Bowne et al. 2006), and our study is unique in that we were able to regularly sample all sites within a relatively pristine system largely isolated from other wetlands. This allowed us to estimate movement rates with associated variance, together with knowledge of the source, destination, and timing of these movements across a large area. Overall, we found that inter-wetland movement rates were high, and all sampled wetlands had some degree of connection with another. However, movement timing, frequency, and number of connections with other wetlands were not uniform across the landscape, highlighting not only the complexity of turtle movements in the system, but also the importance of particular wetlands and the existence of strong habitat quality gradients that drive such movements.

The majority of studies of freshwater turtle population dynamics do not report rates of movement among wetlands. This may reflect a genuine high degree of isolation within the wetland for some aquatic turtle populations, but when sampling is restricted to a single wetland or is only occasionally extended into some of the nearby water bodies, potentially important movements (even if infrequent) could be overlooked. Studies designed to systematically sample all or a subset of wetlands in an area often reveal that a considerable proportion of individuals in various systems move between wetlands. For instance, it is estimated that 5.1% of *Trachemys scripta* in Carolina Bays (Gibbons et al. 1990), 5 – 36% of

Table 6.3. Movement probabilities (± SE) of adult turtles between wetland pairs in the Blacks-Steamers wetland system[a]. Wetlands are classified as either temporary (T) or permanent (P).

origin wetland (*j*)			destination wetland (*i*)			
	period	n	S1 (T)	S2 (P)	BL (P)	SB (T)[b]
S1 (T)	2	12	**0.67**	0.33 ± 0.14	0.00	0.00
	3	23	**0.42**	0.47 ± 0.11	0.00	0.11 ± 0.05
	4	21	**0.47**	0.43 ± 0.17	3:21	0.10 ± 0.08
	5	16	**11:16**	1:16	0.00	0.00
	6	18	**0.63**	0.37 ± 0.11	0.00	0.00
S2 (P)	2	17	0.52 ± 0.13	**0.48**	0.00	0.00
	3	11	0.24 ± 0.13	**0.76**	0.00	0.00
	4	19	2:19	**17:19**	0.00	0.00
	5	29	0.38 ± 0.09	**0.62**	0.00	0.00
	6	28	4:28	**24:28**	0.00	0.00
BL (P)	2	28	0.02 ± 0.02	0.01 ± 0.01	**0.88**	0.09 ± 0.06
	3	39	0.00	0.00	**0.37**	0.63 ± 0.09
	4	28	0.00	0.00	**0.92**	0.08 ± 0.08
	5	39	0.00	0.00	**0.13**	0.87 ± 0.06
	6	25	1:25	0.00	**0.58**	0.42 ± 0.29
SB (T)[b]	2	4	0.00	0.00	0.41 ± 0.23	**0.56**
	3	4	0.00	0.00	0.24 ± 0.22	**0.76**
	4	26	0.01 ± 0.01	0.01 ± 0.01	0.82 ± 0.07	**0.16**
	5	9	0.00	0.00	0.28 ± 0.24	**0.72**
	6	29	0.02 ± 0.02	0.00	0.16 ± 0.06	**0.82**

[a] Ratios are reported for parameters fixed to zero to achieve model convergence, but where movement was known to have occurred. Probability of remaining within a wetland is one minus the sum of movement probabilities to other wetlands. Wetlands where captures were too few or inconsistent were not included in the model (IB, AB, EM, MA, CK1, CK2).

[b] Owing to their close proximity, SB and SB2 were grouped together to increase sample Sizes.

Table 6.4. Movement probabilities (± SE) of adult turtles between wetland pairs in the McKenzie-Windermere wetland system[a]. Wetlands are classified as either temporary (T) or permanent (P).

origin wetland (*j*)			destination wetland (*i*)		
	period	n	W (P)	M (P)	R (T)
W (P)	2	19	**1.00**	0.00	0.00
	3	62	**0.94**	0.06 ± 0.03	0.00
	4	37	**0.95**	0.05 ± 0.04	0.00
	5	68	**0.87**	0.11 ± 0.06	0.02 ± 0.03
	6	71	**0.99**	0.01 ± 0.03	0.00
M (P)	2	33	0.00	**0.97**	0.03 ± 0.05
	3	101	0.01 ± 0.01	**0.98**	0.01 ± 0.02
	4	53	0.02 ± 0.02	**0.98**	0.00
	5	60	0.01 ± 0.01	**0.92**	0.07 ± 0.07
	6	66	< 0.01 ± < 0.01	**0.40**	0.60 ± 0.67
R (T)	2	51	0.02 ± 0.02	0.75 ± 0.10	**0.23**
	3	41	0.00	0.40 ± 0.37	**0.60**
	4	11	0.00	0.14 ± 0.19	**0.86**
	5	4	0.00	2:4	**2:4**
	6	4	0.00	1:4	**3:4**

