



Life in the suburbs: Behavior and survival of a freshwater turtle in response to drought and urbanization

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ABSTRACT

Urbanization fundamentally alters the abiotic and biotic components of landscapes, presenting wildlife with serious challenges to which they must respond in order to avoid excess mortality from urban dangers. In this study, we used radio-telemetry to examine the behavior and survivorship of an Australian freshwater turtle, *Chelodina longicollis*, in a suburban environment compared to a control group on an adjacent nature reserve. We expected turtles in the suburbs to be less mobile, but the suburban environment did not inhibit the ability of turtles to traverse large areas and make frequent movements among several different wetlands. In fact, suburban turtles were more vagile, moving distances twice as far as those on the nature reserves. Turtles on the nature reserve responded to dropping water levels during drought by estivating for several months in sheltered woodland micro-habitats. Suburban turtles did not estivate terrestrially, in part because their water bodies experienced dampened water level fluctuations and retained water during drought, though the relative unavailability of suitable estivation sites and perceived threats could also account for their avoidance of extended forays into the terrestrial environment. Annual survival rate was 95.3% in the reserves compared to 87.6% in the suburbs, but this 7.7% decrease in survival from road mortality was not significant in our survivorship models. The continued ability of suburban turtles to remain vagile without suffering from high mortality rates is likely a product of the availability of vegetated drainage lines and under-road “box” culverts that allow turtles to travel safely throughout the suburban landscape.

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1. Introduction

Urbanization is one of the most damaging and rapidly expanding forms of habitat fragmentation and alteration worldwide, often completely restructuring the physical landscape and the associated biotic community (Adams et al., 2006; Shochat et al., 2006). Wildlife in urban areas must contend with substantial deterioration of habitat quality and reduction in its extent including (but not limited to) exposure to environmental pollutants, changes in primary productivity, resource availability and microclimate, novel intra-specific and inter-specific interactions, or the outright loss of landscape features with critical resources (McDonnell and Pickett, 1990; Savard et al., 2000; Germaine and Wakeling, 2001; Marzluff, 2001; Adams et al., 2006; Shochat et al., 2006). Furthermore, remnants of otherwise suitable habitat patches such as urban water bodies, green spaces, or nature reserves are typically isolated from one another by inimical landscape features. Urban areas are typi-

cally bisected by dense road networks and associated traffic, which can isolate individuals from critical resources by impeding their movements, or serve as a source of mortality (Forman and Alexander, 1998; Trombulak and Frissell, 2000). The ability of a species or population to persist in urban environments depends in large part on their tolerance to habitat changes brought about by urbanization and their ability to avoid urban dangers (Germaine and Wakeling, 2001; Koenig et al., 2001; Riley et al., 2006; Pattishall and Cundall, 2008).

Freshwater turtles show a wide range of responses to urbanization. On the one hand, some species persist or even thrive in urban waterways such as waste and stormwater drainage lagoons, golf course ponds, lakes, reservoirs, rivers, or streams (Gasith and Sidis, 1984; Mitchell, 1988; Lindemann, 1996; Conner et al., 2005; Plummer et al., 2008; Burgin and Ryan, 2008; Giles et al., 2008). However, even if suitable aquatic habitat exists, populations may be impacted by modifications to the surrounding terrestrial landscape. Turtles can encounter dangers when they leave the water to nest, estivate, hibernate, migrate, or disperse to another water body (Semlitsch and Bodie, 2003; Roe and Georges, 2007), and the high incidence of vehicular mortality from crossing roads is thought to adversely affect turtle populations (Gibbs and Shriver,

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2002; Marchand and Litvaitis, 2004; Steen and Gibbs, 2004; Arecco, 2005a). Life-history characteristics associated with high adult survivorship, such as low annual recruitment and delayed sexual maturity, may constrain the ability of turtle populations to absorb this excess mortality (Congdon et al., 1993, 1994). Consequently, roads and other habitat modifications that increase mortality, restrict movements, or reduce the availability of critical resources in the wider landscape may eventually eliminate some species from urban areas, or restrict populations to natural habitat remnants large enough to buffer against urbanization (Rubin et al., 2001; Edwards et al., 2004; Giles et al., 2008).

Most of our understanding of how freshwater turtles are influenced by urban development comes from intensive examinations of urban populations (Mitchell, 1988; Conner et al., 2005; Grgurovic and Sievert, 2005; Plummer et al., 2008; Burgin and Ryan, 2008; Giles et al., 2008) or by drawing inferences from patterns of abundance, diversity, and population demographics along a gradient of land-use types (Marchand and Litvaitis, 2004; Steen and Gibbs, 2004; Rizkalla and Swihart, 2006). Landscape-scale studies can provide correlational evidence of land-use features associated with impacts, but by themselves cannot identify a mechanistic basis for the impact. For example, roads can adversely impact turtle populations (Marchand and Litvaitis, 2004; Steen and Gibbs, 2004; Arecco, 2005a; Gibbs and Steen, 2005), but whether this results from road mortality, road avoidance behavior, or some combination these or other factors is not always clear. Intensive examinations of urban turtle ecology can better identify the specific mechanisms of impact, but to our knowledge no studies have directly investigated freshwater turtles in urban settings while simultaneously examining another cohort in nearby natural habitats as a control.

