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Identifying Critical Habitat for Australian Freshwater Turtles in a Large Regulated Floodplain: Implications for Environmental Water Management

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Abstract Freshwater turtles face many threats, including habitat loss and river regulation reducing occupancy and contributing to population decline. Limited knowledge of hydrological conditions required to maintain viable turtle populations in large floodplain wetlands hinders effective adaptive management of environmental water in regulated rivers. We surveyed three turtle species over 4 years across the Lower Murrumbidgee River floodplain, a large wetland complex with a long history of water resource development. Using site and floodplain metrics and generalized linear models, within a Bayesian Model Averaging framework, we quantified the main drivers affecting turtle abundance. We also used a hierarchical modeling approach, requiring large sample sizes, quantifying possible environmental effects while accounting for detection probabilities of the eastern long-necked turtle (*Chelodina longicollis*). The three species varied in their responses to hydrological conditions and connectivity to the main river channel. Broad-shelled turtles (*Chelodina expansa*) and Macquarie River turtles (*Emydura macquarii macquarii*) had restricted distributions, centered on frequently inundated wetlands close to the river, whereas the eastern long-necked turtles were more widely distributed, indicating an ability to exploit variable habitats. We conclude that turtle communities would benefit from long-term management strategies that maintain a spatiotemporal mosaic of hydrological conditions. More specifically, we identified characteristics of refuge habitats and stress the importance of maintaining their integrity during dry periods. Neighboring habitats can be targeted during increased water availability years to enhance feeding and dispersal opportunities for freshwater turtles.

Keywords Turtle · Floodplain · Wetland · Environmental flows · Ecological monitoring · Occupancy models

Introduction

Freshwater turtles are one of the world's more endangered taxonomic groups, with 52% of 335 species extinct or threatened (Bohm et al. 2013; Van Dijk et al. 2014). While exploitation and unregulated trade are the primary causes for sharp declines in many species, habitat loss and fragmentation also drive population declines (Gibbons et al. 2000; Van Dijk et al. 2014). Freshwater turtles are vulnerable to changes in aquatic and terrestrial habitats with loss and fragmentation of terrestrial and riparian habitats disrupting overwintering and nesting sites, and restricting emigration and dispersal among wetlands (Bodie 2001; Bowne et al. 2006). Elimination of aquatic habitat reduces critical feeding and breeding areas (Cosentino et al. 2010; Gibbons et al. 2000; Marchand and Litvaitis 2004) as do

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changes to hydrological regimes through regulating structures and water extraction altering occupancy patterns, population growth, and reproduction (Ashton et al. 2015; Hunt et al. 2013).

River regulation is associated with declines and extinctions of freshwater fishes, waterbirds, frogs, and turtles (Chessman 2011; Kingsford et al. 2006; Meador and Carlisle 2012; Poff and Zimmerman 2010). Changing water availability alters permanent and temporary wetlands through fragmentation and loss of connectivity (Arthington and Balcombe 2011). Determining how these drivers affect turtles is critical for improving environmental management and conservation at landscape scales (Bodie and Semlitsch 2000). Current understanding of these processes lags for turtles, compared with other vertebrates (Chessman 2011; Tucker et al. 2001).

We investigated the poorly known responses to flow availability and variability of three turtle taxa (broad-shelled turtle [*Chelodina expansa*], eastern long-necked turtle [*Chelodina longicollis*], and Macquarie River turtle [*Emydura macquarii macquarii*]) (Georges and Thomson 2010); herein referred to as "species") distributed throughout the lowland floodplain rivers and wetlands of the Murray–Darling Basin (south-eastern Australia). All three species occupy permanent lentic and lotic habitats, but were predicted to vary in their responses, given their differing physiological and behavioral adaptations. Eastern long-necked turtles are known to occur in many different freshwater and terrestrial habitats due to short periods of estivation and an ability to limit water loss and increase water uptake (Chessman 1984a) for traveling overland (Stott 1987). In contrast, the broad-shelled and the Macquarie River turtles are restricted to rivers and permanent slow flowing or still waterbodies, such as lakes or billabongs (Chessman 1988; Spencer and Thompson 2005). Both species have lower resistance to desiccation than the eastern long-necked turtle and neither of the species displays estivation abilities (Chessman 1984a, 1988). Refuges close to the main river channel may be particularly important for all species, providing dependable food supply and nursery areas (Kennett and Georges 1990). Current understanding is primarily based on limited flow scenario analyses (Bower et al. 2012; Rees et al. 2009; Roe and Georges 2008b; Tucker et al. 2001) with relatively little known of responses to large variation in flooding.

We tested the responses of three species of turtles to landscape and site-scale conditions over different sized flood (2008–2014) on the Lower Murrumbidgee floodplain, a large regulated floodplain wetland in the Murray–Darling Basin, Australia. We predicted that the three species would have differing responses to flow and inundation metrics, which reflect their habitat preferences, with broad-shelled turtles and Macquarie River turtles potentially uncommon in variably flooded wetlands. We used the results to identify characteristics of critical habitat across the broader floodplain. Understanding relationships between hydrological regimes and dependent aquatic organisms is critical for provision of effective adaptive management of environmental water (Commonwealth of Australia 2013; New South Wales Government 2008).

Methods

Study Area

The Murray–Darling Basin is a heavily regulated river system (Kingsford 2000; Tucker et al. 2001). Most significant wetlands are in the low-relief, semi-arid, or temperate regions of the Basin, sustained by river flows (Kingsford et al. 2004). This includes the Murrumbidgee River, one of the larger catchments (81,527 km^2) in the Basin, with over 100 years of water resource development (Kingsford 2003). Its lower floodplain (the "Lowbidgee") is downstream of most irrigation and extraction development in the semi-arid zone where the average annual rainfall is low (313.35 mm ± 116.39 SD, gauge number 075049, data range = 1900–2015) (BOM 2016). The floodplain is a large complex of interconnected creeks that formally covered more than 304,000 ha (Kingsford and Thomas 2004). River red gum forest (*Eucalyptus camaldulensis*) and spike rush (*Eleocharis* spp.) characterize the more frequently inundated wetlands near the Murrumbidgee River, with black box-lignum (*Eucalyptus largiflorens-Duma florulenta*) wetlands across the less frequently flooded, higher areas of the floodplain. Areas of functional wetland have been reduced over the past 50 years as a result of the construction of levees, clearing of native vegetation across the floodplain, and upstream diversion for irrigation (current size 128,000 ha) (Kingsford and Thomas 2004). Despite significant hydrological alteration and land clearing, the Lowbidgee floodplain remains one of Australia's most ecologically significant wetland landscapes (Bino et al. 2015).

Apart from years of widespread flooding, inflows to the Lowbidgee wetlands are managed with regulators, channels, and weirs that allow water to be moved onto the floodplain, even during periods of low flow in the main river channel. State and Commonwealth governments deliver environmental water to this wetland complex to support permanent and semi-permanent wetland vegetation and wetland-dependent fauna groups with water availability varying in a given season according to prevailing climatic conditions (New South Wales Government 2008). Consequently, waterbodies vary in their permanency and connectivity,

allowing an opportunity to test flow-ecology relationships over a large landscape.

Surveys

We surveyed 23 sites (Table 1) in October, December, February, and April during the 2008–2009, 2009–2010, 2010–2011, and 2013–2014 spring–summer seasons (total of four survey seasons), coinciding with annual spring flood events (natural or managed environmental flow release). The 2008–2009 and 2009–2010 survey seasons were during a prolonged drought ("Millennium Drought": 1996–2010; Ummenhofer et al. 2009), following a long period (since 2005) of low flows and limited local rainfall to the Lowbidgee floodplain. Small environmental water releases (~2500 ML) and stock and domestic flows (~5000 ML) occurred during 2008–2009. In the 2009–2010 season, winter rain coincided with environmental water releases (~25,000 ML) with further managed releases over spring–summer 2009–2010 (~16,700 ML in total). In winter 2010, large managed environmental water releases took place (~59,000 ML) from July–October, which were followed by widespread natural flooding over November 2010–January 2011 (Fig. 1). Another large natural flood occurred in autumn 2012 (Fig. 1) with managed environmental releases targeting areas of the Lowbidgee floodplain occurring before and after the natural flood in 2011–2012 and 2012–2013 (33,542 ML and 2700 ML, respectively). The 2013–2014 survey season coincided with large managed releases (~200,000 ML). The same sites (wetlands) were surveyed within each survey season, but limited accessibility meant that the 23 sites were not consistently surveyed. Between 10 and 18 sites were surveyed each season, with three sites surveyed in all four seasons (see Table 1). Sites during the 2011–2012 and 2012–2013 seasons were surveyed with different sized nets that were not comparable to the other years, and these seasons were not included in the analysis.

