Urban tolerance of raptors at the global, regional, and local level

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Thesis Summary

Urbanisation is a key driver of biodiversity loss worldwide, causing irreversible ecosystem changes at the global, regional, and local level. While the impacts of urbanisation on wildlife, particularly in an urban setting, have been studied extensively for some taxa, there is a lack of understanding of how raptor species may differ in their ecology from urban to rural landscapes, especially in the Southern Hemisphere. This study investigates the factors that influence urban tolerance of raptors at multiple scales.

Using data sourced from community science projects (also referred to as citizen science) in combination with observational raptor data collected in the field, this study explores how urban tolerance and the use of urban green spaces vary amongst Kestrel species across the globe (Chapter 1), which traits influence urban tolerance in Australian raptor species (Chapter 2), and how the richness and diversity of Australian raptors vary along an urban-rural gradient (chapter 3). At the global level, urbanisation was the most important predictor of Kestrel occurrence and count for all three species modelled, which were all urban avoidant. Urban green space, particularly grassland, shrubland, and cropland, were important predictors of Kestrel occupancy in cities. At the regional level, out of the 24 Australian raptor species analysed, 13 species were urban tolerant, while 11 species were urban avoidant. Many of the urban tolerant species were bird specialist feeders. Smaller Australian raptor species were found to be more tolerant of urban areas than larger raptor species. At the local level, species richness analyses revealed that a greater number of species were observed in towns compared to cities, and a greater number of individual birds were observed in the rural zone compared to the urban zone of towns. Species diversity analyses showed no significant difference in the diversity of birds observed across cities and towns and their urban zones. Trait-based analysis revealed that body mass, diet breadth and habitat breadth were not significant predictors of where birds were observed across locality types and zones.

The use of large-scale datasets and complex statistical analysis has given insight into the urban tolerance of raptors in the Southern Hemisphere, which has traditionally been poorly understood. This study bolsters our knowledge of how raptors respond to urbanisation as well as the underlying traits associated with urban tolerance across the urban-rural interface. It also draws attention to the importance of urban green space in cities and their benefit to urban-adapted wildlife in the form of foraging and breeding grounds. The distribution of raptors in the Southern Hemisphere is being impacted by urbanisation across large spatial scales, and the results of this study highlight the need to conserve suitable natural habitats that support raptor survival beyond urban areas.

Declaration

‘I certify that this thesis: 1. does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university 2. and the research within will not be submitted for any other future degree or diploma without the permission of Flinders University; and 3. to the best of my knowledge and belief, does not contain any material previously published or written by another person except where due reference is made in the text and 4. has been completed without the use of generative artificial intelligence tools.’

Signed: Taylor Headland

Date: 25/02/2025

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Statement of Authorship/Contribution

	Chapter 1	Chapter 2	Chapter 3	Chapter 4	Chapter 5
Writing/editing	100% - TH	N/A	N/A	N/A	100% - TH
Research Design	N/A	60% - TH, 10% - SK, 10% DCN, 10% - PS, 10% - CTC	60% - TH, 10% - PS, 10% - CTC, 10% -DCN, 10% - SK	60% - TH, 10% - SCS, 10% - PS, 10% - DCN, 10% - SK	N/A
Data collection	N/A	TH - 100%	70% - TH, 10% - PS, 10% - CTC, 10% - SCS	80% - TH, 10% - PS, 10% - SCS	N/A
Statistical analysis	N/A	80% - TH, 20% - PS	70% - TH, 15% - PS, 15% - CTC	80% - TH, 20% - PS	N/A
Manuscript writing	N/A	100% - TH	100% - TH	100% - TH	N/A
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All work presented within this thesis adhered to the legal and ethical requirements of Flinders University.

Publications associated with this thesis

Information from this thesis has been published in peer-reviewed journals as follows:

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Chapter 1 – Introduction

Anthropogenic change and urban biodiversity

Anthropogenic land conversion is one of the leading causes of habitat and biodiversity loss globally, leading to species declines and extinctions (Simkin et al., 2022, Aronson et al., 2014, Shochat et al., 2010, Callaghan et al., 2024). Urbanisation, or the physical expansion of urban areas due to the increased presence of buildings, roads and infrastructure, is occurring at an unprecedented rate, and, by 2050, approximately 68% of the world's population will live in cities and the urban population will grow by 2.5 billion people, mostly in Africa and Asia (United Nations, 2019). Current global projections of urban expansion predict that between 2015 and 2050, approximately 0.82–1.53 million km^2 of natural land will have been transformed into urban landscapes, which is triple the urban extent of 2015 (Simkin et al., 2022). This expansion can cause direct and indirect losses of natural habitat, particularly the indirect loss of forests due to cropland displacement from urban expansion (van Vliet, 2019). Mitigating the impacts of urban land conversion is therefore critical to halt further biodiversity decline worldwide (Huang et al., 2018, McDonald et al., 2020).

The delineation of urban and non-urban areas is the subject of much debate (Weeks, 2010, Fang et al., 2025, de Bellefon et al., 2021). However, in recent times, the UN and other international organisations have developed a method to delineate urban areas known as the 'Degree of Urbanisation', which is based according to the definitions in 'Cities in the World: A New Perspective on Urbanisation (Commission, 2020):

1. Cities - consist of contiguous grid cells that have a density of at least 1 500 inhabitants per km2 or are at least 50% built up. They must have a population of at least 50,000.
2. Towns and semi-dense areas - consist of contiguous grid cells with a density of at least 300 inhabitants per km2 and are at least 3% built up. They must have a total population of at least 5,000.
3. Rural areas - cells that do not belong to a city or a town and semi-dense area. Most of these have a density below 300 inhabitants per km2.

This definition translates to the urban/peri-urban/rural gradient that is commonly referred to in ecological studies (Blair, 1996, Hindmarch and Elliott, 2014, Banaszak-Cibicka and Żmihorski, 2012), where cities and towns and semi-dense areas have higher levels of built areas and human populations density compared to rural areas, which are mostly comprised of natural landscapes or agriculture (Haase and and Nuissl, 2010, Martellozzo et al., 2018).

