Responses of an Australian freshwater turtle to drought-flood cycles along a natural to urban gradient

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Abstract Urban areas provide habitat for numerous native species, but life in towns and cities presents many challenges. The effect of climate on the ecology and the behaviour of non-volant vertebrates inhabiting urban habitats have received little attention. In this study, we investigated demography, growth rates, movements and reproduction of a semi-aquatic freshwater turtle, *Chelodina longicollis*, along a natural to urban gradient during a period of relatively high rainfall (2011–2014) and compared this to a previous study in the same system during drought (2006–2007). In addition to changes in rainfall, urbanization increased considerably over the same time period and a pest-exclusion fence was constructed to mitigate against urban hazards encroaching on the adjacent reserve. Turtles grew at similar rates, had similar abundances and sex ratios and had similar reproductive output across the gradient from urban to non-urban sites during the wet period. Despite increasing urbanization, recruitment occurred at all sites and survivorship estimates were similar among sites. Turtles moved among wetlands at high rates and over long distances (6 km), underscoring the importance of movements in urban landscapes. Our results contrast with those for the same system during drought, when turtles were less abundant and grew slower in the nature reserve compared with the urban environment. Our results underscore the strong influence climate can have on population dynamics and resilience of species to changes brought about by urbanization. Further monitoring is required to understand the long-term population responses of long-lived species to drought cycles.

Key words: climate cycles, dispersal, El Niño, longitudinal study, urbanization.

INTRODUCTION

Urbanization rates are expected to increase worldwide in the next decades (World Resources Institute *et al.* 1996; Gakenheimer 1999). Growth of cities and the associated urban sprawl encroaches on natural habitats with negative consequences for many native species (McKinney 2002, 2008; Pauchard *et al.* 2006). An increasing body of work details how vertebrates are impacted by urbanization (Pautasso 2006; McKinney 2008), including mitigation measures to protect them from urban hazards (Clevenger & Waltho 2005; Bond & Jones 2008), and how generalists species can cope with the life in the city (Chace & Walsh 2006; Bateman & Fleming 2012). Less well understood is how climate, and in particular drought cycles, influences behaviour and population responses along the interface between natural or rural and urban habitats, and how interactive and cumulative effects of climate cycles and urban expansion influence vertebrate populations. Climate change predictions are for an increase in the frequency of drought and flood events (Hughes 2003), which in turn increases urgency to improve this

understanding. Vagile vertebrates (e.g. many birds and mammals) can disperse among habitat patches either within or outside the urban area (Takekawa & Beissinger 1989; Goad *et al.* 2014), but less vagile species may be more limited in their responses to spatial and temporal variation in habitat quality resulting from climate cycles.

Freshwater turtles represent a useful model species to investigate the effects of urbanization and the interactions with climate. Populations can be easily and repeatedly sampled within a series of discrete patches (waterbodies) across targeted land-use gradients (Gibbons 1968). Long lifespans also make turtles amenable to capture–mark–recapture studies that span short-term climactic cycles (Congdon *et al.* 1994; Roe & Georges 2008a,b) and anthropogenic land-use changes (Plummer & Mills 2008; Eskew *et al.* 2010). Freshwater turtles rely on movements among waterbodies and to nearby terrestrial habitats for nesting and other critical behaviours (Steen *et al.* 2006; Roe & Georges 2007), making them particularly sensitive to loss of connectivity arising from roads and other aspects of urbanization (Gibbs & Shriver 2002; Marchand *et al.* 2002; DeCatanzaro & Chow-Fraser 2010; Eskew *et al.* 2010). Alternatively, some species may benefit from increased productivity of urban waterways, leading to faster growth, higher

fecundity and ultimately higher population abundances compared with natural populations (Brown et al. 1994; Lindeman 1996; Souza & Abe 2000). Such benefits are water-dependent and so under the influence of drought cycles characteristic of the Australian temperate climate.

The Australian eastern long-necked turtle (Chelodina longicollis) is a generalist and opportunistic species with a marked propensity for overland movement (Roe & Georges 2008a; Rees et al. 2009), enabling it to exploit a wide range of temporary and permanent aquatic habitats (Kennett et al. 2009), including urban waterbodies (Rees et al. 2009; Roe et al. 2011; Stokeld et al. 2014; Hamer et al. 2016). Chelodina longicollis appears to be somewhat resilient to at least some degrees of urbanization, with site occupancy and population demographics in urban areas similar to rural and natural areas (Roe et al. 2011; Stokeld et al. 2014; Hamer et al. 2016). In some cases, they have been shown to grow faster, achieve larger body size and reach higher abundances in urban habitats compared with nearby natural areas (Roe et al. 2011). However, the mechanisms involved in such population responses in urban landscapes are not completely understood and may depend on a suite of interacting factors, including climate (Rees et al. 2009; Roe et al. 2011), environmental contamination (Stokeld et al. 2014) and influence of exotic predators (Spencer & Thompson 2005). Most studies examining turtle responses to urbanization, including for C. longicollis, are limited to short-term snapshots of a few consecutive years (Roe et al. 2011; Stokeld et al. 2014), which can lead to an incomplete understanding of temporal trends in urban impacts.

Here, we examine attributes of the population biology, including demography, growth rates, movements and reproduction, of C. longicollis during a period of high rainfall (wet period; 2011–2014) influenced by La Niña, and we compare these with earlier studies in the same system during a period of low rainfall influenced by El Niño (drought; 2006–2007) (Rees et al. 2009; Roe et al. 2011). In conducting a longitudinal study over nearly a decade, we aimed to better understand vertebrate responses to drought cycles within natural-urban gradients. We also examine how turtles respond over time to additional changes in the system with potential importance for population regulation, including expanding urbanization and the implementation of a barrier fence to mitigate urban impacts in neighbouring nature reserves.

METHODS

Study area

From October 2011 to March 2014, we studied turtle populations in 14 water bodies distributed along a gradient extending from suburb to rural to nature reserve (urban gradient) in the Gungahlin region of the Australian Capital Territory (ACT), southeastern Australia (Fig. 1). The nature reserve site was Mulligans Flat Nature Reserve comprising 791 ha of woodland, grassland, ponds and upper tributaries of Ginninderra Creek. In June 2009, a predator-proof barrier fence was erected, as part of a wildlife restoration project, enclosing 485 ha of the reserve to isolate it from the impacts of encroaching urbanization, exclude invasive species and allow reintroduction of locally extinct native species (Manning et al. 2011). We sampled turtles in five wetlands within the enclosure. The nature reserve site was defined here as having a low degree of anthropogenic impact isolated by the fence enclosure.

