The Journal of Wildlife Management 75(7):1544–1552; 2011; DOI: 10.1002/jwmg.219

Research Article

Suburbs: Dangers or Drought Refugia for Freshwater Turtle Populations?

JOHN H. ROE,[1] *Department of Biology, University of North Carolina, Pembroke, NC 28372, USA*
MARTHA REES, *Institute for Applied Ecology, University of Canberra, Canberra, ACT 2601, Australia*
ARTHUR GEORGES, *Institute for Applied Ecology, University of Canberra, Canberra, ACT 2601, Australia*

ABSTRACT Urbanization is one of the most rapidly expanding forms of habitat alteration worldwide. Wildlife differs in their responses to urbanization depending upon species and site-specific factors. We used capture-mark-recapture to examine the abundance, population demographics, growth, and movements of the eastern long-necked turtle (*Chelodina longicollis*) in Australia over 1 year in a suburban environment and an adjacent nature reserve during drought. Contrary to expectations, sex ratios, injury incidence, and frequency of juvenile size classes did not differ between turtles in the suburbs and the nature reserve. Moreover, turtles in the suburbs were nearly 3 times more abundant, grew 5 times faster, and had populations comprised of more adults in the larger size classes than nature reserve populations. These findings, together with net movements from the nature reserves into the suburbs, suggest that suburban water bodies were the higher quality habitat, effectively buffering turtles from temporal fluctuations in environmental conditions during drought. However, reserve managers and urban planners need to recognize that suburban water bodies have the potential to attract turtles from nearby reserves during drought, and that even low levels of persistent mortality during these travels across reserve boundaries may have consequences for populations of long-lived vertebrates.

KEY WORDS Australia, *Chelodina longicollis*, ecological trap, estivation, herpetofauna, population demographics, population sink, reptile, road mortality, urbanization.

Urbanization is one of the most rapidly expanding forms of habitat alteration worldwide (Adams et al. 2006, Shochat et al. 2006). Urbanization can have profound impacts on wildlife populations, though the direction and magnitude of response depends in part upon the type and degree of habitat alteration and intrinsic attributes of the species in question. For instance, roads are a prevalent form of urban habitat modification that can affect mobile animals more than sedentary ones (Manserg and Scotts 1989, Bonnet et al. 1999, Carr and Fahrig 2001, Roe et al. 2006), while species with a high capacity for reproduction may be more resilient to additional mortality from urban hazards than those with life-history strategies associated with long lifespan (Jaeger et al. 2005, Row et al. 2007). Sealed surfaces, buildings, exotic vegetation, or managed green spaces in urban areas can negatively impact some species, yet these same habitat modifications can be neutral to or even benefit others by providing suitable habitat, augmenting resources, or modifying inter-specific interactions, trophic dynamics, and local climate (Germaine and Wakeling 2001, Marzluff 2001, Parris and Hazell 2005, Shochat et al. 2006).

Turtles as a group may respond in a number of ways to urbanization. Some species can persist or even thrive in modified habitats such as gardens, stormwater drainage lagoons, golf course ponds, and other urban water bodies (Conner et al. 2005, Burgin and Ryan 2008, Plummer et al. 2008, Ryan et al. 2008, Eskew et al. 2010). In some respects these disturbed habitats can be of high quality, as turtles using these habitats may be able to grow faster, mature at an earlier age, and have higher fecundity than those inhabiting less developed areas (Lindemann 1996, Budischak et al. 2006). However, considering the vulnerability of turtles to road mortality, (Gibbs and Shriver 2002, Marchand and Litvaitis 2004, Steen and Gibbs 2004, Aresco 2005*a*), subsidised predators (Marchand et al. 2002, Harden et al. 2009), and other disruptive human activities (Garber and Burger 1995, Brisbin et al. 2008), populations of many species may ultimately be extirpated from these areas or restricted to small habitat remnants (Rubin et al. 2001, Edwards et al. 2004).

Another potentially problematic aspect of urban landscape modification is the creation of attractive but low quality habitat. Water bodies are often integrated into urban design or created for stormwater retention, storage reservoirs, recreation, and even for wildlife habitat and aesthetic purposes (Tilton 1995). Wildlife can be attracted to these sites, but if these water bodies are of low quality, or if animals experience high mortality while traveling to them, these habitats could potentially act as mortality sinks or ecological traps (Pulliam 1988, Schlaepfer et al. 2002).

Received: 26 August 2009; Accepted: 27 February 2011;
Published: 2 August 2011

---

[1] *E-mail: john.roe@uncp.edu*

In a previous radio-telemetry study, we determined that the eastern long-necked turtle (*Chelodina longicollis*) inhabiting suburban areas suffered only a small (and statistically insignificant) increase in adult mortality compared to those in adjacent nature reserves during a 1-year investigation (Rees et al. 2009). However, no examination of the broader population-level implications or quality of available habitats for urban eastern long-necked turtles has been conducted. Given the tendency of eastern long-necked turtles to move overland between wetlands and traverse large areas, and to estivate and nest terrestrially as part of their annual or seasonal cycles (Stott 1987; Roe and Georges 2007, 2008*a*, *b*; Roe et al. 2008), we suspected turtles would be consistently exposed to urban hazards each year. Given their life history traits associated with long lifespan (Parmenter 1985, Roe et al. 2009), we hypothesized that even small levels of chronic mortality would accumulate and negatively impact eastern long-necked turtles at the population level over time (Congdon et al. 1993, 1994). To this end, we assessed whether and to what extent urbanization impacted population abundance and demographics of eastern long-necked turtles in a suburban region relative to their counterparts on adjacent reserve lands. Given the propensity of eastern long-necked turtles to travel long distances overland and to successfully navigate to aquatic habitats using scent and visual cues (Graham et al. 1996), we also expected turtles to move between nature reserve and suburban water bodies. Determining the frequency and directionality of overall population emigration and immigration rates would allow for more effective management and mitigation activities at the interface between reserves and urban areas.