Globally, urban ecosystems are characterised by distinct biodiversity patterns of reduced species richness and diversity and altered patterns of abundance (Li et al., 2022, McKinney, 2006, Aronson et al., 2014). Species richness refers to the number of species observed in a given area, and diversity per species describes an index that combines the number of species with a measure of the evenness of the abundance per species (Peet, 1974). For example, when comparing two communities with equal species richness, the evenness or relative abundance of the species across the communities dictates the potential difference in level of diversity, such that high species richness and low diversity is a result of low evenness. Such patterns can be measured across an urban to non-urban gradient, where the urban core typically harbours lower species richness and altered abundance, and diversity tends to increase with closer proximity to non-urban areas (Sol et al., 2014, McKinney, 2008, Faeth et al., 2011, Melliger et al., 2018). The reduced species richness and altered abundance patterns may be the result of anthropogenically imposed biotic and abiotic elements during landscape transformation, such as impervious surface cover, commercial and residential buildings, transport infrastructure, and artificial lighting (Grimm et al., 2008), but also pollution from chemicals, lights, noises (Gaston, 2010) and elevated temperatures (Phelan et al., 2015, Sumasgutner et al., 2023). For example, elevated noise levels were associated with reduced bird richness and diversity in urban green spaces in south-eastern Brazil (Perillo et al., 2017), and bird richness declined with increasing housing cover across 30 residential landscapes in Melbourne, Australia (Humphrey et al., 2023). Understanding how species richness and diversity are impacted by landscape level changes is important to prevent further biodiversity decline as urbanisation intensifies.

Native species are among the most affected by natural land conversion (Davis et al., 2013, McKinney, 2002, Shochat et al., 2010). Urbanisation significantly alters the spatial configuration of available habitat types and causes fragmentation and reduced connectivity of non-urban lands (McKinney, 2002, Nor et al., 2017b, Nor et al., 2017a), modifying species compositions and assemblages (Gibb and Hochuli, 2002, Concepción et al., 2015, Fahrig, 2003). In general, native species richness and diversity decline as anthropogenic habitat modification increases (McKinney, 2008, Luck and Smallbone, 2010). As native species are displaced from urban habitats, invasive species may replace them, leading to biotic homogenisation and a higher overall biomass in urban ecosystems compared to neighbouring rural areas, even though urban areas exhibit lower species richness (McKinney, 2006, McKinney and Lockwood, 1999, Knop, 2016). This is due to the ability of synurbic species (species that colonise urban environmens) to effectively exploit anthropogenic resources, such as food, as demonstrated by the House sparrow (*Passer domesticus*), an invasive, aggressive, and efficient forager, that outcompete native species, such as the Lesser goldfinch (*Carduelis psaltria*) and the Black-throated sparrow (*Amphispiza bilineata*) in Phoenix, Arizona (Shochat et al., 2010). Examples of successful urban adapted species that have colonised cities around the world are the Rock Dove (*Columba livia*) (Farfán et al., 2019, Buijs and Van Wijnen, 2001) and the Black Rat (*Rattus rattus*) (Byers et al., 2019, Feng and Himsworth, 2014).

Natural land interspersed within urban landscapes, referred to as urban green space, are resource-rich areas for urban wildlife (Aronson et al., 2017, Lepczyk et al., 2017). While urban green spaces can range from natural remnant vegetation and wetlands to man-made golf courses and green roofs, they vary in their management intensity (Aronson et al., 2017, Gaston et al., 2013) and are often highly fragmented throughout the urban landscape (Zhou and Wang, 2011, Nor et al., 2017a, Byomkesh et al., 2012). Urban green spaces can harbour high biodiversity due to the resources they provide for urban wildlife in the form of foraging grounds (Yabsley et al., 2021, Wojcik and McBride, 2012, Partridge and Clark, 2018), breeding grounds (Ding et al., 2023, Morrison et al., 2016, Threlfall et al., 2015), and resting areas

(Bradsworth et al., 2021, White and Main, 2005). However, the extent of biodiversity supported by urban green spaces is highly variable and depends upon the type of green space, its structure and composition, and its connectivity to other green spaces (Lepczyk et al., 2017, Aronson et al., 2017, Beninde et al., 2015). When urban green space is managed to enhance biodiversity – by planting native species and creating diverse canopy structures (Threlfall et al., 2017, Threlfall et al., 2016) or by promoting green space heterogeneity (Callaghan et al., 2019a, Chang et al., 2017) – such efforts can result in an increase in species richness and abundance, thereby benefitting ecosystem functioning (Belaire et al., 2022, Berthon et al., 2021). Large patches of urban green space have been demonstrated to have positive effects on species biodiversity (Beninde et al., 2015, Leveau, 2022, Aida et al., 2016), and their protection is crucial as urban expansion increases (Simkin et al., 2022).

Tolerance of wildlife to urbanisation

Urbanisation acts as a strong selective filter of wildlife distribution, where behavioural traits influence species' ability to survive in urban areas (Aronson et al., 2016, McDonnell and Hahs, 2015, Croci et al., 2008, Neate-Clegg et al., 2023). Broadly, urban tolerant species are those that adapt to living in or use urban environments in spite of significant anthropogenic landscape transformation from natural to non-natural land and high levels of human disturbance (Rodewald and Gehrt, 2014). Species that are more tolerant of environmental change typically exhibit a wider niche breadth (Callaghan et al., 2019b, McKinney and Lockwood, 1999, Callaghan et al., 2021a, Devictor et al., 2008). Specifically, diet and habitat generalists are usually more urban tolerant than specialist species because they can exploit a wider variety of food resources and tolerate a broader range of landscape characteristics (Ducatez et al., 2018, Callaghan et al., 2019b, Neate-Clegg et al., 2023, Bonier et al., 2007). Previous studies have determined that traits such as behavioural flexibility (Lowry et al., 2013, Murray et al., 2018), high fecundity (Croci et al., 2008, Neate-Clegg et al., 2023, Evans et al., 2011), tolerance of human disturbance (Samia et al., 2015, Lowry et al., 2013, Møller and Díaz, 2017), degree of sociality (Skandrani et al., 2017, Kark et al., 2007) and dispersal ability (Møller, 2009, Vélová et al., 2023) are strong predictors of urban tolerance. However, the contribution of these traits to persistence is species or taxa specific (Neate-Clegg et al., 2023, Santini et al., 2019, Curti et al., 2024) and can be influenced by the composition of the urban landscape (Ibáñez-Álamo et al., 2024). There are also other factors that influence species' ability to exist within urban environments apart from behavioural traits, such as resource requirements and vulnerability to predation (Lowry et al., 2013, Rodewald and Gehrt, 2014). Nonetheless, identifying traits that shape urban tolerance is vital to understanding mechanisms that enhance local biodiversity and to protect species that are vulnerable to anthropogenic landscape changes.