In this study, we used radio-telemetry to compare the behavior and survivorship of eastern long-necked turtles (*Chelodina longicollis*) in a suburban area to those in an adjacent nature reserve. Though the behavior of *C. longicollis* can be highly variable (Roe and Georges, 2008a,b), it is not known whether or to what extent this species can alter behavior to avoid urban dangers. To this end, we assessed aspects *C. longicollis* movement and habitat use

behaviors to determine if they become less mobile and more aquatic in response to the hazards and altered habitats typical of urban areas. Alternatively, if turtles do not change behavior in response to urbanization, we would expect them to suffer higher mortality rates than in the nature reserve. Our comparative approach should allow for an assessment of both the magnitude and mechanisms of urban effects, or identify aspects of turtle behavior that allow individuals to avoid threats and persist in urban areas. This information will also identify specific management actions and features of urban design that could help mitigate impacts to turtle populations in metropolitan areas.

2. Methods

2.1. Study area

We studied turtles between September 2006 and November 2007 in suburban Gungahlin and in an adjacent nature reserve of the Australian Capital Territory (ACT), Australia (Fig. 1). Gungahlin has a history of livestock grazing (National Capital Development Commission, 1988) and was developed in 1975, though construction of its outer suburbs was still occurring during this study. The suburbs are characterized by large areas of residential and industrial development, high road densities, and intensively managed urban green spaces including golf courses, urban parks, sports ovals, and gardens (Fig. 1). There are also many suburban water bodies, including two large reservoirs (each 25 ha in surface area), several golf course and stormwater drainage ponds, and a chain of small and shallow wetlands that become temporarily connected during high water flows along the Ginninderra Creek drainage (Fig. 1).

Two connected natural areas, Mulligans Flat and Goorooyaroo nature reserves, border the suburbs and together contain one of the largest protected areas of native vegetation in the Gungahlin area (Lepschi, 1993). Habitats on the reserves consist of woodlands, grasslands, a number of ponds that were originally used for stock (largest pond 7.1 ha), as well as the upper tributaries of

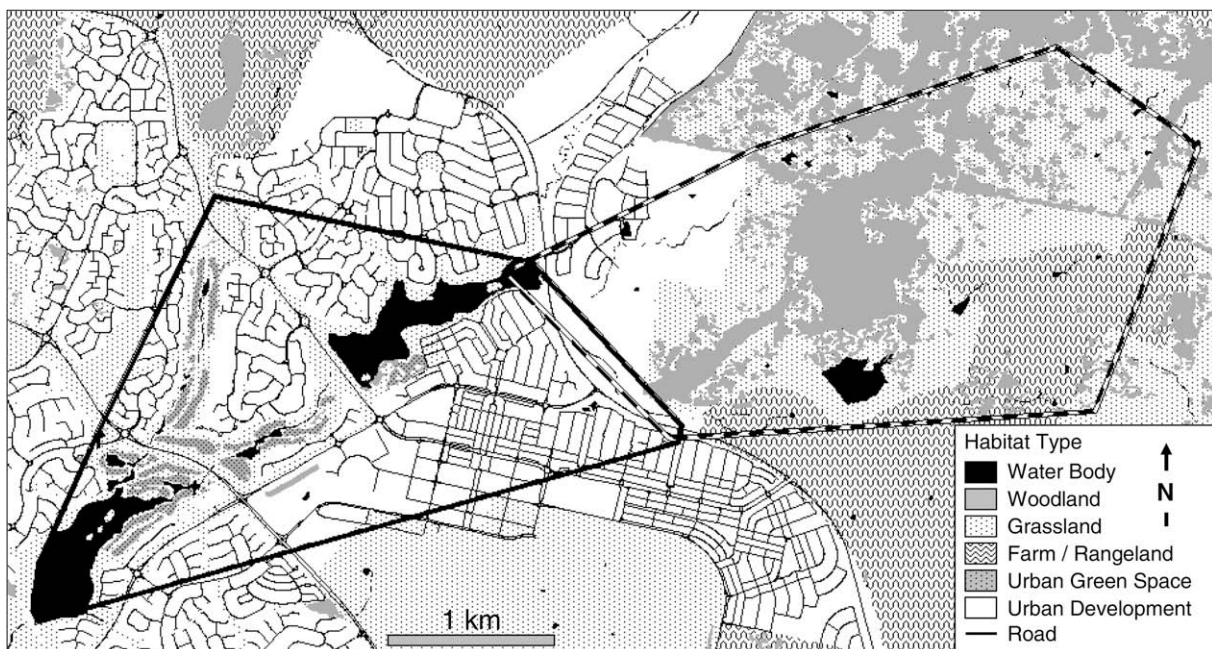


Fig. 1. Habitat composition and road networks in the suburban (solid polygon) and nature reserve (dashed polygon) study sites. Each study site was defined by drawing a minimum convex polygon around the outermost locations of turtles originally captured on their respective study sites and followed for approximately 1 year using radio-telemetry.

Ginninderra Creek. These reserves are surrounded by sheep and cattle rangeland on the rest of their borders (Fig. 1).