STUDY AREA

We studied turtles between September 2006 and November 2007 in water bodies of Gungahlin, a suburb of Canberra, and in adjacent nature reserves of the Australian Capital Territory (ACT), Australia (Fig. 1). Gungahlin was initially established in 1975, though development has continued up to (and throughout) the period of this study. The Gungahlin suburbs were characterized by large areas of residential, industrial, and agricultural development, as well as urban green spaces such as golf courses, urban parks, and sports ovals. There were also many suburban water bodies including two large reservoirs >25 ha, several smaller golf course and stormwater drainage ponds, and a network of streams in the Ginninderra Creek drainage. Two natural areas, Mulligans Flat, and Goorooyaroo nature reserves, bordered the suburbs and consisted of woodlands, grasslands, a number of ponds, as well as the upper tributaries of Ginninderra Creek. The reserves were initially established in 1995, and together formed an area of 1,600 ha and were surrounded by rangeland on the rest of their borders. More detailed descriptions and maps of the study sites are given by Rees et al. (2009).

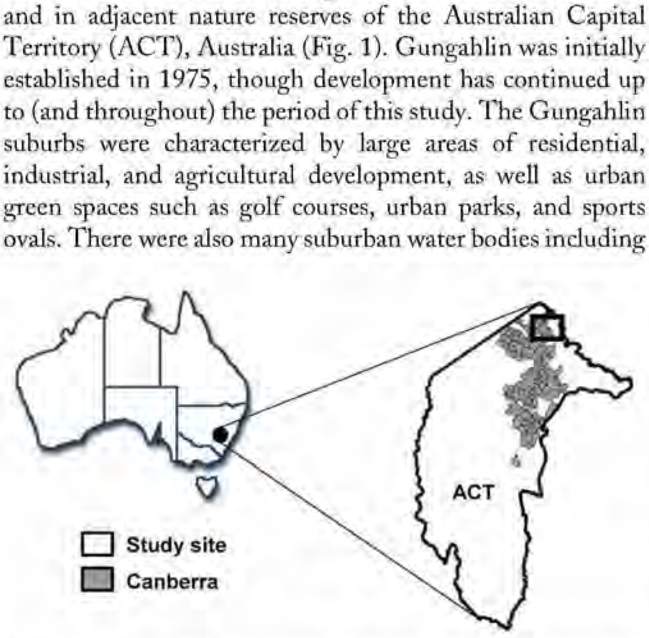

Figure 1. Location of Canberra and the eastern long-necked turtle study area (box in upper right) within the Australian Capital Territory (ACT), Australia, 2006–2007.

METHODS

Environmental Variables

We sampled 19 water bodies (10 suburban and 9 reserve) within a 55 km^2-area along an urban to rural gradient. We measured several environmental variables associated with water bodies, including surface area, maximum depth, pH, conductivity, coverage by emergent vegetation, and relative prey abundance. We measured water depth biweekly using a digital sounder (PS-7; Hondex, Toyohashi City, Japan) and depth gages, and measured dissolved oxygen, pH, and conductivity during each trapping period using a water quality analyzer (Hydrolab Surveyor 4A; Loveland, Colorado). We measured the amount of emergent vegetation during summer by setting up equally spaced transects across wetlands and assessing the proportional coverage of surface vegetation along each transect. We estimated standing-crop biomass of prey by sampling each wetland in March 2007. We conducted 4 time-constrained (30 s) searches in each wetland by sweeping a 34 cm × 28 cm dipnet (250 μm mesh) in the littoral zone around available structures (e.g., macrophytes, rocks, and debris) and by agitating the sediment. We stained samples with rose Bengal and preserved them in 10% formaldehyde for later sorting. We placed samples in a sorting tray divided into 16 sections. We removed prey items until 2 min of searching revealed no further items. We stored sorted samples in 90% ethanol, and then dried on absorbent paper for 10 min before weighing (+0.01 g). We only recorded potential prey items if they occurred in the diet of eastern long-necked turtle (see Chessman 1984, Georges et al. 1986).

We also measured several landscape metrics within a 500-m radius of each wetland. We chose a 500-m radius because this distance encompassed the distance eastern long-necked turtles would typically travel from wetlands for terrestrial activities (Roe and Georges 2007, Rees et al. 2009). Landscape metrics included road density and proportional coverage by several habitat classes including grassland, woodland, farm and rangeland, urban infrastructure (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), and water body (stock dams, stormwater drainage ponds, reservoirs, streams, and wetlands). We digitized habitat polygons from aerial photographs using a Geographic Information System (ArcView 3.1; Environmental Systems Research Institute, Redlands, CA). We also determined distance to nearest road for each wetland. The ACT Planning and Land Authority provided spatial data for the road network. We chose these local wetland and landscape environmental variables either because of their demonstrated importance to freshwater turtle populations, impacts on turtle prey, or their inclusion in previous studies examining urban impacts on turtle populations (Marchand and Litvaitis 2004, Steen and Gibbs 2004).

Turtle Sampling

We sampled the same 19 water bodies for turtles from September 2006 through November 2007. We captured turtles using crab traps baited with liver and sardines set for 48-hr periods on 4 separate occasions: September and November 2006 and January and October 2007. One nature reserve and 1 suburban water body had dried and could not be trapped in January. On all other sampling occasions, 5 traps were set in each water body, 3 of which were modified with a snorkel that allowed traps to sit on the bottom in up to 2 m of water while allowing turtles to surface for air, and 2 unmodified traps were set in shallow water (<0.5 m). We checked traps every 24 hr. Due to low recapture rates (see "Results" Section) and evidence from concurrent radio-telemetry (Rees et al. 2009), we suspected that many turtles had moved to nearby unsampled water bodies. To bolster recaptures for growth and movement estimates, we sampled an additional 6 water bodies (2 suburban and 4 nature reserve) opportunistically using traps and hand capture techniques.

Upon initial capture, we marked each turtle by filing notches into a unique combination of marginal scutes on the carapace using a hacksaw or scissors. We measured the mass of each turtle on a top-loading digital balance and measured straight-line carapace length (CL) and midline plastron length (PL) using callipers. Turtles with a CL < 145 mm were classified as juveniles. We only determined sex for turtles with a CL > 145 mm by examining the plastron curvature, as sex cannot be reliably determined from external morphology below this size (Kennett and Georges 1990). We classified males with CL > 145 mm and females with CL > 165 mm as adults, while females between CL 145.0 mm and 164.9 mm were classed as subadults (Kennett and Georges 1990). We also noted injuries to the shell and limbs. We immediately released turtles at their site of capture following measurements. This research was approved by the University of Canberra Committee for Ethics in Animal Experimentation (CEAE 04/6), and the Environment ACT (LT2006222).