Five wetlands were sampled in the rural landscape, including two wetlands in the Ginninderra Experimental Station and three wetlands in Goorooyarroo Nature Park. The Ginninderra Experimental Station consists of areas with native grasses and eucalypts, in addition of areas with crops and pastures (Webster & Butler 1976). Goorooyarroo is adjacent to Mulligans Flat Nature Reserve, with similar vegetation species composition, but is not enclosed by the barrier fence. Together the rural sites of Ginninderra Experimental Station and Goorooyarroo were defined as having intermediate degree of anthropogenic impact, including agriculture, low-level urban development and exposure to invasive predators such as the European fox.

Finally, four wetlands were sampled in a suburban site located in the central Gungahlin suburb, including a large reservoir, a golf course pond, a canal and a storm water drainage pond. This area is subject to industrial and residential development, including high road densities and managed urban green spaces such as golf courses, parks, gardens and sport ovals (Rees et al. 2009; Roe et al. 2011). This site was defined as having high degree of anthropogenic impact, including urbanization and exposure to invasive and domestic predators.

The climate of the ACT is temperate, with a mean annual rainfall of 633 mm (1974–1988, Australian Bureau of Meteorology). Rainfall in southeast Australia is highly variable, with long periods of drought punctuated by flood. The most recent drought occurred from 2001 to 2009, with a yearly below median rainfall of 483 mm year^{-1}, mainly influenced by El Niño events (van Dijk et al. 2013). There are also periods of elevated rainfall, influenced by La Niña events (Beard et al. 2011) such as in 2012 and 2013 with annual rainfall of 694 and 534 mm, respectively (Canberra Airport weather station, Australian Bureau of Meteorology).

Trapping and marking

Turtles were captured using traps baited with sardines and bovine liver once per month (five consecutive days of trapping per month) from October 2011 to March 2014, excluding months when turtles are inactive (April–August). Two ponds in each of the nature reserve, rural and suburb sites, hereafter referred to as the fixed sites, were sampled monthly to describe reproductive biology of the turtles. Additional ponds were sampled twice per year to increase sample sizes in other demographic analyses (three ponds
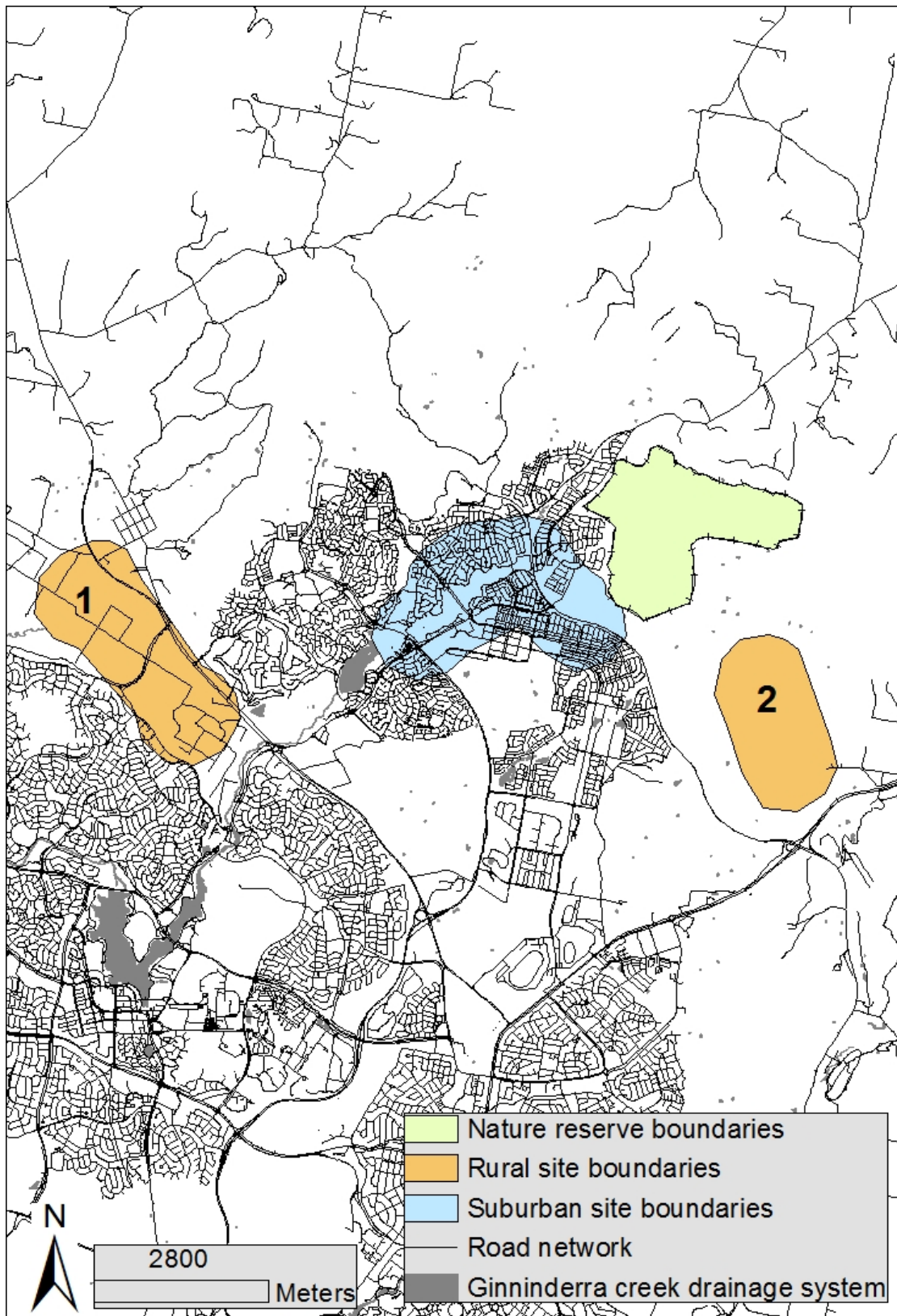
Fig. 1. Nature reserve, rural and suburban study sites in Gungahlin, northern Canberra, Australian Capital Territory. Study sites were defined by drawing 700-m polygons around sampled ponds and then joining the polygons to delimit each site. The polygons in the nature reserve were contracted to delimit the area only included within pest-fencing. Number 1 denotes the Ginninderra Experimental Station and number 2 the Goorooyarroo Nature Park, both part of the rural sites.

each in the nature reserve and rural sites, and two in the suburb site) and are referred to hereafter as the occasional sites. We used two to six traps per pond depending on pond size. We marked captured turtles with unique codes by notching the shell and measured maximum straight-line carapace length (CL), carapace width (CW), midline plastron length (PL) and plastron width (PW) with callipers (±0.1 mm) and body mass with a scale (±5 g). Turtles with a CL <145 mm were considered juveniles; those for which CL >145 mm were classified as males or females on the basis of external morphological features (see Kennett & Georges 1990). All turtles were released at their point of capture.