2.2. Habitat mapping

Habitat polygons were digitized from aerial photographs using a Geographic Information System (ArcView 3.1, [Environmental Systems Research, 1992](#)). Obscure habitat boundaries were verified by ground-truthing with a GPS unit (GPS III Plus, Garmin Corp., Olathe, Kansas) with an error of 1–7 m. Macrohabitat classifications included grassland, woodland, farm/rangeland, urban development (high density residential and industrial development, including land cleared in the process of being developed), urban green space (intensively managed landscapes including golf-courses, city parks, and sports fields), or water body (stock dams, stormwater drainage ponds, reservoirs, streams, and wetlands). The borders of water bodies were mapped at their high water flood levels, but to describe fluctuations in depth, maximum water depth was assessed on a monthly basis in several suburban and nature reserve wetlands.

For analytical purposes, the boundaries of the suburban and nature reserve study sites were delineated by drawing a minimum convex polygon (MCP) encompassing all radio-locations for turtles originally captured from their respective study sites using the Animal Movements extension for ArcView (Fig. 1). The areas of each habitat type and total road lengths were calculated for both the suburban and nature reserve sites using the X-tools function in ArcView.

2.3. Capture and radio-transmitter attachment

Turtles were initially captured using traps or by hand from 11 wetlands distributed across both study sites (four wetlands in suburbs, seven wetlands in nature reserves). Turtles were originally captured from wetlands ranging from 0.05 to 7.1 ha, excluding the two large reservoirs in the suburbs. Forty-three adult turtles were fitted with radio-transmitters, 20 (13 females and 7 males) from the suburbs and 23 (13 females and 10 males) from the nature reserves. We originally attached radio-transmitters manufactured by Sirtrack Ltd. (Havelock North, New Zealand), but owing to numerous premature transmitter failures, we switched to equivalent transmitters from Holoohil Systems, Ltd. (Carp, Ontario, Canada). Detailed descriptions of our transmitter attachment protocol are described in [Doody et al. \(2009\)](#). Initial plastron lengths and mass of suburban females was 172.3 ± 15.7 mm (mean \pm standard deviation) and 1098 ± 335 g, and for nature reserve females was 171.6 ± 16.9 mm and 956 ± 354 g. Initial plastron lengths and mass of suburban males was 151.1 ± 8.4 mm and 709 ± 115 g, and for nature reserve males was 142.6 ± 5.9 mm and 596 ± 82 g. Transmitters were 1.4–6.4% of the turtles' initial body mass.

2.4. Radio-telemetry data collection

Turtles were located twice per week during their typical active season (September to March) and once per week over the inactive season (April to August). Where possible, coordinate positions were determined using GPS units held directly above the turtle, but when the turtle could not be closely approached we plotted its location on an aerial photograph by triangulation. We then plotted location coordinates on habitat maps using ArcView.

Several variables were used to describe the movement behavior for each turtle. To estimate the size of the area traversed by each individual, we used the minimum convex polygon (MCP) technique. We also calculated the linear range length, measured as the Euclidian distance between the two most widely spaced locations. As an index of inter-patch movement extent and frequency,

we calculated the number of different wetlands that a turtle visited, and the number of times that a turtle moved between these wetlands. Next, we estimated movement distance as the sum of Euclidian distances between sequential radio-locations for each individual. Estimations of area use and distances were performed with the Animal Movements extension for ArcView.

We also assessed several aspects of habitat use behavior. At each location, we noted the macro-habitat class that the turtle was using, with a particular focus on whether the turtle was in an aquatic or terrestrial habitat. From these observations, we calculated the following variables to describe terrestrial behaviors: (1) terrestrial duration, the number of consecutive days a turtle spent in terrestrial habitats without returning to a wetland, (2) terrestrial habitat proportional use, calculated as the proportion of radio-tracked time that turtles spent in terrestrial habitat, and (3) distance from water body, the Euclidian distance from a terrestrial location to the nearest wetland. Due to the extended durations that *C. longicollis* typically spends in out of water for estivation and hibernation ([Roe and Georges, 2007, 2008b](#)), our tracking intervals likely provided good relative estimates of time spent in terrestrial habitats.

At each terrestrial refuge site used for an extended duration (i.e., several weeks), we measured micro-habitat features. Canopy openness (%) was determined using hemispherical photography and gap light analysis ([Doody et al., 2006](#)). Hemispherical (180°) photographs were taken with a Nikon Coolpix[®] 995 digital camera with a Nikon FC-E8[®] fisheye converter lens held directly above the ground. Photographs were then analysed using the program Gap Light Analyzer Version 2.0 ([Frazer et al., 1999](#)). Litter depth was determined at four random locations within a 1 m quadrat centered over the turtle. We also determined the minimum distance to the nearest protective structures (i.e., tree, shrub, log or stump). To investigate whether turtles chose terrestrial refuge sites randomly, these micro-habitat variables were also measured at 40 random locations. For each turtle, five random sites were randomly selected using the Random Point Generator function of ArcView, constrained to a 500 m radius around the wetland the turtle most recently used, which is the furthest distance from water that *C. longicollis* is known to estivate ([Roe and Georges, 2007](#)).

2.5. Data analyses

Statistical analyses were performed with SPSS Version 14.0 ([SPSS, 2006](#)), SAS Version 8.2 ([SAS Institute, 2001](#)), and the program MARK version 4.2 ([White and Burnham, 1999](#)). The assumptions of normality and homogeneity of variances were examined where appropriate and when data failed to meet these assumptions, data were transformed to approximate normal distributions and equal variances; otherwise, non-parametric tests were used. Statistical significance was accepted at the $\alpha = 0.05$ level unless specified otherwise, and means are reported as ± 1 standard error.