Two unbaited fyke hoop nets with 2×10 m wings, a 1 m drop, and 12 mm tricot mesh were set at each site to survey turtles. Nets were set late afternoon (1 or 2 h before sunset) and cleared within 2 h of sunrise. The nets were set with the end secured out of the water, so that turtles were able to access air after they entered the net. Turtles were identified to species (Georges and Thomson 2010) and measured for maximum straight carapace and plastron length (mm). We used carapace and plastron lengths for hatching size from literature to estimate the number of recent hatchlings: eastern long-necked hatchling size (~30 mm carapace length; Kennett et al. 2009), Macquarie River turtles (~27 mm plastron length; Spencer 2001), and broad-shelled turtle (~35 mm carapace length; Bower and Hodges 2014). Eastern long-necked turtle less than 180 mm carapace length were classed as juveniles following Chessman (2011) in order to calculate the total number and relative proportion of juveniles (number of juveniles divided by total number of turtles) in each survey season. Each turtle was released back into the wetland as soon as possible after capture.

Environmental Metrics

We collected site data on hydrology, inundation, and water temperature at three temporal scales: survey (October, December, February, and April), annual (June–July "water" year, which coincides with water delivery over austral spring and summer), and long term (July 1988–June 2014) (Table 2). Coinciding with field surveys, we determined inundation metrics using inundation maps, and surveyed for fish, aquatic vegetation cover, and average water temperature. Inundation maps for the Lowbidgee floodplain were derived from Landsat Thematic Mapper satellite imagery (25×25 m cell size) by combining water and vegetation spectral indices to classify different inundation states that were merged to map inundation at a point in time (Thomas et al. 2015). Inundation map dates were matched with the survey occasion date (maximum 30 days between survey occasion and map date). For each site, an inundation metric for each survey occasion was calculated as the proportion of cells inundated within the area of a 500-m radius from the center of the survey site.

We included fish catch-per-unit-effort (CPUE) as eastern long-necked and broad-shelled turtles are obligate carnivores, and high fish densities may also influence behavior through competition (Chessman 1984b; Spencer et al. 1998). We calculated CPUE as the average of the sum of fish across four nets using the two large-sized nets and two additional small-sized mesh nets (2-mm mesh) to ensure capture of small and large-sized species. Aquatic vegetation forms an important structural component for turtles and may also influence behavior, given that dense vegetation can restrict movement (Marchand and Litvaitis 2004). During surveys, we visually estimated the summed percentage cover of all four types of aquatic vegetation: tall emergent (>30 cm, i.e., *Typha* spp.), short emergent (<30 cm, i.e., *Eleocharis acuta*), floating (i.e., *Ludwigia peploides*), and submerged (i.e., *Myriophyllum* spp.). In addition, we collected three site measurements of water temperature using a hand-held multi-parameter water quality meter (EXO2 Multiparameter Sonde, YSI Incorporated).

To obtain an annual (i.e., water-year) metric of inundation, we spatially overlaid all inundation maps within a water-year to create an annual total inundation area map (inundated cell value = 1). From each map we calculated the annual total inundation extent for the Lowbidgee floodplain and for each site we calculated the proportion of

Table 1 Site characteristics and summary of sampling regime

Site code	Dominant vegetation	Longitude	Latitude	Long-term inundation frequency[a]	Dist. to river (m)	No. of surveys	Site surveyed during spring–summer season			
							2008–2009	2009–2010	2010–2011	2013–2014
IAS	River red gum	143.804	−34.381	0.62	47.69	7	Y	Y		
AVA	Black box/Lignum	143.9174	−34.5812	0.45	37 790	13	Y	Y	Y	Y
EUL	Lignum	144.1855	−34.5596	0.48	14 093	7	Y	Y		
GAB	River red gum	143.641	−34.5771	0.42	32 098	1		Y		
GAS	River red gum	143.6301	−34.5723	0.23	30 898	1		Y		
LOO	River red gum	143.8921	−34.6168	0.42	37 790	4				Y
MER	River red gum	145.5109	−34.3791	0.61	147	11	Y	Y	Y	Y
MON	Black box/Lignum	143.822	−34.4799	0.53	63 700	5	Y	Y		
MUR	River red gum	143.6502	−34.5354	0.31	26 468	3		Y	Y	
NAP	Black box/Lignum	144.1016	−34.4366	0.59	11 393	5		Y	Y	Y
NRC	River red gum	143.7735	−34.3778	0.45	41	1	Y			
PCS	River red gum	143.7932	−34.374	0.26	977	4	Y			Y
PIG	River red gum	143.7622	−34.4262	0.49	7 483	7		Y	Y	Y
RIV	River red gum	143.6114	−34.6336	0.33	44 148	7		Y	Y	Y
SES	Lignum	144.1984	−34.5956	0.43	16 979	6	Y	Y		
SPR	River red gum	143.643	−34.5429	0.23	27 636	1		Y		
STE	River red gum	143.6767	−34.4825	0.38	21 818	6		Y	Y	Y
SUI	Lignum	144.0504	−34.5448	0.5	25 865	3			Y	
TBR	River red gum	143.7918	−34.4046	0.48	10 781	10	Y	Y	Y	Y
TEL	River red gum	144.0248	−34.514	0.46	38 997	7	Y	Y	Y	
WAG	River red gum	143.8793	−34.3885	0.7	3 629	11	Y	Y		Y
WAR	Black box/Lignum	143.9847	−34.5875	0.53	33 954	9	Y	Y	Y	
YAN	River red gum	143.5916	−34.7046	0.4	100 936	3		Y	Y	
					Total sites		12	18	12	10

[a] Average long-term (July 1988–June 2014) frequency of inundation (probability) of cells within a 500-m radius of center of the site based on overlaying the annual total inundation area maps, counting the number of times a cell was inundated and dividing by number of years

Fig. 1 Rainfall (mm) (**a**, gauge number 075049 Maude [Nap Nap]) and river flows (monthly cumulative volume) (**b**, gauge 410040) for the Lowbidgee floodplain over the study period (July 2008–June 2014) and survey occasions (*open circles*)
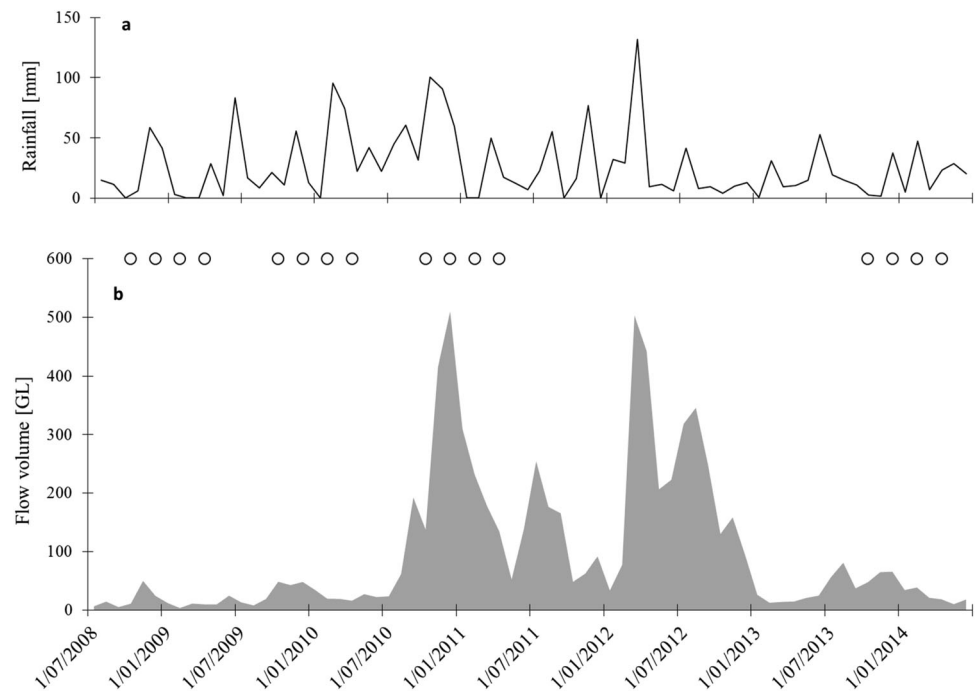
inundated cells within the 500-m radius area. We obtained an annual metric of fish CPUE, vegetation cover, and temperature by averaging the four survey occasions for each variable.