For all recaptured animals, we measured growth as the change in CL between captures. We calculated growth rates by dividing change in shell length by the fraction of the 6-month activity season (15 Sept–15 Mar) elapsed between initial and final captures (Kennett and Georges 1990, Roe and Georges 2008*a*). We also assessed whether recaptured individuals had moved between sites since their most previous capture.

Statistical Analysis

We performed statistical analyses with SPSS Version 16.0 (SPSS Inc., Chicago, IL), SAS Version 9.1 (SAS Institute, Cary, NC), and the Program MARK version 4.2 (White and Burnham 1999). We examined the assumptions of normality and homogeneity of variances where appropriate, and when data failed to meet these assumptions we transformed it to approximate normal distributions and equal variances. We accepted statistical significance at the $\alpha < 0.05$ level unless specified otherwise.

Where the 500-m radius buffer from a water body included another study water body, we combined them into a single buffer. In these cases, we calculated a single mean value for all turtle and environmental variables. We compared environmental variables within the water bodies between nature reserve and suburban sites using analysis of variance (ANOVA). We $\log_{10}$-transformed surface area, maximum depth, prey biomass, pH, dissolved oxygen, and conductivity and arcsin square-root transformed proportion emergent vegetation prior to analysis. In the 500-m buffers, we compared proportional landscape coverage by woodland, grassland, and wetland between sites using ANOVA, and compared road density, proportional coverage by urban, urban green space, and farm and rangeland between sites using Mann–Whitney *U* tests. In the above analyses, we arcsin transformed all proportions. Finally, we compared distances to the nearest road between sites using ANOVA on $\log_{10}$ distances.

In the 19 core wetlands where we were able to standardize trapping, we compared turtle relative abundance and proportion females captured between nature reserve and suburban water bodies using ANOVA, with $\log_{10}$ total number of turtles captured and arcsin square-root transformed proportion females as the dependent variables, and site as the independent variable.

To determine whether and to what degree sampling bias influenced comparisons of population metrics, we used Cormack–Jolly–Seber (CJS) open population capture–recapture models in Program MARK to derive and compare estimates among groups (adult male, adult female, and juvenile), between sites (reserves and suburbs), and over time (sampling occasions). Based on evidence from concurrent radio-telemetry of eastern long-necked turtles in the same area (Rees et al. 2009), we started with models where survivorship (Φ) was held constant but capture probability (ρ) was allowed to vary over time, among groups, and between sites. We then fit a series of reduced parameter models and ranked them based on Akaike's Information Criterion (AIC). If competing models had AIC values of ≤ 2.0, we considered them as having some support (Lebreton et al. 1992). We assessed the fully saturated model's adequacy to describe the data using a bootstrap goodness-of-fit test with 500 simulations and an overdispersion parameter ($\hat{c}$) was derived by dividing the model deviance by the mean of simulated deviances (Cooch and White 2004). If there was evidence for overdispersion ($\hat{c} > 1$), we adjusted the models with the derived $\hat{c}$ to improve model fit and calculated a quasi-likelihood estimator, $QAIC_c$ (Burnham and Anderson 1998).

In the wider group of 25 wetlands, we determined if injury incidence differed between the nature reserves and suburbs using a Fisher's exact test. Next, we performed a chi-square test using the PROC FREQ procedure in SAS to examine overall differences in the size-frequency distributions between suburban and nature reserve sites, with the null hypothesis of equal frequency between sites for all size class groups. We followed the overall test with a series of chi-square tests to determine where specific differences existed. We lowered significance values for this series of comparisons to $\alpha < 0.004$ using the Dunn–Sidak correction. To assess whether growth rates differed between sites, we used analysis of covariance (ANCOVA), with $\log_{10}$ growth rate as the dependent variable, site as the independent variable, and $\log_{10}$ initial CL as a covariate.

RESULTS

Environmental Variables

Overlap of the 500-m radius buffers occurred for 4 wetland pairs (2 in reserves and 2 in suburbs), reducing the number of independent study sites to 7 water bodies (or water body groups) in the nature reserves, and 8 in the suburbs. The surface area, maximum depth, coverage of emergent vegetation, prey abundance, and dissolved oxygen did not differ between suburban and nature reserve wetlands (Table 1). The only water body variables to differ between sites were conductivity and pH, both of which were higher in suburban water bodies (Table 1). Vegetation in suburban water bodies was dominated by the sedges *Typha orientalis*, *Eleocharis acuta*, *Scirpus validus*, and *Phragmites australis* and the waterweeds *Vallisneria gigantea* and *Potamogeton tricarinatus*. Species in the reserves were comprised of sedges *Typha orientalis* and *Eleocharis acuta* and the waterweeds *Potamogeton tricarinatus* and *Myriophyllum crispatum*.

Suburban water bodies were nearer to roads, and surrounded by higher road densities and land in urban infrastructural development and green space (Table 1). The landscapes surrounding reserve water bodies were comprised of higher proportions of woodland and grassland habitats (Table 1). The sites did not differ in the relative amount of farm and rangeland or wetland habitat in the surrounding landscape (Table 1).

Turtles

The eastern long-necked turtle was the only species of turtle encountered in our sampling. We captured a total of 546 turtles from the 19 core wetlands where sampling was standardized. Relative turtle abundance was 2.9 times higher in suburban water bodies compared to those in the nature reserves (Table 1). However, there was no difference in the proportion of females between suburban and nature reserve water bodies (Table 1).

The model with capture probability constant over time, among groups, and between sites had the most support (Table 2). Models with variable capture probability between adults and juveniles, and among adult male, adult female, and juveniles also had some support (Table 2). Models with constant capture probability between suburbs and nature reserves had 2.7 times more support than models with variable capture probability between sites (Table 2). Capture probabilities were higher for adults than juveniles at both sites (Table 3).

We made 787 captures of 686 individual turtles in the wider group of 25 wetlands. Size–frequency distributions differed between the suburbs and nature reserves (overall $\chi^2_{10} = 75.8$, $P < 0.001$), with the only significant disparities occurring in the adult size classes (Fig. 2). Turtles 120.0–

Table 1. Comparison of eastern long-necked turtle captures and local wetland and landscape variables within a 500-m radius of 7 wetlands on a nature reserve and 8 wetlands in the suburbs of the Australian Capital Territory, Australia, 2006–2007.