Analysis of covariance (ANCOVA) was used to investigate differences in movement and area-use estimates. Response variables for each analysis were \log_{10} MCP, range length, and \log_{10} total movement distance, with site, sex, and their interaction as the discrete factors, and PL the covariate. Analysis of variance (ANOVA) was used to investigate inter-patch movements, with number of wetlands used and frequency of inter-wetland movements the response variables, and site, sex, and their interaction as the discrete factors.

A series of Mann–Whitney *U* tests were used to examine site- and sex-specific differences in terrestrial habitat use, using the proportion of time spent in terrestrial habitats as the response variable. The first Mann–Whitney *U* test combined sexes and examined only site-specific differences. Next, we examined sex-specific differences in terrestrial habitat use only for nature reserve

turtles, given that we detected no terrestrial habitat use in suburban turtles (see Section 3). The Dunn-Sidak adjusted α level for these related Mann–Whitney tests was $\alpha \leq 0.025$. We used ANOVA to investigate differences in micro-habitat variables between turtle estivation sites and random sites, with canopy coverage, litter depth, and \log_{10} distance to nearest refuge structure as the response variables, and type (turtle or random) as the main effect.

Survivorship analyses were conducted using known fate models in the program MARK (White and Burnham, 1999). Maximum likelihood survival probabilities were estimated over monthly intervals. We started with a fully-saturated model in which survival probability was dependent on site, month, and initial plastron length as a covariate, then fitted a series of reduced-parameter models. Time periods where radio-signals could not be detected (i.e., transmitter failure or undetected long-distance movements) were censored from the analysis. The Akaike Information Criterion (AIC) was used to rank candidate models; if competing models had AIC values of ≤ 2.0 , they were considered as having some support for the model (Lebreton et al., 1992).

3. Results

3.1. Habitat composition

The suburban study site comprised an area of 539.8 ha, while the nature reserve site was 615.4 ha (Fig. 1). The study sites overlapped slightly where two turtles from the nature reserve entered the suburbs. Not surprisingly, habitat composition varied considerably between the two sites, with the suburbs having relatively higher proportional coverage of urban development, urban green space, and water bodies, and the nature reserve with higher coverage of woodlands, grasslands, and farm/rangeland (Table 1, Fig. 1). Average road density was 19 times higher in the suburbs (12.75 km/km²) than in the nature reserves (0.64 km/km²).

A complete set of monthly water level data was only available for six nature reserve and five suburban wetlands from November 2006 through June 2007. In July 2007, a major flood following heavy rainfall dislodged and inundated most of our water level monitoring stations, so data is presented only up to this point. Some wetlands' data were discarded because of equipment theft and tampering. Despite the limited scope of these data, it is apparent that water bodies on the nature reserve experienced greater drying than did suburban water bodies during a drought that extended through June 2007 (Fig. 2).

3.2. Movements

Turtles were radio-tracked for an average of 320 ± 20 consecutive days, over which we obtained 51 ± 3 locations for each individual. During this time, suburban turtles traversed areas equivalent to those in the nature reserves based on MCP estimates, while males used larger areas than females on both sites (ANOVA site: $F_{1,30} = 2.921$, $p = 0.098$; sex: $F_{1,30} = 7.532$, $p \leq 0.01$; site \times sex: $F_{1,30} = 0.805$; Table 3; Fig. 3). Linear range lengths did not differ between sites, and were also larger for males than females (ANOVA site: $F_{1,30} = 1.206$, $p = 0.281$; sex: $F_{1,30} = 7.481$, $p \leq 0.01$; site \times sex: $F_{1,30} = 0.110$, $p = 0.743$; Table 3). However, suburban turtles moved greater total distances than did those on the nature reserves, and

Table 2

Models of survivorship probability (S) between sites (site) over monthly time intervals (time). Plastron length (pl) was used as a covariate.

Model	AICc	Δ AICc	Weight	N	Deviance
S (time)	28.32	0.00	0.365	2	24.29
S (time \times site)	28.73	0.413	0.297	3	22.68
S (time) pl	29.73	1.41	0.181	3	23.67
S (time \times site) pl	30.12	1.793	0.149	4	22.10
S (.)	37.54	9.21	0.004	1	35.53
S (site)	38.94	10.62	0.002	2	34.92
S (.) pl	39.05	10.72	0.002	2	35.02
S (site) pl	40.56	12.13	0.001	3	34.40

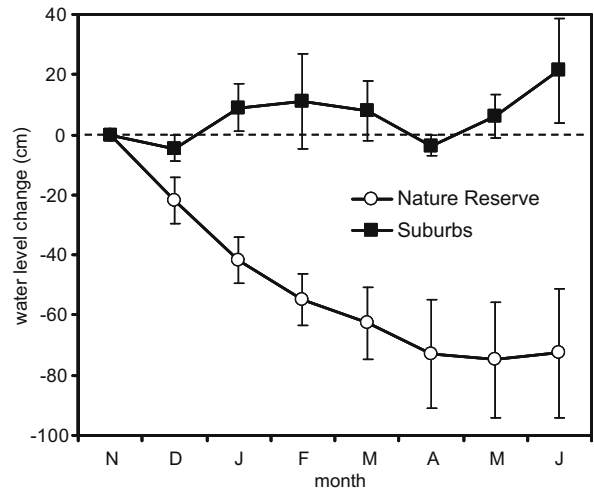


Fig. 2. Water level change relative to the beginning of the study (November 2006) in nature reserve and suburban water bodies. Values are mean ± 1 standard error.

males moved longer distances than females (ANOVA site: $F_{1,30} = 14.736$, $p \leq 0.01$; sex: $F_{1,30} = 15.788$, $p < 0.001$; site \times sex: $F_{1,30} = 1.051$, $p = 0.313$; Table 3). Plastron length was not a significant predictor of any movement variable ($p \geq 0.452$), so this variable was removed as a covariate from the analyses.