Long-term metrics measured inundation frequency and connectivity (distance between the main Murrumbidgee River and each mapped wetland). The long-term inundation frequency of the floodplain was estimated by first calculating annual total inundation areas from 1988 to 2014 and then calculating the long-term ($n = 26$) annual probability each cell was inundated. We then calculated the site average of the long-term inundation within the 500-m radius area. We calculated two distance metrics between each wetland and the nearest section of the Murrumbidgee River. The straight-line distance (calculated using Near tool in ArcGIS ver9.3) was considered to be biologically relevant for the eastern long-necked turtle as they move overland, while a "hydrological-path" distance (Table 1) was considered relevant to the broad-shelled and Macquarie River turtles, as movement tends to be restricted to streams or channel. For the hydrological-path distances, major creeks and irrigation channels were first mapped using LiDAR Digital Elevation Model and aerial imagery, and the distances between wetlands and the river via those pathways, calculated using the Calculate Geometry tool in ArcGIS ver9.3.

Modeling Approach

We assessed any association between maximum straight carapace length of the three species and three explanatory variables: long-term inundation frequency, total inundation extent of that year, and survey season, with generalized linear models assuming Gaussian distribution of errors, using a Bayesian Model Averaging (BMA) approach. We implemented this in the BMA package (Raftery et al. 2011), within the R statistical software (R Core Team 2014).

We quantified the association of environmental and habitat variables and abundance of the three turtle species. As we had sufficient sample sizes for the eastern long-necked turtle, we used a robust hierarchical modeling approach that enabled estimation of the association of environmental and habitat variables, while accounting for confounding effects of environmental conditions on detection. We employed a BMA approach, with generalized linear models for the broad-shelled turtle and Macquarie River turtle, due to the low sample sizes. We also analyzed the eastern long-necked turtle data using the BMA, to allow a more consistent comparison of variable associations among the three species and avoid comparisons across different modeling approaches.

The hierarchical modeling approach allows estimation of the abundance of mobile species with imperfect detection, not uniquely marked. It is based on a repeated measures survey design of count data from multiple sites within multiple seasons, and jointly estimates abundance (λ), annual availability emigration (φ), and detection probability (p) (Chandler et al. 2011; Royle 2004; Royle and Nichols 2003). The advantage of separating abundance, the probability the individual is available, and detection probabilities is that estimates of abundance are explicitly modeled and

Table 2 Description of the variables included in the modeling of turtle abundance using two methods, a generalized linear modeling within a BMA framework and a hierarchical modeling approach (calculated for each site)

Scale	Name	Description
Survey	Water temperature (W.T.)	Average of water temperature during each of the survey occasions (October, December, February, and April)
	Inundation (Inun.)	Inundation extent during each of the sample occasions (October, December, February, and April) based on proportion of cells classified as inundated within 500-m radius of the center of the site
Annual	Yearly water temperature (Y.W.T.)	Average water temperature across the four survey occasions in each survey season
	Fish	Average CPUE (average of the sum of fish across four nets using two large-sized mesh and two small-sized mesh nets) of the four survey occasions in each survey season
	Aquatic vegetation (Veg.)	Average percent aquatic vegetation cover across all survey occasions in each survey season
	Yearly inundation (Y.Inun.)	Annual total proportion of cells inundated within 500-m radius of the center of the site using all available inundation maps from a year (July to June)
Site (long-term)	Distance to river (D.Riv.)	Hydrological-path distance (m) to Murrumbidgee River along major creeks and channels
	Long-term inundation (L.T.Inun.)	Average long-term (July 1988–June 2014) frequency of inundation (probability) of cells within a 500-m radius of center of the site based on overlaying the annual total inundation area maps, counting the number of times a cell was inundated and dividing by number of years

not confounded by changes in availability among survey seasons or by imperfect detection during survey visits (Chandler et al. 2011; Guillera-Arroita et al. 2014). The model assumes that availability of an individual is contingent on the probability it is present and provided it is detected during the survey. This model takes the form:

$$M_i \sim Poisson(\lambda), \ N_{it} \sim Binomial(M_i, \varphi_{it}),$$
$$and \ y_{it} \sim Multinomial(N_{it}, \pi_{it}),$$

where M_i is the total number of individuals that could be detected at patch i; N_{it} is the number of individuals present in patch i at time t; y_{it} is a vector of counts made in patch i at time t; and π_{it} is a vector of multinomial cell probabilities derived from a detection probability function. These models require that within a survey season, sites are sampled several times and assumes that abundances do not change (Chandler et al. 2011). By excluding sites that were only surveyed once, confining our sampling to the 6 month spring–summer season that coincides with peak activity for the species and not including hatchlings in our analysis, we consider the population closure assumption reasonably met. We considered mortality occurring during a single season highly unlikely because of the high adult survivorship of the species (Parmenter 1985; Roe et al. 2009). We also had no reason to suspect that among year temporary emigration rates (affecting annual availability) were asymmetric and assumed that completely random emigration would not affect abundance estimations (Chandler et al. 2011).

We used the total number of individuals caught during each survey as the response variable. Variation at each

parameter can be directly modeled as a function of variables. For the abundance parameter we used the site-level covariates: long-term inundation frequency and distances (straight and hydrological-path) to the main river, where each distance metric was included in the model set separately. Annual availability is represented at the annual scale; for this parameter we considered factors suspected to influence movement among the survey years. This included the total inundation extent of that year, and average annual fish CPUE and average annual aquatic vegetation cover. We considered detection would be influenced by water temperature as turtles are ectotherms (Huey 1982). We also included the inundation extent during each survey occasion as a detection variable as the probability of detecting individuals may be influenced by the amount of water around each site. We compared all possible combinations of variables but excluded models with both straight-line distance and hydrological-path distance in the same model (128 combinations in total). Model performance was assessed using the akaike information criterion (AIC) criteria, considering models within four AIC units from the lowest score as plausible models. We then used AIC model weights to predict abundances and annual availability of eastern long-necked turtle at each of our surveyed sites.

Dealing with the count data for the BMA approach, we assumed Poisson distribution of errors. The model averaging approach enabled us to combine predictions from several candidate models, while accounting for model uncertainty. BMA combines the predictions of a large sample of possible models, using a weighted averaging algorithm based on Bayes' theorem, with weights proportional to the posterior

probability representing the relative strength of evidence in favor of each model (Wintle et al. 2003). The BMA process assumes that all considered models partially explain the data, but only a subset chosen on the basis of the Bayes information criterion (BIC) are combined to improve the overall predictive power of the final model (Hoeting et al. 1999). The final model then incorporates the variables and their averaged coefficients weighted according to the BIC scores. We examined the relationship between average annual abundance of each species and six covariates: annual proportion of inundation extent, average annual fish CPUE, average annual aquatic vegetation cover, average annual water temperature, long-term inundation frequency, and distance to main river metrics. We implemented this using the BMA package (Raftery et al. 2011), within the R statistical software (R Core Team 2014).