Anthropogenic impact

Anthropogenic impact was measured by calculating road density (km of road/km^2) within 700 m of each of the 14 ponds using 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 *et al.* 2009). If the buffer encompassed areas within the predator-proof fence, the buffer was rearranged following the fence line, as the fence completely impedes turtle movements (Ferronato *et al.* 2014).

Primary and secondary productivity

We estimated a surrogate for primary productivity by measuring total phosphorus and nitrogen (TP and TN; ~0.2 L) from water samples in each pond, once per month from December 2012 to February 2013. Water samples were kept on ice in an insulated container during transportation to the lab and analysed using oxidation with $K_2S_2O_8$ and low-pressure microwave digestion (Maher *et al.* 2002). We measured secondary productivity as the standing-crop biomass of potential prey items, sampling wetlands once per month from December 2012 to February 2013. On each occasion, we conducted four time-constrained (30 s) searches in each pond by agitating the sediment and searching in the littoral zone around available structures (e.g. rocks, debris, macrophytes) with the use of a 34 × 28 cm dipnet (250 μm mesh; Roe *et al.* 2011). Samples were preserved in 90% ethanol for later sorting (see Roe *et al.* 2011). We only considered potential prey items that are known to be eaten by *C. longicollis* (Georges *et al.* 1986). We compared primary (TP and TN) and secondary (prey biomass) productivity among study sites using analysis of variance (ANOVA). TP and prey biomass were $\log_{10}$ transformed and TN was square root transformed to meet the assumptions of normality.

Reproduction

Adult female turtles were transported to the University of Canberra for radiographic examination (AJEX Meditech Ltd; Model: AJEX160H; settings: 50 kV, 1.20 mAs, 0.02 s, 70 cm high) and then released within 7 days at their point of capture. Egg length (EL) and egg width (EW) were measured with callipers from the X-ray films, and egg volume (EV) was estimated with the formula

$$EV = \pi * X * Y^2/6$$

where X is the EL and Y is the EW (Vanzolini 1977). The proportion of mature females that were gravid was compared among sites with a chi-square contingency analysis. We used analysis of covariance (ANCOVA) to test whether clutch sizes differed among sites, with site as the factor, clutch size as the response variable and CL as a covariate.

Growth rates and movements

We calculated growth rates over both long-term (individuals initially encountered in 2006–2007 sampling and recaptured in 2011–2014, spanning both the drought and wet periods) and short-term (individuals initially encountered and recaptured in 2011–2014 sampling, during the wet period only) intervals. We then compared growth rates among turtles from natural, rural and suburban areas considering the long-term and the short-term scenarios. Annual growth was measured as change in CL, divided by the fraction of the 6-month growing season (15 September to 15 March) that had elapsed between captures. We only included individuals in the analysis if they were recaptured in the same study area and if the period between captures spanned at least one-half of a growing season.

Individuals were determined to have grown appreciably only if the growth increment exceeded the accuracy of measurements (±0.5 mm), and the proportion of individuals that grew appreciably was also determined for each study site. Data from individuals that had not grown appreciably were otherwise excluded from analyses of growth rates. The analysis of growth was as in the previous *C. longicollis* study during drought (2006–2007) to allow comparisons (Roe *et al.* 2011). The proportion of individuals showing appreciable growth was compared among study areas with a series of chi-square contingency analyses (juveniles and adults separate). Growth rates were compared among sites using ANCOVA, with site as the factor, $\log_{10}$ carapace growth rate as the response variable and initial CL as a covariate. Growth rates analyses were performed for both long-term and short-term recaptures.

We assessed if recaptured individuals had moved among study sites (not including movements between ponds within a study system), considering both long- and short-term recapture intervals. We calculated minimum straight-line distances animals moved with ArcGIS (version 9.3.1: ESRI 2009).

Demographic parameters

We compared proportion of females, estimated population size, size–frequency distributions, survivorship and recapture probability among study sites. Proportion of females was compared with ANOVA, with site as the factor and proportion of females as the response variable. For estimation

of population size, we used the Horvitz–Thompson type estimator (Seber 1982):

$$N = \frac{n}{p}$$

where N is the estimated population size, n is the number of unique turtle captures in each pond and p is the capture probability. Population size was compared with ANCOVA, with site as the factor, estimated population size as the response variable and pond surface area as a covariate. Overall differences in size–frequency distributions among sites were examined with a chi-square test using the PROC FREQ procedure in SAS. We followed the overall test with a series of chi-square tests to examine in which size classes differences occurred. We used the Dunn–Sidak correction to adjust the per comparison significance ($\alpha < 0.004$) to accommodate compounding error that occurs in multiple related comparisons.

Survivorship and capture probability were estimated using Cormack–Jolly–Seber (CJS) open population capture–recapture models in Program MARK. We estimated parameters among groups (adult male, adult and subadult female, and juvenile), sites (nature reserve, rural and suburb) and over time (sampling occasions). We collapsed capture histories into two occasions of approximately equal duration per year (September–December and January–March) owing to the different sampling effort in our fixed and occasional trapping sites. We started with models where survivorship (Φ) and capture probability (ρ) were allowed to vary over time, among groups and among sites. We then fitted a series of reduced parameters models and ranked them based on Akaike's information criterion (AIC). If competing models had AIC values ≤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 the simulated deviances (Cooch & White 2014). 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 & Anderson 1998). All parameters were estimated using model averaging.