Turtles in the suburbs and nature reserves did not differ with respect to the number of wetlands they used, nor the frequency with which they moved between them. Males used a greater number of wetlands than did females at both sites, though the frequency of inter-wetland movements did not differ between sexes (ANOVA number of wetlands; site: $F_{1,30} = 0.660$, $p = 0.422$; sex: $F_{1,30} = 4.70$, $p < 0.05$; site \times sex: $F_{1,30} = 0.56$, $p = 0.461$; inter-wetland movements: site: $F_{1,30} = 1.23$, $p = 0.277$; sex: $F_{1,30} = 1.62$, $p = 0.213$; site \times sex: $F_{1,30} = 0.28$, $p = 0.602$; Table 3).

3.3. Habitat use

Terrestrial habitat use differed markedly between sites (Mann–Whitney U test: $Z = -3.427$; $df = 32$; $p < 0.01$). Turtles in the nature reserves spent 108 ± 34 days (range = 0–281) in terrestrial habitat, representing $28.0 \pm 7.6\%$ (range = 0.0–77.7%) of their time in the study. In contrast, turtles in the suburbs were never detected in terrestrial habitats, though several must have spent at least some

Table 1
Habitat composition (%) of the suburban and nature reserve study sites.

	Grassland	Woodland	Urban development	Farm/rangeland	Urban green space	Water body
Suburbs	21.0	0.6	63.2	0	4.8	10.4
Nature Reserve	37.1	28.6	14.3	17.5	0	2.5

Table 3
Movement behavior and spatial ecology of suburban and nature reserve turtles.

	MCP ^a (ha)		Range length (km)		Distance moved (km)		Wetlands used (n)		Inter-wetland movements (n)	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
<i>Suburbs</i>										
Male	39.6 ± 8.7	3.7–59.9	1.7 ± 0.3	0.4–2.3	6.4 ± 1.1	2.9–9.3	3.5 ± 0.6	1–5	3.0 ± 0.8	0–6
Female	14.2 ± 4.7	0.3–37.2	0.8 ± 0.2	0.1–1.9	3.0 ± 0.6	0.7–6.6	2.3 ± 0.4	1–5	1.9 ± 0.7	0–6
<i>Nature reserve</i>										
Male	12.3 ± 3.7	1.6–24.8	1.2 ± 0.2	0.2–2	2.4 ± 0.2	1.9–3.4	2.9 ± 0.4	1–4	2.0 ± 0.4	0–3
Female	8.7 ± 2.2	0.7–31.8	0.6 ± 0.2	0.2–1.9	1.5 ± 0.2	0.7–2.9	2.3 ± 0.3	1–4	1.5 ± 0.4	0–4

^a Minimum convex polygon.

