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Research paper

Adaptation to urban environments promotes high reproductive success in the tawny frogmouth (*Podargus strigoides*), an endemic nocturnal bird species

M.J. Weaving[a], J.G. White[a], B. Isaac[b], A.R. Rendall[a], R. Cooke[a,*]

[a] School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, Victoria 3125, Australia
[b] Monash University, School of Biological Sciences, Wellington Road, Clayton, Victoria 3800, Australia

HIGHLIGHTS

- Urban tawny frogmouths show very high reproductive success.
- Increasing urbanisation influences tawny frogmouth nest location.
- Native rough-barked *Eucalyptus* tree species are preferred nest trees.
- Environmental factors drive time of breeding not urbanisation.

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ABSTRACT

The tawny frogmouth (*Podargus strigoides*) is an endemic, nocturnal bird species widespread throughout Australia with high numbers in urban environments but very limited information exists on its ability to cope with urban systems. We investigated the reproductive behaviour of this species in response to a continuum of urbanisation. Firstly, we asked does the degree of urbanisation influence the availability of suitable nesting locations. Secondly, does broad and/or local scale factors surrounding a nest influence reproductive success? And finally, does the degree of urbanisation influence time of breeding? We located 158 nest sites and monitored 189 breeding attempts across four breeding seasons (2010–2013). One hundred and thirty three of these attempts successfully fledged 177 chicks. We categorized 75 attempts as first known attempts for that season resulting in 77 fledged chicks. In some pairs, repeated attempts occurred after failure. We observed double brooding by three pairs, a strategy largely unknown in this species. Spatial modelling revealed that birds selected more vegetated areas of the gradient within which to locate their nests, avoiding more highly urbanized areas. We identified no association between land-use type and breeding success at both broad and local scales. Birds selected native rough-barked *Eucalyptus* tree species more frequently than other trees for nesting. The key drivers for the commencement of breeding were climatic variables, in particular rainfall. The ability of the species to synchronize breeding attempts to coincide with optimal environmental conditions resulted in extremely high reproductive success suggesting high individual fitness and an adaptation to local environmental conditions.

1. Introduction

As one of the most extreme forms of landscape transformation, urbanisation substantially modifies natural ecosystems resulting in dramatic and often irreversible changes (McKinney, 2002; Seto, Güneralp, & Hutyra, 2012). Urbanization creates heterogeneous landscapes characterised by highly modified urban cores, moderately disturbed urban fringe areas extending to forested landscapes on the city margin (McDonnell & Pickett, 1990).

The effects of urbanisation on avian community composition are well described (Blair, 1996; Garaffa, Filloy, & Bellocq, 2009; Sol, González-Lagos, Moreira, Maspons, & Lapiedra, 2014). Less studied, and subsequently less understood, is how landscape modification by urbanisation impacts on critical life history elements such as reproduction. The effect of urbanisation on avian breeding is likely to be highly complex and species specific. In addition,

* Corresponding author.
E-mail addresses: mweaving@deakin.edu.au (M.J. Weaving), john.white@deakin.edu.au (J.G. White), bronwyn.isaac@monash.edu (B. Isaac), a.rendall@deakin.edu.au (A.R. Rendall), raylene.cooke@deakin.edu.au (R. Cooke).

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factors such as the type and intensity of urbanisation, the related shifts in resource availability and predation are likely to substantially modify breeding responses (Chace & Walsh, 2006; Chamberlain et al., 2009). Studies spanning urban gradients have demonstrated various differences in reproductive behaviour between urban and rural populations, and have suggested the key roles of factors such as prey availability (Newhouse, Marra, & Johnson, 2008), habitat type (Dykstra, Hays, Daniel, & Simon, 2000), degree of predation (Antonov & Atanasova, 2003; Beck & Heinsohn, 2006) and human-subsidized food resources (Rollinson & Jones, 2002) as influential in these differences. Many studies have highlighted a clear and consistent pattern demonstrating the association between the degree of urbanisation and the timing of breeding onset, with factors such as food abundance (Eden, 1985; Schoech, Bowman, & Thompson, 2003), elevated prey density (Boal & Mannan, 1999) and increased ambient temperatures (Chamberlain et al., 2009) contributing to the early onset of breeding in comparison to their rural counterparts.

Breeding is a critical life history event, as such, breeding birds will actively select specific habitats and habitat elements that maximise reproductive success (Bailey & Thompson, 2007; Degraaf & Wentworth, 1986). If resources are unavailable or lack sufficient quality, as is often the case in urban areas, there is significant implications for the demographics of the urban population (Cody, 1985). For species with specialised breeding requirements such as hollow-dependant breeders, urbanized environments often lack the resources required for breeding and as such breeding outputs are substantially reduced by urbanisation (Cooke, Wallis, Hogan, White, & Webster, 2006; Hindmarch, Krebs, Elliott, & Green, 2012; Isaac, Cooke, Ierodiaconou, & White, 2014; Rottenborn, 1999). Where species have less demanding breeding habitat requirements, novel habitat types and abundant food resources common to urban systems, may enhance breeding outcomes resulting in population levels higher than those in more natural environments (Stracey & Robinson, 2012). Studies that focus on avian reproduction in urban areas are essential as they provide critical information about the patterns and processes driving reproductive outcomes in response to landscape modification.