[a] Ratios are reported for parameters fixed to zero to achieve model convergence, but where movement was known to have occurred. Probability of remaining within a wetland is one minus the sum of movement probabilities to other wetlands. The Claypits and HH were not included in the models due to different sample methods and few captures, respectively.
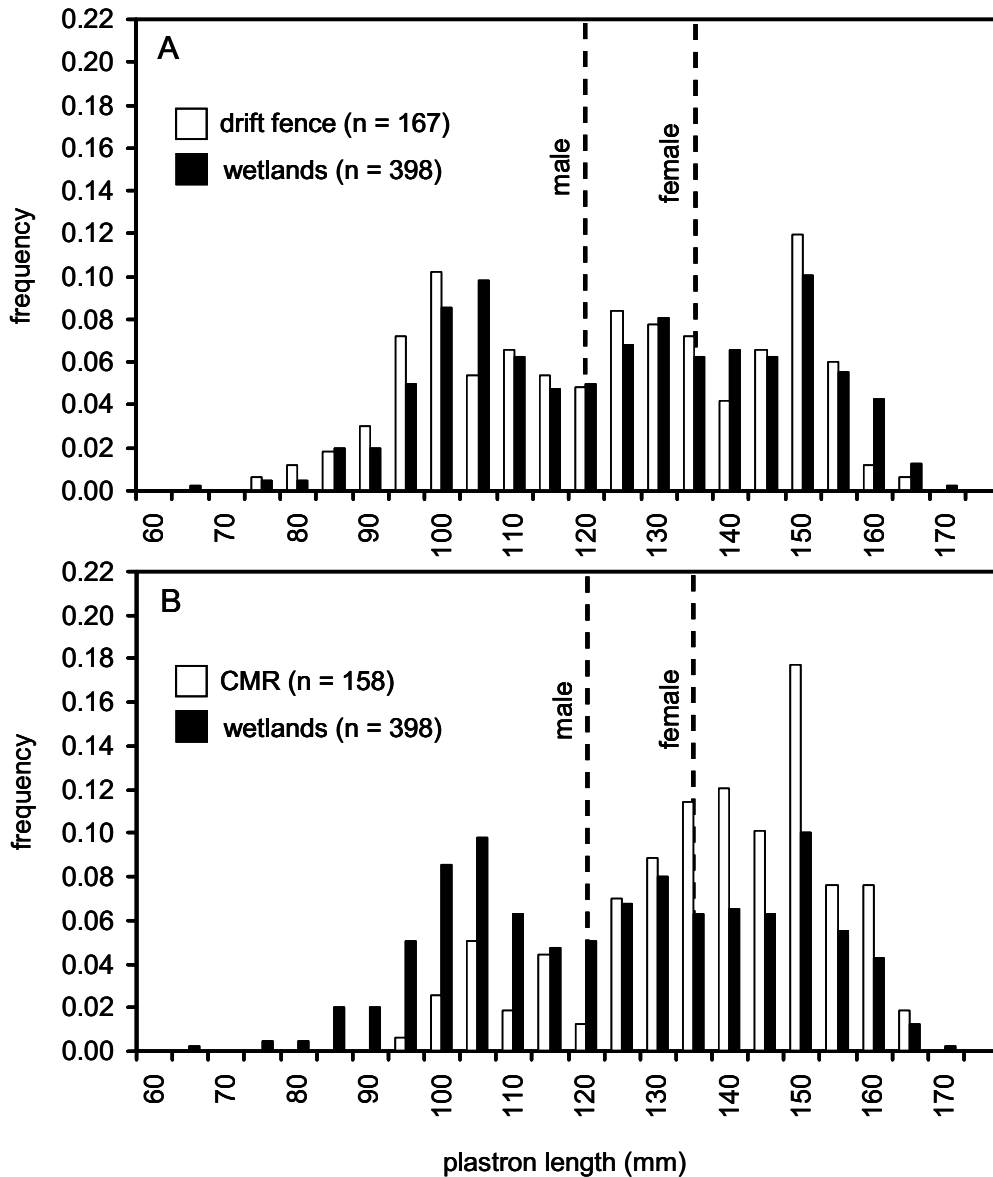
Figure 6.5. Size frequency distributions of all turtles captured in wetlands near the drift fence compared to A) those that were captured moving overland at the drift fence and B) those that were detected to have moved between wetlands by examining capture histories of turtles encountered during standard wetland sampling protocols (trapping and snorkelling). The sizes at which males and females mature are indicated by the vertical dashed lines.

Chrysemys picta in the E.S. George Reserve marshes (Scribner et al. 1993), and 46% of *C. picta* in Virginia farm ponds (Bowne et al. 2006) move between wetlands. Additionally, 33 – 57% of *Graptemys pseudogeographica* and 33 – 40% of *T. scripta* adults moved between different wetland habitats in a Missouri River floodplain (Bodie and Semlitsch 2000b), and 5.7% of *Malaclemys terrapin* moved between estuarine creeks of the Kiawah River (Gibbons et al. 2001). Though the latter two examples do no necessarily involve overland movements between discrete wetlands, they nevertheless indicate a significant shift in location by individuals. *Chelodina longicollis* in Booderee appears to make especially frequent inter-patch transitions (Table 6.1). After scaling the mean movement rate of 33% to the number of generations elapsed during the study (time to maturity 8 – 12 yrs; Chessman 1978), *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 recorded for any terrestrial or aquatic vertebrate or invertebrate included in a recent literature review of inter-patch movements (Bowne and Bowers 2004).

The large proportion of individuals that moved between wetlands indicates a high degree of inter-wetland connectivity, but it is also important to understand the spatiotemporal structuring of connections in the landscape. Our network analysis and transition probabilities demonstrate several salient features regarding the movements of turtles within the wetland system at Booderee. First, we identified two wetland complexes within which connections were numerous and movement probabilities high at times (Tables 6.3 and 6.4), but exchanges between them were infrequent and detected only in our long-term sampling (Fig. 6.1). This suggests the existence of two "patchy populations" (Harrison 1991) with strong connectivity among wetlands within a 2 – 3 km distance and over an area of several hundred hectares, which are then connected to one another, perhaps as a metapopulation, by long-distance (>3.5 km) and occasional dispersal. A similar spatially-stratified classification of population structure has been proposed for other reptiles in a variety of wetland systems (Burke et al. 1995, Joyal et al. 2001, Roe et al. 2003, Bowne et al. 2006).