Results

Annual total wetland area of the Lowbidgee floodplain was limited to a small area during the 2008–2009 and 2009–2010 survey season (3608 and 8597 ha, respectively) (Fig. 2a, b). The 2010–2011 survey season coincided with a natural flood, which inundated 183,200 ha of the Lowbidgee floodplain (Fig. 2c), while the managed environmental flow event in 2013–2014 inundated 37,800 ha (Fig. 2d).

During 132 site surveys, we captured a total of 529 turtles (Table 3). The eastern long-necked turtle was the most frequently captured ($n = 346$), with at least one individual caught in each site (Fig. 3). Less broad-shelled turtles and Macquarie River turtles were caught ($n = 59$ and 21, respectively) at fewer sites ($n = 6$ and 7, respectively) (Fig. 3, Table 3) than the eastern long-necked turtle. At least one individual from all three species was caught during each survey season. We caught an average of 2.6 eastern long-necked turtles per site survey (± 4.4 SD, range = 0–27), 0.45 broad-shelled turtles (± 1.4 SD, 0–10), and 0.16 Macquarie River turtles (± 0.6, 0–4). The highest average number of captures per site for all three species was during the 2009–2010 survey season (Table 3).

Recent hatchlings were recorded in only two sites, both river red gum-spike rush wetlands adjacent (<500 m) to the Murrumbidgee River (Fig. 3). Two eastern long-necked turtles were within the size range for hatchlings (18 mm, February 2009 and 23 mm, September 2014) both from Mercedes Swamp (MER, Table 1). Three Macquarie River turtles close to hatchling size were caught; two at MER (28 mm, February 2010; 36 mm, February 2011) and one at Paul Coates Swamp (PCS, Table 1) (36 mm, April 2014). No hatchling broad-shelled turtles were detected.

Maximum carapace lengths appeared to be generally consistent across survey seasons for the broad-shelled turtle and the Macquarie River turtle, though small sample sizes prevented us from making any statistical inference (Fig. 4). We caught a higher absolute number and relative proportion of eastern long-necked juvenile-sized turtles during the 2013–2014 season compared with the other seasons (number of juvenile turtles = 20, relative proportion = 0.40; 2008–2009: 14, 0.07; 2009–2010: 14, 0.05; 2010–2011: 7, 0.11) (Fig. 4). This was reflected in the modeling as sizes of eastern long-necked turtles decreased significantly in the last survey season (2009–2010: BMA covariate coefficients = 0.71 ± 2.49 SD, BMA posterior probability of inclusion (pp) = 10.8; 2010–2011: -1.62 ± 4.32 SD, pp = 15.6; 2013–2014: -31.49 ± 6.40 SD, pp = 1.00), but did not have a significant association with either long-term inundation frequency (-1.95 ± 8.51 SD, pp = 10.8) nor with annual total inundation extent (-5.16 ± 10.15 SD, pp = 25.2) (Fig. 4, Table 3).

Connectivity of the wetlands to the Murrumbidgee River measured as hydrological-path metric performed better in the models compared with the straight-line distance. Hierarchical model and BMA models of eastern long-necked turtles were consistent except for yearly inundation that was not significant using the BMA approach, but was supported as an important variable on annual availability in the hierarchical modeling (Tables 4 and 6). Abundance, availability, and detection of the eastern long-necked turtle were all influenced by at least one of the long-term, annual, or survey-level variables, respectively (Table 2). The four models in the best model set consistently included long-term inundation frequency and hydrological-path distance to the Murrumbidgee River (Table 4) as an influence on abundance, where abundance was negatively related to increasing distance from the river and positively related to increasing inundation frequency, though this latter relationship was not as well supported (i.e., SE larger than the coefficient, Table 5).

All three annual variables featured in the best model set were related to annual availability of eastern long-necked turtles. Fish CPUE and aquatic vegetation had a negative relationship with annual availability among water-years (Table 5). The annual total inundation extent was also negatively related to emigration but only included in two of the four top models. Detection probability of the eastern long-necked turtle was consistently associated with water temperature during surveys, where detection increased slightly with increasing water temperatures. After correcting for detectability, the hierarchical models predicted an average abundance of 24.48 ± 4.58 SD (range 19.99–36.44) eastern long-necked turtles per site.

Associations with hydrological and environmental covariates from the BMA varied between the three species (Table 6, Figs. 5, 6 and 7), excluding yearly inundation that was a common influence on all species though the direction of the relationship varied). Long-term inundation frequency of the site was positively associated with abundances of
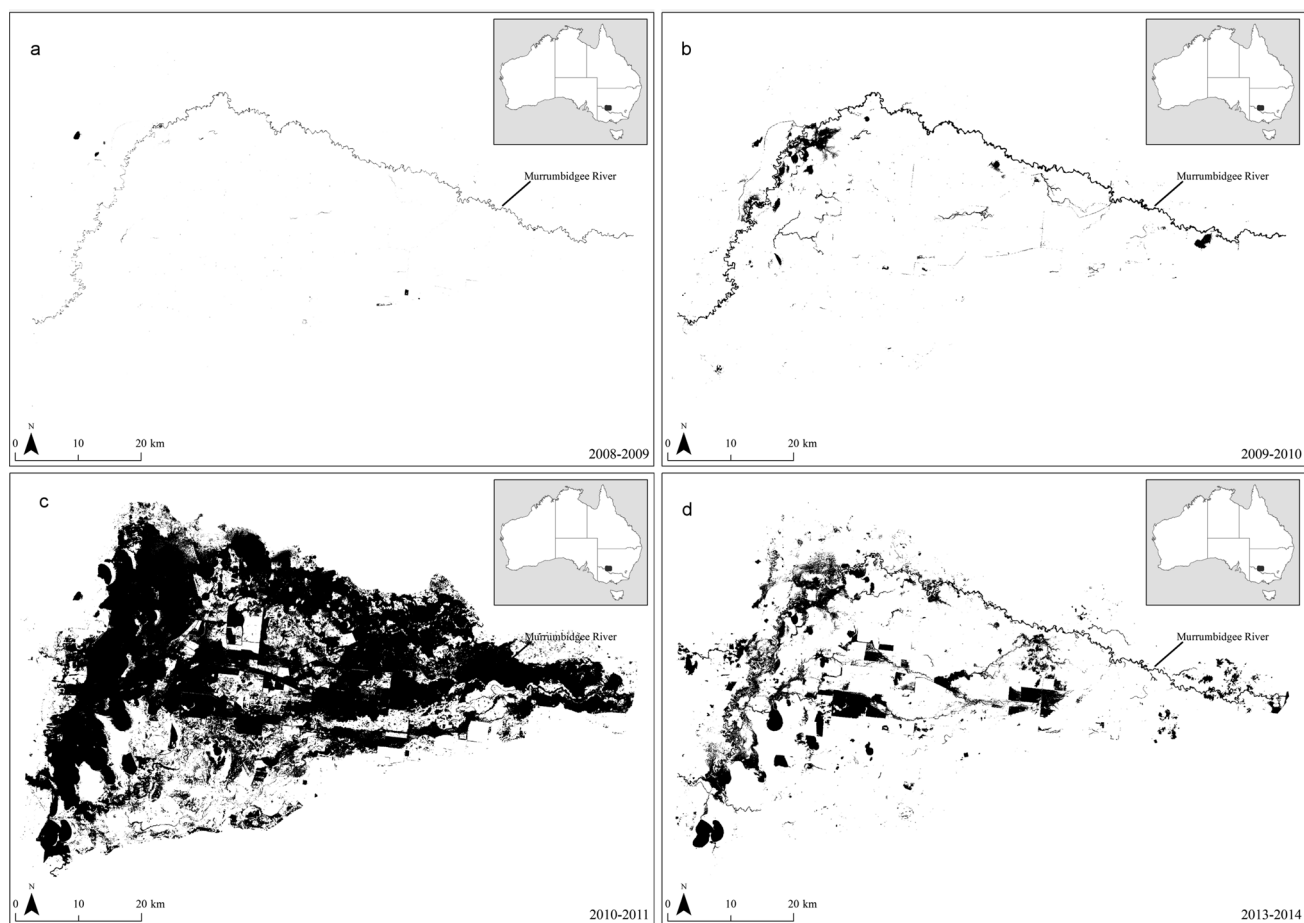
Fig. 2 The total area of Lowbidgee River floodplain inundated for each survey season: **a** 2008–2009, **b** 2009–2010, **c** 2010–2011, and **d** 2013–2014

both broad-shelled and Macquarie River turtles, with broad-shelled turtles having the strongest association (Fig. 5, Table 6). Distance to the river had a small but significantly negative association with abundance of the Macquarie River turtle (Fig. 7), where abundance decreased slightly with increasing distance along hydrological pathways. Annual inundation extent around the site was significantly negatively related to broad-shelled turtle abundance (Fig. 5) but not to the Macquarie River turtle (Fig. 7). Annual fish CPUE had a small but significant negative association with abundance of the broad-shelled turtle (Fig. 5, Table 6). Unlike the eastern long-necked turtle, water temperature and vegetation were not related to abundance of broad-shelled turtle or the Macquarie River turtle (Table 6, Figs. 5, 6 and 7).