Variable	Reserve		Suburbs		Test statistic	P
	$\bar{x}$	SE	$\bar{x}$	SE		
Turtle captures						
Turtles (n)	15.1	4.1	44.2	12.6	4.72^{a}	0.049*
Female (%)	53.5	9.4	66.9	3.7	1.82^{a}	0.200
Local wetland variables						
Prey abundance (g)	3.3	0.8	2.6	0.6	0.01^{a}	0.943
Surface area (ha)	0.7	0.49	1.15	0.48	1.95^{a}	0.188
Maximum depth (m)	1.84	0.28	1.81	0.32	0.11^{a}	0.750
Dissolved oxygen (mg/L)	10.2	0.6	10.5	0.5	0.05^{a}	0.829
Conductivity (μS/cm)	76	13	485	89	32.39^{a}	<0.001**
pH	5.8	0.1	6.5	0.1	10.12^{a}	0.008*
Emergent vegetation (%)	46.1	14.8	54.7	13.9	0.03^{a}	0.862
Landscape variables						
Road density (km/km^2)	0.0	0.0	7.6	1.6	−3.42^{b}	<0.001**
Distance to road (m)	1,060	173	142	60	26.07^{a}	<0.001**
Urban (%)	1.2	1.2	42.6	10.6	−3.05^{b}	0.001*
Urban green space (%)	0.0	0.0	5.7	1.8	−2.41^{b}	0.040*
Farm and rangeland (%)	10.1	6.4	22.1	14.5	−1.00^{b}	0.397
Grassland (%)	52.2	7.7	21.7	5.8	9.61^{a}	0.008*
Woodland (%)	35.3	7.0	4.7	1.7	28.50^{a}	<0.001**
Wetland (%)	1.3	0.6	3.2	1.2	3.23^{a}	0.095

[a] Analysis of variance tests.

[b] Mann–Whitney U tests.

[*] Significance at $\alpha < 0.05$.

[**] Significance at the Dunn–Sidak adjusted $\alpha < 0.006$.

Table 2. Models comparing variation in capture probability (ρ) over time, between sites (suburbs, nature reserves), and among groups (adult male, adult female, juvenile) for eastern long-necked turtles in the Australian Capital Territory, Australia, 2006–2007. Survivorship (Φ) was held constant in all models. Models were compared and ranked using a quasi-likelihood Akaike's Information Criterion (QAIC$_c$) estimator corrected for model overdispersion.

Model	QAIC$_c$	ΔQAIC$_c$	Weight	Parameters	Deviance
Φ (·) ρ (·)	304.40	0.000	0.342	2	38.94
Φ (·) ρ (group)[a]	304.47	0.063	0.331	3	36.98
Φ (·) ρ (group)[b]	306.20	1.799	0.139	4	36.68
Φ (·) ρ (site)	306.41	2.003	0.126	3	38.92
Φ (·) ρ (site × group)[a]	308.09	3.688	0.054	5	36.53
Φ (·) ρ (site × group)[b]	311.76	7.360	0.009	7	36.10
Φ (·) ρ (time × site × group)[a]	327.34	22.946	0.000	19	26.30

[a] Model considers adult and juvenile as groups.

[b] Model considers adult male, adult female, and juvenile as groups.

134.9 mm PL were more frequent in the nature reserves ($\chi^2_1 = 8.6$, $P < 0.025$), but turtles from 135.0 mm to 164.9 mm PL ($\chi^2_1 > 16.6$, $P < 0.001$) and 165.0 mm to 194.9 mm PL ($\chi^2_1 > 8.2$, $P < 0.025$) were more frequent in the suburbs.

Because juvenile growth rates were considerably higher than adults and growth could only be assessed for 1 juvenile turtle in the suburbs (Table 4), we examined site-specific growth rates for subadults and adults only. We also combined sexes to increase analysis power. Growth rates were more than 5 times higher in suburban water bodies than in the nature reserves (ANCOVA site: $F_{1,59} = 4.011$, $P = 0.050$; CL: $F_{1,59} = 0.728$, $P = 0.397$; site × CL: $F_{1,59} = 3.638$, $P = 0.061$). The marginally significant site × CL interaction reflects decreasing growth rates with increasing size for suburban turtles ($F_{1,40} = 3.95$, $P = 0.054$), but constant and lower growth among a similar size range in the nature reserves ($F_{1,19} = 1.33$, $P = 0.262$; Fig. 3). Intervals between captures were 103.5 ± 49.7 (mean ± SD) days for suburban adults, 138.0 ± 67.5 days for nature reserve adults, 62 days for the 1 suburban juvenile, and 179.8 ± 61 days for the nature reserve juveniles.

Injury incidence did not differ between sites, with 7.8% and 10.9% of turtles from the nature reserves and suburbs, respectively, having injuries to either the shell or appendages ($P = 0.334$). Of the 31 recaptured turtles originally captured on the nature reserve, 3.2% moved into suburban wetlands. None of the 43 turtles from the suburban wetlands were recaptured in the nature reserves.

DISCUSSION

The suburban environment was characterized by many features typically associated with negative impacts on turtle populations including high road densities and extensive residential and industrial development. Turtle populations in similar landscapes often have male-biased sex ratios indicating increased female mortality from nesting forays, altered age class distributions reflecting poor recruitment of young turtles, and a high incidence of injury or mortality from interactions with urban threats such as vehicles or predators (Gibbs and Shriver 2002; Marchand and Litvaitis 2004; Steen and Gibbs 2004; Aresco 2005*a*, *b*). Semi-aquatic turtles that exhibit extensive terrestrial behaviors, like the eastern long-necked turtle, are typically most impacted by urbanization (Gibbs and Shriver 2002, Eskew et al. 2010). Surprisingly, we found evidence suggesting populations responded either neutrally or somewhat positively to suburban development relative to their counterparts on nearby reserve lands. Sex ratios did not differ between suburban and reserve populations, nor did the incidence of injury or frequencies of young age classes. However, turtles in the suburbs were several times more abundant, grew faster, and had populations comprised of more adults in the larger size classes than nature reserve populations. These findings were

Table 3. Probability of capture for adult male, adult female, and juvenile eastern long-necked turtles in suburban and nature reserve water bodies in the Australian Capital Territory, Australia, 2006–2007. Parameter estimates were derived as weighted averages based on their quasi-likelihood Akaike's Information Criterion (QAIC$_c$) values, adjusted for model overdispersion.