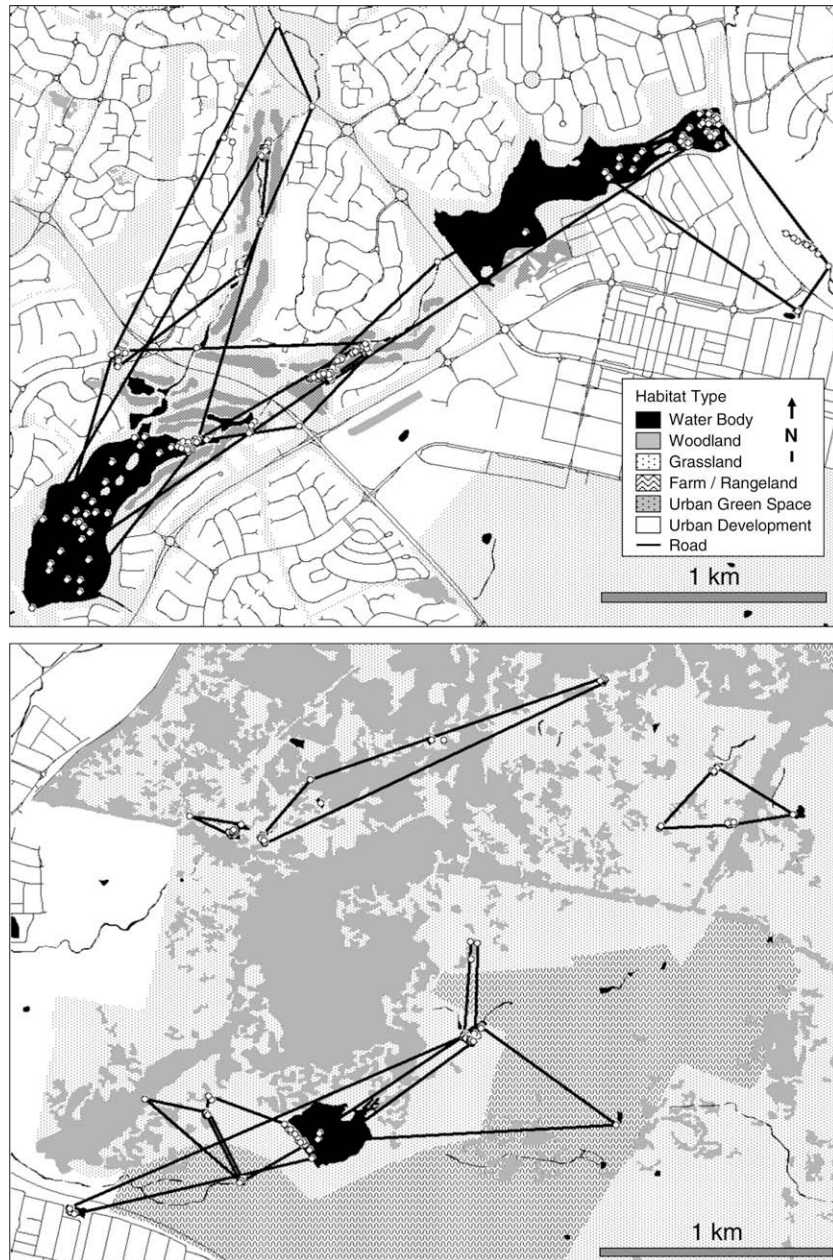


Fig. 3. Radio-locations (white circles) and minimum convex polygons (thick black lines) of six turtles on the suburban site (above), and eight turtles from the nature reserves (below). The key to the habitat map applies to both figures.

time moving overland between wetlands. Turtles on the nature reserve moved into terrestrial refuge sites for estivation beginning in December 2006, where most remained through October 2007, but

long-term terrestrial estivation was a behavior employed only by females (Mann–Whitney U test: $Z = -2.369$; $df = 27$; $p < 0.02$; Fig. 4).

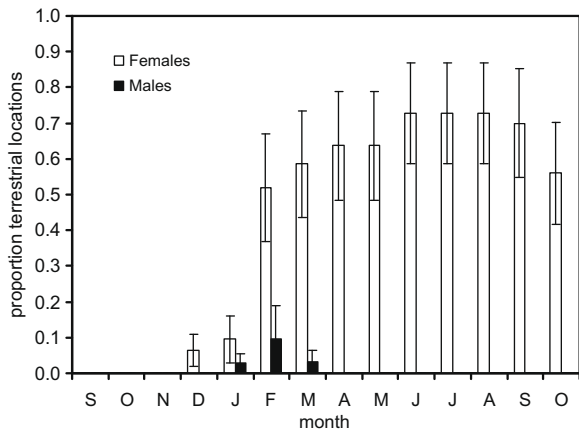


Fig. 4. Monthly use of terrestrial habitats for estivation in female and male *Chelodina longicollis* on the nature reserve. Values are mean \pm 1 standard error. Values are not shown for suburban turtles because they did not estivate in terrestrial habitats.

Estivation sites were located 152 ± 45 m (range = 38–394 m) from the nearest wetland. Estivation sites were all in woodland habitat where the turtle either completely or partially buried under debris. Turtles chose estivation sites non-randomly with respect to several micro-habitat variables (Table 4). Estivation sites had lower canopy openness, deeper leaf litter, and were nearer to cover structures such as logs, shrubs, trees, or stumps than were random sites (ANOVA: $F_{1,32} \geq 7.60$, $p \leq 0.01$).

3.4. Survivorship

We found little evidence that survival probability differed between the suburban and nature reserve sites. The model including monthly variation in survivorship with site held constant had the most support, with some evidence that survival probability was lower for suburban turtles only in December 2006 (Table 2, Fig 5). Monthly survivorship probabilities over the duration of the study averaged 0.996 ± 0.004 for the nature reserve turtles, and 0.989 ± 0.008 for the suburban turtles. One turtle from each of the two sites died of an unknown cause immediately following a brief cold spell in November 2006, and one turtle was killed by a vehicle while crossing a road in the suburbs in December 2006.

4. Discussion

To our knowledge, this is the first study to compare the behavior and survival of freshwater turtles living directly within an urban area to a control group in a nearby non-urbanized landscape. Even though turtles in our control site should not be considered as existing completely free of influence from nearby developed lands, the close proximity of urban and nature reserve sites coupled with their simultaneity of study did standardize geographic, climactic, seasonal, genetic, and methodological factors that could

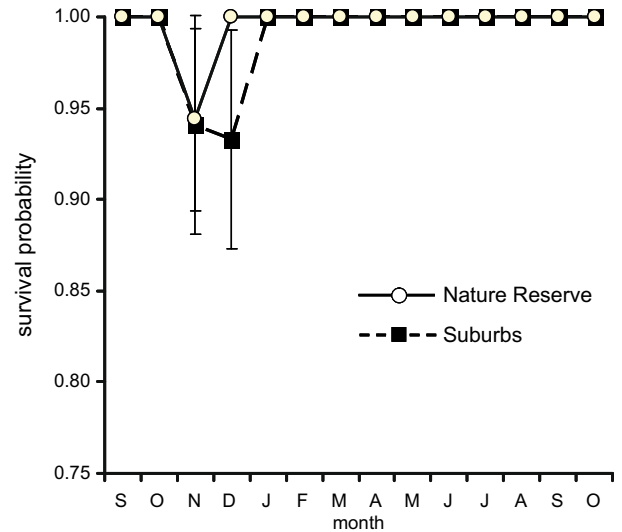


Fig. 5. Monthly survival probabilities for suburban and nature reserve turtles. Error bars are \pm 1 standard error.

otherwise make such comparisons difficult to interpret. Such a design allowed us to answer questions pertaining to both the mechanistic basis and magnitude of urban impacts on *C. longicollis* populations while limiting potentially confounding factors as much as possible.