Discussion

Responses of freshwater turtles to variable flooding regimes at landscape scales are poorly known. Abundances of three turtle

Table 3 Annual captures (sum, mean ± 2SD [min–max]) of three turtle species caught at 23 sites on the Lowbidgee floodplain

Species	Water year	Turtle counts
Broad-shelled turtle	2008–2009	24, 0.75 ± 2 (0–10)
(*Chelodina expansa*)	2009–2010	25, 0.86 ± 1.64 (0–5)
	2010–2011	1, 0.03 ± 0.16 (0–1)
	2013–2014	9, 0.26 ± 1.08 (0–5)
Eastern long-necked turtle	2008–2009	125, 3.91 ± 4.56 (0–16)
(*Chelodina longicollis*)	2009–2010	119, 4.1 ± 6.57 (0–27)
	2010–2011	61, 1.65 ± 2.66 (0–10)
	2013–2014	44, 1.29 ± 2.56 (0–11)
Macquarie River turtle	2008–2009	1, 0.03 ± 0.18 (0–1)
(*Emydura macquarii*	2009–2010	10, 0.34 ± 0.94 (0–4)
macquarii)	2010–2011	7, 0.19 ± 0.74 (0–4)
	2013–2014	3, 0.09 ± 0.29 (0–1)

species differed with flow variability and wetland features on the highly regulated Lowbidgee floodplain. The eastern long-necked turtle exploited a wide range of aquatic habitats, while
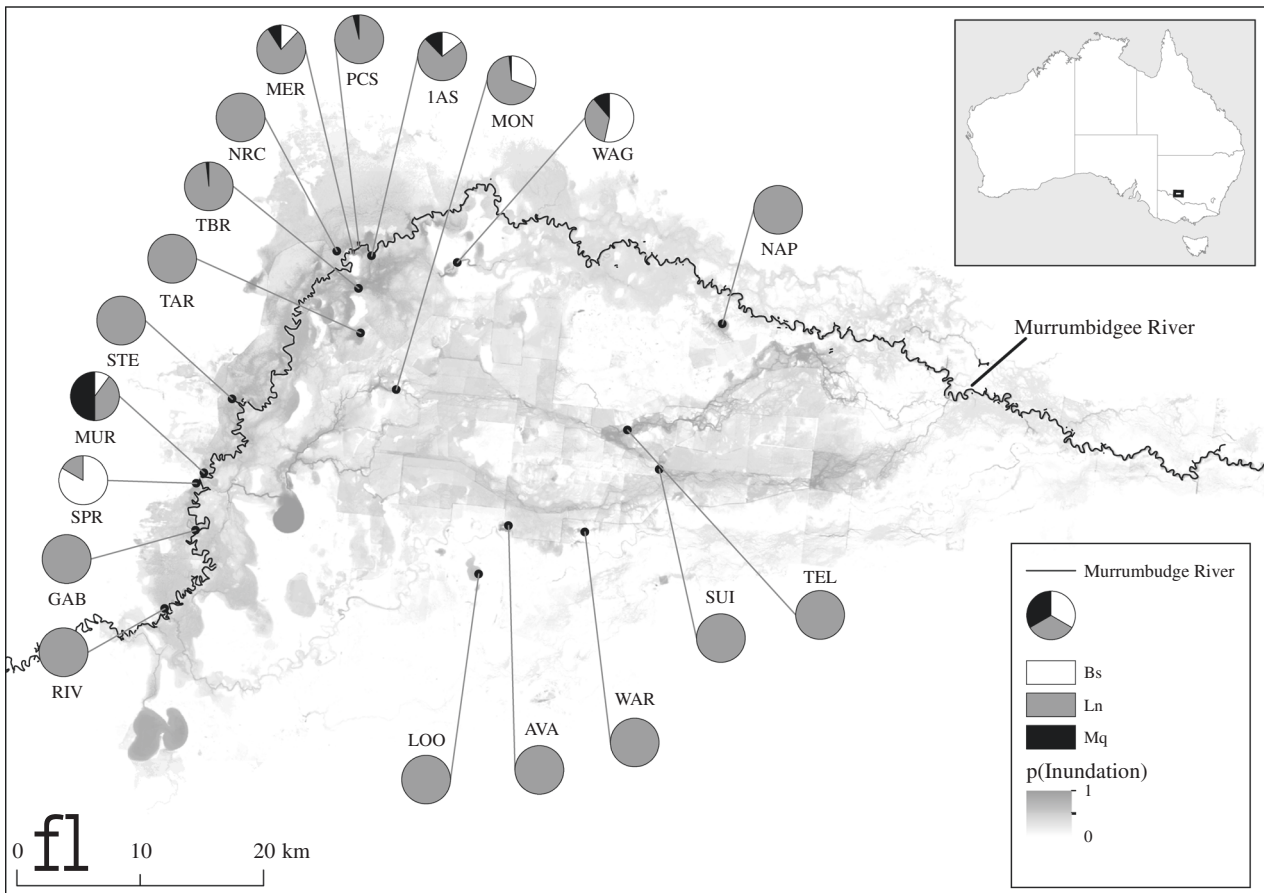
Fig. 3 Inundation probability across the Lowbidgee floodplain (July 1988–June 2014, increasing *gray* indicates increasing flood frequency) and site locations (*black circles*) with relative capture proportions of the three turtle species (*open* = broad-shelled turtle [Bs], *gray* = eastern long-necked turtle [Ln], *black* = Macquarie River turtle [Mq]) (2008–2014). The site codes are detailed in Table 1. Sites where recent hatchlings were caught were MER and PCS

the two predominantly riverine species, Macquarie River and broad-shelled turtles, had restricted distributions, closely associated with wetlands with high inundation frequency and close to the river (Fig. 3). There were critical habitats for all species during dry periods, with mobility and exploitation of highly productive temporary waterbodies during flood periods, reflecting findings of other small-scale studies (Chessman 1988; Spencer and Thompson 2005).

Landscape-Scale Influences and Critical Habitat

For eastern long-necked turtles, concurrence between the robust hierarchical modeling and the BMA suggested that, even when detectability was separable, the explanatory variables with strong associations were still identified. Eastern long-necked turtle populations persist by using a spatiotemporal mosaic of wetlands, with varying inundation duration. Permanent waterbodies are less favorable to eastern long-necked turtles (Roe and Georges 2007) due to competition with the larger broad-shelled and Macquarie River turtles and fish (Chessman 1984b, 1988; Kennett and

Georges 1990). While eastern long-neck turtles move overland to feed on high prey densities in temporary wetlands and ponds (Kennett and Georges 1990), they still require critical refuge habitats during extended drought scenarios, as estivation is limited by fat reserves and dehydration, rarely lasting more than 7 months (Roe et al. 2008).

