

WILDLIFE RESEARCH

Finding Ngabi (Hemiaspis damelii): factors affecting the use of modified floodplain wetlands by an endangered snake

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ABSTRACT

Context. River regulation, coupled with climate change, has caused significant declines in global freshwater biodiversity. In Australia, water extraction within the Murray–Darling Basin (MDB) has reduced the frequency, extent and duration with which floodplains are inundated, resulting in widespread declines in wetland-dependent biodiversity, including reptiles. The endangered Ngabi (Hemiaspis damelii) is associated with floodplain systems in the MDB, yet its distribution and ecological requirements are poorly understood, hampering conservation actions. Aims. We sought to validate an assumption that Ngabi is associated with wetland vegetation communities before investigating factors affecting its probability of detection in the lower Murrumbidgee catchment in southern New South Wales. We predicted Ngabi occurrence patterns would relate to frog abundance, wetland hydrology, microhabitat attributes and meteorological variables. Methods. We compared Ngabi observations from 16 paired wetland and dryland vegetation transects to evaluate associations with vegetation type. We then used generalised linear mixed models to relate snake presence and absence to prey (frog abundance), microhabitat (logs and ground cover), wetland hydrology (water depth and inundation frequency) and meteorological conditions, using 12 repeat surveys between September 2018 and March 2021. Key results. Fiftyeight snakes were observed at five of eight wetlands during the study. Ngabi was exclusively recorded in river red gum/spike rush or lignum vegetation communities, and was absent from sandhill woodland or chenopod communities. The probability of detecting Ngabi increased with ambient temperature and weakly with wetland inundation frequency, but not frog abundance, microhabitat attributes or year. Conclusions. Ngabi is strongly associated with floodplain vegetation communities and, to some extent, frequently inundated wetlands in southern NSW, suggesting water management agencies should incorporate threatened floodplain snake species into future wetland management plans. The use of environmental water to restore aspects of flow regimes, improve wetland health and aquatic diversity is likely to benefit other wetlanddependent snake populations across the MDB. Implications. The positive relationship between Ngabi detections and ambient temperature will be important for designing an effective monitoring program for the species across the MDB. Furthermore, our findings provide insight into the benefits of using environmental water to create wetland refuges to maintain floodplain snake populations during droughts.

Keywords: amphibian diversity, environmental water, flow regime, Murray–Darling Basin, Ngabi, snake conservation, threatened species conservation, wetland restoration.

Introduction

Snake populations have declined on a global scale (Gibbons *et al.* 2000; Reading *et al.* 2010), yet they are among the most neglected vertebrate taxa in conservation programs (Böhm *et al.* 2013; Roll *et al.* 2017; Guedes *et al.* 2018). Their lack of representation is partly attributed to the difficulties of detecting snakes in natural environments (Mazerolle *et al.* 2007; Durso *et al.* 2011), but also due to lack of funding and community support for their conservation compared with more 'charismatic' fauna (Mullin and Siegel 2009;

Ballouard *et al.* 2012). Changing public attitudes and perceptions about snake ecology and behavior can improve snake welfare (Ballouard *et al.* 2012). However, in many cases, targeted management interventions are necessary to reverse population declines, and to be effective, conservation intiatives require knowledge on species distributions, ecological requirements, and the factors influencing their presence (MacKenzie *et al.* 2005; Guillera-Arroita *et al.* 2010; Durso *et al.* 2011; Goldingay 2017).

In floodplain and wetland environments, some snake species are difficult to encounter due to their cryptic behaviour, nocturnal activity patterns, arboreality (Shelton et al. 2018) or natural rarity (Durso et al. 2011; Shelton et al. 2020). For relatively common and detectable species, population estimates often exceed several hundred individuals per hectare (Winne et al. 2005; Sewell et al. 2015). At these densities, snakes may influence food webs, and in some systems, play important roles in transferring nutrients from aquatic to terrestrial environments (Moss 2017). However, freshwater habitats are one of the most endangered ecosystems in the world (Vörösmarty et al. 2010), and consequently, many freshwater snake species have declined due to habitat loss (Roe et al. 2004), altered flow regimes (Willson et al. 2006; Escoriza and Pascual 2021), water pollution (Drewett et al. 2013; Lettoof et al. 2020, 2022), overexploitation (Todd et al. 2010; Chuanwu et al. 2019) and reductions in prey availability (Matthews et al. 2002; Llorente and Santos 2009). The loss of snake diversity and abundance, especially smaller species that are preyed on, could cascade upward through effects on higher-order predators, such as raptors and mammals, potentially causing substantial changes to food web dynamics (Zipkin et al. 2020). It is therefore crucial that snake research is prioritised and threatened snake species included in management plans and monitoring programs, especially in modified or rapidly changing landscapes (Michael et al. 2018).