To describe species tolerance to urbanisation within a conservation framework, Blair (1996) proposed three distinct classifications: urban avoider, urban adapter and urban exploiter. Urban avoiders usually become extirpated from urban environments or are rarely observed in them, either because they are sensitive to human disturbance or urban habitats no longer fulfil their ecological requirements. This often occurs in forest or ground-nesting species (Kark et al., 2007, McKinney, 2002, Conole and Kirkpatrick, 2011). Urban adapters typically use native and non-native vegetation within residential districts, are associated with open and edge habitat, and tend to come from granivore, omnivore, and nectarivore foraging guilds (Conole and Kirkpatrick, 2011, McKinney, 2002, Lim and Sodhi, 2004). Urban exploiters, which are often indigenous or invasive coloniser species, possess the necessary traits to thrive in urban environments, such that they reach higher population densities in cities than surrounding natural areas (Conole and Kirkpatrick, 2011, McKinney, 2002, Evans et al., 2011). They are able to exploit anthropogenic resources, particularly novel food sources, such as waste from rubbish dumps, food crumbs from eateries, and provisioning from residential animal feeders, and have been observed nesting on buildings ledges and cavities (Willmott et al., 2022, Callaghan et al., 2019b, Lowry et al., 2013). This classification was later challenged by Fisher et al. (2015), who advocated updating the terms to urban avoider, urban utiliser, and urban dweller to better reflect the responses of wildlife to urbanisation, but the original classification from Blair (1996) is still the most widely used.

Currently, it is recognised that species responses to urbanisation do not fit this simplified categorisation but instead occur across a continuous spectrum from urban tolerant to urban avoidant (Callaghan et al., 2021a, Callaghan et al., 2020, Callaghan et al., 2019b). Advances in the use of remote sensing variables as proxies of urbanisation, such as artificial light at night (ALAN) (Zhang and Seto, 2013, Ma et al., 2012, Pandey et al., 2013) are now often used for characterisation matrices, given that such variables are available at the global scale at relatively high resolution, are accessible to download from platforms such as Google Earth Engine, and provide continuous (rather than categorical) measurement scores that enable researchers to evaluate species across a continuous urban tolerance-avoidance scale. A continuous measurement of urbanisation also has the advantage of assessing the magnitude of the effect of urbanisation on the species of interest rather than solely classifying the species as an urban avoider, adapter, or exploiter, as per Blair (1996). This style of analysis has been undertaken for birds (Callaghan et al., 2019b, Fanelli et al., 2022, Yang et al., 2023), butterflies (Callaghan et al., 2021a), frogs (Liu et al., 2021), bats (Wolf et al., 2022), and a multi-taxon study including mammals (Curti et al., 2024).

Predators in urban ecosystems

Predator ecology and behaviour differ between urban and non-urban ecosystems due to the structural, ecological, and anthropogenic changes associated with urban expansion (Bateman and Fleming, 2012, Gehrt et al., 2010). Urbanisation, which entails habitat loss, fragmentation and increased human activity, impacts predator movement patterns as individuals navigate heterogeneous landscapes, relocate to more suitable habitat patches, and/or reduce their home range (Bradsworth et al., 2022, Wang et al., 2017, Parsons et al., 2019, O'Bryan et al., 2022). Large apex predators, such as the African Lion (*Panthera leo*) and the European Brown Bear (*Ursus arctos arctos*), are particularly sensitive to anthropogenic disturbance, changes in prey availability and habitat loss, and become extirpated from urban environments (Ripple et al., 2014, Riggio et al., 2013, Lesilau et al., 2021, Keinath et al., 2024, Corradini et al., 2021). In contrast, smaller predator species, such as coyotes (*Canis latrans*) and bobcats *(Lynx rufus*), have adapted to urban environments (Young et al., 2019, Lombardi et al., 2017, Murray and St. Clair, 2017).

These species are able to exploit novel anthropogenic food sources and alter their activity patterns to minimise human conflict (Tigas et al., 2002, Fedriani et al., 2001, George and Crooks, 2006, Larson et al., 2015, Larson et al., 2020).

Urban predators provide ecosystem services in cities (Gilbert et al., 2021, O'Bryan et al., 2018, Bonetti et al., 2024) by regulating prey populations through top-down control of food webs by consuming both carnivorous and herbivorous prey (Terraube and Bretagnolle, 2018, Warren et al., 2006, Faeth et al., 2005). In some cases, their diet is disproportionately composed of invasive species, which tend to be abundant in urban settings (McCabe et al., 2018, Méndez et al., 2020, Gámez et al., 2022). Scavenging species such as vultures (orders *Cathartidae* and *Accipitridae*) remove organic waste and carcasses from urban areas, which can spread diseases (O'Bryan et al., 2018, Donázar et al., 2016, Henriques et al., 2018). The absence of the Indian vulture (*Gyps indicus*) in India, due to the use of the veterinary drug diclofenac, has led to an increase in the stray dog population (*Canis lupus familiaris*) and rabies exposure due to dog bites (Markandya et al., 2008). This example highlights the important role of scavengers in disease control and public health.

Beyond ecological functions, urban predators provide cultural and aesthetic values, whilst also serving as flagship species for conservation success. For example, the citizens of New Delhi, India, feed meat scraps to Black Kites (*Milvus migrans*) and House Crows (*Corvus splendens*) as part of religious offerings (Gupta and Kumar, 2024, Kumar et al., 2019), and the Peregrine Falcon (*Falco peregrinus*), particularly in cities across the USA, is a flagship species for conservation efforts due to its recovery after sharp population declines from DDT usage (Gahbauer et al., 2015, Cade et al., 1994, Donázar et al., 2016, Cade et al., 1988).

