

Urban hazards: spatial ecology and survivorship of a turtle in an expanding suburban environment

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Abstract Urbanization poses a threat to long-lived vertebrates, particularly from road mortalities that can threaten population persistence. We studied movements, behavior and survivorship in a semi-aquatic turtle, *Chelodina longicollis*, during a La Niña period of above average rainfall (wet period) from 2012 to 2013. Our goals were to compare female turtles in a suburban environment to those in an adjacent nature reserve, and to interpret our results relative to a previous study in the same system during an El Niño period of drought from 2006 to 2007. During the wet period, turtles from suburban and nature reserve environments exhibited largely similar movements and use of space, and turtles did not aestivate terrestrially despite prolonged periods of aestivation during the 2006–2007 drought. Additionally, turtles from suburbs had reduced annual survivorship (0.67) compared to turtles in the nature reserve (1.00) during the wet period, which contrasts with previous estimates during drought, when survivorship did not differ between environments. Such a reduction in survivorship for suburban turtles resulted largely from vehicular collisions and may be a consequence of rapid increases in human population (79 %) and traffic volume (76 %) over the eight-year study period. Our study demonstrates that turtle behavior and survivorship can be variable in space and time, and that both urban development and climatic conditions can interact and change relatively quickly to influence important aspects of turtle behavior and population biology.

Keywords Freshwater turtle · Road mortality · Survival · Radiotelemetry · Urbanization · Climate cycles

Introduction

Urbanization is a leading cause of biodiversity loss and local extinction (McKinney 2002, 2006; Shochat et al. 2006). The habitat alteration and land conversion from urban development

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results in a complete restructuring of landform, vegetation and species composition (McKinney 2002; Miller and Hobbs 2002). Cities are dynamic entities (Button 2002), where human population growth, urban sprawl and increase in road traffic are expected, especially in developing countries (World Resources Institute et al. 1996; Gakenheimer 1999; Schafer and Victor 2000). Biologically, urban environments typically show a pattern of reduced species richness and an increase in abundance for urban-tolerant species (Shochat et al. 2006; McKinney 2008).

Several studies have revealed how urbanization can affect vertebrate population dynamics (Chase and Walsh 2006; Glista et al. 2008; Delaney et al. 2010), including that of turtles (Dodd et al. 2004; Aresco 2005a; Rees et al. 2009; Roe et al. 2011). For freshwater turtles, roads are a major factor responsible for mortalities, skewed sex ratios and other changes in population structure (Steen and Gibbs 2004; Aresco 2005a; Eskew et al. 2010a, b; Hamer et al. 2015). Nonetheless, suburban areas with high levels of connectivity among habitat patches and increased productivity from urban green spaces (e.g. golf courses) can have abundant and healthy turtle populations (Rees et al. 2009; Roe et al. 2011; Guzy et al. 2013; Stokeld et al. 2014). Many strategies have been applied to mitigate the impacts of urbanization on turtles, such as the use of under-road culverts and fencing to promote movements through safer passages while minimizing mortality (Dodd et al. 2004; Aresco 2005b; Rees et al. 2009).

Monitoring wildlife populations is essential to understand changes in population dynamics through time (Witmer 2005; Marsh and Trenham 2008), but the time scales over which studies occur must be tailored to the study species, system, and research questions. Single short-term studies may be suitable for measuring population responses for some species and for targeted research questions (Waide 1991; Schmiegelow et al. 1997), but may be of limited effectiveness in more dynamic systems and other species (Krebs 1996; Fryxell et al. 1998). Turtles have a suite of life history traits associated with long lifespans, including high adult survival, low nest and hatchling survival, and delayed sexual maturity, all of which make turtle populations especially sensitive to even slight increases in adult mortality (Congdon et al. 1993; 1994). Thus, longer-term or repeat studies, perhaps extending several decades, may be required to fully understand factors responsible for population regulation (Stickel 1978; Roe and Georges 2008a). Monitoring responses of turtles to dynamic threats such as urbanization is key to understanding their persistence in urban environments (Eskew et al. 2010a; Guzy et al. 2013), and studies should cover durations that capture changing urban development patterns, as well as dynamic environmental phenomenon, such as climate cycles (Roe and Georges 2008a; Roe et al. 2011). In particular, it is essential to understand the effect of wet and dry cycles on freshwater turtles, as turtles can move extensively among water bodies in response to such changes and incur risk of mortality while travelling overland (Rees et al. 2009; Roe et al. 2011; Ferronato et al. 2014).