In the Murray-Darling Basin (MDB) of Australia, water extraction has reduced the frequency, extent and duration with which floodplains are inundated, resulting in widespread declines in fish (Gehrke et al. 1995), amphibians (Wassens and Maher 2011), freshwater turtles (Chessman 2011) and water bird populations (Brandis et al. 2018). Consequently, restoring wetland health and aquatic biodiversity is a key objective of basin-wide environment programs (Reid and Brooks 2000). Using environmental water to restore aspects of flow regimes is one avenue the Australian government uses to improve floodplain systems (Reid and Brooks 2000). However, balancing competing water demands for consumptive purposes with environmental needs in a changing climate presents challenges for water managers because many wetlands currently experience unnaturally prolonged dry periods. Semi-aquatic snakes are particularly sensitive to changes in wetland hydrology (Roe et al. 2004; Vogrinc et al. 2018; Escoriza and Pascual 2021), mediated by prey availability (Rose and Todd 2017) and wetland permanence (Willson et al. 2006; Durso et al. 2011). In the United States of America, semi-aquatic snakes use several strategies for surviving in dynamic wetland environments, including strong dispersal ability or the ability to aestivate during dry periods, and high reproductive potential, enabling them to rapidly repopulate vacant habitats (Willson *et al.* 2006). However, in temperate regions of Australia, the effects of altered hydrology on snakes associated with wetland environments and their response to floodplain management remains poorly understood.

Two threatened anurophagus (frog-eating) snake species inhabit wetland environments in the MDB, the critically endangered mud adder (Denisonia devisi) (Victoria, Flora and Fauna Guarantee Act 1988) and the nationally endangered Ngabi (grey snake; Hemiaspis damelii) (Commonwealth, Environmental Protection and Biodiversity Conservation Act 1999). Currently, basic information on their ecological requirements is undocumented. To bridge this knowledge gap, we undertook the first empirical investigation into the ecological requirements of Ngabi. First, we tested an assumption that Ngabi is associated with floodplain habitats by sampling vegetation communities influenced by markedly different inundation frequencies. We then sought to examine whether prey (frog) abundance, wetland hydrology, microhabitat and meteorological variables explain occupancy (presence/absence) and detectability. Given its specialised dietary requirements (Shine 1987), we predicted occurrence patterns would be influenced by frog abundance and wetland management, and detectability would be influenced by weather conditions at the time of survey. Our findings will be useful for designing an effective monitoring program for this species and provide insight into the potential benefit of using environmental water to improve habitat for wetlanddependant reptile populations in modified floodplain systems.

Material and methods

Study species

The names Ngabi and Nhiibi are from the Indigenous Yuwaalayaay and Gamilaraay (also Gamilaroi/Kamilaroi) language groups from northern NSW. In the absence of an equivalent Nari Nari or Muthi Muthi Indigenous name from southern NSW, the word Ngabi is respectfully used in this study. Ngabi is a relatively small elapid (mean snout-vent length = 42.6 cm, max = 60 cm) (Shine 1987) found across central inland NSW, extending north through the interior of south-eastern Queensland to coastal areas near Rockhampton (Wilson and Swan 2021). It is crepuscular and nocturnal, feeds primarily on frogs and gives birth to 4-16 live young between January and March (Shine 1987). In Queensland and northern NSW, it occurs in Brigalow (Acacia harpophylla) and Belah (Casuarina cristata) woodlands on heavy, cracking clay soils, particularly in association with water bodies, areas with small gullies and ditches, or flood-prone environments