The suburban landscape of our study was typical of many urbanized areas, with patches of wildlife habitat surrounded by heavily built-up residential and industrial areas and high road densities (McDonnell and Pickett, 1990; Adams et al., 2006). Several water bodies including stormwater retention lagoons, golf course ponds, reservoirs, and a network of streams represented potentially suitable habitat for turtles. These types of water bodies are often integrated into urban landscapes and can provide an attractive habitat rich in resources for wildlife (Tilton, 1995). Because these aquatic habitats were imbedded within the suburban matrix, we expected that turtles would respond in one of two ways – by altering behavior to reduce encounters with potential threats, or by behaving normally and suffering higher rates of mortality as a result. We found that suburban turtles behaved differently from their counterparts in the nature reserve with respect to both movements and habitat use, and that this behavioral variation did not translate into differences in survivorship.

4.1. Behavior

C. longicollis is nominally an aquatic turtle that is vagile and sometimes makes extensive use of terrestrial habitats. This species frequently moves overland between several water bodies separated by hundreds of meters, and in addition to nesting, it commonly seeks extended refuge in terrestrial environments for estivation and hibernation (Stott, 1987; Roe and Georges, 2007, 2008a,b; Roe et al., 2008, 2009). Highly mobile wildlife may be especially vulnerable to threats in developed areas due to their in-

Table 4
Microhabitat features associated with turtle estivation sites on the nature reserve versus randomly selected locations.

	Canopy openness (%)		Litter depth (cm)		Distance to structure (m) ^a	
	Mean \pm SE	Range	Mean \pm SE	Range	Mean \pm SE	Range
Estivation site	38.9 \pm 2.1	32–48	10.7 \pm 1.3	6–16	0.9 \pm 2.0	0–2
Random	66.8 \pm 2.7	36–89	1.3 \pm 0.3	0–6	9.1 \pm 1.8	0–62

^a Structures include logs, stumps, trees, or shrubs.

creased encounter rates with inimical landscape features or human activities (Gibbs, 1998; Bonnet et al., 1999; Carr and Fahrig, 2001; Roe et al., 2006; Attum et al., 2008), and turtles in particular are often victims of mortality and collecting when they move overland in areas of even moderate human activity (Garber and Burger, 1995; Ashley and Robinson, 1996; Haxton, 2000; Brisbin et al., 2008). Such a high degree of vagility and terrestriality would presumably bring *C. longicollis* into frequent contact with urban threats, requiring them to employ some behavioral modifications to become less mobile and/or terrestrial if they are to subsist in developed areas. Contrary to our expectations, *C. longicollis* did not reduce mobility in the suburbs, but instead continued their typical behavior of moving among several distant water bodies and traversing large areas, moving even longer distances than their counterparts on the nature reserve (Fig. 3; Table 3).

Though the suburbs did not inhibit the movements or spatial ecology of *C. longicollis*, their use of terrestrial habitats for estivation was substantially different in the suburban landscape. Female turtles in the nature reserve exited wetlands as early as December 2006 and estivated for several months until the following spring, though males spent very little time on land (Fig. 4). However, suburban turtles did not estivate terrestrially, but instead remained in water bodies throughout the study. Nature reserve turtles selected estivation sites in woodlands with specific micro-habitat attributes that offered shelter from predators and desiccation. These habitat types were rare in the suburban environment and would have required considerable travel to reach them. Thus, it is possible that suburban turtles did not estivate because suitable habitat was unavailable, or that they avoided extended forays into terrestrial sites because of perceived threats.

It is important to note that terrestrial estivation is a plastic behavior in *C. longicollis* which depends on whether wetlands dry and their proximity to other water bodies that are more resilient to drought (Roe and Georges, 2008a). Whereas water levels in wetlands on the nature reserve dropped substantially, suburban water bodies fluctuated relatively little and remained mostly flooded (Fig. 2). At the peak of the drought in July 2007, nearly all nature reserve wetlands had either dried completely or were less than half a meter deep, whereas most suburban wetlands remained flooded to a depth of at least one meter. The hydrology of urban water bodies can be greatly altered by irrigation inputs, increased runoff from impervious surfaces, and intentional manipulation of water levels (Tilton, 1995; Paul and Meyer, 2001; Adams et al., 2006), all of which are factors that we observed impacting suburban wetlands during our study. Even though a few suburban wetlands experienced some degree of drying, the larger urban reservoirs offered access to water several meters deep throughout the study. The majority of suburban turtles (62%) had moved into the two large suburban reservoirs by mid summer. Thus, an alternative explanation for the variation in terrestrial habitat use between sites is that dampened water level fluctuations and continuous availability of deeper reservoirs in the suburbs may have given little reason for turtles to estivate. Whether variation in estivation behavior between sites was a proximal consequence of terrestrial habitat suitability or availability, hydrological stability during drought, or some combination of these factors is not immediately apparent, but ultimately all can be attributed either directly or indirectly to the influences of urbanization.

