Received: 25 May 2023 | Revised: 14 December 2023 | Accepted: 28 December 2023
DOI: 10.1002/aqc.4085

RESEARCH ARTICLE

WILEY

# Long-term habitat degradation affects nest site selection behaviour by a freshwater turtle (*Chelodina oblonga*) in Western Australia

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**Funding information**
This project was supported by the Holsworth Wildlife Research Endowment and the Ecological Society of Australia. Additional funding was provided by Murdoch University and the City of Cockburn.

## Abstract

1. Freshwater turtles are one of the most endangered vertebrate groups with >60% of species threatened globally. Terrestrial nesting habitat degradation is a major threat to freshwater turtles, but the characteristics of nesting habitat remain poorly understood. This study investigated the nest site selection of the southwestern snake-necked turtle (*Chelodina oblonga*) to improve the conservation prospects for this species in an urbanized wetland area.
2. In total, 235 depredated and 86 non-depredated nest sites and 320 non-nest locations were surveyed at Bibra Lake, Western Australia, during the Austral spring–summer, 2018–2023. A suite of environmental variables was measured at nest sites and non-nest locations. Analysis of similarities was used to determine whether nest sites and non-nest locations differed in their environmental characteristics. Generalized linear mixed models were used to identify environmental variables that best explained the nesting preferences.
3. The environmental characteristics of nest sites differed from those of non-nest locations, with turtles nesting mainly in remnant natural habitat with greater canopy cover. Turtles generally avoided nesting in modified environments such as lawns and impervious surfaces.
4. Factors influencing nest site selection are probably associated with the conditions necessary for regulating incubation temperatures and ease of nest excavation.
5. This study suggests that modification of terrestrial vegetation around wetlands is adversely affecting freshwater turtle recruitment by removing or altering preferred nesting habitat. Protection and restoration of natural habitats fringing urban wetlands is important for the conservation of remnant freshwater turtle populations, and local partnership projects can help to achieve this.

KEYWORDS
climate change, nesting habitat, oblong turtle, riparian zone, urbanization, wetland conservation

## 1 | INTRODUCTION

Urbanization has brought about profound transformations in natural landscapes, often resulting in the fragmentation and degradation of ecosystems, including wetlands (McDonnell & Pickett, 1993). Wetlands, renowned for their ecological significance, are often surrounded by impervious surfaces such as concrete and asphalt in urban areas (Boyer & Polasky, 2004; Ehrenfeld, 2000; Halse, 1989), leading to changes in hydrology, water quality and vegetation composition (Alberti, 2005; Forman & Alexander, 1998; Paul & Meyer, 2001; Schueler, 1994). These changes have far-reaching effects on wildlife inhabiting wetland ecosystems by altering the composition of species assemblages and reducing biodiversity (McKinney, 2002; McKinney, 2008).

Freshwater turtles are a vital component of aquatic ecosystems, playing a crucial role in nutrient cycling and serving as indicators of ecosystem health (Gibbons, Lovich, et al., 2000; Seigel & Dodd, 2002). They nest on land, and their life cycles and successful recruitment are dependent on aquatic and terrestrial environments found in wetlands (Burke et al., 2000; Steen et al., 2012). Declines in many freshwater turtle populations have been linked to habitat fragmentation, degradation and loss, typically as a result of urban and agricultural development (Gibbons, Scott, et al., 2000; Klemens, 2000; Stanford et al., 2020). Consequently, freshwater turtles are one of the most endangered vertebrate groups with 61% of species either threatened with extinction or already extinct (Lovich et al., 2018; Stanford et al., 2020).

A key aspect of the freshwater turtle life history is nest site selection as this influences reproductive success and therefore the viability of turtle populations (Doody et al., 2004; Spencer, 2002). Nesting behaviour and site selection of most freshwater turtle species are unknown; however, those that have been studied generally select nest sites that provide conditions suitable for egg incubation (Czaja et al., 2020; Foley et al., 2012; Kolbe & Janzen, 2002a; Petrov et al., 2018; Wilson, 1998). The temperature regime of a nest affects the duration of embryonic development, hatchling sex ratios (in species with temperature-dependent sex determination), as well as offspring characteristics such as size, post-hatching growth rate, locomotor performance and behaviour (Kolbe & Janzen, 2002a; Refsnider & Janzen, 2010). Conversely, it has been suggested that some species do not use environmental cues for nest site selection but choose nest sites through social facilitation, such as following other females (Escalona et al., 2009).

Human disturbance can cause female turtles to nest in sub-optimal locations (Moll & Moll, 2004; Moore & Seigel, 2006; Piczak & Chow-Fraser, 2019) or lead to females travelling further in search of suitable sites, which increases their risk of mortality from predation, road traffic collision and illegal poaching (Ferronato et al., 2015; Kiviat, 1997). Generally, the risk of nest depredation decreases with increasing distance of the nest site from water (Moll & Moll, 2004; Spencer, 2002). Determining whether turtles select nest sites using environmental variables, and identifying the preferred habitat for nest sites, should help to improve conservation measures for remnant turtle populations.

*Chelodina oblonga* is a freshwater turtle endemic to the south west of Western Australia. It inhabits a wide range of permanent and seasonal wetlands such as natural and artificial lakes, swamps, rivers, creeks, reservoirs and ponds (Burbidge, 1967; Cann & Sadlier, 2017; Santoro et al., 2020). Urban populations of the species appear to be declining because of a lack of recruitment (Santoro et al., 2020). Although *C. oblonga* is currently listed as Near Threatened by the International Union for Conservation of Nature (IUCN) (Tortoise & Freshwater Turtle Specialist Group, 1996), this assessment has not been updated for over 25 years. To compound matters, the IUCN assessment also appears to have been made when the taxonomic name *C. oblonga* was attributed to the northern snake-necked turtle (now *Chelodina rugosa*). Current knowledge about *C. oblonga* nesting behaviour is based on natural history observations that took place over 40 years ago. These observations suggested that the nesting season usually begins in September and lasts for several months (Burbidge, 1967; Clay, 1981). However, no mention was made about the specific environmental characteristics of nest sites (*cf*. Burbidge, 1967; Clay, 1981).