along the lower reaches of several major westerly flowing rivers such as the Condamine, Gwydir, Namoi, Macquarie and Lachlan systems (Michael et al. 2020). In 2018, Ngabi was recorded on the lower Murrumbidgee (Lowbidgee) floodplain in southern NSW after an absence from official records for over 65 years (Michael et al. 2020). This population appears to be separated from populations in northern NSW by over 500 km and may represent a significant conservation unit. The species has declined due to habitat loss, predation by pest animals (e.g. feral pigs; Sus scrofa) and in northern NSW and Queensland, poisoning from ingesting the introduced cane toad (Rhinella marinus) (Vanderduys et al. 2017). Worst case climate projections based on CSIRO global circulation models predict the species could potentially lose up to 68% of its climatically suitable habitat by 2050 (Cabrelli et al. 2014). Due to the paucity of historical records in southern NSW, it is not possible to determine how widespread the species was prior to river regulation, or how the population has responded since environmental water allocations were delivered to parts of the floodplain.

Study area

We conducted this study within Yanga National Park (761266.53 E, 616115.23 S) and Gavini (251991.67 E, 6173151.98 S), a large wetland complex managed by the Nari Nari Tribal Council, in the Murrumbidgee catchment (Lowbidgee), southern NSW (Fig. 1). The Lowbidgee covers more than 2000 km² and supports a range of ephemeral wetlands dominated by river red gum (Eucalyptus camaldulensis) woodlands, lignum (Duma florulenta) swamps and paleochannels dominated by lignum-black box (E. largiflorans) communities (Wassens et al. 2022). Low energy meandering river channels and deltas, and a semi-arid climate, characterise the Lowbidgee, which supports over 150 000 ha of nationally significant wetlands. Flows in the Murrumbidgee River are driven by winter and spring rainfall and snow melt, inundating large areas of the floodplain (Frazier and Page 2006), although 45-50% of its average annual flow is diverted for agriculture or consumptive uses (Burrell et al. 2017). These changes have significantly altered flow regimes and lateral habitat connectivity across the floodplain (Page et al. 2005). The wetlands in this study are part of a braided

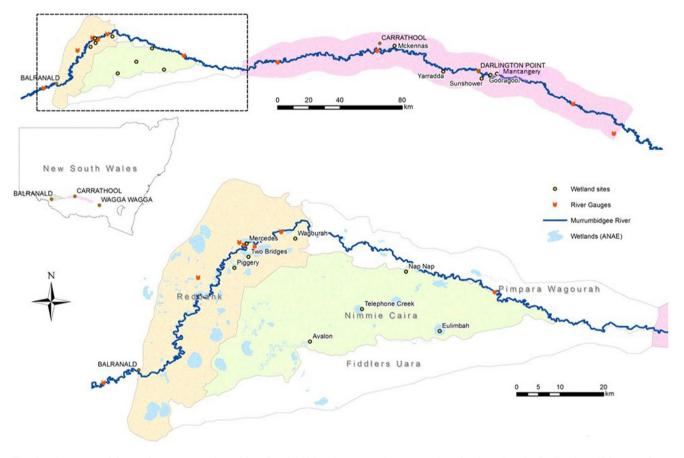


Fig. 1. Location of the study area in southern New South Wales showing eight surveyed wetlands within the Redbank and Nimmie-Caira zones on the lower Murrumbidgee floodplain. Additional wetlands in the Carathool region where Ngabi has not been detected are also shown.

floodplain system, but they only connect naturally during La Niña years or when high environmental water allocations are available during above-average rainfall years.

In 2007, Australian governments introduced water reforms for sustainable water resource management to address ecological declines in river systems across the MDB (Docker and Robinson 2014). Since 2014, over 1 million ML of Commonwealth environmental water has been delivered to targeted wetlands across the Lowbidgee floodplain (Wassens *et al.* 2022). In 2016–17, there was above-average rainfall in the catchment, contributing to increasing tributary inflows and unregulated river flows that inundated significant areas of the floodplain. Between 2017–18 and 2019–20 there was 50% below-average rainfall across much of the MDB but in 2020–21, the Murrumbidgee catchment received above average-annual rainfall resulting in the delivery of over 300 000 mL of environmental water and wetland reconnections across the system (Wassens *et al.* 2022).