	Suburbs		Nature reserves	
Group	$\bar{x}$	SE	$\bar{x}$	SE
Male	0.213	0.069	0.216	0.073
Female	0.220	0.069	0.221	0.073
Juvenile	0.153	0.066	0.160	0.072

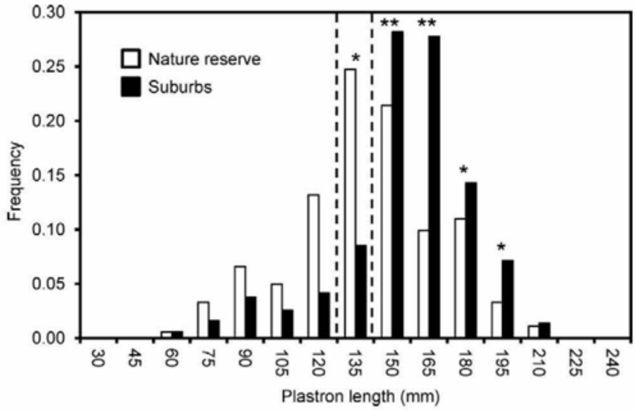

Figure 2. Size frequency distributions of 686 eastern long-necked turtles captured in the nature reserve and suburban water bodies in the Australian Capital Territory, Australia, 2006–2007. Sample sizes for each group are 106 juveniles, 406 subadult and adult females, and 174 adult males. The horizontal dashed lines show sizes at which male and female eastern long-necked turtles become sexually mature, with males maturing at a smaller size than females. Single and double asterisks indicate size classes that differed in frequency of occurrence between sites at the $\alpha < 0.025$ and $\alpha < 0.001$ levels, respectively.

Table 4. Growth rates of juvenile, adult male, and adult female eastern long-necked turtles in the nature reserves and suburbs of the Australian Capital Territory, Australia, 2006–2007.

	Growth rate (mm/yr)[a]			
Group	*n*	$\bar{x}$	SE	Range
Nature reserve				
Juv	8	6.01	1.96	0.0–14.5
M	11	0.23	0.16	0.0–1.7
F	10	0.27	0.11	0.0–1.0
Suburbs				
Juv	1		7.0	
M	13	1.29	0.37	0.0–4.3
F	29	1.28	0.25	0.0–4.6

[a] Based on a growth year spanning the typical activity season (15 Sep to 15 Mar).

not influenced by potential biases in capture probability for different demographic groups between sites or among sampling occasions.

One possible factor contributing to the persistence of the eastern long-necked turtle in this suburban area is its ability to move naturally about the landscape without suffering from excessive mortality. Eastern long-necked turtles normally move overland between many water bodies separated by several hundred meters to meet its resource needs (Stott 1987; Roe and Georges 2007, 2008*a*, *b*; Roe et al. 2009), though data in a concurrent radio-telemetric study indicates that turtles used vegetated drainage lines and under-road culverts when moving about the suburban environment. These features of the developed landscape apparently facilitate turtle movements while limiting mortality from vehicular collisions and other threats (Rees et al. 2009). However, the ability of eastern long-necked turtles to avoid catastrophic mortality during terrestrial sojourns alone cannot explain why they responded somewhat positively to urbanization.

The higher relative abundance, faster growth rates, and larger sizes of adult turtles in the suburbs suggest suburban water bodies were higher quality habitats than those on reserve lands during the study period. A comparison of micro-habitat and chemical features does not indicate any obvious differences that could account for the apparent differences in habitat quality. Most abiotic and biotic variables did not differ between sites, though suburban water bodies were marginally less acidic and more conductive than those on the nature reserves. Conductivity can be higher in urban waterways from runoff of solutes from impervious surfaces (Prowse 1987). High concentrations of dissolved salts could impair freshwater turtle physiology and growth (Dunson 1986, Dunson and Seidel 1986), but the highest conductance levels detected in urban water bodies were not at levels likely to present significant challenges to turtles. Turtles could be indirectly affected by changes in their prey base, but elevated conductivity and acidity tends to degrade larval amphibian and macro-invertebrate communities (Rowe et al. 1992, Walsh et al. 2001, Brainwood and Burgin 2006), the primary prey bases for this species (Chessman 1984, Georges et al. 1986).

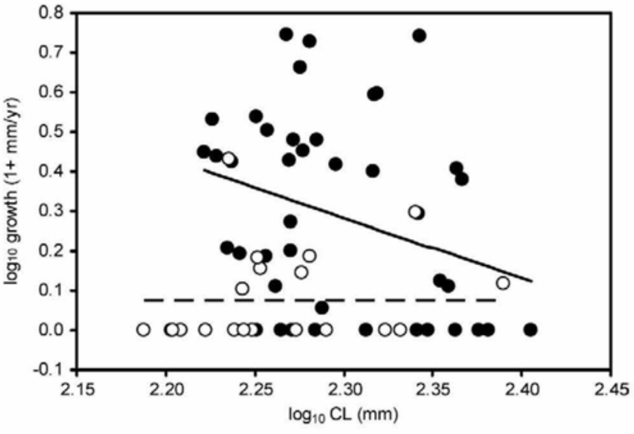

Figure 3. Relationships between growth rate and initial carapace length for adult eastern long-necked turtles in the suburbs (filled circles, solid line) and nature reserves (open circles, dashed line) of the Australian Capital Territory, Australia, 2006–2007.

From the landscape perspective, it is also unlikely that more roads and urban development in the surrounding terrestrial landscape could directly translate into higher habitat quality. In fact, we would expect the opposite (Marchand and Litvaitis 2004, Steen and Gibbs 2004, Aresco 2005*b*). We also suggest that neither site was limited in the availability of nesting sites in the surrounding landscape. Most freshwater turtles prefer to nest in habitats with open canopies due to the thermal benefits of incubation (Janzen and Morjan 2001, Spencer and Thompson 2003). When open-canopied terrestrial habitats of grassland, farm and rangeland, and urban green spaces are combined, nature reserve wetlands had only slightly higher availability of potential nesting habitats (62.3%) compared to suburban wetlands (49.5%). However, while eastern long-necked turtles nest in all open habitats mentioned above (J. Roe, University of North Carolina, unpublished data), it is unclear how nest site quality varies among the different habitat types or between reserve and urban environments. Lack of information on nest site quality is a significant limitation of our study, given that both the availability and quality of nest sites influences freshwater turtle demographics in urban regions (Marchand et al. 2002, Marchand and Litvaitis 2004).