Another conclusion from the network analysis is that connections appear to be organized as a scale-free network, where the majority of wetlands have few connections and an increasing minority are highly connected and referred to as hubs (Fig. 6.3; Barabási and Albert 1999). If turtles simply move to the nearest wetland when transitioning between patches, this type of network pattern may be an artefact of landscape structure, reflecting only the more centralized locations of the hub wetlands. Alternatively, such a pattern could result from selection of higher quality patches. The attributes of wetlands with a high number of connections suggest that habitat quality is the most likely factor determining its status as a

hub in our study system. For instance, three of the six wetlands with the highest number of connections ($k = 5 – 9$; S1, C1, M, B, C4, and S2) were on the periphery of their respective wetland complexes, and thus less centrally located than several others with a lower number of connections (Fig. 6.1). However, five of these six were permanent lakes, habitats that have been previously shown to be of higher quality for individual fitness than temporary wetlands during the drought-like conditions that pervaded the majority of our study (Roe and Georges 2008). Permanent wetlands not only had a larger network of connections, but also received a greater proportion of immigrants during periods of low rainfall (Fig. 6.4). During drought, permanent lakes offer long-term refuge where large numbers of turtles from several drying wetlands in the region converge and await the return of flooding. The critical role of permanent wetlands in maintaining regional connectivity and long-term persistence of some reptile populations inhabiting temporally dynamic freshwater systems has been highlighted in several other studies (Gibbons et al. 1983, 1990, Bowne et al. 2006, Willson et al. 2006).

The importance of permanent wetlands for aquatic reptiles during times of drought may seem obvious, but natural resource managers are often faced with significant challenges to ensuring that habitats surrounding them remain permeable to animals. One significant threat to connectivity in contemporary landscapes is the occurrence of roads that bisect travel routes (Dodd et al. 2004, Aresco 2005), even in areas designated as wildlife refuges (Bernardino and Dalrymple 1992, Ashley and Robinson 1996). Roads posed no great threat in our study system, but in Australia, exclusion fences are both an historic and increasingly popular way to address feral pest problems (Moseby and Reed 2006), and may also present a significant threat to localized landscape connectivity for non-target animals. Such a fence was constructed during the winter of 2006 to surround Lake McKenzie, which we identified to be one of the most highly connected wetlands in the entire system (Figs. 6.1 and 6.4, Table 6.4). However, without measuring actual connectivity the importance of this lake to the regional system may have been difficult to predict a priori from landscape structural features alone. For instance, this lake is not especially close to other wetlands, it is not the largest, nor is it directly connected via a drainage line to any other wetland, all of which are physical landscape attributes that one would expect to be associated with patch connectivity (Bowne and White 2004, Calabrese and Fagan 2004). The majority of connections from Lake McKenzie to other wetlands were at distances of over 1100 m, well above the typical movement distances for turtles in this study (412 – 700 m), and it is considerably smaller (11 ha) than the neighboring Lake Windermere (54 ha). The high connectivity of Lake McKenzie relative to other lakes in the region may reflect its historic status of offering higher quality resources (Georges et al. 1986, Norris et al. 1993, Kennett and Georges 1990), though we did

not detect any substantial fitness advantages in Lake McKenzie during the time frame of this study (Roe and Georges 2008, JHR unpublished data). Regardless of the underlying cause, based on our findings that Lake McKenzie was so highly connected and that the loss (or isolation) of a critical hub in a scale-free network could severely impact population dynamics in the region (Rhodes et al. 2006), park rangers constructed turtle passages where the fence intersected the identified movement routes (see Roe and Georges 2007). We can now report that movements between this lake and other wetlands have continued (Table 6.4).

Even though our findings highlight the importance of permanent wetlands as hubs for regional connectivity, the value of temporary wetlands should not be overlooked. After all, connectivity implies movement to or from another patch, and given the potential risks involved, such movements should be undertaken with the expectation of certain benefits to the individual (Gibbons et al. 1990). The highest movement rates were consistently between temporary wetlands and nearby permanent lakes. In fact, these movements occurred in large numbers at several places, involving the vast majority of turtles in particular wetland groups, but movement direction depended upon rainfall (Tables 6.3 and 6.4, Fig. 6.4). For example, over 80% of turtles in the shallow wetlands SB and SB2 moved to the deeper and permanent Blacks Waterhole coinciding with the lowest recorded rainfall during the study (period four), immediately followed by an equally large exodus from Blacks back to the same temporary wetlands upon the return of heavier rainfall and flooding in periods five and six (Table 6.3). Similar changes in movement between other permanent and temporary wetland pairs signify a response to anticipated shifts in habitat quality, as temporary wetlands offer *C. longicollis* higher quality foraging resources and associated fitness benefits than permanent lakes in non-drought conditions (Chessman 1984a, Kennett and Georges 1990). These movement patterns do not necessarily conform to classical source / sink dynamics (Pulliam 1988), as the higher quality habitat and predominant direction of movement shifts with environmental conditions over short time-frames. Instead, the high degree of movement and shifts in direction between temporary and permanent wetlands with rainfall suggests both wetland types are relied upon at times, and that movements are in response to strong and changing fitness gradients between them. Based on the historical patterns of rainfall variation at our site, several such shifts are likely to occur over the lifetime of a turtle (Roe and Georges 2008).