Study design

We surveyed eight wetlands ranging in size from 11 to 1050 ha (mean = 307 ha) in the Redbank and Nimmie-Caira zones on the Lowbidgee floodplain (Fig. 1). These wetlands form part of a broader long-term ecological monitoring program spanning wetlands between Narrandera and Balranald (Wassens et al. 2022), and were selected based on the recent discovery of Ngabi in the area. At each of the eight wetlands, two independent transects 250 m long by 20 m wide and 250-1000 m apart were established along the wetland edge or along levee banks bisecting the wetland. Wetland sites were dominated by river red gum or lignum on cracking clay soils, and were surveyed on four occasions per year between September 2018 and March 2021. To test the assumption that the species is associated with wetland vegetation communities, on four occasions during September 2019 and March 2020, 16 dryland transects were surveyed at 100-200 m from, and immediately after, the wetland transects. The dryland transects correspond with an adjoining vegetation community and were classified as sandhill woodland or chenopod shrubland dominated by bramble wattle (Acacia victoriae) or saltbush (Atriplex sp.) on sandy soils. Inundation frequency spatial layers were used to validate transect placement to ensure they represented areas that experienced frequent inundation (>17 out of 20 years) versus infrequent (<3 out of 20 years) inundation events (Hall et al. 2019).

Survey protocol

Snakes and frogs were counted between 1900 and 2400 h, using a head lamp or hand-held spotlight, by scanning the ground for active individuals along a 250-m transect. Where available, ground cover such as logs, leaf litter and soil cracks were inspected for sequestered animals. One observer searched each transect for 30 min, alternating start times across the season to ensure all wetlands were visited at different times. For each snake captured by hand, sex, mass (g), snout–vent length; SVL (cm) and total length; TL (cm) were recorded. Sex was determined by examination of tail length and morphology.

Collection of predictor variables

Hydrological and meteorological variables were collected at the wetland scale during each survey period. Water depth and inundation frequency were derived from depth loggers and GIS spatial layers (Hall et al. 2019), and averaged across survey periods (September-March). The time frames (5 years and 10 years) and spatial scales (90 m and 150 m) were used to calculate inundation history at the midpoint of each transect, the latter temporal scale corresponding with the commencement of environmental water allocations in the region. This measure represented the number of inundated 30-m cells over two spatial scales (90 m² or 150 m²), and ranged between 9 and 25 inundated cells per year, which we converted to percentage inundation frequency as a proxy for wetland permanence. Minimum overnight temperature and rainfall a week prior to and including each survey was extracted from the Bureau of Meteorology database by converting raw data to shapefiles and appending the data to precise site locations (BOM 2021) in R Studio (R Core Team 2022).

Habitat variables were measured at each site during the same month as the herpetofauna surveys. Percentage estimates of vegetation ground cover (derived from combining plant functional groups such as grasses, sedges, forbs and subshrubs) and number of logs (>10 cm diameter) were measured along transects aligned perpendicular to the wetland boundary. On 30 occasions log data was not collected. Variables were collected along three 90–150-m transects depending on whether the wetland was dry or not. Measurements were collected within 10–30 1 × 1-m plots spaced every 5 m, beginning from the high-water mark extending to the water's edge or into the wetland if the site was dry. Values across transects were averaged to the site level.

Data analysis

An independent *t*-test was used to compare mean SVL and mass between sexes. Due to high zero counts, we used presence/absence for each site as the response variable, specified as having a binomial distribution with a log link function. Rainfall on the day, 1 week prior and the cumulative amount over 7 days, were highly correlated (>0.7 Pearson's correlation coefficient), so the latter variable was retained in the final model. Similarly, bare ground, leaf litter and ground cover vegetation were highly correlated, as were hydrological metrics; therefore, we retained ground cover and inundation frequency (10 years/150 m). Generalised linear mixed models (GLMMs) were used to relate Ngabi

presence at a site (conditional on it occupying all wetlands) to water depth (m), inundation frequency (%), minimum temperature (°C), cumulative rainfall (mm), ground cover (%), number of logs and total frog abundance, in addition to year, which was included as a categorical variable with four levels (2018, 2019, 2020, 2021) to account for annual variation in detection, specifying 2018 as the reference category. Site was included as a random factor because sites were revisited on multiple occasions over 4 years, resulting in non-independence among sampling periods (Zuur et al. 2009). After removing observations with missing data (e.g. logs), we were left with 151 observations in our analysis. A global model (i.e. all explanatory variables included in the model) was fitted to generate parameter estimates for all explanatory variables. Model fit was assessed using marginal and conditional R^2 (Nakagawa and Schielzeth 2013). Fitting the full model using the lme4 package (Bates et al. 2015) resulted in singularity issues, so it was refit within a Bayesian framework using the blme package (Bates et al. 2015). Model diagnostics were examined (QQ plots, residual vs predicted values) using the DHARMa package (Hartig 2022), which did not reveal any significant issues.