Perth (the capital city of Western Australia) increased in size by 45% from 1990 to 2015 (MacLachlan et al., 2017). This expansion has affected most of the remnant wetlands, with riparian vegetation typically converted to parkland habitat or replaced by roads or other impervious surfaces (Chester et al., 2013; Hiller et al., 2013). Predation pressure on *C. oblonga* has increased as a result of this urbanization, notably an increase in the abundance of the red fox (*Vulpes vulpes*) (Saunders et al., 1995; Short et al., 2002), and proliferation of Australian raven (*Corvus coronoides*) (Recher & Serventy, 1991; Stewart, 1997).

At present, there are no government/legislation-based conservation or management plans for *C. oblonga*. However, owing to increasing mortality of nesting females and destruction of nests (Santoro, 2022; Santoro, Chambers, et al., 2023), conservation action has been taken by local authorities, notably by the City of Cockburn at Bibra Lake (Figure 1). These actions include fox removal, creating nesting refuges and installing signage on roads around wetlands. In addition, a citizen science programme called 'Turtle Trackers' has been implemented (Santoro, 2022).

This study aimed to improve the understanding of nest site selection behaviour by *C. oblonga* in an urban setting by investigating the environmental characteristics of nest site location. Improved understanding of preferred nesting site habitat should help conservation measures for *C. oblonga* such as protecting and restoring suitable terrestrial habitats around wetlands as well as contributing more broadly to the understanding of nesting behaviour of freshwater turtles in the context of land use and climate change.

## 2 | METHODS

### 2.1 | Study site

The study was conducted at Bibra Lake (Figure 1), located within Beeliar Regional Park in Perth, Western Australia. The Park covers approximately 3400 ha and contains some of the only remnant bushland on the Swan Coastal Plain, as a result of protection from land clearance that has occurred widely since the arrival of Europeans (Government of Western Australia Parks and Wildlife Service, 2017). The Mediterranean climate is characterized by hot, dry summers and cool, wet winters (Sturman & Tapper, 1996).

Bibra Lake is a large (108 ha) seasonal wetland that has been affected by habitat degradation. Urban areas encroach from several directions; roads fragment the remaining natural areas to the north and west, whereas the eastern side retains natural buffer zones of between ~300 and 800 m (Figure 1). The proximity of roads to the lake varies from <20 to >500 m. The resulting pattern of natural and modified terrestrial environments provided an ideal site to investigate the impact of urbanization on *C. oblonga* nesting site preference.

### 2.2 | Land use change

To assess how much of the terrestrial environment surrounding Bibra Lake had been urbanized in the >40 years since the studies of Clay (1981) and Burbidge (1967), two aerial images of Bibra Lake were compared: one from 2018 (Google Earth, 2023) and the other from 1974 (Landgate, 2023). QGIS was used to draw polygons around areas that had been modified. Three buffers of varying distances from the lake's edge were created. The first, set at 100 m, represents the average distance from water that nests (both plundered and protected) were found. The second, at 300 m, encompassed most observed nests. The third, spanning 800 m, covered the maximum distance at which a nest had been observed. The percentage of change within each buffer zone was then calculated by comparing the altered area within the buffer to the total buffer area.

### 2.3 | Nest site locations

A combination of depredated and non-depredated *C. oblonga* nests were used in the study. In 2018 and 2019, the land adjacent to Bibra Lake was searched for depredated nests, readily recognized by turtle eggshells scattered around shallow holes dug in the ground (Figure 2). During the nesting season (October–December) in each year, two 2-day searches were made in the zone up to 800 m from the water's edge—this

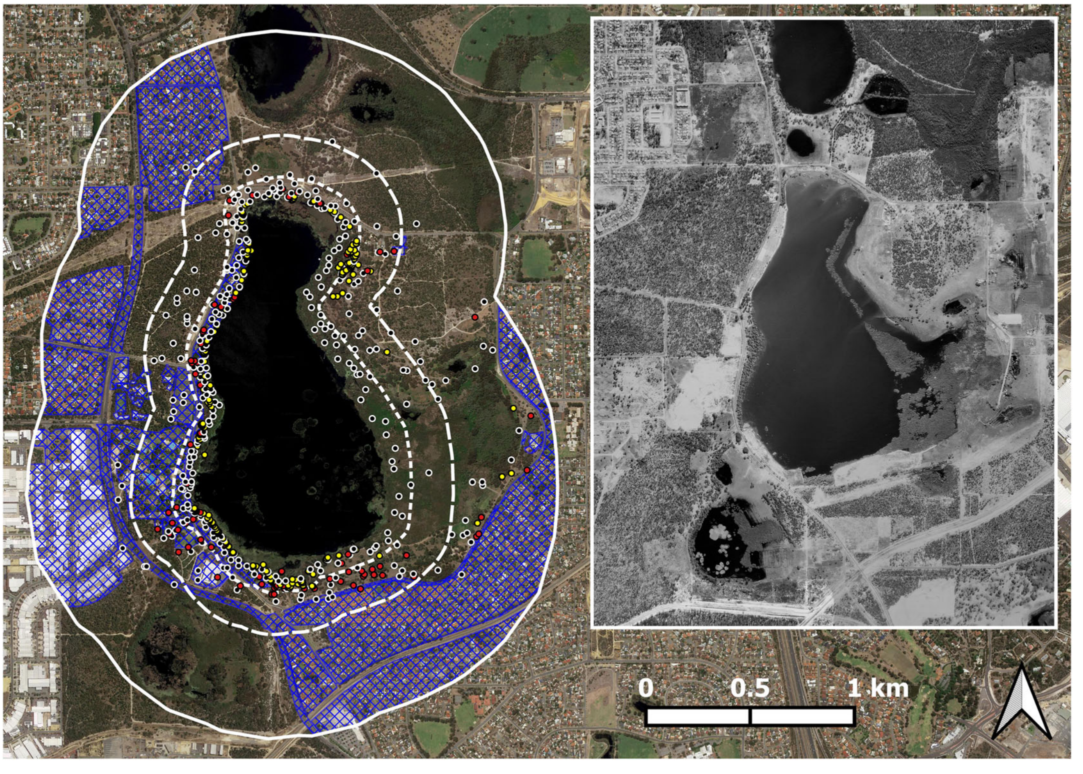


FIGURE 1 Aerial image of Bibra Lake and the surrounding terrestrial areas showing the various points of urban encroachment and distances between water's edge and roads. Dots indicate locations of depredated nest sites (yellow), non-depredated nest sites (red) and non-nest locations (black). White lines indicate buffers of various distances from the lake's edge (dot = 100 m, dash = 300 m and solid = 800 m). Hashed blue zones indicate the area that has been modified since 1974 (shown in the inset).