Radio-telemetric studies of *C. longicollis* in this system suggest that neither sex nor body size influences individual behavior, but these previous examinations were limited to a relatively small sample of adult turtles (Roe and Georges 2007, in press). This study, drawing from a much larger set of individual observations, uncovered some subtle demographic differences in overland movement behavior partially consistent with other species of

freshwater turtles. Long distance and dispersal movements by males are in agreement with the reproductive strategies hypothesis (Morreale et al. 1984) proposed to explain sex-related movement differences often seen in turtles (e.g., Kiester et al. 1982, Tuberville et al. 1996), though male and female *C. longicollis* did not differ in their frequency of movement. With respect to age- and size- specific behavior, larger turtles tended to move longer distances than smaller ones, though this relationship was weak and several juveniles moved long distances as well (Fig.6.2). Additionally, juveniles moved overland with less frequency than adults (Table 6.1), a finding that at first appears to closely agree with the conclusions of others that small and immature turtles are less likely to travel between wetlands (Chessman 1978, Gibbons et al. 1990, Scribner et al. 1993). However, these findings are not particularly convincing given the biased sampling methodology detected in our study. Juvenile turtles are notoriously difficult to encounter in wetlands due to their small size, secretive behavior, and choice of microhabitats with complex structure (Congdon et al. 1992, Pappas and Brecke 1992), which was reflected in their low capture probability in our study. Using only wetland captures, the capacity for immature turtles to move between wetlands was grossly underestimated compared to captures at the drift fence (Fig. 6.5), which is a preferred sampling technique for terrestrially-active reptiles (Gibbons and Semlitsch 1981, Ryan et al. 2002). Encounters at the drift fence reduced the minimum size at which turtles in the area were known to undertake such movements by more than 20 mm PL (24 mm CL), the equivalent of a 2 – 3 year age difference based on the highest growth rates for turtles this size (9 – 10 mm / yr CL, JHR unpublished data). We should mention that small turtles encountered at the drift fence were seldom recaptured in wetlands (not surprisingly), so whether these movements were ultimately successful is not known. Nevertheless, movement between wetlands in response to resource variation in our study system is likely to be just as important for small and immature turtles as for other demographic groups.

Implications for conservation and management

In addition to providing useful information for on-site applications of park management, our study has several broader implications. First, in systems where individuals move frequently between wetlands, important ecological processes regulating aquatic animal populations and community structure in a focal wetland should not be viewed as operating independently of other nearby wetlands. However, variable degrees of inter-dependence should be recognized across the landscape at different spatial scales. Turtles occupying clusters of temporary and permanent wetlands within a distance of approximately 1.5 km certainly warrant

consideration as an integrated demographic unit in Booderee, but the lower rates of inter-wetland exchange among these sub-populations at longer distances are more consistent with that of a metapopulation. This study is part of a growing list of examples where inter-wetland connectivity is thought to strongly impact local and regional population processes and community structure in diverse wetland vertebrates including amphibians (Semlitsch 2000, Marsh and Trenham 2001), birds (Haig et al. 1998), and reptiles (Willson et al. 2006, Roe and Georges 2007). Such inter-wetland linkages seem especially important in allowing animals to respond to changes in resource quality in temporally dynamic systems.

Examining how connectivity varies across the landscape and over time in an area minimally impacted by human development can also provide an important reference for comparisons to more heavily modified areas. In terms of setting a baseline for other studies, perhaps our most important contribution is that inter-wetland connectivity was highly variable over space and time. Both the frequencies and directions of movement between the same wetland pairs varied considerably over time, not according to changes in the matrix though which turtles were travelling, but presumably in response to changes in intra-patch quality and associated shifts in the fitness gradient between permanent and temporary wetlands (sensu Fretwell 1972, Spendelow et al. 1995). Thus, just as structural connectivity can have little bearing on the actual movements of animals (Tischendorf and Fahrig 2000, Calabrese and Fagan 2004), there is also the danger that measures of actual connectivity may not reflect the degree to which different landscapes impede or facilitate movements unless motivation to move is first understood and then standardized (Bélisle 2005). To this end, we suggest that some understanding of spatial and temporal variation in intra-patch processes (e.g., quality and extent) and the expected movement responses of animals (e.g., habitat selection) would greatly advance our understanding of landscape connectivity, especially in studies of short duration relative to the life-span of the organism in question. In the same vein, we reiterate that even direct and detailed measures of actual connectivity can be very sensitive to methodological biases for particular demographic groups, a finding that should be of concern to those researching any species with life-stages that are inherently difficult to study.

SYNOPSIS

Picture: Turtle tracks leading into Lake McKenzie

Even though the findings contained in this thesis are presented as a series of stand-alone entities, several inter-related themes course through the chapters that, when taken together, contribute to a more holistic understanding of the terrestrial and aquatic ecology of a nominally aquatic animal. I believe this work, in fulfilling the primary aims and objectives of the thesis, makes significant contributions to an understanding of the inter-workings of both aquatic and terrestrial systems (mechanistic ecology) as well as for their management (applied ecology). Below I highlight some of the most significant, original and surprising insights that have emerged from this thesis and discuss some promising and exciting avenues for future work.