It is also possible that suburban water bodies were more productive via runoff from urban green spaces, roads, and wastewater effluent (Mallin and Wheeler 2000, Lee et al. 2006). Though we did not directly measure nutrient loads, secondary productivity (as measured by standing-crop biomass of macro-invertebrate, and small vertebrate prey items) was similar between water bodies in the suburbs and reserves. Our technique of prey sampling has been demonstrated to capture an adequate representation of the major components of the invertebrate and vertebrate diet of this carnivorous turtle (Georges et al. 1986), as well as to detect considerable variation among water bodies that differ in relative productivity (Roe and Georges 2008*b*). However, we caution that our sampling was limited to a single event that did not account for seasonality, and our index of prey abundance does not account for production which may be higher in some sites but subject to greater predation levels.

Another plausible explanation for the effects on the eastern long-necked turtle is that the suburbs ameliorated the impact of drought to the benefit of turtle populations. The ACT was in drought conditions throughout much of the study period, with severely reduced rainfall for 12 of the 15 months and 32% below average precipitation for the study period (Fig. 4). In spite of these conditions, suburban water bodies remained mostly flooded compared to the drying of the nature reserve sites (Rees et al. 2009). The majority of nature reserve turtles responded to falling water levels by estivating terrestrially for up to 9 months, whereas suburban turtles were able to remain aquatically active (Rees et al. 2009). This prolonged activity period extended foraging opportunities for suburban turtles by several months over their counterparts on the nature reserves, offering perhaps the most likely explanation for the faster growth rates, larger adult body sizes, and higher abundances.

Net movement rates of turtles from nature reserve to suburban water bodies were low, but movement timing and direction was consistent with telemetry studies (Rees et al. 2009), and factors that influence the migratory and dispersal behavior of turtles in general. Freshwater turtles often move in response to apparent changes in habitat quality associated with flood–drought cycles (Gibbons et al. 1990, Bowne et al. 2006, Roe and Georges 2007, 2010). When wetlands dry, many turtles respond by moving into permanent water bodies that are more resilient to drought (Kennett and Georges 1990, Roe and Georges 2008*a*, Roe et al. 2009). Suburban water bodies offered such drought refuges for turtles from the nature reserves, but these travels required turtles to occasionally cross roads. For instance, we documented 46 turtles either dead or alive on 1 road between reserve and suburban water bodies (J. Roe, unpublished data). It is thus possible that the lower abundances of turtles on reserve lands reflect either low and persistent levels of mortality as they attempt to enter suburban water bodies, or their temporary exodus from drought conditions on the reserves. Longer-term population studies would be required to assess whether nature reserve populations are declining as a consequence of mortality along bordering roads, or whether immigration and emigration movements reverse direction if or when wet conditions in the nature reserves return.

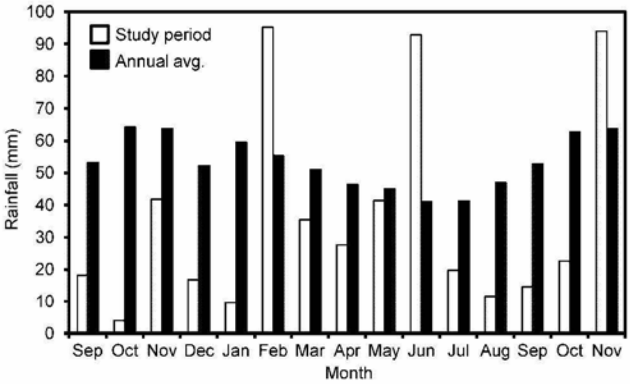

Figure 4. Monthly rainfall amounts from Sep 2006 to Nov 2007 compared to monthly averages collected from a weather station at the Canberra airport (Australian Bureau of Meteorology), located approximately 15 km southeast of our eastern long-necked turtle study site in the Australian Capital Territory, Australia.

MANAGEMENT IMPLICATIONS

Land managers in urban areas are presented with the challenges of meeting the conservation needs of natural lands and wildlife as well as those for urban development. Our results indicate that urbanization can modify ecosystems to buffer against temporal fluctuations in environmental conditions by providing a stability or bolstering of resources uncharacteristic of nearby natural areas. Populations of eastern long-necked turtles were more abundant and turtles grew at higher rates in the urbanized area of our study, though it should be noted that we did not directly assess some important aspects of habitat quality such as predation pressure and nest site quality. Nevertheless, if wildlife can avoid urban dangers, either by virtue of their behavior or the design of the urban landscape (Rees et al. 2009), populations can take advantage of the attenuated environmental fluctuations and respond positively to some degrees of urbanization relative to their counterparts on nearby reserve lands (Noske 1998, Germaine and Wakeling 2001, Parris and Hazell 2005, Shochat et al. 2006). Urban waterways, such as those in our study, are often buffered from natural fluctuations in hydrology due to irrigation inputs, increased runoff, and intentional manipulation of water levels (Tilton 1995, Paul and Meyer 2001, Adams et al. 2006). For freshwater turtles in arid regions, habitat modifications that increase the availability of permanent water bodies and dampen water level fluctuations may provide important sites of refuge from drought that would not have been otherwise available (Roe and Georges 2010).

Natural lands managers and urban planners should realize that urban water bodies have the potential to attract wildlife from nearby reserves, especially during drought. Populations of many species of freshwater turtles may encompass several wetlands that individuals regularly move among (Joyal et al. 2001, Bowne et al. 2006, Roe and Georges 2007, Roe et al. 2009). Thus, factors important in population regulation on reserve lands may also occur outside of the reserve boundaries. When roads or other threats bisect travel routes for turtles moving between nature reserves and urbanized areas, there exists the potential for mortality, such as that from vehicular collisions. If these road-crossing hotspots can be identified, mortality can be mitigated in part by using barrier fencing to keep turtles from entering the road and directing their movements into safe crossing structures, such as under-road culverts (Yanes et al. 1995, Dodd et al. 2004, Aresco 2005*a*, Hagood and Bartels 2008).