**FIGURE 2** A typical *Chelodina oblonga* depredated nest.

distance being the maximum from water that Burbidge (1967) found a *C. oblonga* nest. The total search area was ~200 ha. Searches were made between 08:00 and 17:00 by teams of three or four people. Other depredated nests were located on an ad hoc basis during surveys of non-nest locations (see below) and other related field work from September to February. To prevent duplicate recording, depredated nests were filled in after logging their location. Non-depredated nests were located by direct observation of *C. oblonga* females nesting in 2018, 2019, 2021 and 2022. At each nest, a coordinate position was recorded using the 'Handy' GPS App on a mobile phone (recording accuracy <±5 m).

## 2.4 | Non-nest locations

An aerial image of Bibra Lake was used to construct a sampling framework comprising ~5000 20 × 20 m grid squares within the area searched for nests. One hundred and fifty of these grid squares were selected for survey using a random number generator (Kolbe & Janzen, 2002a). During 2 days in October 2019, a 1-$m^2$ quadrat was located within each of the 150 sample grid squares to represent the most prevalent environmental character (e.g. bush, native grasses, lawn and impervious surface).

## 2.5 | Ad hoc non-nest locations

Nests were predominantly located at short distances from water. Therefore, to achieve a better spatial balance between the numbers of nest and non-nest locations, an additional 150 non-nest locations were sampled between 0 and 50 m from the water and a further 20 located between 51 and 100 m. These additional sample locations were selected as per non-nest locations but within the distance limits specified.

## 2.6 | Environmental variables

Several environmental variables known to influence freshwater turtle nesting (Flitz & Mullin, 2006; Hughes & Brooks, 2006; Petrov et al., 2018) were recorded at all nests, and non-nest locations surveyed in October 2019. Using the 1-$m^2$ quadrat, visual estimates were made of percentage cover of the following: bare ground (naturally unvegetated), leaf litter, native grasses, lawn, other herbaceous plants, woody plants and impervious surfaces such as cycle paths, pavement and roads. Wooden stumps were also included in the impervious surface category because some nests were located next to a wooden stump adjacent to an impervious surface. Canopy cover was estimated using the CanopyApp (University of New Hampshire, 2018). Photographs were taken at a height of 30 cm directly above the nest. Average slope within each quadrat was estimated using one of four categories: 0°, 1° ≤ 15°, 16° ≤ 30°, 31° ≤ 45°. Aspect was also recorded at sloping locations.

Ad hoc non-nest location environmental variables were estimated by a desk study in February 2023 using Google Earth Pro (map dated 2018), Google Street View (images captured Nov 2021), the senior author's collection of images from the study site during 2018 and 2019 and his intimate knowledge of the area.

The GPS coordinates of each nest and all non-nest locations were imported into QGIS. A digital elevation map was used to estimate elevation (Australian Height Datum [AHD]) both of nests and non-nest locations. A polygon of the inundated zone of Bibra Lake was created, based on the high-water mark on 14 November 2018 using Google Satellite Imagery. The field calculator function was used to determine the shortest distance from the aquatic zone to each nest and non-nest location.

**TABLE 1** Mean ± standard error (SE), standard deviation (SD) and range for distance, elevation, canopy cover, slope and each category of ground cover within a 1-m$^2$ quadrat of *Chelodina oblonga* nest sites ($n = 321$) and non-nest locations ($n = 320$).