Urban raptors

Raptors, or birds of prey, are a paraphyletic group of birds from the orders Strigiformes, Falconiformes, Accipitriformes and Cathartiformes (McClure et al., 2019). There are 557 raptor species that occur on every continent except Antarctica (McClure et al., 2018, Buechley et al., 2019). With this near-global distribution of raptors comes great diversity, and species exhibit a range of hunting strategies (Cresswell, 1996, Ellis et al., 1993), activity patterns (Aumann, 2001, Eriksen and Wabakken, 2018), and habitat preferences (Palomino and Carrascal, 2007, Rullman and Marzluff, 2014, Smith et al., 2022). Raptors are generally more sensitive and vulnerable to the impacts of anthropogenic change because of their slow life history and high trophic niche (Sergio et al., 2008, Buechley et al., 2019). Animals with slow life histories are characterised by low reproductive output, late sexual maturity, high parental investment and long generation times (Healy et al., 2019, Tapia and Zuberogoitia, 2018). When raptors experience disturbance or mortality from anthropogenic sources, their populations are vulnerable to reduced breeding success and poor recruitment, leading to long population recovery times compared to species with faster reproductive output (Stearns, 2000, Tapia and Zuberogoitia, 2018). Despite their importance and global population declines, they continue to be understudied (Buechley et al., 2019, McClure et al., 2018).

Raptors have existed within urban areas for centuries (Negro et al., 2020, Boal and Dykstra, 2018). Red Kites (*Milvus milvus*) nested in London, Great Britain, during the 15th century when King Henry VIII was in power (Boal and Dykstra, 2018), and records of Lesser Kestrels (*Falco naumanni*) breeding in building cavities exist dating back to the 15th century (Negro et al., 2020). Today, the most widespread urban raptor around the world is the Peregrine Falcon. This large falcon has a pan-global distribution and is successful in urban areas because of its tolerance to a wide variety of habitats (Fargallo et al., 2022), ability to nest on cliff analogues, such as building ledges and cavities, as well as nest boxes (Mak et al., 2021a, Altwegg et al., 2014, Sumasgutner et al., 2020), and capacity to prey on invasive species such as the Rock Dove and the Common Starling (*Sturnus vulgaris*) (Drewitt and Dixon, 2008, Mak et al., 2023, Altwegg et al., 2014). The abundance of resources that are available to raptors in urban areas, particularly in the form of prey and nesting sites, means that raptors can sometimes be observed in greater densities in urban areas than in the neighbouring rural areas (McPherson et al., 2021). Examples of common urban raptor species include the Eurasian Sparrowhawk (*Accipiter nisus*) (Schütz and Schulze, 2018, Thornton et al., 2017), the Black Goshawk (*Astur melanoleucus*) (Martin et al., 2014, Suri et al., 2017), the Eurasian Kestrel (*Falco tinnunculus*) (Sumasgutner et al., 2018, Sumasgutner et al., 2014a) and the Red-tailed Hawk (Morrison et al., 2016, White et al., 2020).

Urban-dwelling raptors display unique phenotypic and behavioural traits that facilitate successful living in urban ecosystems. In general, raptors occupying urban areas tend to have a smaller body size (Cooper et al., 2022, White et al., 2018). Larger raptors typically become extirpated from urban environments because their spatial and dietary requirements cannot be met (Peery, 2000), in combination with their low tolerance to anthropogenic disturbance (Kettel et al., 2018a, Montaño-Centellas et al., 2023). However, not all larger-bodied raptors are absent from urban areas, as the Crowned Eagle (*Stephanoaetus coronatus*) (Maseko et al., 2023), Osprey (*Pandion haliaetus*), Bald Eagle (*Haliaeetus leucocephalus*) and the African Fish Eagle (*Haliaeetus vocifer*) (McPherson et al., 2021) inhabit urban ecosystems. Raptors that exhibit a specialist diet, particularly avian specialists, and those that display a wide habitat breadth are the most successful urban species (Kettel et al., 2018a, Cooper et al., 2022). This phenomenon can be attributed to the year-round abundance of avian prey in urban areas that feed on the available resources (French et al., 2005), and the ability of certain raptors to tolerate a wide variety of environments (Boal, 2018). On the contrary, prey availability negatively affects the occurrence of raptors that have a generalist or rodent specialist diet in urban areas (Patankar et al., 2021, Sumasgutner et al., 2014a, Hindmarch and Elliott, 2015). However, not all studies have found evidence that diet specialism and habitat breadth affect the urban tolerance of raptors (Leveau et al., 2022), underscoring consideration of many factors potentially influencing urban tolerance in raptors (Neate-Clegg et al., 2023), and the importance of elucidating these factors to aid our understanding of raptor tolerance.

Thesis scope and objective

The chapters of this thesis investigate the urban tolerance of raptors at the continental, regional, and local scale. Using data collected from community science initiatives and observations from road transect surveys, my thesis examines how urbanisation impacts top predators such as raptors to inform conservation management for predators in urban ecosystems.

Specifically, this thesis aims to:

1. Investigate the occurrence rate, urban tolerance and urban green space use of Kestrel species around the world in relation to urbanisation.
2. Examine the urban tolerance of Australian raptors and identify which specific ecological and morphological traits influence their urban tolerance.
3. Explore how raptor richness and diversity change across the urban gradient of eight localities in South Australia and determine which ecological and morphological traits influence where they are observed.

Organisation of the thesis

This thesis is presented as a series of manuscripts that are published (Chapter 3), submitted for publication (Chapter 4) or in preparation for publication (Chapter 2). Some repetition of content is present in this thesis as each chapter is prepared as a standalone manuscript. Chapter 2 examines the influence of urbanisation on kestrel occurrence, as well as the urban tolerance and urban green space use of the American Kestrel, Eurasian Kestrel, and Nankeen Kestrel across their distributions. Chapter 3 investigates the urban tolerance of Australian raptors and the specific traits that influence their urban tolerance. Chapter 4 uses observational data from road transect surveys to assess species richness and Shannon diversity across the urban gradient of South Australia, as well as how behavioural and phenotypic traits influence where raptors are observed. A discussion including a synthesis of the main findings and recommendations for future study concludes the thesis. Included in the appendix (Appendix 2) is a manuscript investigating home range sizes of Nankeen Kestrels across the annual cycle, which uses data collected during the undertaking of this thesis.