ggplot2 and ggeffects were used for plotting (R Core Team 2022). All analyses were performed in R Studio using ggplot2 and ggeffects for plotting (R Core Team 2022).

Results

Ngabi was observed actively foraging on the surface or sequestered within soil cracks on 58 occasions at five of eight wetlands, with a maximum of 14 individuals observed at one wetland (Two Bridges Swamp) in Yanga National Park in March 2021 (see supplementary material). A comparison between dryland and wetland transects revealed Ngabi was exclusively detected in wetland vegetation communities, and was absent from sandhill or chenopod vegetation communities (Fig. 2*a*). Of the individuals measured, mean SVL was 37.9 cm, TL was 44.21 cm, and males were on average larger (F = 14.30, d.f. = 37, P < 0.001) and heavier (F = 8.49, d.f. = 25, P = 0.007) than females (Table 1). Frog abundance was significantly higher along the wetland transects (Fig. 2*b*).

The global model explained >90% of the variance in the data (see supplementary material), and included significant

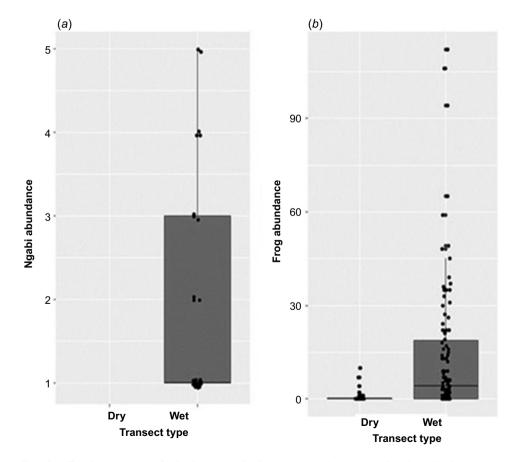


Fig. 2. Total abundance of (*a*) Ngabi and (*b*) frogs recorded on dryland and wetland transects between September 2019 and March 2021. The wetland sites were classified as river red gum or lignum, and the dryland transects were classified as sandhill woodland or chenopod shrubland.

positive relationships with inundation frequency (10 years/150 m) (P < 0.05) and minimum overnight temperature (P < 0.01) (Fig. 3). The effects of inundation and temperature were both non-linear, where the probability of detecting Ngabi increased when inundation frequency exceeded 80% (>8/10 years) and minimum overnight temperature exceeded 20°C (Figs. 4*a*, *b*). None of the microhabitat predictors (percentage ground cover or number of logs), water depth, cumulative rainfall or year were significant in explaining Ngabi occurrence.

Discussion

Effective threatened species conservation requires a sound understanding of a species distribution and ecological requirements. Prior to this study, the distribution and abundance of Ngabi in southern NSW were poorly known and limited to fewer than 15 observations and specimens collected in the 1950's (Michael et al. 2020). Our surveys from a small subset of wetlands in the Lowbidgee confirm the species is associated with wetland vegetation communities on cracking clay soils, and is absent from adjoining vegetation types on sandy soils. Given Ngabi was detected on five of eight wetlands not previously recorded before this study, the species may be more widespread than currently recognised. Furthermore, Ngabi may be locally abundant in areas of suitable habitat, with 14 individuals observed during a single survey at one wetland in 2021. However, concurrent surveys from oxbow lagoons in the mid-Murrumbidgee (Wassens et al. 2022), 165 km upstream from this study area, failed to detect this species using equal amounts of survey effort, suggesting Ngabi may have a geographically restricted distribution in southern NSW, potentially encompassing <500 km² of suitable floodplain habitat. Considering the expansion of cane toads in northern Australia (Shine et al. 2021), and the sensitivity of this species to bufotoxin (Phillips et al. 2003), the Lowbidgee population may represent a significant conservation unit requiring targeted management of specific wetlands, especially in relation to other pest species (e.g. feral pigs) control (DCCEEW 2022).

