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Terrestrial activity, movements and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis*, in a temporally dynamic wetland system

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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 ha (±SE) 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.

Key words: eastern long-necked turtle, ephemeral wetland, home range, migration, movement strategy.

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 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 examination 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

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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, and 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 factors, 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 of aerial photographs taken between 2001 and 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 (PL) 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 3–4 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 & Blouin-Demers 2006; Nilsen *et al*. 2008), we use both methods to estimate the size of total area use (hereafter, home range), while only the kernel methods were used to define core areas (hereafter, activity centres). For kernel density analysis, we used the fixed kernel method and the least

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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^{-1}), 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: (i) 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 (ii) 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 damp course (70 m long, 0.38 m high) buried several centimetres 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 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. Subadult 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 subadult 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 to 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 items 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 s) 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 (Chessman 1984a; Georges *et al*. 1986) 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, they 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 ± 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 centre size), and five predictor variables (inter-wetland distance, wetland size, number of wetlands used, PL, number of days radio-tracked) were then investigated using a series of multiple

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Table 1. Movement and space use estimates (mean±1 SE) 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

KD, kernel density; MCP, minimum convex polygon; RL, range length.

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^{-1}) and $\log_{10}$ range length as the response variables, month and month × 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 αlevel for statistical significance for this group of tests was $\alpha \leq 0.004$.

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: (i) total number of turtles captured; (ii) number of adult turtles capture; (iii) number of immature turtles captured; (iv) number of turtles moving from the permanent to the temporary wetland; and (v) 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 sums of squares being calculated. The Dunn–Sidak adjusted αlevel for statistical significance for this group of tests was $\alpha \leq 0.007$.

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 1). However, in no case did variability in movement and space use measures reflect sex differences (MANOVA: Wilks' $\Lambda = 0.97$, $F_{4,48} = 0.42$, $P = 0.792$; Table 1), and the MCP and 95% kernel density methods yielded similar home range estimates (Table 1). A considerable proportion of total movement distance was through terrestrial habitat (males: 47.2 ± 5.1%, females 46.0 ± 4.7%; Table 1).

Variation in movement and space use was most strongly influenced by attributes of the wetland landscape (Table 2). The inter-wetland distance and wetland size indices explained significant amounts of the variance for every estimate of movement and space

Table 2. Relationships between movement and area use estimates (dependent variables) and independent variables found to be significant for *Chelodina longicollis*

Dependent variable	Independent variables†	Coefficient	d.f.	*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				

†Independent variables are listed in order of their overall contribution to the model. KD, kernel density; MCP, minimum convex polygon; RL, range length.

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% and 86% of variation in movement and space use estimates (Table 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 2).

Seasonal patterns

Twenty-two (10 males, 12 females) and 20 (9 males, 11 females) 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' $\Lambda = 0.32$, $F_{10,198} = 15.36$, $P < 0.001$, month × sex: Wilks' $\Lambda = 0.91$, $F_{10,198} = 0.929$, $P = 0.508$), but in the second year there was an interaction between month and sex (month: Wilks' $\Lambda = 0.66$, $F_{12,214} = 4.05$, $P < 0.001$, month × sex: Wilks' $\Lambda = 0.76$, $F_{12,214} = 2.60$, $P = 0.003$). 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. 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 ($\chi^2 < 14.43$, $P > 0.025$). Females only exhibited significant monthly variation in inter-wetland movement frequency during the first year when movements were more frequent in spring and early summer ($\chi^2 = 19.07$, $P = 0.002$), but did not vary in overall terrestrial habitat use in either year ($\chi^2 > 5.00$, $P > 0.416$; Fig. 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 ($P = 0.949$).

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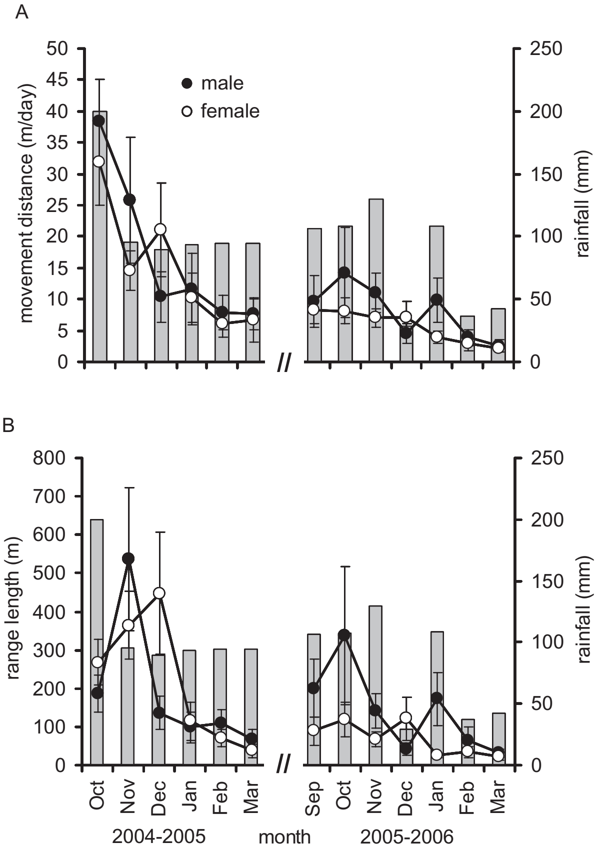

Fig. 1. Relationships between monthly rainfall (bars) and (A) movement distance, and (B) range length for *Chelodina longicollis* studied with radio-telemetry during the active season. Movement variables are mean ± 1 SE.