Chapter 2 - Urbanisation and urban green space shape the distribution of kestrel species at the global scale

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Abstract

Urbanisation is a major cause of biodiversity loss globally. Yet, many species exhibit varying degrees of tolerance to human-dominated landscapes, especially across different spatial scales. Keystone species, such as raptors, play critical roles in ecosystem functioning through the provisioning of ecosystem services and stabilising food webs. Kestrels are small-bodied falcons with a widespread distribution and varying tolerance towards urban stressors, making them an ideal study system to assess the impacts of urbanisation on top predators across different spatial scales. This study aims to quantify the urban tolerance and urban green space use of kestrel species at the global and regional scales. We analysed data from eBird for three kestrel species: the American Kestrel, Eurasian Kestrel and Nankeen Kestrel across their distribution ranges. To determine the relative importance of land cover predictors, we used the output from eBird derived random forest models. Urban tolerance of kestrel species was quantified by an index based on general additive models (GAMs), ranking species from urban tolerant to urban avoidant. Lastly, to assess urban green space use and tolerance of urbanisation at the regional scale, we used occupancy modelling coupled with fine-scale land cover data across 37 cities. Urbanisation, measured via artificial light at night (ALAN) as a proxy, emerged as the most important land cover predictor in explaining kestrel occurrence and count. Urban green space generally had a significant positive influence on occupancy, while urban land cover generally had a significant negative influence on occupancy. Urbanisation is shaping the distribution of kestrels worldwide. Creating and maintaining urban green spaces for breeding, foraging and resting will ensure that Kestrels persist in urban ecosystems. Meanwhile, safeguarding suitable natural habitat is critical for individuals existing outside of urban areas.

Introduction

Urban ecosystems are dominated by humans, with artificial structures predominantly built to support human life (Vitousek et al., 1997, Frantz et al., 2023). Despite the negative consequences of urban living on wildlife (Shanahan et al., 2014, Birnie-Gauvin et al., 2016, Isaksson et al., 2018), some species persist and even thrive within urban environments (Alberti and Marzluff, 2004, McKinney, 2008). At the same time, the exponential growth of the human population within cities (Seto et al., 2012, United Nations, 2019), coupled with accessible technology capable of documenting everyday life (e.g. mobile phones, cameras, etc), presents a unique opportunity for community engagement in science and conservation. Individuals are documenting how urbanisation alters ecological relationships related to species richness and abundance, as well as predator-prey interactions and intra/inter-specific competition (Adler et al., 2020, Kobori et al., 2015, Trouille et al., 2019). Community science projects (also referred to as citizen science), such as eBird (Sullivan et al., 2014, Sullivan et al., 2009, Wood et al., 2011) and iNaturalist (Unger et al., 2021, Mesaglio and Callaghan, 2021), represent invaluable sources of data that can influence species conservation within urban ecosystems around the world. These platforms amass millions of observations annually from dedicated participants, generating data that can impact policy when survey efforts are sustained (Kobori et al., 2015). Given the ecological importance of green spaces, such as parks and gardens in urban areas (Aronson et al., 2017, Threlfall et al., 2017, Dale, 2018), quantifying the impacts of anthropogenic change on wildlife in cities is important to understand how to best mitigate further biodiversity decline.

Keystone species, such as raptors, are well-captured within community science survey efforts (Headland et al., 2023, Cooper et al., 2022). Most comprehensive analyses of raptor assemblages in urban areas stem from data sourced from online community-science-driven platforms (McClure et al., 2018, O'Bryan et al., 2022, Headland et al., 2023, Bradsworth et al., 2017, McPherson et al., 2021). These species are well-known, relatively large-bodied (Callaghan et al., 2021b), and easily recognisable, making them ideal for mobilising conservation efforts as flagship species (Donázar et al., 2016). Raptors play an integral part in ecosystem functioning in urban areas (Reynolds et al., 2021), and can sometimes exist in larger densities within urban ecosystems than in the surrounding rural areas (McPherson et al., 2021, McPherson et al., 2016a, Sumasgutner et al., 2014a, Suri et al., 2017, McCabe et al., 2018). For example, the Peregrine Falcon (*Falco peregrinus*), Crowned Eagle (*Stephanoaetus coronatus*), Black Goshawk (*Astur melanoleucus*) and Lanner Falcon (*Falco biarmicus*) were reported more frequently in urban areas than rural areas in South Africa (McPherson et al., 2021). In general, smaller species are more commonly found within urban areas than larger species (Headland et al., 2023, Cooper et al., 2022), as larger species require vast areas for home ranges (Moss et al., 2014), eat large prey that generally does not exist within the urban ecosystem (Naude et al., 2019), and are sensitive to anthropogenic disturbance

(Dennis et al., 2011). However, larger species, such as the Crowned Eagle in South Africa (Muller et al., 2020, McPherson et al., 2019, McPherson et al., 2016b, McPherson et al., 2016a), the Bald Eagle (*Haliaeetus leucocephalus*) in North America (Goulet et al., 2021, Millsap et al., 2004), and the Osprey (*Pandion haliaetus*) in cities around the world (Forys et al., 2021, Thomson et al., 2019), have demonstrated that large predators can survive in urban environments.

The composition and configuration of urban environments, particularly the presence and connectivity of green spaces, are key factors that may influence the ability of raptors to thrive in cities (Maseko et al., 2023, Boal, 2018). Urban green spaces provide raptors with the necessary space to hunt, breed and rest, and therefore these pockets of land are especially useful to raptors. For example, urban Eurasian Kestrels (*Falco tinnunculus*) in Vienna, Austria, nest on buildings close to backyards with greenery for ease of hunting wildlife that use green spaces (Sumasgutner et al., 2014b). Similarly, Peregrine falcons (*Falco peregrinus*) in London, Great Britain, nest close to public parks and gardens (Mak et al., 2021a). Unlike the aforementioned species that nest within the urban core, Crowned Eagles in Durban, South Africa, nest within forested patches in the urban mosaic, which provides them with breeding sites and close proximity to prey (McPherson et al., 2016b, McPherson et al., 2016a). Furthermore, natural forest cover is a significant predictor of Crowned Eagle occupancy (Maseko et al., 2023). Therefore, urban tolerance, in conjunction with habitat and prey preferences and availability, represent major factors in determining the occurrence of raptors within the urban matrix, and whether raptors are present year-round or only seasonally. The spatial distribution of urban green space, as well as the size of green patches, can also influence where raptors are observed. For example, the occurrence of the Harris Hawk (*Parabuteo unicinctus*) in Buenos Aires, Argentina, is positively associated with connectivity to other larger urban green space patches (Leveau, 2021), while the winter distribution of Eurasian Sparrowhawks (*Accipiter nisus*) in Vienna is positively associated with urban park size (Schütz and Schulze, 2018). Similarly, the species richness of raptors across South American cities increased in proportion to the size of the urban green space patch (Leveau, 2022). These examples display the utility of urban green space for raptors and their presence in urban areas.