Effect of temperature

Temperature is widely recognised as being an important factor influencing snake activity patterns (Webb and Shine 1998), with many studies reporting increased snake activity with ambient temperature, weather conditions and season (Nelson and Gregory 2000; Dyugmedzhiev *et al.* 2020; Shelton *et al.* 2020). We found the probability of detecting Ngabi increased with increasing minimum temperature, with overnight temperatures of 20–25°C resulting in a 20–50% chance of detection. In the Lowbidgee region, average minimum temperatures above 15°C occur between December and March (BOM 2021), representing a relatively small window of opportunity for detecting the species during optimal weather conditions. Approximately 25% of our surveys were conducted on evenings that reached a minimum of <10°C, reducing out detection rate and potentially influencing relationships with other variables such as inundation.

In addition, prey activity can also influence snake activity patterns. Nocturnal snakes feed on species that are either active at night or sequestered within retreat sites, and many species have physiological adaptations to facilitate metabolic activity during cool weather. For example, the closely related nocturnal marsh snake (*H. signata*) was found to select a body temperature of 22°C in an indoor thermal gradient (Llewelyn *et al.* 2005). Ngabi shelters within deep soil cracks during the day and is likely to thermoregulate by selecting thermally suitable retreat sites, as well as maintaining preferred body temperature via conduction with the soil substrate. Further research on Ngabi should focus on understanding its activity patterns, thermal ecology and relationship to other environmental variables when surveys are conducted above suitable ambient temperatures.

Effect of wetland hydrology

As predicted, the probability of detecting Ngabi was related to a component of wetland hydrology, particularly inundation frequency, with detection probability exceeding 20% at wetlands inundated on a near-annual basis over a 10-year period. Although we found this variable to be weakly significant, with high confidence intervals, wetland permanence is an important factor in explaining occupancy patterns in aquatic (Durso *et al.* 2011) and semi-aquatic snake species (Vogrinc *et al.* 2018), and is likely to be important in explaining occupancy patterns in terrestrial snakes associated with floodplain habitats. The relationship between Ngabi detection and wetland inundation frequency may have important implications for managing wetlands in context of climate change and periods of drought, which are

 Table 1.
 Mean and range of snout-vent length, total length and mass of male and female Ngabi from the lower Murrumbidgee region in southern NSW.

Sex	N	Snout-vent length (cm)	Total length (cm)	Mass (g)
Male	24	41.78 (34.90–50.10)	49.02 (42.00–60.20)	37.10 (25.00–60.00)
Female	15	32.83 (17.60-44.20)	37.73 (19.50–51.50)	23.75 (3.00–59.00)
Total	39	37.91 (17.60–50.10)	44.21 (19.50–60.20)	31.16 (3.00-60.00)

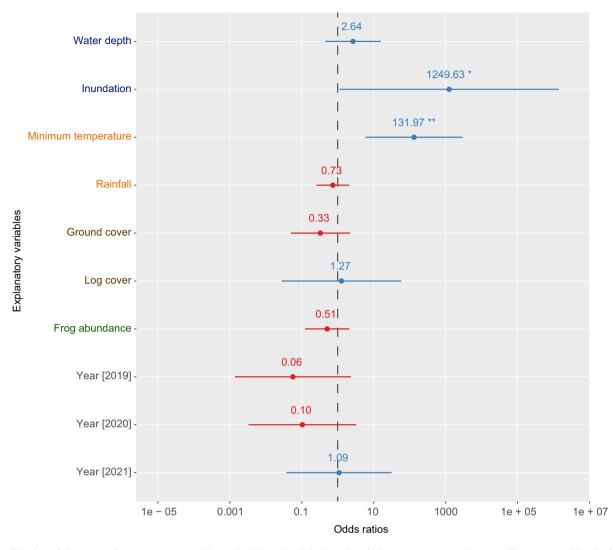


Fig. 3. Odds ratios for predictor variables included in the global model of Ngabi occurrence showing effects size and level of significance (***P < 0.001, **P < 0.01, *P < 0.05). Colours indicate positive (blue) or negative (red) effect sizes.