Identified as sensitive to landscape modification, long-lived sedentary species are considered useful models for investigating ecological responses to urbanisation (Sekercioglu, Daily, & Ehrlich, 2004). The tawny frogmouth (*Podargus strigoides*), is a long-lived, sedentary, large-bodied (350–550 g) endemic nocturnal species widespread throughout Australia (Higgins, 1999). This species exhibits a range of generalist habitat requirements with no apparent dependency on any one or more habitat resources (Higgins, 1999). Dietary items consist of terrestrial and aerial invertebrates and some small vertebrates (Rose & Eldridge, 1997). The species has a protracted annual breeding season (July to January) with pairs capable of repeated breeding attempts if prior attempts in that season fail (Higgins, 1999). As a non-hollow dependant species, tree branches are used for diurnal roosting and nesting (Körtner & Geiser, 1999a, 1999b; Rae, 2009). Pairs construct very basic nests from small woody twigs, locating them in the fork of a tree branch or trunk/branch junction or occasionally utilizing an abandoned bird nest (Schodde & Mason, 1980). Breeding activities are shared between the sexes (Higgins, 1999).

Whilst a common species, many aspects of tawny frogmouth ecology and behaviour remain largely unknown. Most studies have focused on birds associated with woodlands or more forested environments (Körtner & Geiser, 1999a, 199b; Rae, 2009). In comparison to more wooded areas, high numbers of tawny frogmouths have been shown to occupy urbanized environments (Weaving, White, Isaac, & Cooke, 2011) suggesting some degree of adaptation to the landscape changes associated with urbanisation.

Using the tawny frogmouth as a case study, this research investigates whether the degree of urbanisation has an influence on key breeding parameters. Firstly, does the degree of urbanisation influence the availability of suitable nesting locations across a continuum of urbanisation? We predict that nesting habitat will not be uniform across the urban landscape and will become limited as urbanisation intensifies. Secondly, we investigate whether broad and/or local scale factors around a nest site influence the degree of reproductive success of tawny frogmouths. We predict that breeding success will be negatively associated with the degree of urbanisation around the nest at both broad and local scales. Finally, we investigate whether the degree of urbanisation influences the timing of the commencement of breeding. We predict that the onset of breeding will be earlier where nesting attempts occur in increasingly urbanized locations.

2. Methods

2.1. Study site selection and land cover quantification

Our study was located in the north-east of Melbourne, Australia and covered approximately 52,000 ha and represents a continuum of urbanisation (Fig. 1). Our definition of urbanisation was based on the proportion of impervious surfaces occurring in the study zone, with increasing cover of impervious surfaces indicating increasing urban intensification. To quantify the urban landscape a Normalised Difference Vegetation Index (NDVI), which measures the amount of living green vegetation in the landscape (Leslie, Sugiyama, Ierodiaconou, & Kremer, 2010), was created in Environment for Visualizing 4.7 (ENVI 4.7). The NDVI landscape scale map was created from SPOT 5 ('Systeme Pour 1' Observation de la Terre) imagery using four high-resolution satellite images with a pixel size of 10 m × 10 m. These images were corrected for differences in brightness, colour and contrast then mosaicked together, using one image as the base and a feather distance of 100 pixels to overlap the images (ITT Visual Information Solutions, 2010a). The resulting image was then processed to create an NDVI layer.

Using the NDVI layer we then classified the landscape into five broad land-use types that could define the urban landscape: – grass, impervious surfaces, trees, rivers and permanent water bodies. The land use layer was created by defining Regions of Interest (ROI's), with each land-use type being defined by 107 ROI's. Supervised classification was then undertaken with the ROI's using the maximum likelihood function. This function gives each pixel a probability of belonging to a land-use type and then assigns it to the land-use type with the highest probability (ITT Visual Information Solutions, 2010b).

2.2. Field survey methods

Between July and January, over four consecutive breeding seasons (2010–2013), parks, vacant land, bushland reserves and streetscapes within the study zone were searched on foot, during the daytime to locate nesting birds. Using binoculars, tree branches were systematically scanned to locate nesting or roosting birds. To avoid bias with the data collection, a single data collector (MW) conducted all surveys using a systematic and consistent search method. Breeding bird locations were also reported by members of the public and ornithology groups and these locations were all visited and confirmed by MW. A small set of nest locations were also found by radio telemetry as we were radio-tracking some birds for other research questions (Weaving, White, Hower, Isaac, & Cooke, 2014).

Once a nest site was found, the location was recorded and the following attributes measured: tree type (native, exotic), Genus (*Eucalyptus*, *Pinus*, *Acacia*, other), bark type (rough, smooth and