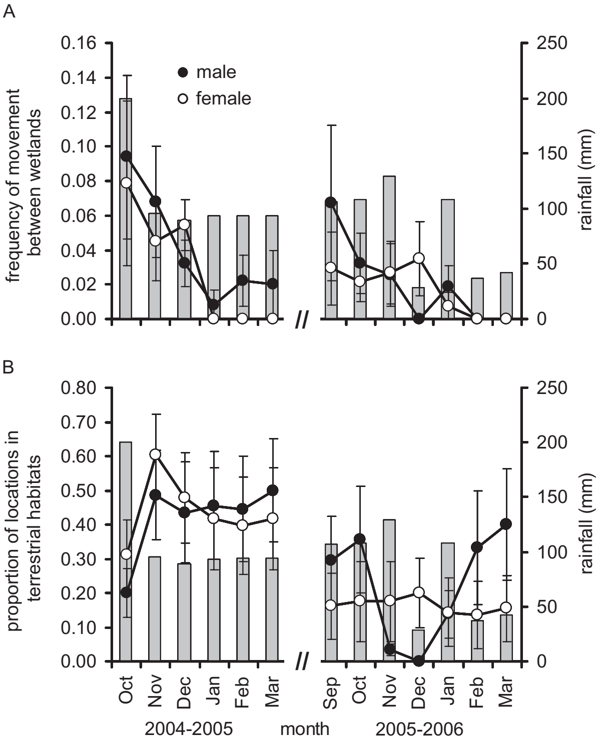

Fig. 2. Relationships between monthly rainfall (bars) and use of terrestrial habitats for (A) overland movement between wetlands, and (B) overall terrestrial habitat use for *Chelodina longicollis* studied with radio-telemetry during the active season. The independent variable is the proportion of locations in each month where a movement between wetlands or terrestrial habitat use was observed. Habitat use variables are mean ± 1 SE.

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. 3). Coarse patterns of monthly movement were not related to rainfall or temperature ($P > 0.231$ in all cases, Fig. 3), but daily movements were significantly related to rainfall (Table 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 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 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. 4E, J. Roe, pers. obs). 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 per sample; Fig. 4A–C), and in one case complete absence when the wetland dried (Fig. 4A). In permanent wetlands, there were generally smaller absolute changes in prey availability among months (maximum changes of between 1.1–9.1 g per sample; Fig. 4D–F), and no times of complete absence of prey. Likewise, water levels changed more dramatically in temporary wetlands (62–100% loss of maximum water level; Fig. 4A–C) than in permanent wetlands (18–51% loss of maximum water level; Fig. 4D–F).

DISCUSSION

Our large sample size of turtles from several wetlands allowed us to simultaneously examine how numerous

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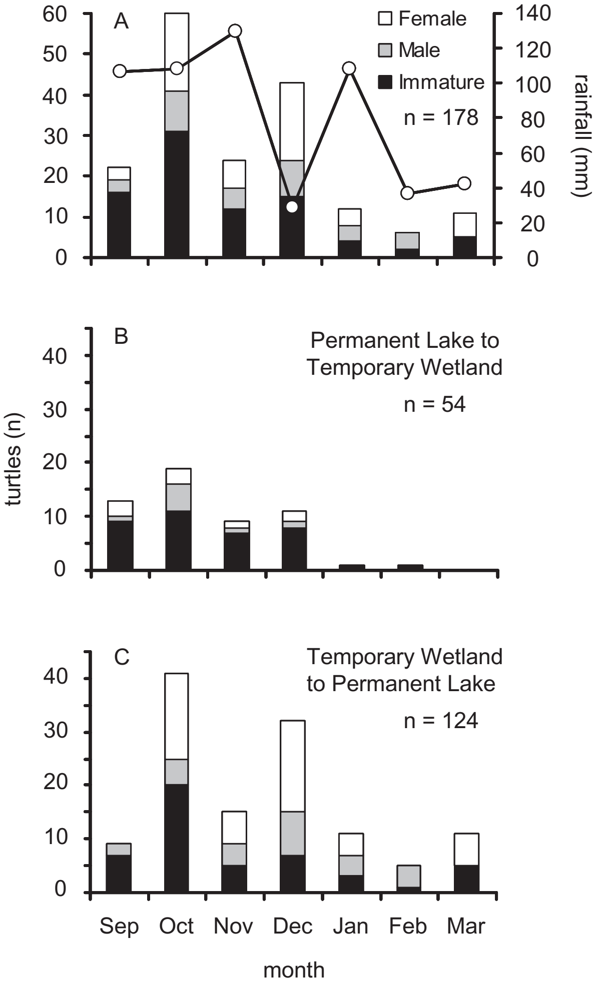

Fig. 3. Relationship between monthly rainfall (circles) and number of turtles captured along a drift fence while moving overland between two wetlands for (A) all individuals, (B) individuals moving from the permanent lake to the temporary wetland only and (C) individuals moving from the temporary wetland to the permanent lake only.