Eastern long-necked turtle populations probably decline during long dry periods due to crowded permanent refuges and loss of subsequent productive, temporary wetlands (Chessman 2011). The many juveniles caught during 2013–2014 season in the Lowbidgee floodplain, compared with drought years (2008–2009 and 2009–2010 seasons), likely reflected a new cohort entering the population after multiple years of flooding (Fig. 1), similar to along the River Murray (Chessman 2011).

The distribution of broad-shelled and Macquarie River turtles indicated they had limited mobility, although individuals are known to have some capacity to move to connect wetlands (Bower et al. 2012; Katie Howard personal communication). Frequently inundated wetlands and deep
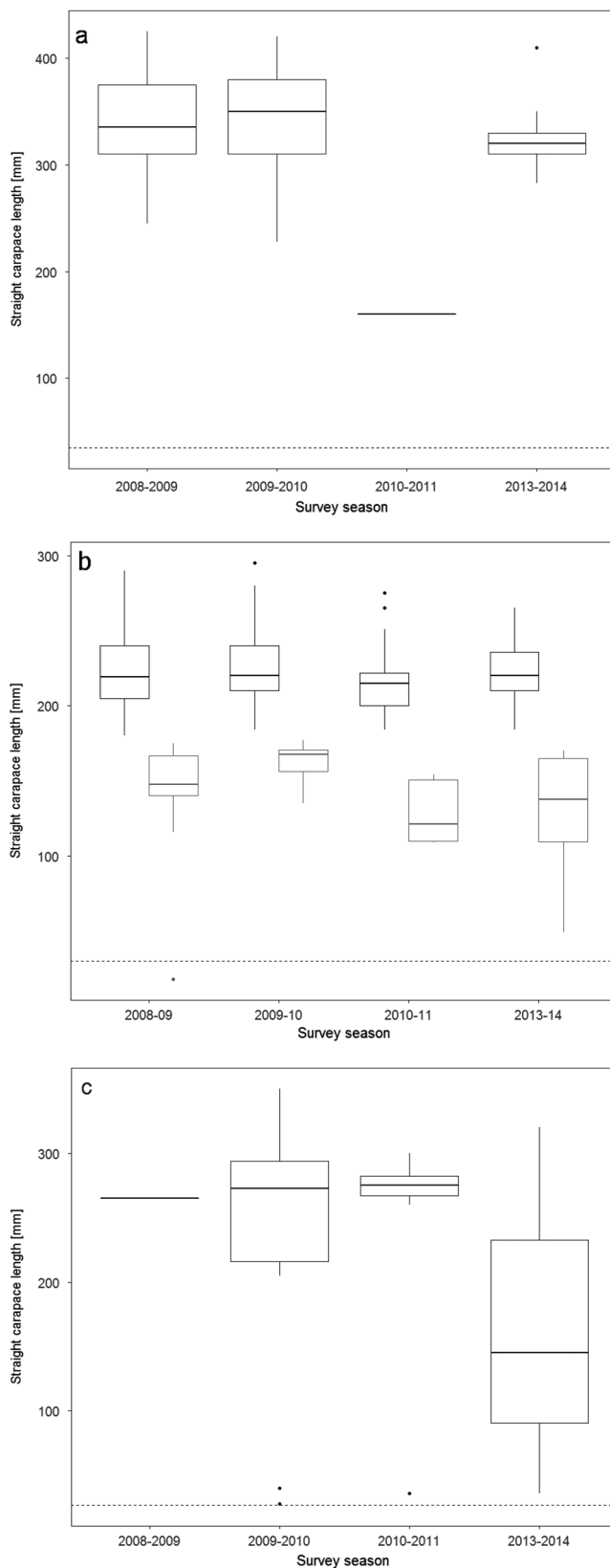
Fig. 4 Boxplots of straight carapace length of **a** broad-shelled turtle, **b** eastern long-necked turtle, and **c** the Macquarie River turtle during the four survey seasons. Eastern long-necked turtle individuals were separated into adults (*black lines*) and juveniles (*gray lines*) following Chessman (2011). The lower and upper "hinges" correspond to the first and third quartiles (the 25th and 75th percentiles). The numbers underneath the box indicate the number of individuals on which the boxplot is calculated. *Dashed line* indicates hatchling length (carapace length used for broad-shelled turtle and eastern long-necked turtle, plastron length used for Macquarie River turtle.)

Table 4 Results of the hierarchical model selection process, showing the best explanatory models (ΔAIC < 2) for the eastern long-necked turtle (*Chelodina longicollis*) (abundance = λ, temporary emigration = φ, and detection probability = p)

Model	K	AIC	ΔAIC
λ(L.T.Inun+D.Riv) φ(Fish+Veg+Y.Inun) p(W.T.)	9	611.7699	0
λ(L.T.Inun+D.Riv) φ(Fish+Veg) p(W.T.)	8	612.0343	0.2644
λ(L.T.Inun+D.Riv) φ(Fish+Veg) p(W.T. +Inun)	9	612.8311	1.0612
λ(L.T.Inun+D.Riv) φ(Fish+Veg+Y.Inun) p(W.T.+Inun)	10	613.7094	1.9395

Table 5 Parameter estimates ($\beta \pm$ SE, log scale) for covariates from averaged models within four ΔAIC of highest ranking models affecting abundance (λ), availability (φ), and detection rates (p) of the eastern long-necked turtle (*Chelodina longicollis*)

| Covariate	$\beta \pm$ SE
Intercept (λ)	3.19 ± 0.44
D.Riv (λ)	-0.16 ± 0.06
L.T.Inun (λ)	0.24 ± 0.6
Intercept (φ)	4.24 ± 1.22
Fish (φ)	-1.33 ± 0.48
Veg (φ)	-0.86 ± 0.29
Y.Inun (φ)	-1.34 ± 1.01
Intercept (p)	-2.99 ± 0.43
W.T. (p)	0.07 ± 0.02
Inun (p)	-0.21 ± 0.31

lagoons that retained water for long periods in the Low-bidgee probably constituted core habitat from which individuals dispersed, given both species have limited capacity to wait out dry periods by moving or estivating (Chessman 1984a, 1988). Given this, occupancy across the Lowbidgee floodplain may reflect site fidelity in the persistent water-bodies further from the main river channel and opportunistic movement into wetlands close to the river.

The comparatively low numbers of broad-shelled and Macquarie River turtles, particularly the Macquarie River turtles (cf. Chessman 1988; Francis 2015; Howard et al. 2013, Cultural conservation of freshwater turtles in Barmah-

Table 6 Covariate coefficients (± SD) and significance levels (pp = posterior probability (pp) of inclusion, where pp value is positive correlated with significance) from BMA of generalized linear models for three turtle species

Covariate	Broad-shelled turtle	Eastern long-necked turtle	Macquarie River turtle
Intercept	−4.46 ± 1.59 (pp=1.00)	0.71 ± 0.71 (pp=1.00)	−3.58 ± 3.21 (pp=1.00)
L.T.Inun	**8.70 ± 1.92 (pp=1.00)**	0.46 ± 0.74 (pp=0.38)	1.31 ± 2.66 (pp=0.29)
D.Riv	0.01 ± 0.07 (pp=0.11)	**−0.29 ± 0.07 (pp=1.00)**	**−0.44 ± 0.33 (pp=0.75)**
Y.Inun	**−5.43 ± 1.37 (pp=1.00)**	−0.06 ± 0.20 (pp=0.18)	**1.86 ± 1.83 (pp=0.64)**
Fish	**−0.60 ± 0.54 (pp=0.66)**	**−0.71 ± 0.19 (pp=1.00)**	−0.07 ± 0.35 (pp=0.14)
Veg	−0.05 ± 0.19 (pp=0.16)	**−0.50 ± 0.11 (pp=1.00)**	−0.21 ± 0.44 (pp=0.27)
Y.W.T.	−0.003 ± 0.02 (pp=0.17)	**0.12 ± 0.02 (pp=1.00)**	0.07 ± 0.10 (pp=0.43)