Data analysis

Statistical analyses were performed with SPSS (Version 21), Program MARK version 7.1 (White & Burnham 1999) and SAS Version 9.1 (SAS Institute 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.

RESULTS

Anthropogenic impact

Road density around sampled ponds ranged from 15.7 to 19.3 km/km^2 at the urban site, from 0.0 to 5.8 km/km^2 at the rural site, and no roads were within 700 m of ponds in the nature reserve.

Primary and secondary productivity

The nature reserve and rural ponds had TP and TN similar to one another and higher than suburban ponds (TP: ANOVA: $F_{2,39} = 10.08$, $P < 0.001$; TN: ANOVA: $F_{2,39} = 47.90$, $P < 0.001$; Table 1). However, there was no difference in prey biomass among sites (ANOVA: $F_{2,39} = 0.35$, $P = 0.70$; Table 1).

Reproduction

Shelled eggs were detected only from October to December in each year (Fig. 2). Of 299 adult females captured during the breeding season, only 8.4% were gravid, and the percentage of gravid females did not vary significantly among sites (nature reserve: 10.7%; rural 5.8%; urban: 8.4%) ($X^2 = 0.70$, d.f. = 2, $P = 0.71$). After controlling for carapace length, clutch sizes were similar among study sites (ANCOVA site: $F_{2,19} = 0.72$, $P = 0.50$; CL: $F_{1,19} = 24.57$, $P < 0.005$; Table 2). The interaction between site and CL was not significant ($P = 0.60$) and was dropped from the analysis.

Table 1. Primary and secondary productivity measurements in ponds inhabited by *Chelodina longicollis* among study sites, Australian Capital Territory, Australia

	Primary		Secondary
	TP (mg/L)	TN (mg/L)	Prey biomass (g)
Nature reserve ($n = 15$)	0.11 ± 0.01[A] (0.04–0.26)	1.42 ± 0.09[A] (0.89–2.28)	2.66 ± 0.39[A] (0.96–5.50)
Rural ($n = 15$)	0.08 ± 0.01[A] (0.05–0.15)	1.47 ± 0.08[A] (1.03–2.01)	3.35 ± 0.58[A] (0.27–6.58)
Suburb ($n = 12$)	0.05 ± 0.01[B] (0.02–0.09)	0.61 ± 0.03[B] (0.46–0.76)	2.52 ± 0.56[A] (0.52–6.89)

Mean, SE; superscripts indicate similarities or differences among study sites within columns.
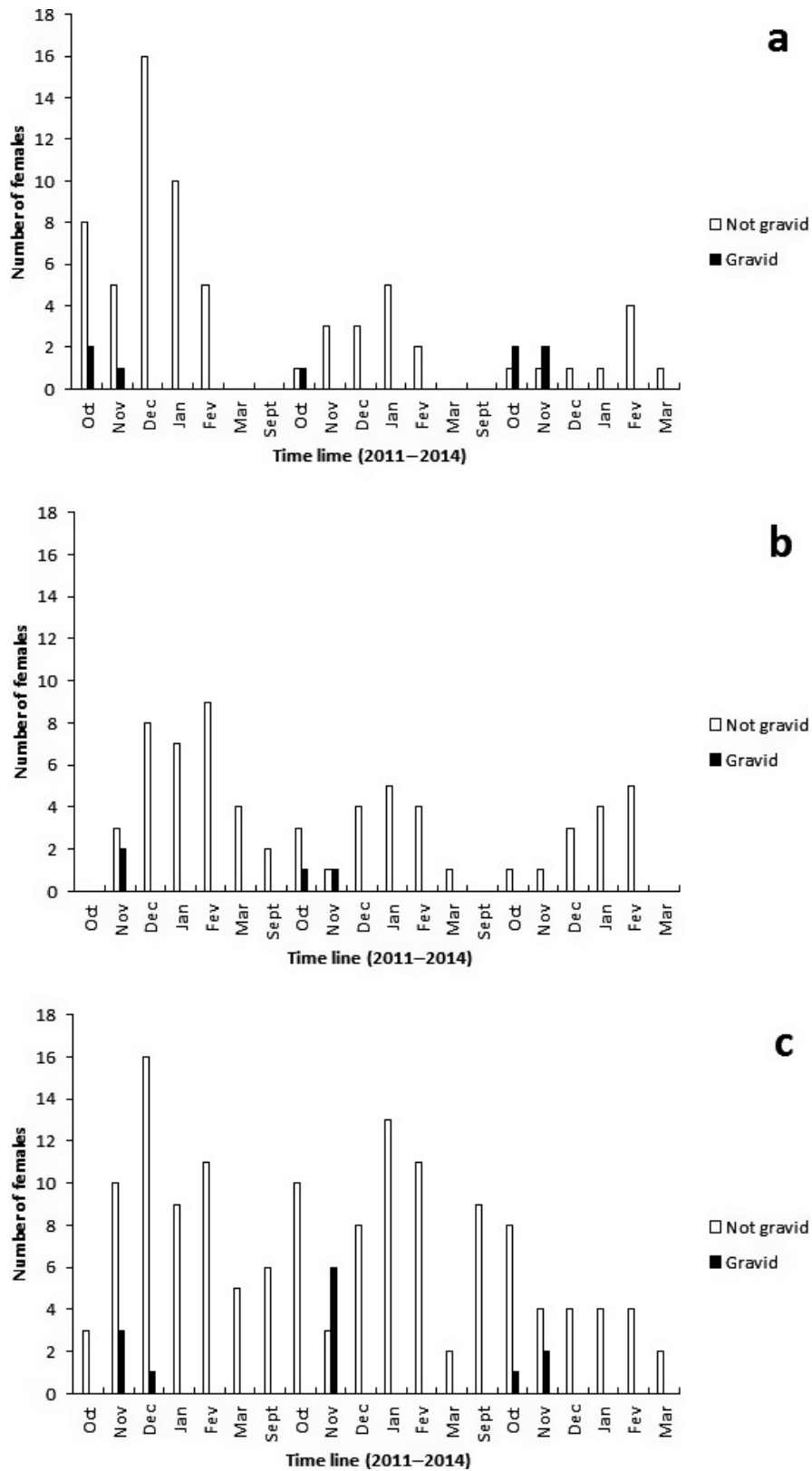
Fig. 2. Gravid females *Chelodina longicollis* inspected through X-ray in nature reserve (a), rural (b) and suburban (c) sites, in Australian Capital Territory, Australia. X-rays performed from October 2011 to March 2012, September 2012 to March 2013 and September 2013 to March 2014.