| | | Mean ± SE | | SD | | Range | |
|---|---|---|---|---|---|---|---|
| Analysis | Variable | Nest | Non-nest | Nest | Non-nest | Nest | Non-nest |
| All | Distance (m) | 68.6 ± 5.7 | 112.9 ± 7.1 | 102.5 | 127.5 | 2–703 | 0–746 |
| | Elevation (m) | 16.3 ± 0.1 | 17.4 ± 0.2 | 1.7 | 3.5 | 14–33 | 14–40 |
| | Canopy cover (%) | 42.5 ± 1.7 | 35.2 ± 1.9 | 30.8 | 34.4 | 0–100 | 0–100 |
| | Slope (%) | 12.2 ± 0.7 | 5.8 ± 0.5 | 13.1 | 9.7 | 0–45 | 0–45 |
| | Bare ground (%) | 25.7 ± 1.4 | 14.6 ± 1.3 | 25.7 | 23.3 | 0–100 | 0–100 |
| | Leaf litter (%) | 10.3 ± 1.0 | 10.2 ± 1.1 | 18.2 | 20.0 | 0–100 | 0–100 |
| | Native grasses (%) | 39.5 ± 2.1 | 23.1 ± 1.8 | 36.9 | 31.4 | 0–100 | 0–100 |
| | Herbaceous plants (%) | 13.9 ± 1.2 | 17.7 ± 1.5 | 21.6 | 27.0 | 0–100 | 0–100 |
| | Woody plants (%) | 2.7 ± 0.5 | 7.3 ± 0.8 | 8.6 | 15.2 | 0–60 | 0–100 |
| | Lawn (%) | 2.5 ± 0.7 | 15.4 ± 1.9 | 12.4 | 34.6 | 0–100 | 0–100 |
| | Impervious (%) | 5.5 ± 0.8 | 11.7 ± 1.6 | 14.7 | 29.4 | 0–75 | 0–100 |
| 0–50 m | Distance (m) | 20.4 ± 0.9 | 30.7 ± 1.1 | 13.0 | 14.9 | 2–50 | 0–50 |
| | Elevation (m) | 15.7 ± 0.0 | 15.8 ± 0.1 | 0.7 | 1.0 | 14–18 | 14–19 |
| | Canopy cover (%) | 44.1 ± 2.3 | 45.7 ± 2.9 | 32.3 | 37.0 | 0–100 | 0–100 |
| | Slope (%) | 16.5 ± 1.0 | 5.4 ± 0.8 | 13.8 | 10.2 | 0–45 | 0–45 |
| | Bare ground (%) | 29.6 ± 1.9 | 12.9 ± 1.6 | 27.1 | 20.2 | 0–100 | 0–95 |
| | Leaf litter (%) | 9.6 ± 1.3 | 5.9 ± 0.7 | 18.6 | 9.4 | 0–100 | 0–50 |
| | Native grasses (%) | 29.6 ± 2.5 | 24.8 ± 2.3 | 35.5 | 29.5 | 0–100 | 0–100 |
| | Herbaceous plants (%) | 19.7 ± 1.8 | 13.6 ± 1.7 | 24.5 | 22.5 | 0–100 | 0–100 |
| | Woody plants (%) | 1.6 ± 0.4 | 10.8 ± 1.4 | 6.1 | 18.5 | 0–40 | 0–100 |
| | Lawn (%) | 3.1 ± 1.0 | 20.5 ± 3.0 | 14.5 | 39.2 | 0–100 | 0–100 |
| | Impervious (%) | 6.7 ± 1.2 | 11.5 ± 2.3 | 16.1 | 29.6 | 0–75 | 0–100 |
| 51–100 m | Distance (m) | 74.4 ± 1.7 | 77.3 ± 2.2 | 14.2 | 14.5 | 51–100 | 51–100 |
| | Elevation (m) | 16.7 ± 0.3 | 17.1 ± 0.2 | 2.4 | 1.5 | 15–33 | 15–21 |
| | Canopy cover (%) | 42.6 ± 3.6 | 19.3 ± 4.2 | 29.3 | 27.0 | 0–100 | 0–85 |
| | Slope (%) | 5.9 ± 1.0 | 6.1 ± 1.5 | 8.3 | 9.4 | 0–30 | 0–30 |
| | Bare ground (%) | 15.3 ± 2.5 | 20.6 ± 4.6 | 20.3 | 29.6 | 0–70 | 0–100 |
| | Leaf litter (%) | 10.2 ± 1.9 | 8.7 ± 3.5 | 15.6 | 22.8 | 0–80 | 0–90 |
| | Native grasses (%) | 59.7 ± 4.3 | 13.5 ± 3.7 | 35.0 | 24.1 | 0–100 | 0–100 |
| | Herbaceous plants (%) | 4.5 ± 1.2 | 21.4 ± 4.9 | 9.8 | 31.4 | 0–40 | 0–100 |
| | Woody plants (%) | 4.1 ± 1.3 | 4.0 ± 1.5 | 10.6 | 9.9 | 0–50 | 0–40 |
| | Lawn (%) | 2.7 ± 1.4 | 13.8 ± 4.8 | 11.2 | 31.4 | 0–70 | 0–100 |
| | Impervious (%) | 3.6 ± 1.5 | 17.6 ± 5.6 | 12.6 | 36.1 | 0–60 | 0–100 |
| 101–250 m | Distance (m) | 144.9 ± 5.1 | 170.6 ± 4.9 | 35.4 | 41.0 | 102–229 | 105–245 |
| | Elevation (m) | 17.5 ± 0.3 | 19.5 ± 0.5 | 1.8 | 4.0 | 15–23 | 15–32 |
| | Canopy cover (%) | 39.9 ± 3.7 | 25.8 ± 3.1 | 25.9 | 25.6 | 0–94 | 0–81 |
| | Slope (%) | 5.8 ± 1.3 | 6.4 ± 1.2 | 9.1 | 9.7 | 0–30 | 0–45 |
| | Bare ground (%) | 24.7 ± 3.5 | 15.9 ± 3.0 | 24.3 | 25.0 | 0–100 | 0–100 |
| | Leaf litter (%) | 13.6 ± 3.1 | 18.1 ± 3.3 | 21.4 | 27.3 | 0–100 | 0–100 |
| | Native grasses (%) | 49.2 ± 4.5 | 19.1 ± 3.9 | 31.7 | 32.6 | 0–100 | 0–100 |
| | Herbaceous plants (%) | 4.3 ± 1.5 | 26.8 ± 3.9 | 10.4 | 32.4 | 0–45 | 0–100 |
| | Woody plants (%) | 5.2 ± 1.9 | 3.6 ± 1.1 | 13.0 | 9.3 | 0–60 | 0–45 |
| | Lawn (%) | 0.4 ± 0.4 | 6.8 ± 3.0 | 2.9 | 24.8 | 0–20 | 0–100 |
| | Impervious (%) | 3.1 ± 1.6 | 9.8 ± 3.2 | 11.4 | 27.0 | 0–50 | 0–100 |

(Continues)

TABLE 1 (Continued)

| Analysis | Variable | Mean ± SE Nest | Mean ± SE Non-nest | SD Nest | SD Non-nest | Range Nest | Range Non-nest |
|---|---|---|---|---|---|---|---|
| 250+ m | Distance (m) | 504.6 ± 42.2 | 387.7 ± 17.8 | 146.2 | 114.1 | 273–703 | 251–746 |
| | Elevation (m) | 18.8 ± 0.6 | 20.8 ± 0.9 | 2.1 | 6.0 | 17–25 | 16–40 |
| | Canopy cover (%) | 26.2 ± 8.4 | 24.3 ± 4.6 | 29.2 | 29.3 | 0–100 | 0–84 |
| | Slope (%) | 3.8 ± 2.0 | 6.6 ± 1.3 | 6.8 | 8.2 | 0–15 | 0–30 |
| | Bare ground (%) | 22.9 ± 5.3 | 13.4 ± 3.9 | 18.5 | 25.1 | 0–55 | 0–90 |
| | Leaf litter (%) | 8.8 ± 2.4 | 15.7 ± 4.4 | 8.3 | 27.9 | 0–25 | 0–90 |
| | Native grasses (%) | 49.2 ± 9.8 | 32.8 ± 6.2 | 34.0 | 39.9 | 0–100 | 0–100 |
| | Herbaceous plants (%) | 10.8 ± 5.8 | 15.2 ± 4.0 | 20.2 | 25.8 | 0–50 | 0–100 |
| | Woody plants (%) | 2.5 ± 1.8 | 2.3 ± 1.3 | 6.2 | 8.2 | 0–20 | 0–50 |
| | Lawn (%) | 0.0 ± 0.0 | 10.4 ± 4.5 | 0.0 | 28.8 | 0 | 0–100 |
| | Impervious (%) | 5.8 ± 4.0 | 10.1 ± 3.8 | 13.8 | 24.6 | 0–40 | 0–95 |

*Note*: Analysis column indicates the distance range within which nest sites and non-nest locations were included.