Kestrels are a group of diurnal birds of prey that belong to the monophyletic family *Falconidae*, subfamily *Falconinae* (Fuchs et al., 2015). Kestrels are globally distributed and occupy a wide range of habitats and regions (Costantini and Dell'Omo, 2020). They are frequently observed perched on natural (e.g. trees, shrubs) or artificial structures (e.g. powerlines, telecommunications towers) at roadsides, or hovering, their distinctive hunting style, that allows them to scan the area below them for prey across a range of habitat types – over grassland, cropland, shrubland, coastal dunes or any other open area (Costantini and Dell'Omo, 2020). The urban affinity of the Eurasian Kestrel, (Sumasgutner et al., 2018, Sumasgutner et al., 2014b, Sumasgutner et al., 2014a), Nankeen Kestrel (Headland et al., 2023) and American Kestrel (Smallwood and Bird, 2020) have been previously documented, but it is unclear whether urban tolerance trends at the fine scale match those at the broad scale, and whether urbanisation is an important predictor of kestrel occurrence and count. These three Kestrel species are ideal for studying the impacts of urbanisation on raptor distribution due to their collective near-global presence, varied habitat use, and differing strategies of urban affinity, making them excellent indicators of how raptors can adapt to urban environments.

Our objective was to quantify the impact of urbanisation on the distribution of the American Kestrel, Eurasian Kestrel and Nankeen Kestrel at the broad scale (i.e. range-wide) and fine scale (i.e. across cities). First, we used model outputs from the eBird Status and Trends team that measure occurrence, count and relative abundance for each species. We extracted the predictor importance (how much each variable contributed to the performance of the model) of environmental variables (see table S2.1 for the list of variables) from the occurrence and count models, as the relative abundance predictor importance was not provided. We were particularly interested in the rank of artificial light at night, a suitable proxy for urbanisation across large scales (Zhang and Seto, 2013, Ma et al., 2012) that is used as a model predictor. We predicted that ALAN would influence the occurrence and count of the kestrel species across their range, and that this proxy for urbanisation that is associated with urban land cover would have equal or greater relative importance than other land cover types (Sumasgutner et al., 2014a, Kettel et al., 2018a). We then constructed an urban tolerance index to quantify the direction and magnitude of the association to urbanisation. Second, we conducted finer-scaled occupancy modelling to understand the influence of urbanisation, urban green space and landscape composition on occupancy. Certain kestrel species, such as the Eurasian Kestrel in Vienna, exhibit a particular affinity for urban areas (Sumasgutner et al., 2014b), despite the fact that developed, built areas represent less favourable habitat. Previous studies have demonstrated that urban green space is a key predictor for the occupancy of raptors in urban spaces (Zúñiga-Vega et al., 2023, Maseko et al., 2023, Boal, 2018). Therefore, we predicted that urban green space would positively influence the occupancy of kestrels within cities. We predicted that kestrels would be more likely to occupy cities with a greater percent landcover of grassland, shrubland and cropland, and a lower percent landcover of tree cover and urban land cover. We also predicted that kestrels would be more likely to occupy cities with a lower edge density of grassland, shrubland and cropland and a higher edge density of tree cover and urban land cover. This is because large patches of urban green space that are less fragmented generally support higher amounts of biodiversity (Beninde et al., 2015, Aronson et al., 2014).

Methods

Kestrel observation data and modelled data

We sourced observations of kestrel species from eBird (Sullivan et al., 2014, Sullivan et al., 2009, Wood et al., 2011), a global citizen science program where observers submit checklists of the birds they hear or see whilst birdwatching. Custom eBird datasets that contained the observation data for each kestrel species up until March 2023 were downloaded (ver. ebd_rel_*speciesname*_Mar-2023; available at: https://ebird. org/data/download), along with the corresponding sampling event data (ver. ebd_rel_sampling_Mar-2023) for occupancy modelling as well as urban tolerance modelling. Data from checklists between the periods of 1 January 2010 to 31 December 2022 were used. Checklist data for urban tolerance modelling was cropped to be within the known ranges for each kestrel using shapefiles from the eBird status and trends dataset (Fink et al., 2023) (Figure 1). Checklist data for occupancy modelling was cropped to be within cities across the distribution of the Nankeen Kestrel (Australia), Eurasian Kestrel (Europe) and American Kestrel (North and South America), and city shapefiles were sourced primarily from the Global Administrative Areas Database, the Urban Centres and Localities of Australia dataset, and the US Census Urban Areas dataset. Please refer to supplementary materials table S2.2 for the full list of sources. We sourced random forest model output data from random forest models predicting the occurrence, count, and relative abundance of American, Eurasian and Nankeen Kestrels across their range from the eBird Status and Trends product version 2023 (Fink et al., 2020) These products come in the form of rasters (digital images) and contain checklist data from 1 January 2009 to 31 December 2023.

Data filtering and preparation

Prior to analyses, we filtered the checklist data for the urban tolerance and occupancy analysis to remove biases that exist within community science datasets such as eBird (Bird et al., 2014, Backstrom et al., 2024a). We followed the eBird best practices guide (Strimas-Mackey et al., 2023) to ensure data filtering was done correctly and robustly.

Checklists were included in the analyses if they were ‘complete’, meaning a birdwatcher had submitted a checklist containing all the birds they had heard/seen whilst birdwatching. To reduce observer variation effort, only travelling or stationary checklists were used, and checklists were restricted to less than 24 hours in duration, less than 10km in length, at speeds below 100km/h, and with 10 or fewer observers (Strimas-Mackey et al., 2023, Johnston et al., 2021).

To eliminate spatial and temporal bias that is often present within community science data (i.e. data is collected close to where people live or commute to and at times that are convenient) (Bird et al., 2014), we subsampled the checklist data to include one checklist from each 3x3 km hexagonal grid cell for each week of the year from 2010 to 2022 for the urban tolerance analysis, and from 2017 to 2022 for the occupancy modelling. To help alleviate class imbalance within the data (i.e. many more non-detections present than detections), detection and non-detection data were sampled independently (Johnston et al., 2021).