Chelodina longicollis is an Australian freshwater turtle that inhabits a wide range of water bodies in both natural and developed environments (Kennett et al. 2009). The behavior of this turtle is variable and depends on local environments and climate (Roe and Georges 2008a). Given our comprehensive understanding of *C. longicollis* ecology during drought in 2006–2007 (Rees et al. 2009; Roe et al. 2011), we were interested in monitoring the species in the same system following several environmental changes. The 2006–2007 study was conducted during the early stages of suburban development, and the region has since experienced rapid population growth and associated suburban infrastructure, including additional roads, houses, and a pest-exclusion fence designed in part to isolate the nature reserve from encroaching suburban threats. Second, climate conditions were appreciably wetter in 2012–2013 than in

2006–2007. The effect of such changes could potentially affect turtle behavior and ultimately alter important population vital rates such as survivorship. Specifically, we aimed to (1) compare the behavior of *C. longicollis* in a suburb and an adjacent nature reserve during a wet period, (2) evaluate the survivorship of *C. longicollis* between environments, and finally (3) contrast these findings from the wet period to results from the earlier drought period of 2006–2007 following such changes to the system.

Methods

Study area

This study was undertaken from January 2012 to April 2013 in suburban Gungahlin and an adjacent nature reserve of the Australian Capital Territory (ACT), Australia. Gungahlin, established in 1975 and encompassing 9060 ha, is a fast growing district in Canberra and development continued throughout our study. The Gungahlin suburbs are characterized by large areas of residential, industrial and agricultural development, in addition to high road densities and suburban green spaces such as sport ovals, golf courses, gardens and suburban parks. There are also several suburban water bodies, including two large reservoirs >25 ha, smaller golf course and stormwater drainage ponds, and several streams that form the Ginninderra Creek drainage (Rees et al. 2009). Adjacent to Gungahlin, there are two connected natural reserves, Mulligans Flat (791 ha) and Goorooyaroo (703 ha), which consist of woodlands, grasslands, several ponds and the upper tributaries of Ginninderra Creek. Both nature reserves are surrounded by suburban development and farmlands. For a detailed description of the study sites, see Rees et al. (2009) and Roe et al. (2011).

In 2009, a predator-proof fence was established in Mulligans Flat Nature Reserve to allow the managed re-introduction of locally extinct species of animals and consequently protect native species against invasive and pest species such as foxes, hares, rabbits, feral cats and dogs (Shorthouse et al. 2012). The fence is 11.5 km in length and encloses 485 ha of the reserve (Shorthouse et al. 2012).

The climate of the ACT is temperate, with mean monthly maximum air temperature ranging from 11 °C in July to a peak 27 °C in January and February, and a mean monthly minimum air temperature ranging from 0 °C to 13 °C in the same months (Palmer-Allen et al. 1991). Although the mean annual rainfall is 600 mm (Palmer-Allen et al. 1991), the weather in Australia is unpredictable, with long periods of drought. The most recent, known as the “Millennium drought”, occurred during 2001–2009, with a yearly below median rainfall of 483 mm/yr., mainly influenced by El Niño events (van Dijk et al. 2013). In contrast, there are periods of elevated rainfall and flooding, influenced by La Niña events, such as in 2010–2012 (BOM 2012; Letnic et al. 2013). Our study took place during a La Niña period, with elevated rainfall, totaling a 965 mm of rainfall from Jan. 2012 to Apr. 2013, or 772 mm/year (Australian Bureau of Meteorology).