## 2.7 | Data analysis

### 2.7.1 | Analysis of similarity

All of the following analyses were performed in R (v4.3.0) (R Core Team, 2023). Using the 'vegan' package (Oksanen et al., 2022), an analysis of similarities (ANOSIM) was used to test whether environmental characteristics of nests and non-nest locations (including ad hoc non-nest locations) were significantly different. The Euclidean similarity metric was used. Elevation, canopy cover and slope, together with the percentage of bare ground, leaf litter, native grasses, lawn, other herbaceous plants, woody plants and impervious surfaces, were included in the analysis. To standardize the values of environmental variables, the recorded values of elevation, distance and slope were each scaled to have a minimum and maximum value of 0 and 100, respectively. A non-metric multidimensional scaling (NMDS) ordination was used to illustrate the distribution of nests and non-nest locations in low-dimensional space based on the aforementioned environmental variables (Figure S1).

### 2.7.2 | Generalized linear models

To assess which of the environmental variables best explained the differences between nests and non-nest locations (including both the locations assessed in situ in October 2019 and the ad hoc non-nest locations estimated in February 2023), a global generalized linear model (GLM) with a binomial distribution and logit link function was generated, using the 'lme4' package (Bates et al., 2015). Distance was not included as anthropogenic habitat modification may result in preferred habitats being unavailable at various distances. Leaf litter was not included as there was minimal difference between nests and non-nest locations (Table 1), and when included, the variation inflation factor (VIF)—which determines the correlation of the predictor with all other predictors—of several predictors was excessive (ranging from 9 to 19). Possible collinearity between variables was checked by undertaking pairwise correlation analyses, which confirmed all pairwise correlations were <0.34 (Table S1). Subsequently, VIFs were determined with a maximum of 3.22 (Table S2), well below the value of 10, which is generally considered to indicate excessive collinearity (Myers, 1990).

To assess whether distance from water had an influence on the environmental variables of nest sites and whether any differences between nest and non-nest sites were related to distance from water, nest sites and non-nest sites were subset into four distance categories: 0–50 m, 51–100 m, 101–250 m and >250 m. GLMs were built for each distance category as for all sites above. Elevation and native grasses were excluded from the >250 model due to high pairwise correlation (Table S1) and VIF (Table S2), respectively. All remaining pairwise correlations were <0.40 (Table S1). All remaining VIFs were <4.05, except for native grasses in the 0–50 m model, which was 6.43 (Table S2).

For selection of the most parsimonious model within each category, models containing all possible combinations of predictors were ranked based on the Akaike information criterion, corrected for small sample size (AICc), using the MuMIn package (Barton, 2023). As there were multiple models within two AICc units of the top-ranked model for each category, model averaging was undertaken to determine the probability of each variable occurring in the top model, and the average value of each coefficient across the models was calculated. Model assumptions were confirmed using diagnostic plots.

## 3 | RESULTS

### 3.1 | Land use change

Eleven hectares of the terrestrial environment within the 100-m buffer (21% of the area) has been modified since 1974, with 38 ha

(22%) and 201 ha (35%) modified within the 300- and 800-m buffers, respectively (Figure 1). These modifications include the conversion of bushland areas into residential, industrial, recreational and road land uses (Figure 1).

### 3.2 | Nest condition

A total of 321 nests were recorded, comprising 235 depredated and 86 non-depredated nests. In 2018 and 2019, 127 and 108 depredated nests were recorded, respectively, and five, 22, 32 and 27 non-depredated nests were recorded in 2018, 2019, 2021 and 2022, respectively.

### 3.3 | Analysis of similarity

There was a small but significant difference between the environmental characteristics of nests and non-nest locations ($R = 0.07$, $p < 0.001$). The NMDS returned a low stress level (0.20). There was considerable overlap of nests and non-nest locations. However, nests had a tighter distribution within the larger distribution of non-nest locations (Figure S1).

### 3.4 | Environmental variables

#### 3.4.1 | All nest and non-nest sites

On average, nests had approximately twice the percentage of bare ground and native grasses when compared with non-nest locations (Table 1). At non-nest locations, mean canopy cover was approximately three-quarters of that at nest locations (Table 1). On average, non-nest locations had six times the percentage of lawn, twice as much impervious surface, and were half as steep as nest sites (Table 1). Nests and non-nest locations were within similar ranges from shore; however, the average distance to shore of nests was approximately two-thirds that of non-nest locations (Table 1). Nests and non-nest locations had similar average elevations; however, nests were within a smaller range than non-nest locations (nests: 14–33 m [AHD]; non-nest locations: 14–40 m [AHD]; Table 1). Flat sites and easterly facing aspect accounted for 46% and 41% of nests, respectively, with south, north and west accounting for 6%, 5% and 1%, respectively.

#### 3.4.2 | Distance-based nest and non-nest sites

Nest sites had an average of ~40% canopy cover at all distance categories, except for >250 m where it was 26% (Table 1). By comparison, non-nest sites had consistently less average canopy cover (~20%), except at the 0- to 50-m category where it was 45% (Table 1). Nest and non-nest sites had similar average slopes (5%) at all distances except within the 0- to 50-m category where nest sites were located on steeper slopes (16%) than non-nest sites (5%) (Table 1). On average, nest sites had greater percentage cover of bare ground and native grasses than non-nest sites at all distances except 51–100 m and 0–50 m, respectively (Table 1). The average percentage of lawn, impervious surfaces and herbaceous plants was less at nest sites than non-nest sites at all distances, except 0–50 m for herbaceous plants (Table 1).

### 3.5 | Generalized linear model

#### 3.5.1 | All nest and non-nest sites

The best-fitting GLM explaining the probability of a site being a nest or non-nest location explained ~32% of the deviance. It contained the following variables: canopy cover, elevation and slope, and also bare ground, native grass, lawn and woody plants (Table 2). The probability of being a nest location increased as elevation and the percentage cover of woody plants and lawn decreased, and also as slope, canopy cover and percentage of bare ground and native grasses increased (Table 3).