4.2. Survival

Surprisingly, survivorship of suburban turtles did not differ significantly from those on the nature reserve despite the high vagility maintained by turtles in the suburban landscape. Monthly survival probabilities extrapolate to annual rates of 95.3% in the nature reserves and 87.6% in the suburbs, both of which are within

the normal range of *C. longicollis* elsewhere (Roe et al., 2009) and in freshwater turtles in general (Shine and Iverson, 1995). We expected a high incidence of road mortality in the suburbs, but only one turtle was killed by a vehicle, representing a 7.7% reduction in survival relative to nature reserve turtles. Though perhaps not statistically significant during the 1-year time frame of our study, chronic adult mortality at the level we observed in the suburbs may eventually be of biological consequence for a turtle population. Long-term demographic and modelling studies indicate that as little as a 2–3% increase in adult annual mortality can severely limit population growth and persistence in long-lived turtles (Brooks et al., 1991; Congdon et al., 1993, 1994), not accounting for potential density-dependent compensation, immigration, and habitat productivity (Lindemann, 1996; Fordham et al., 2007; Roe et al., 2009). Further studies of *C. longicollis* demographics and growth in this system could illustrate whether this low level of mortality has population-level implications.

4.3. Management implications

Land managers in urban areas are presented with the particular challenges of meeting simultaneously the conservation needs of natural lands and wildlife as well as those for urban development. These goals typically conflict, as urbanization has the potential to disrupt the natural connectivity of landscapes by fragmenting remnant habitat patches into isolated units where wildlife are greatly restricted in their ability to move about the landscape (Hitchings and Beebe, 1997, 1998; Riley et al., 2006). For *C. longicollis*, such movements are an integral aspect of the ecology, allowing individuals to respond to seasonal or stochastic fluctuations in aquatic resources across the landscape, especially variations associated with flood-drought cycles (Kennett and Georges, 1990; Roe and Georges, 2007; Roe et al., 2009).

Our study illustrates how features of urban design can potentially combine infrastructural requirements with wildlife conservation to maintain biotic connectivity in urban landscapes. Many of the water bodies in the suburban site are connected to one another via natural or artificial drainages that were often buffered from intensive development by remnant grassland and urban green space (Fig. 1). Additionally, under-road “box” culverts along these drainage lines allowed turtles the opportunity to move between wetlands without having to contend with roads and associated traffic (Fig. 6). These features permit *C. longicollis* to move widely about the suburban landscape without suffering the expected mortality. Vegetated and aquatic corridors have helped facilitate the movements of other species and allow for their persistence in urban areas (Koenig et al., 2001; Pattishall and Cundall, 2008).

Though our analysis did not detect any appreciable differences in mortality rates of suburban turtles, given the vulnerability of turtles and other long-lived vertebrates to chronic levels of additional mortality comparable to what we observed on roads in the suburbs (Gibbs and Shriver, 2002; Row et al., 2007), it would be prudent to identify potential road mortality hotspots and develop mitigating actions that further minimize the incidence of turtle interactions with roads (Langen et al., 2009). Our observations suggest that turtles generally (though not always) travelled along the drainage lines and through culverts where these features were available, but for most movements we had little evidence of the actual path travelled. Observations from a citizen survey of turtle sightings on roads in the area identified mortality hotspots at locations where culverts were not available, or where natural drainages were altered such that culverts were offset from what was likely the natural travel route (M. Rees and J. Roe unpublished data). Such forays could be largely prohibited by using barrier fencing that prohibits wildlife from entering the road surface and



Fig. 6. Example of a typical under-road box culvert along a natural drainage line in the Gungahlin suburbs.

funnels their movements into culverts (Yanes et al., 1995; Dodd et al., 2004; Aresco, 2005b; Hagood and Bartels, 2008). For many freshwater turtles, including *C. longicollis* in the ACT suburbs, such efforts can be focused where drainages intersect with roads, but for species or other populations that do not travel along such easily identifiable landscape features, road crossing hotspots may be more difficult to identify and expensive to mitigate (Beaudry et al., 2008).

Finally, our study highlights the importance of understanding how urban landscapes can alter the natural hydrology of water bodies. We suspect that the continuous availability of flooded water bodies and dampened water level fluctuations were major reasons why suburban turtles did not venture into terrestrial habitats to estivate. Land managers should be aware that hydrology can influence turtle behavior, as any substantial drops in water level (whether controlled or as a consequence of prolonged drought) would likely result in an exodus of turtles from the water and their exposure to urban hazards (Hall and Cuthbert, 2000). On the other hand, the attenuation of seasonal or stochastic fluctuations in resource availability can sometimes extend activity seasons and bolster food and water supplies for urban wildlife (Shochat et al., 2006). It would be interesting to determine whether this prolonged annual activity and access to resources translates into higher growth rates and reproductive output in suburban *C. longicollis* as is the case in other urban animal populations (Noske, 1998; Parris and Hazell, 2005; Budischak et al., 2006).

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