Water levels and suburban growth

To describe fluctuations in water levels, we measured maximum water depth monthly from January 2012 to April 2013 in four ponds each within the suburbs and nature reserve. We obtained data on human populations and traffic volume over the period spanning the 2006–

2007 and 2012–2013 study periods. Human population growth was collected using Census data in 2006 and 2012 (Australian Bureau of Statistics) from five suburbs of the Gungahlin District (Amaroo, Bonner, Forde, Gungahlin, and Ngunnawal) that surround the study sites. We obtained car traffic volume (cars per day) from 2007 and 2011 from Territory and Municipal Services for a major road, Horse Park Drive, which bisects our study site and presumably gives a representative measure of how traffic volume changed through time.

Capture and radiotransmitter attachment

Turtles were captured from five ponds in the nature reserve and four in the suburbs using traps baited with sardines and cow liver. We only selected a single demographic group for this study to increase sample size, and females were chosen owing to their more direct influence on population regulation via reproduction (Congdon et al. 1993). Radiotransmitters were initially attached to 40 females divided equally between the nature reserve and suburban sites. If a turtle died during the study, the radiotransmitter was attached to another individual from the same study site. We used transmitters manufactured by Holohil Systems Ltd. (Carp, Ontario, Canada) (Models: RI-2B and AI-2F, 14 - 21 g). For details on the transmitter attachment protocol, see Doody et al. (2009).

Radiotelemetry data collection

We tracked turtles once per week during the active season (September to April), and once per month during the inactive period (May to August). Location of individuals was estimated from distances and bearing measurements to known points (e.g., triangulation) when the turtle could not be closely approached (Roe and Georges 2007), or when on land we recorded coordinates by holding a GPS (GPS III Plus, Garmin Corp., Olathe, Kansas) above the turtle. We used ArcGIS (version 9.3.1: ESRI, 2009) to plot locations on habitat maps previously developed by Rees et al. (2009), with corrections using a 2012 aerial photograph.

We calculated several movement behavior variables to compare turtles from natural versus suburban habitats. Home range was estimated by the minimum convex polygon (MCP) method, which describes the size of the area traversed by each turtle. Turtles were included in home range analysis if they had at least 30 locations during the active season (Sep - Apr) (Plummer and Mills 2000; Donaldson and Echternacht 2005), as home ranges estimates are sensitive to sample size (Seaman et al. 1999). Linear range length was calculated as the Euclidean distance between the two most widely spaced locations. Movement distance was also calculated, measured as the sum of Euclidean distances among sequential radio-locations for each turtle. In addition, we calculated the number of different wetlands each turtle used, and the number of times each turtle moved between these wetlands, both metrics representing an index of inter-patch movement extent and frequency (Roe and Georges 2007; Rees et al. 2009). We also assessed if turtles were in an aquatic or terrestrial habitat at each location, and assessed the proportion of total locations in terrestrial habitats for each individual. Movement behavior was estimated using Hawth's Tools extension for ArcGIS (version 9.3.1: ESRI 2009).

Data analysis

Statistical analyses were performed with SPSS (Version 21) and the program MARK version 7.1 (White and Burnham, 1999). The assumptions of normality and homogeneity of variances

were checked by analysis of residuals 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.

To compare MCP, range length, distance moved, number of wetlands used, and proportion of time spent in terrestrial habitats between nature reserve ($N = 19$) and suburban ($N = 13$) turtles, we used an independent-samples T-test. We log (ln) transformed MCP, and proportion of terrestrial locations, to better meet the assumptions. We used a Mann-Whitney test to compare inter-wetland movements of turtles from natural and suburban sites. We did not consider the use of analysis of covariance for the comparisons above as carapace length was similar between turtles from nature reserve and suburbs (Mann-Whitney U test: $U = 243.5$, $z = -0.76$, $df = 47$, $p = 0.44$).

We calculated road density around the suburban ponds and correlated it with turtle deaths on roads to help in identifying factors contributing to hotspots of mortality. We initially created 700 m buffers around the suburban ponds with ArcGIS (version 9.3.1: ESRI 2009). This distance was based on typical movement distances of *C. longicollis* determined from previous studies in the region (Rees et al. 2009; Roe and Georges 2007; Roe et al. 2009). Then we calculated road density (km of road/km²) within each buffer.