#### 3.5.2 | Distance-based nest and non-nest sites

The environmental variables contained in the best-fitting GLM, as well as those ranked as significant predictors during model averaging for each distance category, varied (Tables 2 and 3). The effect of each environmental variable on the probability of being a nest site was largely consistent across the distance categories (Table 3). In general, increasing canopy cover and percentage of bare ground and native grasses increased the probability of being a nest site (Table 3). Decreasing elevation and percentage cover of lawn, impervious surfaces, herbaceous plants and woody plants generally decreased the probability of being a nest site (Table 3).

## 4 | DISCUSSION

Nest site selection by freshwater turtles is important because it represents the most vulnerable phase of their life history. The results of this study have several important implications for the conservation of the early life-history stage of *C. oblonga* and has provided a better understanding of nest site selection by freshwater turtles more generally.

This study has demonstrated that *C. oblonga* prefers nest site locations with more canopy cover than at non-nest sites. It is well known that vegetation cover plays an important role in the thermal properties of freshwater turtle nests (Cook et al., 2017; Kamel, 2013; Thompson et al., 2018) and influences incubation (Francis et al., 2019; Janzen & Morjan, 2001; Kolbe & Janzen, 2002a; Shine et al., 1997; Wilson, 1998). Sub-optimal incubation temperatures can reduce survival, post-hatch body size, growth and locomotor performance

**TABLE 2** Summary information for the generalized linear models within two Akaike information criterion (AIC) (small sample) units of the top-ranked model relating to environmental variables of *Chelodina oblonga* nest sites and non-nest locations.

| Analysis | Model | Degrees of freedom | AIC | Weight |
|---|---|---|---|---|
| All | Type ~ Bare Ground + Canopy Cover + Elevation + Lawn + Native Grasses + Slope + Woody Plants | 8 | 717.4 | 0.400 |
| | Type ~ Bare Ground + Canopy Cover + Elevation + Herbaceous Plants + Lawn + Native Grasses + Slope + Woody Plants | 9 | 718.1 | 0.282 |
| | Type ~ Bare Ground + Canopy Cover + Elevation + Herbaceous Plants + Impervious + Lawn + Native Grasses + Slope + Woody Plants | 10 | 719.1 | 0.172 |
| | Type ~ Bare Ground + Canopy Cover + Elevation + Impervious + Lawn + Native Grasses + Slope + Woody Plants | 9 | 719.4 | 0.147 |
| 0–50 m | Type ~ Herbaceous Plants + Impervious + Lawn + Native Grasses + Slope + Woody Plants | 7 | 361.8 | 0.256 |
| | Type ~ Bare Ground + Impervious + Lawn + Slope + Woody Plants | 6 | 362.1 | 0.220 |
| | Type ~ Elevation + Herbaceous Plants + Impervious + Lawn + Native Grasses + Slope + Woody Plants | 8 | 363.3 | 0.122 |
| | Type ~ Impervious + Lawn + Native Grasses + Slope + Woody Plants | 6 | 363.6 | 0.106 |
| | Type ~ Bare Ground + Elevation + Impervious + Lawn + Slope + Woody Plants | 7 | 363.6 | 0.102 |
| | Type ~ Bare Ground + Impervious + Lawn + Native Grasses + Slope + Woody Plants | 7 | 363.7 | 0.098 |
| | Type ~ Canopy Cover + Herbaceous Plants + Impervious + Lawn + Native Grasses + Slope + Woody Plants | 8 | 363.8 | 0.096 |
| 51–100 m | Type ~ Canopy Cover + Elevation + Herbaceous Plants + Native Grasses | 5 | 88.0 | 0.251 |
| | Type ~ Canopy Cover + Elevation + Herbaceous Plants + Native Grasses + Woody Plants | 6 | 88.3 | 0.212 |
| | Type ~ Bare Ground + Canopy Cover + Elevation + Herbaceous Plants + Native Grasses | 6 | 88.8 | 0.168 |
| | Type ~ Bare Ground + Canopy Cover + Elevation + Herbaceous Plants + Native Grasses + Woody Plants | 7 | 89.3 | 0.128 |
| | Type ~ Canopy Cover + Elevation + Herbaceous Plants + Impervious + Native Grasses + Woody Plants | 7 | 89.4 | 0.122 |
| | Type ~ Canopy Cover + Elevation + Herbaceous Plants + Impervious + Native Grasses | 6 | 89.5 | 0.119 |
| 101–250 m | Type ~ Bare Ground + Canopy Cover + Elevation + Herbaceous Plants + Native Grasses + Woody Plants | 7 | 112.4 | 0.510 |
| | Type ~ Bare Ground + Canopy Cover + Herbaceous Plants + Native Grasses + Woody Plants | 6 | 113.9 | 0.252 |
| | Type ~ Bare Ground + Canopy Cover + Elevation + Herbaceous Plants + Native Grasses + Slope + Woody Plants | 8 | 114.0 | 0.238 |
| 250 + m | Type ~ Lawn | 2 | 58.2 | 0.196 |
| | Null Model | 1 | 58.8 | 0.149 |
| | Type ~ Lawn + Slope | 3 | 59.2 | 0.122 |
| | Type ~ Bare Ground | 2 | 59.6 | 0.100 |
| | Type ~ Bare Ground + Lawn | 3 | 59.6 | 0.099 |
| | Type ~ Slope | 2 | 59.7 | 0.096 |
| | Type ~ Herbaceous Plants + Lawn | 3 | 59.9 | 0.085 |
| | Type ~ Impervious + Lawn | 3 | 60.1 | 0.078 |
| | Type ~ Herbaceous Plants + Lawn + Slope | 4 | 60.2 | 0.075 |

*Note*: Analysis column indicates the distance range within which nest sites and non-nest locations were included.