Variable responses and temporally dynamic wetlands

Chelodina longicollis demonstrated a surprising capacity for individual variation in nearly every aspect of its behaviour examined. Most of the variation in space use, movements, activity, as well as terrestrial aestivation could be attributed to extrinsic factors such as the spatial structuring of wetlands in the landscape, wetland size, hydroperiod, seasonal influences and rainfall (Chapters 2, 3, 4 and 6). Behavioural variation was less a result of intrinsic attributes of the individual such as sex, body size, body condition and even maturity status. The only instance where sex was responsible for any of the variance was in distance moved between wetlands in the capture-mark-recapture study (Chapter 6), but there was no difference detected in this same variable measured by radio-telemetry (Chapter 2). Body size was only weakly correlated with overland distance moved and range length (Chapters 4 and 6). Though we have much less detailed data for the behaviour of immature animals, in instances where comparable data could be obtained by using a terrestrial drift fence, overland movements between wetlands appear to occur just as frequently in small and immature turtles as for larger adults (Chapters 4 and 6). These results run contrary to several hypothesis regarding some of the important intrinsic drivers of behaviour in freshwater turtles (Morreale et al. 1984; Schubauer et al. 1990, Gibbons et al. 1990, Plummer et al. 1997) and suggest that *C. longicollis* behaviour in Booderee, irrespective of sex and body size, is strongly shaped by local habitat variation and the spatiotemporal distribution of suitable patches in the landscape. Much of the variation in habitat quality, extent and distribution that underpins these variable behaviours is under the strong influence of season and rainfall.

Perhaps the most surprising aspect of individual variation was the alternate responses to wetland drying. Aestivation in or near the wetland and movement to nearby water bodies are two strategies commonly employed by aquatic animals facing wetland drying (Denoël et al. 2005,

Sayer and Davenport 1991, Cáceres and Tessier 2003, Hall et al. 2004), including turtles (Gibbons et al. 1983, Christiansen and Bickham 1989, Gibbons et al. 1990, Peterson and Stone 2000, Ligon and Peterson 2002), but *C. longicollis* employed variable terrestrial behaviours in the same population and even in the same wetland (Chapter 3). Maintenance of this variation across the population can in part be attributed to the spatial arrangement of wetlands in the landscape and heterogeneity of wetland hydroperiods (i.e., plasticity), but stochastic variation in rainfall and the associated difference in fitness costs and payoffs of each behaviour must also be considered as a possible mechanism responsible for the maintenance of genetic variation in the population. However, the critical assumption of any genetic hypothesis – that the observed behaviours were heritable – has not yet been demonstrated. Perhaps these variable responses to wetland drying should not come as a surprise, as aestivation and movement to another wetland simply reflect two different paths to the same ultimate goal, which is to escape either in time (by aestivation) or in space (by movement to other wetlands) the temporary resource limitations and stressful environmental conditions that are part of the normal flood-dry cycles of temporary wetlands. However, this is the first clear demonstration of variable responses to wetland drying and the factors that maintain them within a population of freshwater turtles.

While these observations contribute greatly to knowledge of how turtles successfully contend with fluctuating environments in order to survive and thrive, it is important to appreciate that both aestivation and inter-wetland movements require a close association with terrestrial habitats. As such, terrestrial habitats feature prominently in the overall ecology of several species of animals inhabiting fluctuating wetlands (Buhlmann 1995, Burke and Gibbons 1995, Dodd and Cade 1998, Buhlmann and Gibbons 2001, Gibbons 2003, Roe et al. 2003, Taylor et al. 2006), highlighting the general importance of habitats that lie beyond the wetland border for aquatic communities in temporally dynamic wetland systems. It is noteworthy that had this study been focused on turtles in a single wetland or for a short period of time, the scope for variation in terrestrial habitat use and other important responses to environmental variation in *C. longicollis* would not have been revealed. To me, such variation reinforces some important lessons for ecologists. First, studies conducted across several localities, either in different habitat types or geographic regions, can reveal some surprising and novel insights into the ecology of a species (Gibbons and Tinkle 1969, Gibbons et al. 1982, Brown et al. 1994, Ligon and Peterson 2002), highlighting the value of studies of a species in different landscape types. Second, short term studies risk missing potentially important environmental variation that can shape a species behaviour. Without data on the fitness benefits for turtles in temporary wetlands during a wet

period (Kennett and Georges 1990), the costly behaviour of long-term aestivation near temporary wetlands (even until death) would have been difficult to interpret, but an understanding of fitness costs and payoffs in permanent and temporary wetlands during both wet and dry periods provided the evidence to put forth a hypothesis for how variable responses may be maintained in the population. Along those same lines, if the capture-mark-recapture study had been conducted only in the first two dry years, the movements I observed would have been biased towards the larger or more permanent lakes, but movements were primarily in the direction of temporary wetlands in the final wet year. Interpreting either of these events in isolation of the other could lead to a misplaced or incomplete perception of *C. longicollis* movements, habitat selection and population dynamics, but taken together they demonstrate the complexity of turtle behaviour, its ties with environmental conditions and the complimentary nature of permanent and temporary wetlands. I concur with others that long-term or repeat studies of a single population may be necessary to capture the wide variability of environmental conditions that have shaped a population's behaviour over time (Gibbons et al. 1990, Krebs 1991, Semlitsch et al. 1996). Continued studies of the *C. longicollis* population in Booderee and parallel examinations of populations elsewhere will certainly uncover much more of the dynamic ecology of this species.