ACKNOWLEDGMENTS

We would like to thank A. Quinn for assistance in capturing turtles. D. Pederson provided valuable assistance with statistical analyses. We are also grateful to the staff in the ACT Nature Parks and the Gold Creek and Gungahlin Lakes golf courses for logistic support and access to field sites. We also thank the Ginninderra Catchment Group, Bush on the Boundary, and Conservation Council for encouragement and collaboration throughout the project. Funding was provided by the ACT Government under the Environment Grants, and to J. Roe from the University of Canberra Vice Chancellors Scholarship, the Weeden award, the Society for Wetlands Scientists, and the Australian Society of Herpetologists.

LITERATURE CITED

Adams, C. E., K. J. Lindsey, and S. J. Ash. 2006. Urban wildlife management. Taylor and Francis, Boca Raton, Florida, USA.

Aresco, M. J. 2005*a*. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549–560.

Aresco, M. J. 2005*b*. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37–44.

Bonnet, X., G. Naulleau, and R. Shine. 1999. The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation 89:39–50.

Bowne, D. R., M. A. Bowers, and J. E. Hines. 2006. Connectivity in an agricultural landscape as reflected by interpond movements of a freshwater turtle. Conservation Biology 20:780–791.

Brainwood, M., and S. Burgin. 2006. An exploration of the relationships between macroinvertebrate community composition and physical and chemical habitat characteristics in farm dams. Environmental Monitoring and Assessment 119:459–480.

Brisbin, I. L., R. A. Kennamer, E. L. Peters, and D. J. Karapatakis. 2008. A long-term study of eastern box turtles (*Terrapene c. carolina*) in a suburban neighborhood: survival characteristics and interactions with humans and conspecifics. Pages 373–385 *in* J. C. Mitchell, R. E. J. Brown, and B. Bartholomew, editors. Urban Herpetology. Herpetological Conservation Volume 3. Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah, USA.

Budischak, S. A., J. M. Hester, S. J. Price, and M. E. Dorcas. 2006. Natural history of *Terrapene carolina* (Box Turtles) in an urbanised landscape. Southeastern Naturalist 5:191–204.

Burgin, S., and M. Ryan. 2008. Comparison of sympatric freshwater turtle populations from an urbanized Sydney catchment. Aquatic Conservation: Marine and Freshwater Ecosystems 18:1277–1284.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Carr, L. W., and L. Fahrig. 2001. Impact of road traffic on two amphibian species of different vagility. Conservation Biology 15:1071–1078.

Chessman, B. C. 1984. Food of the snake-necked turtle, *Chelodina longicollis* (Shaw) (Testudines: Chelidae) in the Murray Valley, Victoria and New South Wales. Australian Wildlife Research 11:573–578.

Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

Congdon, J. D., A. E. Dunham, and R. C. Van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist 34:397–408.

Conner, C. A., B. A. Douthitt, and T. J. Ryan. 2005. Descriptive ecology of a turtle assemblage in an urban landscape. The American Midland Naturalist 153:428–435.

Cooch, E., and G. White. 2004. Program MARK. Analysis of data from marked individuals. A gentle introduction. http://www.phidot.org/software/mark/docs/book/. Accessed 10 Aug 2007.

Dodd, C. K., W. J. Barichivich, and L. L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily travelled highway in Florida. Biological Conservation 118:619–631.

Dunson, W. A. 1986. Estuarine populations of the snapping turtle *Chelydra* as a model for the evolution of marine adaptations in reptiles. Copeia 1986:741–756.

Dunson, W. A., and M. E. Seidel. 1986. Salinity tolerances of estuarine and insular Emydid turtles (*Pseudemys nelsoni* and *Trachemys decussata*). Journal of Herpetology 20:237–245.

Edwards, T., C. R. Schwalbe, D. E. Swann, and C. S. Goldberg. 2004. Implications of anthropogenic change on inter-population movements of the desert tortoise (*Gopherus agassizii*). Conservation Genetics 5:485–499.

Eskew, E. A., S. J. Price, and M. E. Dorcas. 2010. Survival and recruitment of semi-aquatic turtles in an urbanized region. Urban Ecosystems 13:365–374.

Garber, S. D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. Ecological Applications 5:1151–1162.

Georges, A., R. H. Norris, and L. Wensing. 1986. Diet of the freshwater turtle *Chelodina longicollis* (Testudines:Chelidae) from the coastal dune lakes of the Jervis Bay Territory. Australian Wildlife Research 13:301–308.

Germaine, S. S., and B. F. Wakeling. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biological Conservation 97:229–237.

Gibbons, J. W., J. L. Greene, and J. D. Congdon. 1990. Temporal and spatial movement patterns of sliders and other turtles. Pages 201–215 *in* J. W. Gibbons, editor. Life history and ecology of the slider turtle. Smithsonian Institution Press, Washington, D.C., USA.

Gibbs, J. P., and G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647–1652.

Graham, T., A. Georges, and N. McElhinney. 1996. Terrestrial orientation by the eastern long-necked turtle, *Chelodina longicollis,* from Australia. Journal of Herpetology 30:467–477.

Hagood, S., and M. J. Bartels. 2008. Use of existing culverts by eastern box turtles (*Terrapene c. carolina*) to safely navigate roads. Pages 169–170 *in* J. C. Mitchell, R. E. J. Brown, and B. Bartholomew, editors. Urban herpetology. Herpetological conservation volume 3. Society for the Study of Amphibians and Reptiles. Salt Lake City, Utah, USA.

Harden, L. A., S. J. Price, and M. E. Dorcas. 2009. Terrestrial activity and habitat selection of eastern mud turtles (*Kinosternon subrubrum*) in a fragmented landscape: implications for habitat management of golf courses and other suburban environments. Copeia 2009:78–84.

Jaeger, J. A. G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. Tulk von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185:329–348.

Janzen, F. J., and C. L. Morjan. 2001. Repeatability of microenvironment-specific nesting behaviour in a turtle with environmental sex determination. Animal Behaviour 62:73–82.

Joyal, L. A., M. McCollough, and M. L. Hunter. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conservation Biology 15:1755–1762.

Kennett, R. M., and A. Georges. 1990. Habitat utilization and its relationship to growth and reproduction of the eastern long-necked turtle, *Chelodina longicollis* (Testudinata: Chelidae), from Australia. Herpetologica 46:22–23.