**TABLE 3** Association between environmental variables and *Chelodina oblonga* nest sites at Bibra Lake. Variables are ranked by relative importance (i.e. probability of selection in Akaike information criterion (small sample) best-fit model).

| Analysis | Variable | Importance | Estimate | Standard error | *z* | *p* |
|---|---|---|---|---|---|---|
| All | **Bare ground** | 1.00 | 0.022 | 0.005 | 4.325 | **<0.001** |
| | **Canopy cover** | 1.00 | 0.008 | 0.003 | 2.573 | **0.010** |
| | **Elevation** | 1.00 | −0.050 | 0.013 | 3.898 | **<0.001** |
| | **Lawn** | 1.00 | −0.012 | 0.006 | 2.234 | **0.025** |
| | **Native grasses** | 1.00 | 0.015 | 0.004 | 3.653 | **<0.001** |
| | **Slope** | 1.00 | 0.018 | 0.004 | 4.740 | **<0.001** |
| | **Woody plants** | 1.00 | −0.042 | 0.010 | 4.159 | **<0.001** |
| | Herbaceous plants | 0.45 | −0.003 | 0.005 | 0.619 | 0.536 |
| | Impervious | 0.32 | −0.001 | 0.004 | 0.317 | 0.751 |
| 0–50 m | **Impervious** | 1.00 | −0.020 | 0.008 | 2.411 | **0.016** |
| | **Lawn** | 1.00 | −0.029 | 0.008 | 3.427 | **<0.001** |
| | **Slope** | 1.00 | 0.027 | 0.006 | 4.745 | **<0.001** |
| | **Woody plant** | 1.00 | −0.100 | 0.019 | 5.134 | **<0.001** |
| | Native grasses | 0.68 | −0.008 | 0.007 | 1.028 | 0.304 |
| | Herbaceous plants | 0.47 | −0.006 | 0.008 | 0.777 | 0.437 |
| | Bare ground | 0.42 | 0.005 | 0.007 | 0.700 | 0.484 |
| | Elevation | 0.22 | −0.008 | 0.027 | 0.297 | 0.766 |
| | Canopy cover | 0.10 | <0.001 | 0.001 | 0.105 | 0.917 |
| 51–100 m | **Canopy cover** | 1.00 | 0.043 | 0.013 | 3.333 | **<0.001** |
| | **Herbaceous plants** | 1.00 | −0.058 | 0.022 | 2.631 | **0.009** |
| | **Native grasses** | 1.00 | 0.045 | 0.011 | 4.165 | **<0.001** |
| | Elevation | 1.00 | 0.076 | 0.053 | 1.451 | 0.147 |
| | Woody plants | 0.46 | −0.019 | 0.028 | 0.654 | 0.513 |
| | Bare ground | 0.30 | 0.004 | 0.009 | 0.450 | 0.653 |
| | Impervious | 0.24 | −0.003 | 0.008 | 0.352 | 0.725 |
| 101–250 m | **Bare ground** | 1.00 | 0.039 | 0.012 | 3.314 | **<0.001** |
| | **Canopy cover** | 1.00 | 0.034 | 0.012 | 2.966 | **0.003** |
| | **Herbaceous plants** | 1.00 | −0.046 | 0.022 | 2.116 | **0.034** |
| | **Native grasses** | 1.00 | 0.035 | 0.009 | 3.705 | **<0.001** |
| | **Woody plants** | 1.00 | 0.049 | 0.024 | 2.023 | **0.043** |
| | Elevation | 0.75 | −0.034 | 0.030 | 1.140 | 0.254 |
| | Slope | 0.24 | −0.003 | 0.008 | 0.336 | 0.737 |
| 250+ m | Lawn | 0.66 | −0.169 | 29.677 | 0.006 | 0.996 |
| | Slope | 0.29 | −0.007 | 0.017 | 0.440 | 0.660 |
| | Bare ground | 0.20 | 0.003 | 0.008 | 0.340 | 0.734 |
| | Herbaceous plants | 0.16 | −0.002 | 0.008 | 0.268 | 0.789 |
| | Impervious | 0.08 | <−0.001 | 0.006 | 0.141 | 0.888 |

*Note*: Significant predictor variables ($p < 0.05$) are shown in bold. Analysis column indicates the distance range within which nest sites and non-nest locations were included.

(Booth et al., 2004; Mitchell et al., 2013; Riley et al., 2014; Wilson, 1998). The inference from this and other studies is that *C. oblonga* females are likely to choose nest sites within a more natural environment with vegetative attributes needed to optimize incubation temperatures and regime. As 30%–90% of wetlands have been modified or destroyed globally (Junk et al., 2012), generally reducing canopy cover (Hutto & Barrett, 2021), protecting or restoring the natural canopy cover of those that remain may be essential for reversing the decline of freshwater turtles.

Maximum daily air temperatures in Perth during summer average ~31°C (Bureau of Meteorology, 2021) but commonly exceed 40°C (Bureau of Meteorology, 2020). Increased embryo mortality occurs in some turtle species when eggs are incubated at or above 32°C (Du & Ji, 2003; Ji et al., 2006; Micheli-Campbell et al., 2011; Roosenburg & Kelley, 1996). Although embryos may be able to survive several days at these higher temperatures, brief exposures to temperatures >35°C are likely to reduce hatching success (Ewert, 1979; Hays et al., 2017; Micheli-Campbell et al., 2012; Telemeco et al., 2013). Freshwater turtle nests are shallow and receive minimal thermal buffering (Refsnider et al., 2013). Consequently, if ambient air temperatures continue to increase as predicted in the Perth region (Hope et al., 2015), there will be problems for *C. oblonga* nesting success in the future. Maintaining suitable vegetation cover for nests is therefore likely to become increasingly important.

Nest sites were preferentially located in areas with more bare ground and native grasses, largely avoiding places within lawns or close (<1 m) to other herbaceous and woody plants. This behaviour concurs with observations of Clay (1981) who noted that nest sites had 'little vegetation except for native grasses'. This might be to avoid roots that could inhibit nest digging and also to reduce the risk of root growth penetrating eggs or hindering the subterranean movement of hatchlings when overwintering or leaving the nest (Bolton & Brooks, 2010; Cook et al., 2017; Feinberg & Burke, 2003). Female turtles are therefore most likely to choose nest sites that are easy to excavate (i.e. without woody roots) and provide suitable vegetation cover for thermal regulation.

Very few nests were located within areas modified since 1974, most probably because these are now dominated by impervious surfaces. The lack of nests in these areas highlights the impact of a 20%–35% loss of suitable habitat owing to urbanization. Lack of recruitment in many *C. oblonga* populations in modified wetlands is a profound consequence (Santoro et al., 2020). Availability of sufficient bare ground and native grasses (as opposed to conversion to lawn, dense vegetation and impervious surfaces) could be crucial for successful nesting and recruitment in freshwater turtle populations.