Note: Significant results in bold
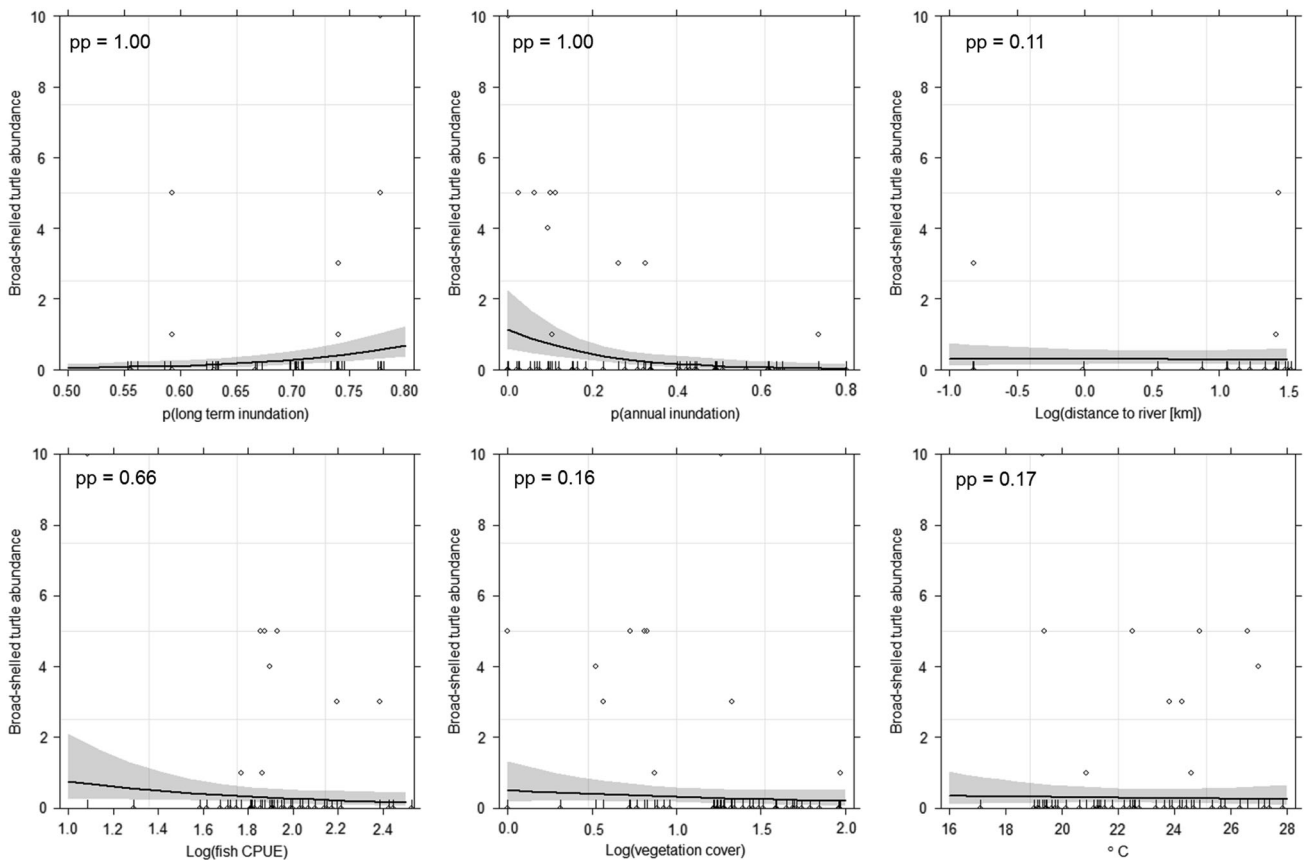
Fig. 5 Predicted average annual abundance and 95% CI of the broad-shelled turtle in response to six site variables: average long-term of inundation probability (L.T Inund), annual inundation (Y.Inun.), average annual fish CPUE (Fish), average annual aquatic vegetation cover (Veg.), hydrological-path distance (D.Riv), and average annual water temperature (W.T.) based on the BMA of Generalized Linear Models. Significance levels indicated by "pp" (posterior probability (pp) of inclusion), where the pp value is positive correlated with significance (see Table 6). *Light gray circles* represent the scatter of values
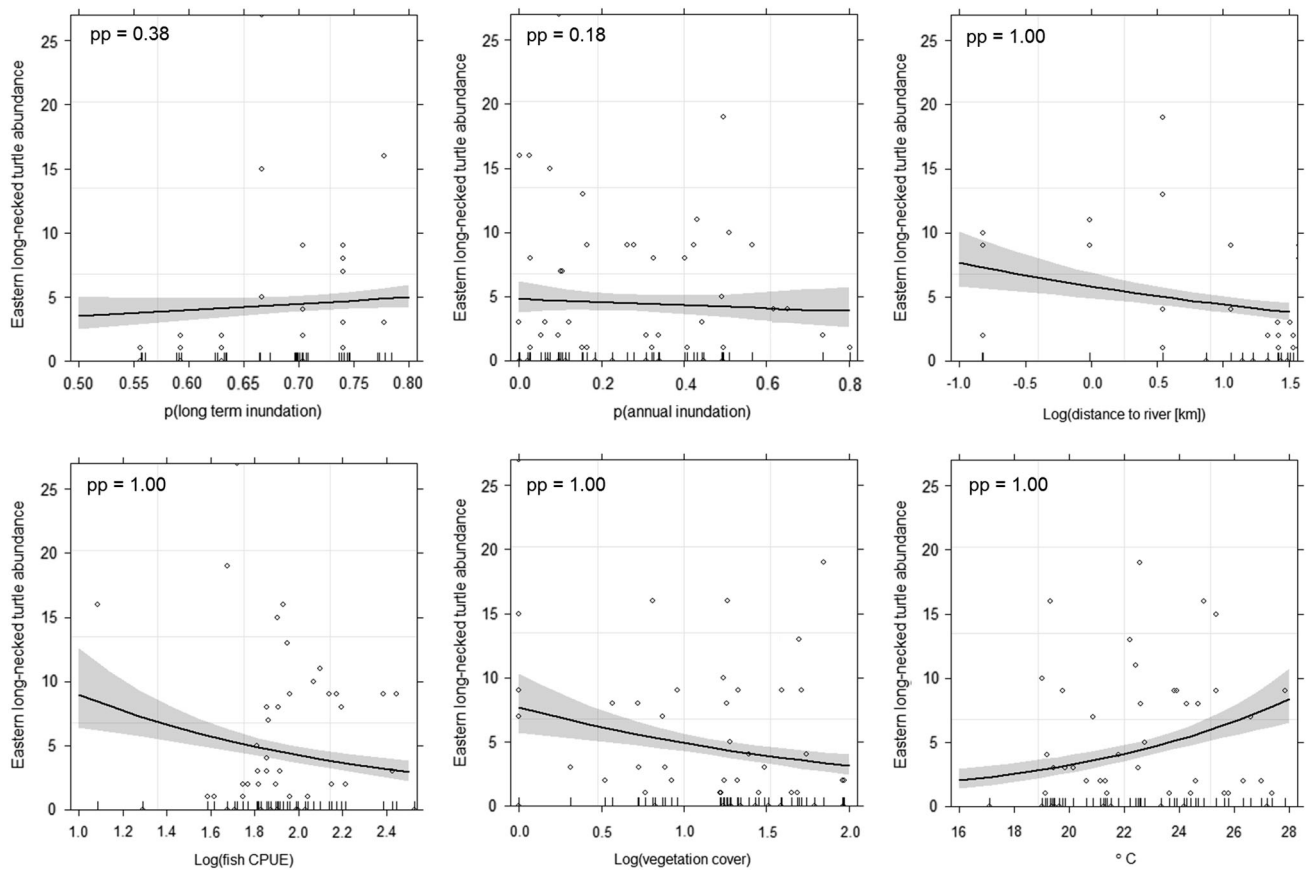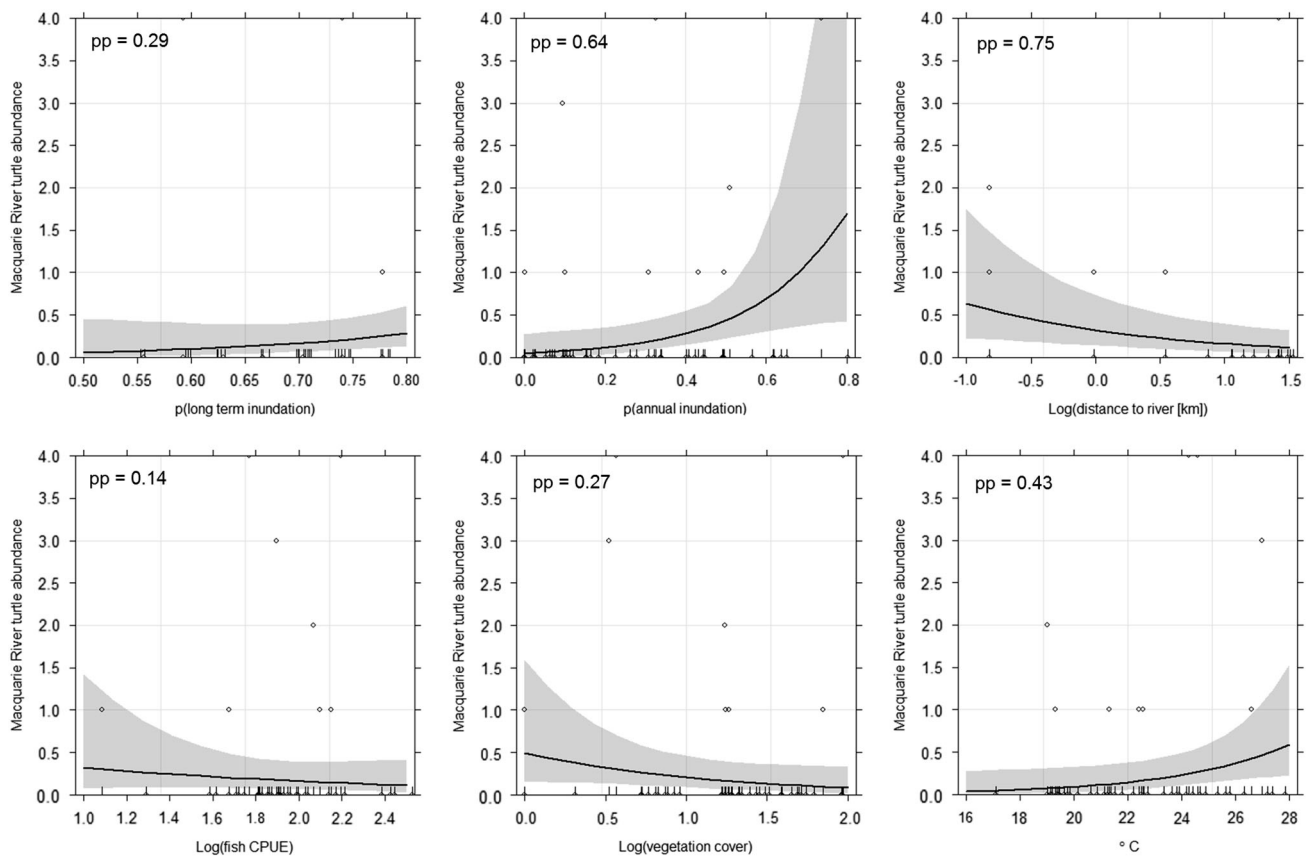
Fig. 6 Predicted average annual abundance and 95% CI of the eastern long-necked turtle in response to six site variables: average long-term of inundation probability (L.T Inund), annual inundation (Y.Inun.), average annual fish CPUE (Fish), average annual aquatic vegetation cover (Veg.), hydrological-path distance (D.Riv), and average annual water temperature (W.T.) based on the BMA of Generalized Linear Models. Significance levels indicated by "pp" (posterior probability (pp) of inclusion), where the pp value is positive correlated with significance (see Table 6). *Light gray circles* represent the scatter of values