Lebreton, J. D., K. P. Burnham, J. Colbert, and D. R. Anderson. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lee, S. Y., R. J. K. Dunn, R. A. Young, R. M. Connolly, P. E. R. Dale, R. Dehayr, C. J. Lemckert, S. McKinnon, B. Powell, P. R. Teasdale, and D. T. Welsh. 2006. Impact of urbanization on coastal wetland structure and function. Austral Ecology 31:149–163.

Lindemann, P. V. 1996. Comparative life history of painted turtles (*Chrysemys picta*) in two habitats in the inland pacific northwest. Copeia 1996:114–130.

Mallin, M. A., and T. L. Wheeler. 2000. Nutrient and fecal coliform discharge from coastal North Carolina golf courses. Journal of Environmental Quality 29:979–986.

Manserg, I. M., and D. J. Scotts. 1989. Habitat continuity and social organization of the mountail pygmy-possum restored by tunnel. Journal of Wildlife Management 53:701–707.

Marchand, M. N., and J. A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18:758–767.

Marchand, M. N., J. A. Litvaitis, T. J. Maier, and R. M. DeGraaf. 2002. Use of artificial nests to investigate predation on freshwater turtle nests. Wildlife Society Bulletin 30:1092–1098.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19–38 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic Publishers, Norwell, Massachusetts, USA.

Noske, R. 1998. Breeding biology, demography and success of the rufous-banded honeyeater, *Conopophila albogularis*, in Darwin, a monsoonal tropical city. Wildlife Research 25:339–356.

Parmenter, J. C. 1985. Reproduction and survivorship of *Chelodina longicollis* (Testudinata: Chelidae). Pages 53–61 *in* G. Grigg, R. Shine, and H. Ehmann, editors. Biology of Australian frogs and reptiles. Royal Society of New South Wales, Sydney, Australia.

Parris, K. M., and D. L. Hazell. 2005. Biotic effects of climate change in urban environments: the case of the grey-headed flying-fox (*Pteropus poliocephalus*) in Melbourne, Australia. Biological Conservation 124: 267–276.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333–365.

Plummer, M. V., D. G. Krementz, L. A. Powell, and N. E. Mills. 2008. Effects of habitat disturbance on survival rates of softshell turtles (*Apalone spinifera*) in an urban stream. Journal of Herpetology 42:555–563.

Prowse, C. W. 1987. The impact of urbanization on major ion flux through catchments: a case study in southern England, UK. Water, Air, and Soil Pollution 32:277–292.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Rees, M., J. H. Roe, and A. Georges. 2009. Life in the suburbs: behavior and survival of a freshwater turtle in response to drought and urbanization. Biological Conservation 142:3172–3181.

Roe, J. H., and A. Georges. 2007. Heterogeneous wetland complexes, buffer zones, and travel corridors: landscape management for freshwater reptiles. Biological Conservation 135:67–76.

Roe, J. H., and A. Georges. 2008a. Maintenance of variable responses for coping with wetland drying in freshwater turtles. Ecology 89:485–494.

Roe, J. H., and A. Georges. 2008b. Terrestrial activity, movements, and spatial ecology of an Australian freshwater turtle, *Chelodina longicollis*. Austral Ecology 33:1045–1056.

Roe, J. H., and A. Georges. 2010. Responses of freshwater turtles to drought: the past, present and implications for future climate change in Australia. Pages 175–190 *in* K. Gow, editor. Metldown: climate change, natural disasters, and other catastrophes—fear and concerns for the future. Nova Science, New York, New York, USA.

Roe, J. H., J. Gibson, and B. A. Kingsbury. 2006. Beyond the wetland border: estimating the impact of roads for two species of water snakes. Biological Conservation 130:161–168.

Roe, J. H., A. Georges, and B. Green. 2008. Energy and water flux during terrestrial estivation and overland movement in a freshwater turtle. Physiological and Biochemical Zoology 81:570–583.

Roe, J. H., A. Brinton, and A. Georges. 2009. Temporal and spatial variation in landscape connectivity for a freshwater turtle in a temporally dynamic wetland system. Ecological Applications 19:1288–1299.

Row, J. R., G. Blouin-Demers, and P. J. Weatherhead. 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biological Conservation 137:117–124.

Rowe, C. L., W. J. Sadinski, and W. A. Dunson. 1992. Effects of acute and chronic acidification on three larval amphibians that breed in temporary ponds. Archives of Environmental Contamination and Toxicology 23: 339–350.

Rubin, C. S., R. E. Warner, and D. R. Ludwig. 2001. Habitat use and movements of radiotagged Blanding's turtles (*Emydoidea blandingii*) in a suburban landscape. Chelonian Conservation and Biology 4:136–141.

Ryan, T. J., C. A. Conner, B. A. Douthitt, S. C. Sterrett, and C. M. Salsbury. 2008. Movements and habitat use of two aquatic turtles *Graptemys grographica* and *Trachemys scripta* in an urban landscape. Urban Ecosystems 11:213–225.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474–480.

Shochat, E., P. S. Warren, H. F. Stanley, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology and Evolution 21:186–191.

Spencer, R.-J., and M. B. Thompson. 2003. The significance of predation in nest site selection of turtles: an experimental consideration of macro- and microhabitat preferences. Oikos 102:592–600.

Steen, D. A., and J. P. Gibbs. 2004. Effects of roads on the structure of freshwater turtle populations. Conservation Biology 18:1143–1148.

Stott, P. 1987. Terrestrial movements of the freshwater tortoise, *Chelodina longicollis* Shaw as monitored with a spool tracking device. Australian Wildlife Research 14:559–567.

Tilton, D. L. 1995. Integrating wetlands into planned landscapes. Landscape and Urban Planning 32:205–209.

Walsh, C. J., A. K. Sharpe, P. F. Breen, and J. A. Sonneman. 2001. Effects of urbanization on streams of the Melbourne region, Victoria, Australia. I. Benthic macroinvertebrate communities. Freshwater Biology 46:535–551.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–138.

Yanes, M., J. M. Velasco, and F. Suarez. 1995. Permeability of roads and railways to vertebrates: the importance of culverts. Biological Conservation 71:217–222.

Associate Editor: John Maerz.