Table 2. Clutch size and egg measurements of gravid female *Chelodina longicollis* (through X-ray evaluation) from different study sites, Australian Capital Territory, Australia

	CS (*n*)	EL (mm)	EW (mm)	EV (mm^3)
Nature reserve (*n* = 7)	10.8 ± 0.8 (8.0–14.0)	29.9 ± 0.7 (28.1–31.7)	21.1 ± 0.3 (20.1–22.5)	7009 ± 312 (6151–8319)
Rural (*n* = 4)	14.2 ± 0.9 (13.0–17.0)	29.7 ± 1.4 (27.5–34.0)	21.1 ± 0.3 (20.1–21.5)	6942 ± 501 (5822–8254)
Suburb (*n* = 12)	12.5 ± 0.8 (8.0–17.0)	29.7 ± 0.4 (27.4–32.6)	20.7 ± 0.3 (19.1–22.7)	6713 ± 207 (5762–8088)

Mean, SE, range; CS, clutch size; EL, egg length; EW, egg width; EV, egg volume.

Table 3. Growth rates of eastern long-necked turtles (*Chelodina longicollis*), and recaptures for juveniles (J) and adults (A), spanning long-term (drought-wet) and short-term (wet) conditions, Australian Capital Territory, Australia

Period	Group	Recaptures (*n*) J	Recaptures (*n*) A	Percentage growing J	Percentage growing A	Carapace growth rate (mm year^{-1})[†,‡] N	Carapace growth rate (mm year^{-1})[†,‡] Mean ± SE (range)
Long-term 2006–2014	Nature reserve	5	19	100	47	14	4.4[A] ± 1.0 (0.8–12.4)
	Rural	5	11	80	73	12	3.8[B] ± 0.8 (0.5–9.1)
	Suburb	3	19	100	74	17	4.5[C] ± 0.8 (0.9–13.9)
Short-term 2011–2014	Nature reserve	4	25	100	48	16	5.7[A] ± 1.7 (0.9–27.3)
	Rural	8	3	100	67	10	8.0[A] ± 3.0 (0.8–26.8)
	Suburb	11	24	100	75	29	7.7[A] ± 1.4 (0.6–28.0)

[†]Based on a growth year spanning the typical activity season (15 September to 15 March). [‡]Carapace growth values not adjusted for carapace length variation (ANCOVA), which if included reveals statistical differences among study sites during the long-term period, but not during the short-term. Superscripts indicate similarities or differences among study sites within columns.

Growth and movements

After controlling for CL, there was a difference in turtle growth rates among sites during the long-term interval spanning both dry and wet periods (ANCOVA site: $F_{2,39} = 12.49$, $P < 0.005$; CL: $F_{1,39} = 95.21$, $P < 0.005$), with urban turtles growing fastest, followed by rural, and then nature reserve turtles (Table 3, Fig. 3). But there was no difference in growth rates among study sites during the short-term interval coinciding with the wet period only (ANCOVA site: $F_{2,51} = 2.22$, $P = 0.12$; CL: $F_{1,51} = 32.49$, $P < 0.005$; Table 3, Fig. 3). The percentage of juveniles and adults growing appreciably did not differ among study sites during the long-term (juveniles: $X^2 = 1.73$, d.f. = 2, $P = 0.42$; adults: $X^2 = 3.37$, d.f. = 2, $P = 0.18$) or short-term intervals (juveniles: not computed as growth was a constant; adults: $X^2 = 3.80$, d.f. = 2, $P = 0.14$; Table 3). We recorded long-distance movements of turtles through capture–mark–recapture, spanning 2006–2014 (Table 4). Over the short-term interval (2011–2014), none of the turtles was recaptured in different study areas.

Demographic parameters

We made 782 captures of 655 different turtles. There was no difference in proportion of females (mean, SE, *n*, range) among sites (nature reserve: 0.49 ± 0.18 (*n* = 5, 0.28–0.72); rural: 0.38 ± 0.14 (*n* = 4, 0.21–0.54); suburb: 0.45 ± 0.12 (*n* = 4, 0.29–0.57)) (ANOVA: $F_{2,10} = 0.35$, $P = 0.60$). Relative population sizes (corrected for variation in capture probability) increased from nature reserve to rural to urban study areas, but after controlling for wetland surface area, population sizes (i.e. densities) did not differ among sites (nature reserve: 47.6 ± 17.5 (*n* = 5, 14.0–110.6); rural: 110.2 ± 36.6 (*n* = 5, 10.2–224.3); suburb: 156.3 ± 35.3 (*n* = 4, 74.2–231.0); ANCOVA: site: $F_{2,10} = 2.19$, $P = 0.16$; wetland surface area: $F_{1,10} = 1.71$, $P = 0.22$). The interaction between site and wetland surface area was not significant ($P = 0.09$) and was removed from the analysis.