Linking behaviour with physiology

Physiology and behaviour are integrally linked aspects of animal ecology, as these traits (along with morphology) interact to allow individuals to respond to day to day challenges they face in their environments (Dorcas and Peterson 1997, Ligon and Peterson 2002). The laboratory physiology of both terrestrial and aquatic reptiles has long been a favourite subject of comparative physiologists (Bennett and Dawson 1976, Mautz 1982; Minnich 1982) and as a result there is a solid understanding of how individuals of different species or populations vary in their abilities to maintain homeostasis or tolerate anhomeostasis. Several studies focus on establishing links between the behaviour and physiology of aquatic reptiles during terrestrial exposure (Belkin 1965, Bentley and Schmidt-Nielsen 1968, Gans et al. 1968, Seidel 1978, Chessman 1984b, Peterson and Stone 2000, Ligon and Peterson 2002). Physiological studies of terrestrial reptiles have moved into the field due to the development of the doubly-labeled water (DLW) method (Lifson and McClintock 1966) and these studies have demonstrated that field studies are an essential companion to laboratory work (Nagy 1982, Nagy et al. 1999). In the case of aquatic reptiles the jump to field-based investigations has been delayed due to the intractability

of this method in freshwater situations (Congdon et al. 1982, Booth 2002). As a result, the critical links between behaviour and physiology for animals behaving naturally in the field, where they are free to respond in ways that influence their survival, remain largely unexplored.

In Chapter 5, I demonstrate the utility of the DLW method for studying the field physiology of freshwater reptiles during terrestrial behaviours. I provide the first estimates of water and energy costs of aestivation and overland movement for any freshwater turtle behaving naturally in the field. One surprising result was the ability of *C. longicollis* to remain hydrated while in terrestrial habitats and that water flux rates during aestivation and overland movement were on par with those of strictly terrestrial turtles (Nagy and Medica 1986, Peterson 1996b, Henen 1997, Penick et al. 2002, Jodice et al. 2006). This ability to remain hydrated was due to a capacity for water intake to offset efflux, which *C. longicollis* can achieve behaviourally through drinking and perhaps by selecting moist microhabitats. This aspect of *C. longicollis* behaviour is previously undocumented in the field and can be added to the suite of physiological means that this species employs to retard water loss and remain terrestrial for extended periods of time. From an energy perspective, I found little evidence of substantial metabolic depression in *C. longicollis*. This result was expected because nearly every turtle in this study remained at least partially active during aestivation and was quick to respond to changing environmental conditions, which agrees with other observations of this species in aestivation (Chessman 1983, Stott 1987).

The physiological models of water and energy relations derived from DLW in Chapter 5 provided valuable insight into observations of turtle terrestrial behaviour (Chapters 2 and 3). For instance, the duration of natural aestivation, ending either at turtle death or eventual movement back to water, was in striking agreement with projections for the depletion of energy reserves. The same projections from water loss rates suggested a capacity for much longer aestivation. Based on these findings, I posit that energy, not water, limits the duration of terrestrial aestivation. This result is contrary to conclusions from several studies examining desiccation tolerances of freshwater turtles in the laboratory (Seidel 1978, Peterson and Stone 2000, Ligon and Peterson 2002), including *C. longicollis* (Chessman 1978, Kilgour 1995). These findings suggest that physiology can be divorced artificially from behaviour in the laboratory leading to misleading interpretations, as animals are restricted in several important behaviours such as natural retreat site choice and drinking, both of which were deemed important for maintenance of homeostasis in *C. longicollis* during terrestrial aestivation.

In Chapter 3, I presented a model to explain the variable responses of individuals to wetland drying, but this model was based on some critical assumptions with respect to the physiological costs of the different terrestrial behaviours. I assumed that aestivation and movement behaviours would differ in their costs to the water and energy budgets of an individual and that the projected difference in these costs in the context of unpredictable flood-dry cycles would in large part govern their response. The DLW measures allowed me to quantify energy as a "currency" with which behavioral or other allocation trade-offs are made. Projecting energy requirements for aestivation and inter-wetland movements for various movement distances and flood-dry scenarios faced by turtles in Booderee, I developed an energy trade-off model to compliment the behavioural model. The energy model was in agreement with the observed behaviours, suggesting that energy consequences are likely to factor into turtle responses when their wetland dries, though other variables such as predation risk from sea eagles (Chapter 3) will also influence behavior.

Several other links between physiology and behavior are worth exploring. For instance, given the variety of wetlands that *C. longicollis* inhabits across their wide geographic range (Cann 1998) and the various challenges that populations would face in these habitats (i.e., infrequent vs. frequent drying), it is plausible that aestivation physiology and behavior are co-evolved traits. This could be examined by collecting turtles from different habitats and taking behavioural observations of activity and physiological measures of metabolism, water loss and blood solutes either in the laboratory (i.e., Peterson and Stone 2001, Ligon and Peterson 2002), in large field enclosures (i.e., Kilgour 1995), or preferably in contrived field exposures as in Chapter 5. This could conceivably be done even within Booderee National Park. The animals used in translocations were captured from a single wetland (Claypits), but would turtles from Lake Windermere, a large permanent lake with a relatively low movement rates and little reason to aestivate exhibit the same behavioural and physiological responses as individuals from the Steamers Waterhole region, where overland movement and aestivation occur much more frequently? Do individuals within a given wetland vary in their physiological responses as they do behaviourally? Further examinations of terrestrial physiology should not be confined to questions regarding terrestrial aestivation, but could also extend to other unresolved issues in freshwater turtle biology where it is important to quantify the cost of overland movement, several of which are discussed in Chapter 5.