Millewa Forest 2011–12, Unpublished Report) limited our ability to model abundance separate from detection. The low capture rates may reflect lack of monitoring sites on the main river, low detectability due to the insufficient survey effort per site, reliance on a single trapping method, or genuinely low population abundances. Increased survey effort is needed in the Murrumbidgee River and closely connected creeks to separate these confounding variables. A low population could be due to nest predation by foxes (Spencer and Thompson 2005) but also from the loss of most of the seasonally inundated and permanent lagoons that once occurred the length of the river through the floodplain (Chessman 2011; Kingsford and Thomas 2004).

Over four seasons, we recorded hatchlings of eastern long-necked and Macquarie River turtles at only 2 of the 23 survey sites (Fig. 2). Little is known of hatchling ecology and behavior of eastern long-necked and Macquarie River turtles, probably because they have a lower capture rate than adults. Both were captured at wetlands frequently inundated via seasonal overbank flows from the Murrumbidgee River and were shallow with warm water and high aquatic emergent vegetation cover, which probably provides crucial protection and refuge (Pappas and Brecke 1992; Rosenberg and Swift 2013).

Annual Flooding and Drying Cycles

Inundation of floodplain wetlands over spring–summer drives patterns of aquatic vegetation growth and germination, and allows wetland fish communities to expand (Arthington and Balcombe 2011; Robertson et al. 2001). However, high densities of aquatic vegetation and fish were found to have negative associations with all three species, though this was not strongly supported for the broad-shelled turtle and the Macquarie River turtle. Macrophytes, algae, and fish at high densities may inhibit hunting success and movement (De Lathouder et al. 2009), and cause competition through crowding, even though forming prey. A mosaic of connected aquatic habitat varying depths and

Fig. 7 Predicted average annual abundance and 95% CI of the Macquarie River turtle in response to six site variables: average long-term of inundation probability (L.T Inund), annual inundation (Y.Inun.), average annual fish CPUE (Fish), average annual aquatic vegetation cover (Veg.), hydrological-path distance (D.Riv), and average annual water temperature (W.T.) based on the BMA of Generalized Linear Models. Significance levels indicated by "pp" (posterior probability (pp) of inclusion), where the pp value is positive correlated with significance (see Table 6). *Light gray circles* represent the scatter of values

vegetation cover each year probably provides opportunities to exploit a range of food resources.

Large inundated areas had a weakly negative impact on annual availability of eastern long-necked turtles and abundance of broad-shelled turtles, suggesting these species dispersed away from monitored sites during larger floods. The positive yet weak association of large inundation on Macquarie River turtle abundance may have been affected by the low number of captures for this species.

Recommendations for Environmental Flow Management

Adaptive management emphasizes integrating management with science to identify key relationships that can be tested over multiple watering events, and inform decisions and strategies where there are specific objectives (King et al. 2010). Environmental flows in regulated rivers can improve ecological outcomes for floodplain wetland-dependent biota by mimicking wetting and drying cycles, and supplementing natural flows to increase inundation extent and duration

(Arthington 2012). Freshwater turtles are seldom considered in environmental flow management, despite their importance for local indigenous communities (Howard et al. 2013, Cultural conservation of freshwater turtles in Barmah-Millewa Forest 2011–12, Unpublished Report) and their significant biomass in floodplain wetland systems (Spencer and Thompson 2005).

All three turtle species on the Lowbidgee floodplain were likely affected by decreased flooding frequencies and inundation duration. Core habitats and long-term refuges for all turtles overlapped, centered on wetlands with high long-term inundation frequency, and had close hydrological connection to the main river. Maintaining the integrity of these sites with environmental water to prevent complete drying will be critical for survival of populations. When high volumes of environmental water are available, we recommend environmental flows should target temporary wetlands close to permanent refuges where they can create feeding and dispersal opportunities for freshwater turtles, particularly the eastern long-necked turtle (Cosentino et al. 2010; Roe and Georges 2008b). Understanding the full

complexities of these relationships, particularly among the three species, requires dedicated and long-term data that can inform adaptive management with objectives for turtle populations. In particular, it is important to understand the role of connectivity and recruitment to maintain resilient turtle populations.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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