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, pers. obs), but the sexes did not differ significantly in behaviour at these times or any other (Table 1; Fig. 1). Females did not nest far from wetlands (e.g. <30 m, J. Roe, pers. obs), 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 2). That turtles traversed larger areas and longer distances with increasing inter-wetland distance is 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) could be a proximal cause for movement among distant wetlands, as such variation

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Table 3. Summary of regression statistics demonstrating there lation ships between rain fall, temperature, and the number of *Chelodinalongicollis* 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	

Relationships were examined using Poisson regression (PROC GENMOD, SAS 1999). *Indicates variables that were significant after adjusting alpha for multiple comparisons.

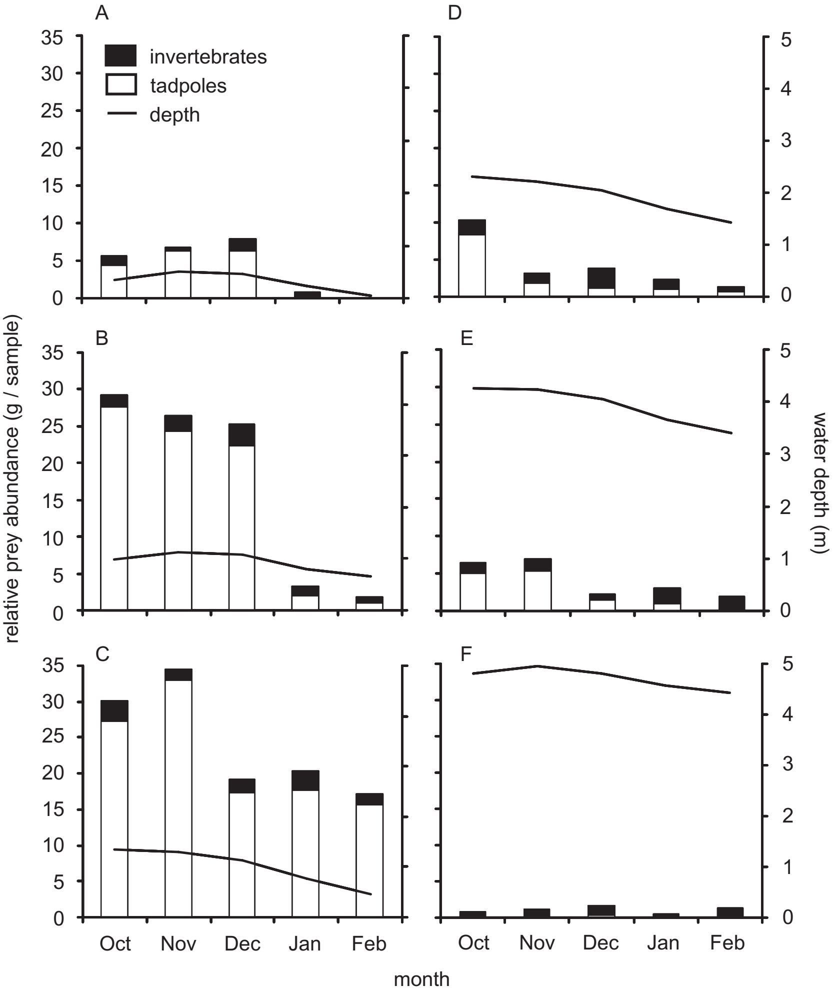

Fig. 4. Monthly variation in relative prey abundance (primary axes) and water depth (secondary axes) in temporary wetlands (A–C) and permanent lakes (D–F). Values for tadpole and invertebrate abundance represent mean wet mass for the three time-constrained sweeps. No small fish were recorded in the prey sampling, though they occur in one of the permanent wetlands, Blacks Waterhole (E).

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 1979). 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 used 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 and tactics in *C. longicollis* is reflected in their high variability in movements and space use (Table 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 1, Fig. 2B). 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 in part result from 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; Christian *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. 3), but terrestrial movements of juveniles were more closely associated with rainfall than for adults (Table 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

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movements between a temporary wetland experiencing dramatic resource fluctuations and a more stable permanent lake (Fig. 4B,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 interesting, however, was that movements from the temporary wetland were less correlated with rainfall than were movements towards the temporary wetland (Table 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. 3,4). Deteriorating conditions in drying wetlands can have severe consequences for turtles that fail to evacuate (Bodie & Semlitsch 2000a; Buhlmann & Gibbons 2001; Fordham *et al.* 2006), 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 suboptimal. 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.

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