becoming more frequent across the globe. Marked temporal changes in wetland snake populations can result from drought (Seigel et al. 1995), affecting different species in different ways (Willson et al. 2006). Terrestrial species associated with specific wetland attributes, and little capacity to migrate to alternative wetland habitats, may take several years to return to pre-drought population levels (Sperry and Weatherhead 2008), or lead to localised extinction. In the MDB, the delivery of environmental water to target wetlands that support Ngabi populations may be important for their survival during below-average rainfall years. During drought years, many wetlands in the Lowbidgee remain dry, and only begin to fill with active management such as using pumps to fill disconnected wetlands from the main river channel. Delivering environmental water to key wetlands is therefore likely to not only benefit Ngabi but also other threatened wetland dependent snakes in the MDB. For example, the first sightings of the threatened mud adder from wetlands in Victoria (e.g. Wallpolla Island) were attributed to improvements in wetland habitat and frog populations associated with environmental water allocations (MDBA 2006).

Relationship with prey and microhabitat

In contrast to our initial prediction, total frog abundance was not a significant factor in explaining Ngabi detection patterns, a result consistent with Shelton *et al.* (2020), who also found habitat use by the pale-headed snake (*Hoplocephalus bitorquatus*) was not influenced by frog abundance. Our findings may be due to the ubiquitous distribution and abundance of the most common frog species in this system (Wassens *et al.* 2013; Littlefair *et al.* 2021), spotted marsh frog (*Limnodynastes tasmaniensis*) and barking marsh frog (*L. fletcheri*), and due to homogeneous distribution in frog abundance between our sites. Ngabi is known to prey

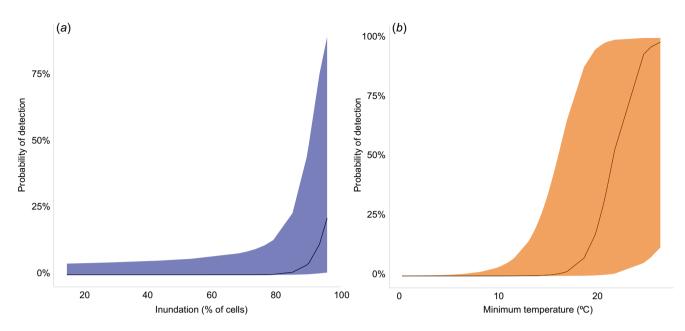


Fig. 4. Significant relationships between Ngabi occurrence and (a) inundation frequency (10 years/150 m), and (b) minimum overnight temperature (°C).

on both species (Michael *et al.* 2022), although frog abundance is unlikely to be a limiting factor in this system. Similarly, we found no significant relationship between Ngabi detection and any of the microhabitat attributes we measured, including percentage ground cover or log abundance. Microhabitat relationships have been reported in nocturnal snakes from forest environments (Webb *et al.* 2004), but logs may be less important to small nocturnal floodplain species that potentially utilise soil cracks as retreat sites instead. Cracking clay soil represents a microhabitat that is both complex and dynamic, changing with season according to natural wetting and drying cycles. Therefore, intrinsic soil properties, such as subterranean cavities, microclimate and temporal stability may be useful variables to investigate occupancy patterns in future research.

Conclusion

We surveyed Ngabi from a small number of wetlands in a modified floodplain environment, and found the species to be locally abundant but restricted to the Lowbidgee floodplain. The apparent absence of Ngabi records in southern NSW prior to this study is likely due to its nocturnal behaviour, limited activity patterns, remoteness and possible confusion with other snake species. Extensive reptile surveys in other habitats surrounding the Lowbidgee floodplain have failed to detect the species (Michael *et al.* 2014, 2015), providing further evidence of its dependency on floodplains. Our findings revealed that the probability of detecting Ngabi increased with minimum temperature and to some extent, inundation frequency. Broader nocturnal surveys across floodplain wetlands in the MDB are required to determine its current distribution and abundance. To improve species detectability, surveys should be conducted when ambient temperatures exceed 15°C, and ideally during La Niña years. Conservation actions for this species might include using environmental water to maintain key wetland refuges during below-average rainfall years and increase wetland connectivity across the landscape to facilitate dispersal and colonisation of vacant wetlands. Further research is required to investigate its spatial and thermal ecology and response to floodplain management.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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