Size–frequency distributions differed among sites (overall $X^2 = 87.2$, d.f. = 24, $P < 0.001$), with significant differences within 60.1–75 mm PL ($X^2 = 12.0$, d.f. = 2, $P < 0.004$) and 105.1–120 mm PL size
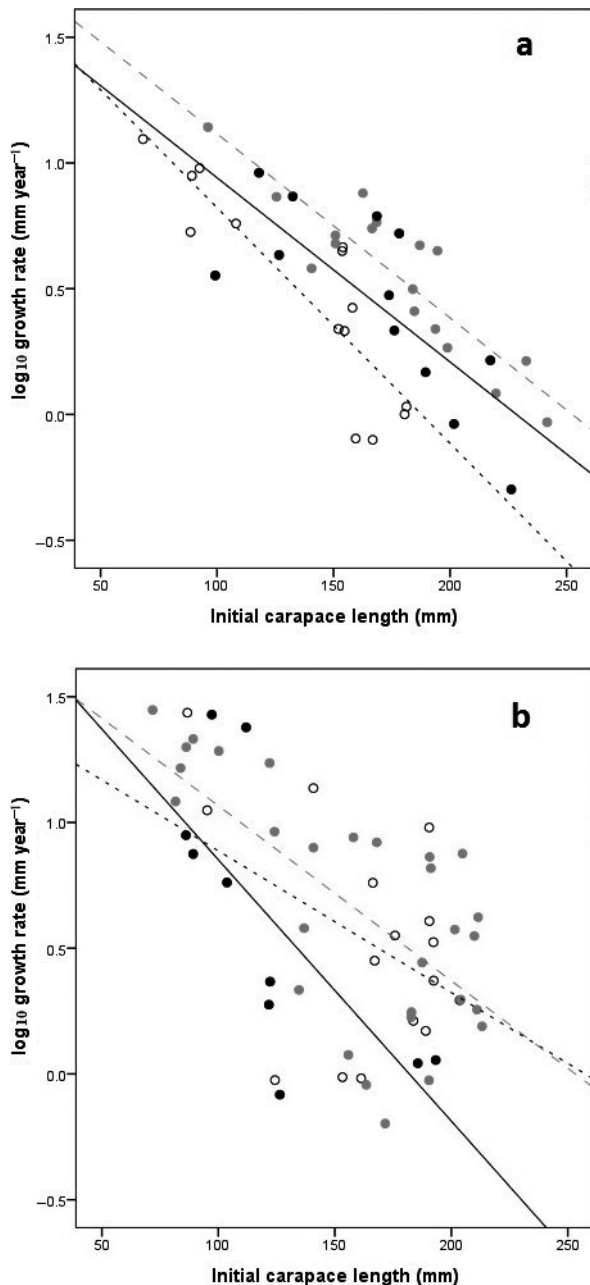
Fig. 3. Relationships of growth and initial carapace length (mm) in *Chelodina longicollis* inhabiting nature reserve (open circles, smaller black dashed line), rural (black filled circles, solid line) and suburban (grey filled circles, larger grey dashed line) habitats, during 2006–2014 period (a) and 2011–2014 (b) period, Australian Capital Territory, Australia.

classes ($X^2 = 14.1$, d.f. = 2, $P < 0.004$), with more individuals in the rural site in both cases, as well as in the 165.1–180 mm PL size class, with more individuals in the rural and urban sites than the nature reserve ($X^2 = 15.0$, d.f. = 2, $P < 0.004$; Fig. 4).

In the capture–mark–recapture analysis, the model with most support had survivorship constant over

time and among groups and sites, and capture probability varying according to site (Tables 5,6). The other competing models had little support according to Δ QAIC$_c$ values (Table 5). Analyses using only the fixed trapping sites supported the same highest ranked model as analyses using both fixed and occasional sampling sites.

DISCUSSION

Populations of plant and animal species can be expected to wax and wane under the influence of climate, extending their ranges during more favourable periods, contracting during less favourable periods (Davis & Shaw 2001; Huntley *et al.* 2008). In the context of drought, critical elements in this process are patches of local persistence during the dry periods, and connectivity with suitable habitat during the wet periods. Often species, both terrestrial and aquatic, will contract and expand their distributions along drainage lines (Burridge *et al.* 2006; Smit *et al.* 2007), and maintaining connectivity is an important management objective (Pringle 2001). Urbanization has a major influence on whether or not local refugia for many species during drought are maintained and in what condition, and to what degree dispersal of species through the urban environment is prevented or impeded. Our study and those that preceded it (Roe *et al.* 2011; Ferronato *et al.* 2014) establish clearly the importance of these factors for the persistence of the eastern long-necked turtle in urban areas within its natural range.

Long-term or repeat studies of turtles inhabiting urban landscapes have focused specifically on demographic parameters and vital rates before and after major habitat alterations (Plummer & Mills 2008; Eskew *et al.* 2010). While we were not able to examine turtle populations before urban development, our study is unique in that we evaluated turtle responses not only to changes in degree of urban development over time and space but also to other potentially interacting stressors such as climate and invasive predators. Our recent sampling from 2011 to 2014 coincided with higher rainfall (mean 602 mm year^{-1}, La Niña event, Beard *et al.* 2011) and a marked increase in urbanization compared to an earlier 2006–2007 sampling when the system was in drought (mean 464 mm year^{-1}, El Niño period, van Dijk *et al.* 2013) and in the early stages of urban development (Rees *et al.* 2009; Roe *et al.* 2011). In addition, a fence was recently built to exclude non-native animals and isolate the nature reserve from encroaching urban hazards with substantial impact on turtle movements (Ferronato *et al.* 2014). Such a longitudinal study across a gradient of anthropogenic impact and following such changes allowed us to

Table 4. *Chelodina longicollis* movements among study sites based on capture–mark–recapture, Australian Capital Territory, Australia

| Group | Trapped in 2006–2007 (n) | Recaptured in 2011–2014[†] (n) | | | Distance moved (m) Mean ± SE (range) |
		NR	R	S	
NR	32	–	–	8	1446.2 ± 431 (540–3800)
R	17	–	–	–	–
S	28	3	4	–	3118.8 ± 582 (1575–6020)

[†]Denotes recaptures outside its original site of capture. NR, nature reserve; R, rural; S, suburb.
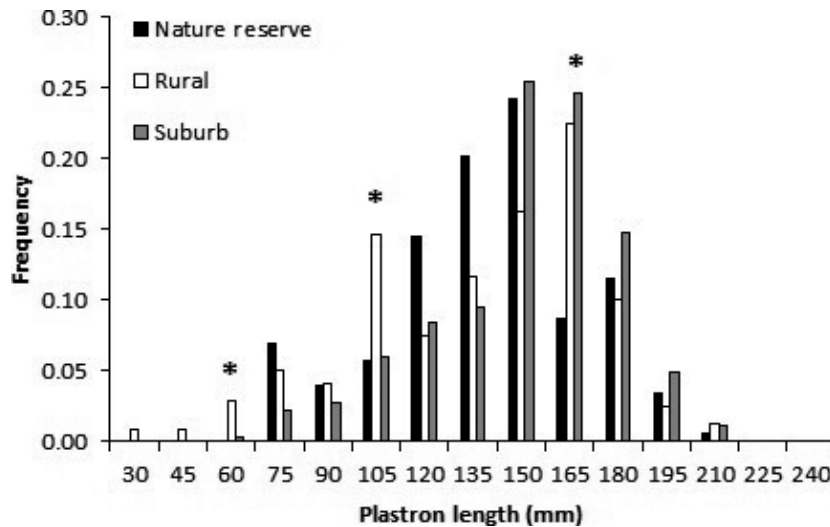
Fig. 4. Size–frequency distributions of *Chelodina longicollis* among study sites, Australian Capital Territory, Australia. Asterisk indicated statistical difference.