Land cover products

For the urban tolerance analysis, we followed the protocols outlined in Headland et al., 2023 and used the Visible Infrared Imaging Radiometer Suite (VIIRS) nighttime lights dataset (Elvidge et al., 2017) as a proxy for urbanisation. This measure of urbanisation is commonly used in studies of urban tolerance, as it provides a continuous rather than categorical estimate, and therefore allows for species to be ranked individually, offering greater insight into the directionality and magnitude of their responses. We also chose VIIRS night-time lights as a proxy for urbanisation due to the availability of the data at the appropriate spatial grain and temporal timeframe of the study. This renders ALAN an appropriate measure to assess the urban tolerance of the Kestrel species. We downloaded yearly rasters of the VIIRS night-time lights dataset from 2012 to 2022 and created a composite image of the average value for each pixel. We imported this raster into R (v 4.3) (R Core Team, 2023) and extracted the mean radiance within a 3km buffer of each checklist.

For the occupancy modelling, we sourced landcover data from the Dynamic World dataset (Brown et al., 2022) in Google Earth Engine (Gorelick et al., 2017). This product provides landcover data at 10m resolution, and we selected five landcover classes for modelling: tree cover, grassland cover, cropland cover, shrubland and scrub cover, and urban land cover. We reduced the image collection of data from 2017 to 2022 to a single composite image of the mode for each pixel (i.e. land cover class most frequently classified for that pixel) over the six-year period for each city. We then summarised the land cover classes around each eBird checklist within the given city at a resolution of 3km.

Statistical analysis

We conducted all analyses using the statistical software R in the integrated RStudio environment. The *tidyverse* (v 2.0) (Wickham et al., 2019) ecosystem of packages along with the *sf* package (v 1.17) (Pebesma, 2018) were used for data manipulation, and the *ggplot2 (v 3.3.5)* package (Wickham, 2011) was used for visualisation of data and model results.

Predictor Importance

To quantify the importance of ALAN in Kestel occurrence and count models, we extracted the top 10 most important land cover predictors range-wide from the random forest models, which is available from the eBirdst package output. We then ranked the land cover predictors based upon their overall importance between the occurrence and count models. Predictive performance metrics (PPMs) for the two models are available in table S2.3.

Urban tolerance

As the predictor importance extracted from the eBird random forest models do not give the magnitude or directionality of the predictors, only the predictive power of the covariates in the model, we ran urban tolerance models using the methods from Headland et al., (2023) for each of the three Kestrel species. We used generalised additive models (GAMs) with a negative binomial error structure, as the data were over-dispersed.

For each model, the response variable was the estimated abundance of each species within the checklist, and the predictor variable was the median value of the VIIRS nighttime lights assigned to each checklist. Smoothing functions were applied to the following variables, which were likely to influence the detection of a species on a checklist: number of observers, latitude and longitude, day of year, effort distance (km), effort speed (kmph), effort hours and ‘time observations started’. Thin plate regression splines were used for the following variables: number of observers, latitude, longitude, duration (min), and day of year. Five degrees of freedom were used for these variables. A cyclic cubic regression spline with seven degrees of freedom was used for ‘time observations started’. For each species' model, the parameter estimate for nighttime lights was obtained to indicate each species' relationship with urbanisation (i.e., positive or negative) and the magnitude of that relationship.

Occupancy modelling

To examine the influence of urbanisation and urban green space on the occupancy of Nankeen, Eurasian and American Kestrels within cities across their range, we fitted occupancy models using the *spOccupancy* package (ver. 8.0) (Doser et al., 2022). This package fits occupancy models under a Bayesian framework using Markov Chain Monte Carlo (MCMC) and Pólya-Gamma data augmentation for efficient computation. Models were fitted using the s*tPGOcc* function, which enables for fitting spatially explicit multi-season occupancy models where it is possible to pool all available data across years to investigate the effects of a covariate on occupancy. This approach was used rather than traditional dynamic occupancy models, as we were not interested in colonisation and extinction rates.

We chose the associated cities included in the occupancy modelling analysis by investigating the amount of checklist data present for each species within a given city across their range. Occupancy modelling requires repeat visits to a locality (i.e. birdwatching site), which can significantly reduce the number of checklists available for analysis. Therefore, we chose those species for which high volumes of data had been collected, and cities that had sufficient checklist data for those species. For the American Kestrel, this included cities in the United States of America, ranging from Los Angeles (on the west coast) to New York (on the east coast) and all cities in between. We included three cities from Canada, as well as four cities from South America. For the Eurasian Kestrel we included eight European cities, ranging from Lisbon (in the east) to Vienna (in the west) and all cities in between. For the Nankeen Kestrel, we included all major capital cities Australia's states and territories, ranging from Sydney (in the east) to Perth (in the west).

Occupancy modelling assumes that the sampling area is closed (i.e. no change in occupancy) during the study duration (MacKenzie et al., 2003). However, for mobile species, such as birds, communities can change across surveys (Si et al., 2018), which violates this critical assumption. Instead of interpreting the results of the models as site occupancy, we interpreted it as site use (Zhang et al., 2024).

Therefore, the results are read as site use probability rather than site occupancy probability. As the Eurasian Kestrel, and to a lesser extent the American Kestrel, are migratory species, we ran the models' using data from the breeding seasons for each species to account for when birds are most likely to be present in their respective ranges (e.g. Eurasian Kestrels in Vienna).

We ran the models for each city until convergence and goodness of fit was obtained. Full information regarding the number of chains, number of burn-in samples and the thinning rate is available in table S2.4. To check for adequate mixing of chains, we examined the Gelman-Rubin statistic and ensured that it was below 1.1, looked at the Effective Sample Size (ESS) and ensured that it was over 100 and visually inspected trace plots. To check for model goodness of fit, we used the *ppcOcc* function from *spOccupancy,* which performs posterior predictive checks. If the Bayesian p-value fell within 0.1-0.9, the model was deemed to fit the data adequately.

In the occupancy sub-model, we included the proportion of grassland cover, cropland cover, shrubland and shrub cover, tree cover and urban land cover at 3km resolution around the checklist. The year was also included to account for pseudo replication of sites across years. In the detection sub-model, we included data from checklists that influence bird detectability, such as the time of day, protocol type (stationary or travelling), the number of observers, distance travelled by the observers and the duration length of the survey. We standardised all continuous covariates to allow for comparisons between covariate values across species.