To assess if turtle movements were associated with environmental variables, we performed multiple linear regression, using weekly movements from each turtle (response variable), location (nature reserve or suburb), season (Summer 2012, Fall 2012, Winter 2012, Spring 2012, Summer 2013, Fall 2013), daily maximum temperature (°C), and rainfall (mm) as the predictor variables. We used weekly movement distances in regression models, and the mean value of daily maximum temperature per week and the rainfall accumulated during the week period. Weekly movements were log (ln) transformed to better meet assumptions. For this analysis, we used the locations of 20 females in the nature reserve, and 26 females in the suburbs.

We used known fate models in the program MARK (White and Burnham, 1999) to evaluate differences in survivorship between sites. Time periods when radio-signals could not be detected (i.e. transmitter failure or undetected long-distance movements) were censored from the analysis. If a turtle died during the study, we fitted the transmitter to another turtle from the same population and entered the data as “staggered” in its capture history (Cooch and White 2014). Akaike information criterion (AIC) were used to rank candidate models; if competing models had AIC values of <2.0 , they were considered as having some support. Maximum likelihood survival probabilities were estimated over monthly intervals. Annual survival probability was estimated by using the monthly probability from the real function parameters and raised to a 12 (months) exponent. We started with a fully-saturated model in which survival probability was dependent on site, time, and their interaction, then we fitted a series of reduced-parameters models.

Results

Water levels

Water levels fluctuated more in nature reserve ponds relative to those in the suburbs (Fig. 1). Nonetheless, ponds from neither site experienced significant drops in water level, and all wetlands remained flooded throughout the study period.

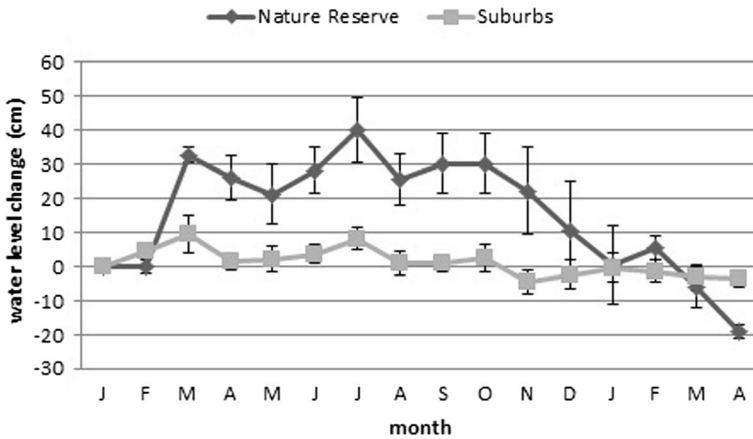


Fig. 1 Water level fluctuation relative to the beginning of the study (January 2012) in nature reserve and suburban ponds, Australian Capital Territory, Australia. Values are mean \pm 1 standard error

Movements

We radiotracked 20 turtles from the nature reserve and 28 turtles from the suburbs. Numbers were higher for suburban turtles owing to mortalities and subsequently radio attachments for other females from the same sites. Initial carapace length and mass for nature reserve turtles ($N = 20$) were 199.8 ± 19 mm (mean \pm standard deviation) and 909.9 ± 229.9 g, respectively, and for suburb turtles ($N = 28$) were 203.9 ± 20 mm and 926.7 ± 242.4 g, respectively. Transmitters were 1.1–3.8 % of the turtle's initial body mass. We radiotracked turtles for an average of 262 ± 18 (7–364) days, and gathered 37 ± 3 (1–52) locations for each turtle. The majority of locations were recorded by triangulation as opposed to direct record above the turtle, owing to a small proportion of turtles found in terrestrial locations (Table 1). There was no difference between turtles from nature reserve and suburban sites in several metrics, including MCP ($t(30) = 0.34$, $p = 0.74$), range length ($t(30) = -0.39$, $p = 0.70$), number of wetlands used ($t(30) = 0.98$, $p = 0.33$), proportion of terrestrial locations ($t(4) = 1.52$, $p = 0.20$) and inter-wetland movement frequency (Mann-Whitney U test: $U = 107.5$, $Z = -0.64$, $df = 31$, $p = 0.52$) (Table 1). However we observed differences in distances moved, with suburban turtles moving longer distances than those on the nature reserve ($t(30) = -2.84$, $p = 0.008$) (Table 1). No radiotracked turtles were observed in prolonged aestivation (several months, Roe et al. 2008; Rees et al. 2009) on land in any of the study sites. The few observations of turtles in terrestrial habitats were of those walking along the predator-proof fence and two individuals in the nature reserve that remained buried under litter for 7–14 days next to the fence (7.6 m and 10 m away) before returning to water. One nature reserve turtle was located outside of the fence and it was possibly moved by a visitor (Fig. 2).