Table 5. Models of survivorship (Φ) and capture probability (ρ) of *Chelodina longicollis* over time (twice per year), among sites (nature reserve, rural and suburb) and among groups (adult male, adult and subadult female, and juvenile) in the Australian Capital Territory, Australia, 2011–2014

Model	$QAIC_c$	$\Delta QAIC_c$	Weight	Parameters	Deviance
Φ (.) ρ (site)	491.7	0.00	0.52	4	115.8
Φ (site) ρ (.)	493.8	2.03	0.19	4	117.8
Φ (.) ρ (.)	494.7	2.97	0.12	2	122.8
Φ (group) ρ (.)	495.6	3.81	0.08	4	119.6
Φ (.) ρ (group)	496.4	4.62	0.05	4	120.4
Φ (site × group) ρ (.)	498.1	6.37	0.02	10	109.9
Φ (.) ρ (site × group)	498.6	6.88	0.02	10	110.4
Φ (site × group) ρ (site × group)	508.0	16.26	0.00	18	103.1
Φ (.) ρ (site × group × time)	552.6	60.89	0.00	46	85.9
Φ (site × group × time) ρ (.)	554.1	62.40	0.00	46	87.5
Φ (site × group × time) ρ (site × group × time)	641.8	150.06	0.00	90	66.5

Models were compared and ranked with a quasi-likelihood Akaike's information criterion ($QAIC_c$) estimator corrected for overdispersion ($\hat{c} = 1.51$).

examine spatial and temporal responses in behaviour, demography and vital rates, yielding insight into the mechanisms related to turtle persistence in urban systems.

The evidence of increased urbanization in the system (Gungahlin suburbs) over the last 8 years includes a 79% growth in human population (Australian Bureau of Statistics 2013), a 76% increase in

Table 6. Estimates of survivorship (Φ) and capture probability (ρ) for *Chelodina longicollis* among different sites and groups in the Australian Capital Territory, Australia, 2011–2014

Site	Group	Φ (bi-annual)	Φ (annual)	ρ[†] (bi-annual)
Nature reserve	Male	0.688 ± 0.076	0.473 ± 0.005	0.117 ± 0.028
	Female	0.702 ± 0.074	0.492 ± 0.005	0.121 ± 0.029
	Juvenile	0.687 ± 0.076	0.471 ± 0.005	0.118 ± 0.029
Rural	Male	0.648 ± 0.078	0.419 ± 0.006	0.077 ± 0.022
	Female	0.652 ± 0.077	0.425 ± 0.005	0.079 ± 0.022
	Juvenile	0.639 ± 0.079	0.408 ± 0.006	0.077 ± 0.022
Suburb	Male	0.671 ± 0.078	0.450 ± 0.006	0.099 ± 0.029
	Female	0.686 ± 0.076	0.470 ± 0.005	0.102 ± 0.029
	Juvenile	0.668 ± 0.079	0.446 ± 0.006	0.101 ± 0.029

[†]Capture probabilities showed differences among sites according to model selection. Parameters were derived as weighted averages based on their quasi-likelihood Akaike's information criterion (QAIC$_c$) values, adjusted for model overdispersion. Results expressed in mean ± SE.

traffic volume (Territory and Municipal Services, R. Shoukrallah, pers. comm., 2013) and a 130% higher road density compared to the 2006–2007 period (Roe *et al.* 2011). Such an increase in urbanization, especially regarding road density and traffic volume, could pose a threat for turtles with marked propensity for overland movements, although our measures of various behavioural, demographic and population vital rates together with those of earlier studies suggest otherwise (Roe *et al.* 2011). The apparent resilience of *C. longicollis* to such threats is in contrast with demographic responses of several other species to heavy road density and traffic volume elsewhere (Gibbs & Shriver 2002; Marchand & Litvaitis 2004).

Although we considered habitats in the context of being more or less influenced by anthropogenic stressors, we were also interested in understanding potential differences in productivity. Urban areas may have higher productivity and nutrient loads owing to human subsidized resources (DeStefano & DeGraaf 2003; Shochat *et al.* 2006), which can ultimately influence growth rates and reproductive output in turtles (Brown *et al.* 1994; Lindeman 1996). This was not the case in our system, where urban ponds had the lowest primary productivity, a result that could have been influenced by differences in the uptake of resources by organisms and variation in the availability of nutrients during sampling (Jones 1984; Müller 2000). However, availability of food resources for turtles was similar among study sites, suggesting that productivity did not differ in ways relevant to turtle population regulation, a finding in agreement with previous estimates of food availability during drought (Roe *et al.* 2011). The lack of elevated productivity in urban ponds may be related to the lack of sewage contamination in our system, which can be a significant source of nutrient input in urban areas elsewhere (Galbraith *et al.* 1988; Souza & Abe 2000).

Our results demonstrate the strong influence of drought on growth rates. During drought, turtles in urban areas grew five times faster than those in the nature reserve (Roe *et al.* 2011), even though ponds were similar in prey biomass when flooded. The authors hypothesized that the constant availability of water extended the activity period (and thus foraging opportunities) for turtles in suburbs, while ponds in the nature reserve dried and most turtles aestivated on land. Our results support this hypothesis, as growth rates were similar between natural and urban ponds during the wet period, when all ponds remained flooded and no turtles were observed in long-term aestivation (Ferronato *et al.* 2016). Interestingly, long-term growth rates spanning both dry and wet periods remained lowest in nature reserve turtles, indicating a lack of compensatory growth following the return of rainfall. Such responses suggest that the cumulative effects of several wet–dry cycles may further constrain individual growth rates in nature reserve populations relative to their urban counterparts, though we were only able to measure growth responses over one wet–dry cycle. Indeed, growth rates of animals, including *C. longicollis*, are strongly influenced by rainfall patterns in wet–dry cycles characteristic of much of Australia (Kennett & Georges 1990; Madsen & Shine 2000; Greenville *et al.* 2013).