Nests were dug in relatively flat areas except within 50 m of the lake edge; this behaviour concurs with observations by Clay (1981) that the nest site location was 'comparatively flat'. It is worth noting that the strong correlation of eastern aspects and increased slope of nest sites within 50 m of the lake edge in this study is probably the result of several nests located along the artificially modified western bank of Bibra Lake. This modification has increased the bank slope, with a limestone wall constructed along the top of much of its length. The wall acts as a barrier with many nests located at its base. Nests adjacent to the wall also appear to have been more vulnerable to predation by red fox. As these nests were depredated, it was not possible to establish whether conditions on this steeper bank were less suitable for incubation.

Nests were at similar elevations to non-nest locations; this contrasts with the behaviour of many freshwater turtles that prefer higher elevation locations to reduce the risk of nests being flooded (Booth, 2010; Burger & Montevecchi, 1975; Ferreira Júnior & Castro, 2010; Moll & Moll, 2004; Petrov et al., 2018; Spencer & Thompson, 2003). However, at Bibra Lake, there is far less risk of flooded nests because nesting occurs in the austral springtime (September–November) when water levels are at their maximum. Eggs hatch as early as March, with all generally hatched by early winter (June); hatchlings either emerge soon after hatching or overwinter in the nest until rising temperatures trigger emergence (Santoro, 2022). If nests were to be flooded during the winter, they would be most likely to contain hatchlings that can emerge rather than eggs at risk of deoxygenation.

Nests were located on average 69 m from water, which is within the range of spring and summer average distances (i.e., 85 and 25 m, respectively) observed by Clay (1981). However, the range of 2–703 m is much greater than the 20–105 m in the study by Clay (1981). This could be a consequence of the larger sample size of this study and/or the effect of habitat modification (especially the influence of bank steepening and the limestone wall along the western shoreline and conversion of bushland to residential, recreational, industrial and road use). We suggest that the pattern of nest sites around a lake probably reflects the availability of suitable habitat for excavation and successful incubation.

It is possible that some non-depredated nests were located further from the lake edge but were undetected. Nevertheless, there was a significant overlap of environmental attributes associated with nests within different distance categories as well as between non-depredated and depredated nests (see the Supporting Information, Figure S2). A similar pattern of environmental overlap was found in *Emydura macquarii*, both non-depredated and depredated nests (Spencer, 2002), and at a range of distances from the shore (Spencer & Thompson, 2003). This suggests that the environmental factors associated with nest sites identified in this study would also apply at increased distances from the water and that they are important drivers of nest site selection at Bibra Lake.

Nest predation is obviously a major issue for the population at this study site and may be influencing site selection behaviour. Nests of other freshwater turtle species located close to the water's edge often suffer from increased rates of predation (Kolbe & Janzen, 2002b; Spencer, 2002; Strickland et al., 2010). However, nests located near the water's edge may initially enhance hatchling survival because migration distance is low (Kolbe & Janzen, 2001; Refsnider & Janzen, 2010). The risk of predation to females and hatchlings may increase with increasing distance from the shore (Spencer, 2002; Tuttle & Carroll, 2005). For example, *E. macquarii* females were observed nesting closer to the shore when predators were present (Spencer & Thompson, 2003). Therefore nest site selection behaviour may reflect a trade-off between predation risk to the female and nest, against increasing offspring survival post-emergence. Control of known predators around wetlands may help to increase recruitment success by allowing turtles to nest in optimal locations as well as reducing predation pressure.

Protection and restoration of habitats fringing urban wetlands is crucial for the conservation of remnant *C. oblonga* populations, not least in the context of more extreme temperatures as a result of climate change (Hope et al., 2015). Fortunately, action is already being taken in the study area involving a partnership of local council authorities under the auspices of the 'Saving Our Snake-Necked

Turtle' (SOSNT) project (www.sosnt.net.au). This involves training volunteers to search for turtles during the nesting season; with turtles then monitored during migrations to nest sites and located nests subsequently protected with plastic meshing. Using the TurtleSAT system (www.turtlesat.org.au), the location of turtle mortality is also recorded, allowing local councils to determine the best place to locate turtle tunnels under roads (Santoro, Newsome, et al., 2023) as well as where predator control may be required. As part of the SOSNT project, turtle ecologists also conduct annual monitoring of the turtle populations, allowing assessment of the effectiveness of conservation measures taken by the local councils. This partnership approach has the advantage of involving local communities, raising awareness about the need to conserve freshwater and wetland ecosystems generally as well as focusing on *C. oblonga* as a flagship species. Similar programs could be developed for other freshwater turtles to help increase juvenile recruitment and improve their conservation plight.

## AUTHOR CONTRIBUTIONS

Anthony Santoro, Stephen J. Beatty, Jane M. Chambers and Brendan C. Ebner conceived the ideas and designed the methodology; Anthony Santoro and April L. Sturm collected the data; Anthony Santoro and Stephen J. Beatty analysed the data; Anthony Santoro led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study was a chapter of Anthony Santoro's PhD and all authors are local to the country. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

## ACKNOWLEDGEMENTS

The authors would like to acknowledge the Noongar people who are the traditional custodians of the land on which this research took place. We would also like to thank the volunteers who helped with this project, in particular Jake Watsham, Caitlan Davis and Vita Summers. Open access publishing facilitated by Murdoch University, as part of the Wiley - Murdoch University agreement via the Council of Australian University Librarians.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made available on Dryad upon acceptance for publication.

## RESEARCH INVOLVING ANIMALS

This research was undertaken in compliance with the following permits: Murdoch University's Animal Ethics Committee permit no. R3053/18, Department of Primary Industries and Regional Development, Western Australia exemption no. 3137, and Department of Biodiversity, Conservation and Attractions Regulation 25 licence no. FO25000094-4.

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## SUPPORTING INFORMATION

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**How to cite this article:** Santoro, A., Chambers, J.M., Ebner, B.C., Sturm, A.L. & Beatty, S.J. (2024). Long-term habitat degradation affects nest site selection behaviour by a freshwater turtle (*Chelodina oblonga*) in Western Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 34(2), e4085. https://doi.org/10.1002/aqc.4085