Weekly movement distances were positively correlated with daily maximum temperature and rainfall, but these two variables explained only 4 % of the variation ($F_{4, 1738} = 18.45$, $r^2 = 0.04$, $p < 0.001$) (Predictor variables: daily maximum temperature: Beta = 0.19, $p < 0.001$; rainfall: Beta = 0.08, $p < 0.001$). Location (Beta = 0.02, $p = 0.42$) and season (Beta = 0.04, $p = 0.07$) had no influence on movements.

Table 1 Spatial ecology and movements of female *Chelodina longicollis* in nature reserve and suburban habitats comparing a previous (2006–2007) and the present study (2012–2013) in Gungahlin, Australian Capital Territory, Australia. Values expressed in Mean ± SE (range)

		MCP ^b (ha)	Range length (Km)	Distance moved (Km)	Wetland used (n)	Inter-wetland movements (n)	Proportion of terrestrial locations
2006 – 2007 ^a (Drought)	Nature reserve	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)	0.28 ± 0.76* (0–0.77)
	Suburbs	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)	0 ± 0
2012–2013 (Wet)	Nature reserve	17.2 ± 4.2 (0.3–70.6)	0.8 ± 0.1 (0.1–1.5)	3.7 ± 0.3 (1.2–5.5)	1.9 ± 0.1 (1–3)	1.3 ± 0.2 (0–3)	0.01 ± 0.004 (0–0.06)
	Suburbs	11.9 ± 3.7 (1.6–53.5)	0.9 ± 0.1 (0.4–2.1)	4.9 ± 0.3* (3.0–6.4)	1.6 ± 0.2 (1–3)	1.7 ± 0.7 (0–7)	0.001 ± 0.01 (0–0.02)