Turtles in urban systems may have higher fecundity than in natural settings (Brown *et al.* 1994; Lindeman 1996), but we did not detect variation among sites in any measure of reproductive biology, including reproductive season, clutch sizes or percentage of gravid females. That our measures of fecundity were similar across environments is again likely related to similar food availability among sites. *Chelodina longicollis* can lay up to three clutches in a reproductive season in the Murray River and in Gippsland, Victoria (Parmenter 1985; Kennett *et al.* 2009), but we found no evidence of multiple clutches based on X-

ray analysis of females recaptured within a breeding season, a finding corroborated by a previous study in the Canberra region (Vestjens 1969) and likely reflecting climactic constraints on a shortened reproductive season (October to December). Even though we do not have information on reproductive output of *C. longicollis* during drought in our system, females aestivate on land for several months in response to wetland drying (Rees *et al.* 2009) and may cease reproduction during unfavourable drought conditions at other locations in southeastern Australia (Kennett & Georges 1990).

The observation of similar population sizes among study sites at first suggests a different dynamic from the previous drought (2006–2007), where urban turtles were nearly three times more abundant than nature reserve turtles (Roe *et al.* 2011). However, despite statistical analyses, abundance in nature reserve ponds was still 3.2 and 2.3 times lower than the urban and rural sites, respectively, a difference that could be biologically meaningful but biased by low sample size. For instance, even though the same ponds were sampled in each study, sample sizes in the wet period (2011–2014) were smaller owing to the construction of the fence that required the natural site to be divided into two regions, reducing power in the analysis. While nature reserve turtles resumed growth and reproduction during the recent wet conditions, perhaps not enough time had passed for a population-level response to be realized. Additionally, at the same time that the drought broke, the predator-proof fence was erected, isolating that population and preventing remigrations of individuals that had left for the suburban ponds during drought. Indeed, many more turtles were encountered on the outside of the fence following the return of rainfall, which likely represents individuals attempting to return to the flooded ponds in the nature reserve (Ferronato *et al.* 2014). Thus, immigration into nature reserve ponds was eliminated, causing both high mortality and forcing them into other ponds (Ferronato *et al.* 2014, 2016).

The observation of animals in the smaller size classes in all study sites indicates that recruitment has continued despite expanded urbanization. One of the typical challenges facing turtles in urban landscapes is limited recruitment owing to high predation rates and lack of nesting habitats (Spinks *et al.* 2003; Marchand & Litvaitis 2004). The presence of recruitment across all levels of anthropogenic impact examined here is a signal that some females are still safely reaching nesting areas, eggs are successfully incubated, and some hatchlings are capable of travelling to water. Although survivorship did not vary across study sites based on capture–mark–recapture estimates, a concurrent radiotelemetry study demonstrated that adult female urban turtles had lower annual survivorship (0.67) compared with females from the nature reserve (1.00, Ferronato *et al.* 2016), where most mortality of urban turtles was on roads. However, the radiotelemetry study focused only on females, and we identified localized hotspots that could have biased mortality differences in the telemetry owing to small sample sizes (Ferronato *et al.* 2016). The overall mortality in the broader study area could be diffuse at the meta-population scale, yet still significant on local scales. Regardless, survivorship estimates during the wet period (2011–2014) are especially low for *C. longicollis* (Roe *et al.* 2009) and compared to other freshwater turtles (Shine & Iverson 1995), so we question the accuracy of these survival rates. Considering the biology of *C. longicollis* and its ability for frequent and long-distance inter-wetland movements (Ryan & Burgin 2007; Roe & Georges 2008b; Roe *et al.* 2009), there is potential for high emigration to ponds outside the sample locations, which would be interpreted as 'mortalities' in our CJS models (Cooch & White 2014). We did not consider using the Robust Design approach to account for emigration, as females were temporarily removed from the populations for X-ray analysis, which would have violated the assumptions of such models.

Previous research has demonstrated the high vagility of *C. longicollis*, suggesting that single wetlands should not represent the minimum habitat unit harbouring a population (Roe & Georges 2008b; Roe *et al.* 2009). Rare dispersal events of up to 5.2 km have been described among dune lakes in an undisturbed setting in southeastern Australia (Roe *et al.* 2009), and it is apparent that such long-distance movements (up to about 6 km) also occur within urbanized regions, suggesting that the turtles behave similarly with regard to inter-wetland movements for dispersal or migration even where roads and other threats are encountered. Such movements are important for maintaining connectivity and gene flow among populations (Hansson 1991; Coulon *et al.* 2004), in addition to rescue populations from stochastic events such as drought. However, the current design of the pest-fencing surrounding the nature reserve is disrupting this dynamic in response to wet–dry cycles (Rees *et al.* 2009; Roe *et al.* 2011; Ferronato *et al.* 2014), and causing high mortality for turtles attempting to pass (Ferronato *et al.* 2014). Nevertheless, these long-distance movements demonstrate that our sites do not satisfy the assumption of independence. However, such important behaviour would have not been documented in short-term studies or if we had only sampled wetlands distant from each other (e.g. 10 km apart). Moreover, another limitation in our design is that the construction of the fence enclosure in the nature reserve in 2009 isolated that population from exchange with other nearby ponds.

CONCLUSIONS

Our study expands the current understanding of vertebrate responses to drought cycles within natural-urban gradients and demonstrates the strong influence of rainfall on population dynamics. Together, our findings of similar vital rates, demography and recruitment in all study sites indicate that *C. longicollis* is resilient to the levels of urbanization in our system. Perhaps, the ability of *C. longicollis* to move overland and settle in different habitats (Kennett & Georges 1990; Roe & Georges 2008a,b; Roe *et al.* 2009), in addition to its opportunistic carnivorous feeding behaviour (Georges *et al.* 1986) have also contributed to its successful colonization in urban ponds. As long as turtles can travel safely between natural and urban environments, climate cycles similar to those observed in this study should pose no threat to their persistence in such habitats. A major limitation of our study is the lack of adequate replication, with our study system covering only one gradient of urbanization in a single urban environment. However, taken together with studies in urban environments elsewhere, evidence of *C. longicollis* resilience and establishment across a range of urban settings over broad spatial scales is growing (Ryan & Burgin 2007; Rees *et al.* 2009; Roe *et al.* 2011; Stokeld *et al.* 2014). Finally, even though our repeat study compared population dynamics over an 8-year period, such duration is still relatively short compared with the turtle life spans that may cover several decades (Gibbons 1987), making further monitoring essential for a more complete understanding of turtle population dynamics in urban landscapes.

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