The characterization of freshwater turtle populations
and implications for their management

Defining the boundaries of freshwater turtle populations and determining the processes that contribute to their regulation is a difficult task. The common solution is to consider the group of turtles occupying each wetland as a separate demographic unit capable of occasional interaction with neighbouring "populations" through dispersal (i.e., as a metapopulation; Hanski 1991, Harrison 1991). However, some species use habitats in more complex ways with important implications for population dynamics. In such cases, there are few blueprints on how to go about defining these demographic units, yet such information is critical for their effective management. This thesis provides a case study on how to resolve this issue.

The idea that a *C. longicollis* population could be defined according to aquatic and terrestrial boundaries is quickly refuted by their frequent use of terrestrial habitats, sometimes at long distances from the wetland (Chapter 2). For instance, nearly 25% of all *C. longicollis* locations were in terrestrial habitats and in some months turtles were even more terrestrial (e.g., > 60% in October 2004; Chapter 4). A distance of 370 m from the wetland would include 95% of all *C. longicollis* terrestrial refuge sites, a value towards the high end of the spectrum for terrestrial habitat use in other nominally aquatic animals (Semlitsch and Bodie 2003, Roe et al. 2003, Roth 2005). Not only did turtles use adjacent terrestrial habitats for refuge, but they traveled overland in maintaining associations with multiple wetlands (Chapter 2). The frequency with which individuals moved between wetlands, the proportion of individuals exhibiting this behaviour (both juveniles and adults) and the distances they traveled overland in doing so (Chapters 2, 4 and 6) run contrary to many concepts of freshwater animal behaviour. In fact, the inter-patch movement rates were among the highest among any vertebrate or invertebrate in aquatic or terrestrial systems (Bowne and Bowers 2004). 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. *Chelodina longicollis* populations and the processes that affect them are certainly not confined to a single wetland.

Now that I have refuted one definition of a population, a suitable alternative needs to be put forward. It is at this point that the definition of a population becomes obscure and much more detail needs to be provided. For instance, even though individuals tended to associate with more than one wetland and move between them with high frequency, how many wetlands encompass a

single population? Also, over what spatial scales does a population span before it becomes just a group of populations (i.e., a metapopulation)? In Chapter 6, I used a network analysis to visualize the biotic connections between wetlands (via turtle movements) and found evidence for the existence of two "patchy populations" (Harrison 1991) with strong connectivity among wetlands within a 2–3 km distance and over an area of 290–460 ha, which are then connected to one another as a metapopulation by long-distance (>3.5 km) and occasional dispersal. However, while these specifics adequately describe the spatial structuring of populations in Booderee, what generalities can be used to define the relevant population units for vagile turtles elsewhere? For *C. longicollis*, it is not so much a question of how many wetlands or what size area encompasses a population, but rather what combination of wetland types does a population need in order to thrive? In Chapter 2 and 6, I argue that both permanent and temporary wetlands are key landscape elements contributing to regional carrying capacity and population persistence. These different wetland types offer complimentary resources – temporary wetlands as highly productive patches where turtles capitalize on fitness benefits during persistently wet periods and permanent wetlands as more stable patches of lower productivity for refuge during drought. Chapters 3 and 5 illustrated that terrestrial aestivation near temporary wetlands is not a successful strategy to survive extended drought and populations are likely carried through such droughts by the movements of most individuals to permanent lakes where they can await the return of more favorable conditions before returning to temporary wetlands. In Chapter 6, I demonstrated that turtles move *en masse* from temporary to permanent wetlands during periods of drought, only to immediately return to the same temporary wetlands when the rains return. This latter observation suggests that movements are indeed in response to strong and changing fitness gradients between wetlands and that turtles are selecting habitats based on anticipated shifts in patch quality. Though perhaps not strictly the same, these movements nevertheless reflect a similar phenomenon to the seasonal migrations of some birds, large mammals, fish, invertebrates and larger reptiles in exploiting variable and distant habitats (Swingland and Lessels 1979, Sinclair 1983, Swingland 1983, Madsen and Shine 1996, Alerstam et al. 2003). A key insight from this thesis with respect to defining population units in *C. longicollis* and perhaps other mobile freshwater reptiles is that it is more instructive to understand the functional significance of inter-wetland movements and heterogeneity of habitat types required by individuals than it is to count wetlands or assign spatial constraints.

Unlike many of the world's freshwater turtles, *Chelodina longicollis* is not considered to be in widespread decline. Even so, prudent, conservative and localized management is still

warranted where policies are in obvious conflict with the needs of wildlife, especially in areas designated as ecological reserves (Bernardino and Dalrymple 1992, Ashley and Robinson 1996). This concern is particularly relevant for long-lived, slow growing and late maturing species with high egg and hatchling mortality (e.g., most turtles including *C. longicollis*; Parmenter 1976, Chessman 1978, Kennett and Georges 1990), as these life history traits may hide ongoing population declines and compromise the ability of a population to rebound once declines have begun (Brooks et al. 1991, Congdon et al 1993, 1994, Heppell 1998). Several additional features of *C. longicollis* ecology identified in this thesis have been hypothesized as potentially threatening to other species of freshwater reptiles in the face of anthropogenic landscape changes. These include frequent and long distance movements between patches, large home range size and use of terrestrial habitats (Buhlmann 1995, Gibbs and Shriver 2002, Roe et al. 2003, 2004, Bowne et al. 2006, Roe et al. 2006). In turtles, females are thought to be at particularly high risk from threats such as predators and roads during their terrestrial nesting excursions (Marchand and Litvaitis 2004, Steen and Gibbs 2004, Aresco 2005b, Spencer and Thompson 2005, Gibbs and Steen 2005, Steen et al. 2006). However, I demonstrate that adult females would not be the only individuals at risk in *C. longicollis* given the frequent use of terrestrial habitats by both sexes and the overland movements of immature animals.