*indicate difference between groups during each study period

^a Rees et al. 2009

^b Minimum convex polygon

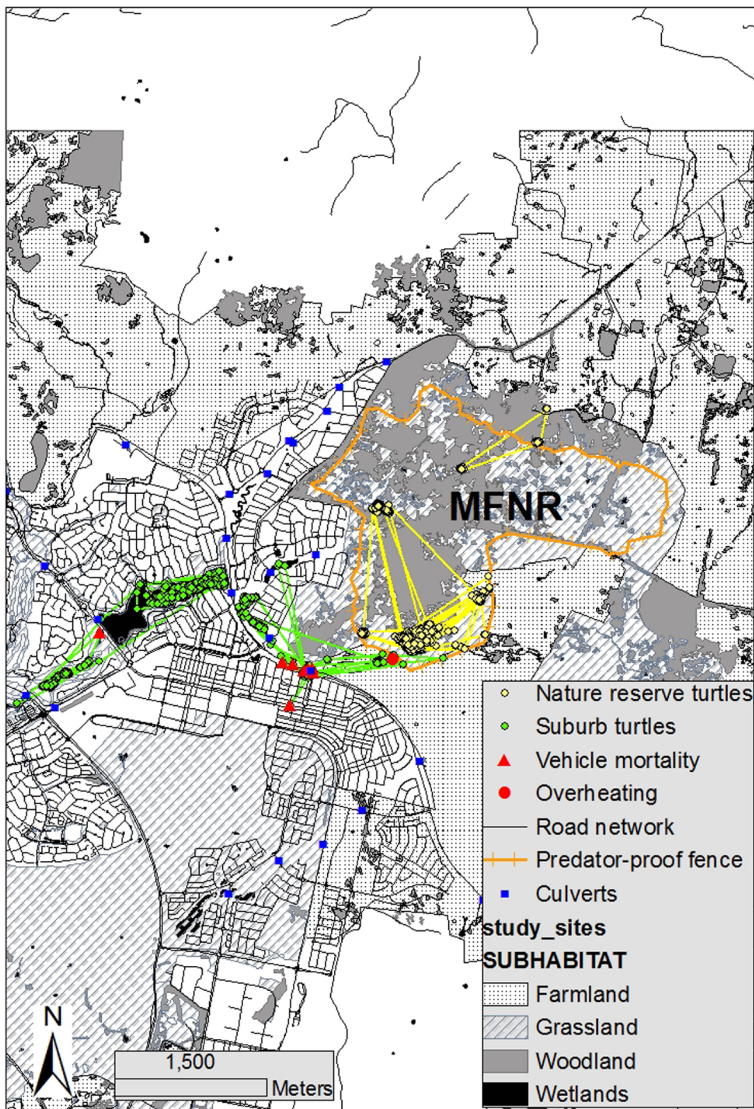


Fig. 2 Movements and mortality of female *Chelodina longicollis* monitored by radiotelemetry in the Gungahlin suburb during wet period, Australian Capital Territory, Australia. (MFNR - Mulligans Flat Nature Reserve)

Survivorship

The model with the most support included only variation between sites, with no support for time-dependent models (Table 2). Estimated survivorship probabilities over the duration of the study were 1.00 ± 0.0 for nature reserve turtles and 0.59 ± 0.1 ($0.38\text{--}0.77$) for suburban turtles, which equates to an annual survivorship of 0.67 ± 0.01 ($0.46\text{--}0.81$) for suburban turtles. Of the nine mortalities for suburban turtles, 89 % were due to vehicular collision, while only one (11 %) was due to overheating (Fig. 2). Most of the turtle mortalities caused by vehicle collisions (75 %) occurred in the vicinity of one pond in the suburbs (Fig. 2).

Table 2 Models of survivorship probability (S) of female *Chelodina longicollis* between sites over monthly time intervals, Australian Capital Territory, Australia

Model	AICc	Δ AICc	Weight	Model Likelihood	N	Deviance
S (site)	83.21	0.00	0.996	1.000	2	19.20
S (.)	94.72	11.52	0.003	0.003	1	32.73
S (time)	106.66	23.45	0.000	0.000	16	13.70
S (time x site)	127.87	44.66	0.000	0.000	32	0.00

Discussion

Our investigation demonstrated the value of a repeated longitudinal study for turtle populations, where we observed their response to both natural (rainfall) and anthropogenic (urbanization) environmental changes over a period of eight years. The most important findings relative to managing turtle populations in suburban environments are as follows. First, the environmental challenges and threats of urbanization may change relatively quickly as suburban areas expand, which can significantly influence important population vital rates, such as survival. This is of broader conservation significance because suburban environments are rapidly growing worldwide, presenting accelerating challenges to suburban wildlife, some of which might not be able to cope and persist. Second, turtle behaviors in and around suburban areas are influenced by environmental conditions in potentially interactive ways, as the behavior of suburban turtles was largely similar in drought and wet periods, while several critical aspects of behavior changed dramatically for nature reserve turtles according to drought/wet cycles. Urban managers and wildlife biologists should realize the dynamic nature of human and wildlife interactions in developed areas, and that longer-term or repeat studies may be necessary to understand wildlife population responses and to mitigate negative impacts.