I observed two clear management policies within the terrestrial habitats of Booderee national park that could seriously impact freshwater turtle populations. First, a prescribed burn in the vicinity of Ryan's swamp to control the invasive bitou bush (*Chrysanthemoides monilithera*) was carried out in late 2007. This fire burned through the forest where turtles aestivated, but because this event occurred after my data collection ended, I could not quantify the impact that this burn had on aestivating turtles. At least some turtles were found dead (Fig. 7.1), so when possible, I recommend that future prescribed burns near temporary wetlands be timed to occur when the wetland is flooded and few turtles are aestivating.

A second management issue that threatened the turtles was the construction of a predator-proof fence completely encircling Lake McKenzie as part of a widespread effort to control an introduced predator, the European fox (*Vulpes vulpes*). Predator-proof fences are commonly constructed in Australia as a means to control feral animals for the purposes of agriculture and native wildlife management (McKnight 1969, Moseby and Reed 2006). These fences can stop the movements of native wildlife and entrap (and kill) them as well and turtles are no exception (personal observation). Based on the evidence that permanent lakes and nearby temporary

Figure 7.1. A turtle burned in the fire while in the forest near Ryan's swamp (left) and passages to allow turtles to cross a predator-proof fence encircling Lake McKenzie (right).

wetlands are complimentary habitats for turtle populations and that Lake McKenzie in particular was one of the most critical wetland hubs for regional connectivity during drought, the park rangers constructed turtle passages to allow turtles to continue these critical movements (Fig. 7.1). Observations from radio-telemetry provided the necessary information for the placement of passage structures (Chapter 2), while the capture-mark-recapture study provided a means to monitor whether the passages were successful in their objective. In Chapter 6, I provide evidence that turtle movements appear to be unaltered by the fence, but I caution that continued long-term monitoring and fence maintenance at a considerable expense to the park management (M. Hudson, personal communication) must be undertaken to ensure the fence remains permeable to the turtles. Also, before the fence is heralded as a success, its effectiveness in excluding foxes and impacts on other non-target species needs to be examined (Coates and Wright 2004). Given these concerns, fences should not be a considered a panacea for feral pest problems, but perhaps only used as a last resort when all other control measures have been exhausted.

Given the suite of life history and behavioral characteristics that presumably place *C. longicollis* at risk from the threatening processes of agricultural and urban development that have severely impacted reptile populations globally (Gibbons et al. 2000), it would be instructive to examine how *C. longicollis* populations fare when faced with these more widespread challenges. I would predict that the overland movement behaviors of *C. longicollis* are likely to expose them to several agents of additional mortality from vehicles, farm equipment, feral and native animals, pets and collection (Garber and Burger 1995, Saumure and Bider 1998, Gibbs and Shriver 2002, Spencer and Thompson 2005), but whether or not these losses would translate to effects at the population level, as they have for other turtle populations (op. cit.), is a question worth exploring. Given the capacity for variable behaviors in *C. longicollis*, it would be especially interesting to see if this species alters its behaviour in response to these threatening processes, either as a plastic response to perceived threats, or as an evolutionary response shaped by differential mortality or other fitness costs incurred by individuals exhibiting alternate behaviors. There is evidence that *C. longicollis* is capable of thriving in some agricultural and suburban settings (i.e., in the rice agroecosystems of New South Wales [Rennie 2002] and in the suburbs of the Australian Capital Territory [M. Rees and J. Roe, unpublished data]), but these may only represent isolated examples that could be challenged by additional study elsewhere.

Summary

Turtle populations and the factors that impact them in Booderee National Park extend well beyond the boundaries of the wetland. Overland movements between wetlands and to aestivation sites are in response to spatiotemporal variation in habitat quality associated with the prevalent rainfall patterns. These results suggest that maintaining the natural heterogeneity of wetland and terrestrial habitats, as well as the continued ability for individuals to move between them should be of primary concern for the management of turtle populations in the park and elsewhere. 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. Instead, permanent and temporary wetlands and adjacent terrestrial habitats are complimentary landscape elements contributing to regional carrying capacity and population persistence. Linkages between these habitat types are especially important in temporally dynamic wetland systems in allowing animals to move in response to changing resource needs.

Chelodina longicollis exhibited an impressive capacity for behavioural variation irrespective of intrinsic individual attributes. Much of this variation may be ascribed to local habitat differences and landscape structure, but even turtles within the same wetland responded to fluctuating environmental conditions in different ways. Aestivation and movements to other wetlands are two different paths to the same ultimate goal, but with vastly different physiological consequences and relative fitness outcomes that are dependent upon unpredictable changes in future environmental conditions (e.g., wetland flooding and drying). To me, this behavioural variation is reflective of the strong proximal and selective influences with which turtles inhabiting stochastically fluctuating wetland systems must contend. Together, these findings not only fill many gaps in our knowledge of the ecology of freshwater turtles, but they also open many new and exciting avenues for future research. The terrestrial ecology of freshwater turtles and other reptiles is an under-explored frontier of research that will contribute greatly to our understanding of their overall ecology.

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