We observed a significant reduction in annual survivorship for suburban female turtles compared to their nature reserve counterparts during the 2012–2013 wet period, a finding in contrast with the 2006–2007 study in the same system during drought, where survival was similar between sites (Rees et al. 2009). Although survivorship estimates in 2006–2007 included males, sex was not a significant predictor variable in models (Rees et al. 2009). Annual survivorship dropped from 88 % in the 2006–2007 period to 67 % in the 2012–2013 period, a reduction of 21 %, while survival increased nearly 5 % in the nature reserve over the same time frame (Rees et al. 2009). It is possible that differences in rainfall explain such increased mortality in the suburbs. For instance, *C. longicollis* overland movements increase during rainfall (Roe and Georges 2008b; Roe et al. 2008), potentially exposing turtles to vehicular mortality and other threats. Indeed, female turtles moved longer total distances in the nature reserve and suburbs during the wet period of 2012–2013 compared to drought of 2006–2007 (Table 1), but two metrics that better reflect frequency of overland movements (number of wetlands used and frequency of inter-wetland movements) were similar between wet and dry conditions (Table 1). It is also possible that terrestrial nesting excursions were more frequent during wet conditions, a behavior that exposes female turtles to increased risk of mortality on roads (Steen and Gibbs 2004; Aresco 2005a; Steen et al. 2006). Reproduction in *C. longicollis* is tightly correlated with rainfall, with fecundity and percentage of gravid females highest during wet conditions (Kennett and Georges 1990). However, we did not

track turtles with high enough frequency to provide details of such overland nesting movements to confirm this as the primary cause of terrestrial movement and subsequent mortality.

An additional explanation for the drop in survivorship for suburban turtles between study periods is rapid changes in human population and associated infrastructure, including heavier road traffic volumes. Human populations increased 79 % from 2006 to 2011 in the expanding Gungahlin suburbs (2006: 13,381 people; 2011: 23,985 people) (Australian Bureau of Statistics), and traffic volume on a major road bisecting our study area increased 76 % over a similar time frame (3086 cars/day to 5435 cars/day; Territory and Municipal Services). Only one radiotracked turtle was killed by a vehicle in the 2006–2007 study period (Rees et al. 2009), compared to eight individuals killed by vehicles in the 2012–2013 period. We propose that the heavier traffic volumes increased the probability of a turtle being killed during road crossings. Numerous studies have modeled or demonstrated increased risk of vertebrate mortality as traffic volume increases (Hels and Buchwald 2001; Mazerolle 2004), including for turtles (Gibbs and Shriver 2002; Aresco 2005b). The survival estimates of suburban turtles in our study are lower than *C. longicollis* elsewhere (Roe et al. 2009), and compared to other freshwater turtles (Shine and Iverson 1995). It would be expected that this reduction in annual survivorship, if chronic, will negatively affect populations of *C. longicollis* in our system over the long-term.

Despite evidence that freshwater turtles are at high risk of road mortality (Gibbs and Shriver 2002; Marchand and Litvaitis 2004; Aresco 2005a), and tend to have reduced survivorship in urbanized landscapes (Eskew et al. 2010a, b), we previously hypothesized that the unexpectedly low mortality rates observed in the 2006–2007 study period were in part owing to the availability of vegetated drainage lines and under-road “box” culverts that facilitated turtle movements while avoiding threats (Rees et al. 2009). Given the new evidence from the 2012–2013 study period, turtles in our system do not always use under-road culverts when available and are thus susceptible to road mortality. However, mortalities were not spread evenly across the suburban landscape, indicating the presence of mortality hotspots. Road densities did not vary significantly among ponds used by suburban turtles (range 16–20 km/km²), but nearly 75 % of road mortalities were near one pond, approximately 35 m away from a major road (Fig. 2). This pond is in close proximity to the nature reserve, and along a major travel corridor for turtles moving between suburban lakes and nature reserve wetlands (Ferronato et al. 2014). However, that there is an under-road culvert at this mortality hotspot suggests these turtles may have been seeking higher ground nesting locations, as *C. longicollis* often follows natural drainages when moving between wetlands, which would have taken them through the culvert instead. Nonetheless, even without a detailed understanding of the context and motivation for these terrestrial movements, the identification of road mortality hotspots is a first step towards mitigating the impact of roads on animal populations on rural highways (Langen et al. 2009; Cureton and Deaton 2012; Crawford et al. 2014) and more heavily trafficked urban areas (Ramp et al. 2006; Wotherspoon and Burgin 2011).

The importance of connectivity for both population and community level resilience for freshwater turtles has been identified in both suburban (Guzy et al. 2013) and agricultural landscapes (Bowne et al. 2006). Our repeat study demonstrates the movement dynamics of *C. longicollis* between natural and suburban ponds and from ponds to terrestrial nesting sites, along with its potential consequences if landscapes become fragmented by inimical elements or barriers. Turtles in our system respond to fluctuating resources by evacuating drying wetlands, most of which are found on the nature reserve, during drought (Rees et al. 2009; Roe et al. 2011), only to move back to nature reserve ponds during wet conditions (Ferronato

et al. 2014), increasing risks from vehicular mortalities or interactions with conservation fences (Ferronato et al. 2014). Access to and from suitable terrestrial nesting sites must also be maintained (Steen et al. 2012). Consequently, land managers need to consider the ecology of species when planning new areas of development and we suggest that landscape connectivity along the natural to suburban continuum, allowing travel among water bodies and to terrestrial nesting and aestivation sites must be maintained to avoid mortalities of vagile vertebrate species. Such movements can be facilitated by use of culverts and partial fencing to direct turtle movements (Dodd et al. 2004; Aresco 2005b) in identified mortality hotspots, or construction of artificial nesting sites in safe areas, though the effectiveness of such applications should be tested and tailored to the behavior of the target species (Paterson et al. 2013; Baxter-Gilbert et al. 2015).

By conducting a repeat study in the same system, we were able to examine how turtle behavior is influenced by dynamic environmental factors, such as rainfall, and how behavioral responses depend on site-specific conditions, particularly urbanization. During drought, most turtles on the nature reserve entered prolonged aestivation (up to 10 months) in terrestrial habitats when ponds dried during 2006–2007 (Rees et al. 2009). In contrast, during the wet period of 2012–2013, there were no periods of extended refuge on land except for relatively short periods (less than 14 days) when turtle's movements were interrupted by the predator-proof fence. Additionally, turtles in the nature reserve moved longer distances and used larger areas in the wet period compared to drought (Table 1). Interestingly, suburban turtles behaved similarly regardless of the dry/wet cycles, as turtles did not aestivate on land during drought or wet conditions, instead remaining active and vagile through the suburban landscape (Table 1). This is possibly a result of the hydrological stability of suburban ponds owing to increased runoff, irrigation inputs, and intentional manipulation (Rees et al. 2009). The dissimilarity in behavior between wet and dry cycles, at least in natural habitats, reinforces the idea that terrestrial aestivation in *C. longicollis* is a behaviorally plastic response influenced by wetland drying and the proximity to other permanent wetlands (Roe and Georges 2008a).

Wildlife inhabiting urban areas face the challenge of dealing with patchy habitats, low connectivity and increased risks of mortality (Blair and Launer 1997; McKinney 2002; Aresco 2005a; Steen et al. 2006). Although many studies have provided guidance and successful management strategies to protect vertebrates against threats such as roads (Yanes et al. 1995; Clevenger et al. 2001; Dodd et al. 2004; Aresco 2005b), continued monitoring is essential to understand responses of animals to urban challenges in space and over time (Cosentino et al. 2010). Many cities worldwide, especially in developing countries, will likely continue to grow in human population and associated infrastructure, such as roads and traffic (World Resources Institute et al. 1996; Gakenheimer 1999; Schafer and Victor 2000). In addition, the effects of climate change might play a role in influencing turtle behavior as future climate scenarios should lead to extreme hydrological conditions, with greater frequency of drought and flood events (Vörösmarty et al. 2000; Hughes 2003; Dudgeon et al. 2006). Managers and conservationists need to be alerted to how such changes can affect native wildlife. We were able to demonstrate that temporal changes in suburban conditions, such as increase in traffic, could lead to a decrease in survivorship of a vertebrate species. Additional research that yields insights on the causes and mechanisms of mortality in suburban animals will help to assist managers with implementing development projects that are more compatible with native species conservation (Shochat et al. 2006).

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