Urban land cover composition

To identify whether landscape composition and configuration influenced kestrel occupancy, we ran linear models. Prior to analysis, we summarised the percent land cover, a measure of landscape composition, and the edge density, a measure of landscape configuration, for each of the 37 cities in the analysis. These metrics are commonly used to summarise land cover data in species distribution modelling (Strimas-Mackey et al., 2023). We then ran linear models for each metric (e.g. percent landcover and edge density) and land cover class (e.g. urban land cover, tree cover, shrubland, grassland, cropland) combination, totalling 10 different models. The response variable was the mean posterior estimate of the land cover type, and the predictor variable was the landscape metric.

Results

Predictor Importance

ALAN displayed high predictive power amongst land cover covariates in explaining the occurrence and count of the American Kestrel, Eurasian Kestrel and Nankeen Kestrel modelled by the eBird Status and Trends team (Figure 2.2). For the occurrence models, ALAN had the most predictive power of the land cover covariates for the American Kestrel, the second most predictive power for the Eurasian Kestrel, and the fourth most for the Nankeen Kestrel. For the count models, ALAN had the most important predictive power amongst land cover predictors for the American Kestrel and the Eurasian Kestrel, while it was the third highest predictive power for the Nankeen Kestrel. Other important land cover predictors explaining kestrel count and occurrence included ‘Dense Herbaceous Cover’ (American Kestrel

– Occurrence rank: 2, Count rank: 3; Eurasian Kestrel – Occurrence rank: 1, Count rank: 3; Nankeen Kestrel – Occurrence rank: 1, Count rank: 2), 'Seasonal Water Cover' (American Kestrel – Occurrence rank: 3, Count rank: 2; Eurasian Kestrel – Occurrence rank: 4, Count rank: 2; Nankeen Kestrel – Occurrence rank: 3, Count rank: 1), 'Herbaceous Cropland' (American Kestrel – Occurrence rank: 6, Count rank: 6; Eurasian Kestrel – Occurrence rank: 5, Count rank: 4; Nankeen Kestrel – Occurrence rank: 7, Count rank: 5), 'Sparse Forests' (American Kestrel – Occurrence rank: 4, Count rank: 4; Eurasian Kestrel – Occurrence rank: 3, Count rank: 5; Nankeen Kestrel – Occurrence rank: 2, Count rank: 4), and 'Open Forests' (American Kestrel – Occurrence rank: 5, Count rank: 5; Eurasian Kestrel – Occurrence rank: 6, Count rank: 7; Nankeen Kestrel – Occurrence rank: 6, Count rank: 9) (Figure 2.2).

Kestrel urban tolerance index

All three kestrel species displayed a negative response profile to urbanisation, indicating they are generally urban avoidant (Figure 2.3). The Eurasian Kestrel displayed the least negative response profile, closely followed by the American Kestrel (Figure 2.3). The Nankeen Kestrel displayed the greatest negative response profile to urbanisation (Figure 2.3).

Importance of urban green space

Urban green space was an important predictor of occupancy for Nankeen Kestrels, American Kestrels and Eurasian Kestrels alike (Figure 2.4 A-E). Kestrels generally displayed a consistent pattern of habitat use, opting to use shrubland, grassland and cropland, while avoiding urban land cover and tree cover, regardless of species or city.

Across Australia (seven cities), Nankeen Kestrels significantly avoided using urban land cover and tree cover in four cities and displayed a significant positive association with shrubland and grassland in five cities, and a significant positive association with cropland in three cities (Figure 2.4A, Table S2.5).

Eurasian Kestrels across Europe (eight cities) significantly avoided using urban land cover in two cities and tree cover in one city and displayed a significantly positive association with grassland in three cities and a significantly positive association with cropland in two cities (Figure 2.4B, Table S2.5).

Within cities based in South America (four cities), there was no significant avoidance of urban land cover or tree cover by American Kestrels, and they displayed a significantly positive association with cropland in one city (Figure 5C, Table S2.5).

Similarly, across North America (18 cities), kestrels significantly avoided using urban land cover in seven cities and significantly avoided using tree cover in six cities. American Kestrels had a significantly positive association with shrubland in seven cities, a significantly positive association with grassland in 10 cities, and a significantly positive association with cropland in eight cities (Figure 2.4D-E, Table S2.5).

Urban land cover composition

Linear models showed that there was a significantly positive association between percent land cover of grassland and the model posterior estimate, such that kestrels had higher occupancy rates in cities with higher percent land cover of grassland (Figure 2.5A, Table 2.1, estimate = 0.06 ± 0.025, LCI = 0.01, UCI = 0.11, p = 0.019). We found no significant relationship between percent land cover of tree cover (Figure 2.5B, Table 2.1, estimate = <0.005 ± 0.012, LCI = -0.02, UCI = 0.03, p = 0.7), urban land cover (Figure 2.5C, Table 2.1, estimate = <0.005 ± 0.008, LCI = -0.02, UCI = 0.01, p = 0.8), shrubland (Figure 2.5D, Table 2.1, estimate = -0.02 ± 0.018, LCI = -0.06, UCI = 0.02, p = 0.3) and the model posterior estimate.

There was a significantly positive relationship between edge density of grassland and the model posterior estimate, such that kestrels had higher occupancy rates in cities where grassland was more fragmented (Figure 2.6A, Table 2.2, estimate = 0.03 ± 0.009, LCI = 0.01, UCI = 0.05, p = 0.003). There was a significantly negative relationship between edge density of cropland and the model posterior estimate, such that kestrels had lower occupancy rates in cities where cropland was more fragmented (Figure 2.6E, Table 2.2, estimate = -0.04 ± 0.012, LCI = -0.06, UCI = -0.01, p = 0.002). We found no significant relationship between edge density of tree cover (Figure 2.6B, Table 2.2, estimate = -0.01 ± 0.011, LCI = -0.03, UCI = 0.02, p = 0.6), urban land cover (Figure 2.6C, Table 2.2, estimate = -0.01 ± 0.013, LCI =-0.04 , UCI = 0.01, p = 0.3) and shrubland (Figure 2.6D, Table 2.2, estimate = 0.01 ± 0.008, LCI = -0.01, UCI = 0.02, p = 0.4) and the model posterior estimate.

Discussion

Using robust occurrence and count models sourced from the eBird Status and Trends team, as well as eBird data covering the distribution range of the American, Eurasian, and Nankeen Kestrels, we analysed approximately 45 million checklists to investigate the influence of ALAN on the three species at the broad and fine scales, giving new insights into kestrel urban tolerance at multiple scales. We unravelled the importance of ALAN in explaining kestrel occurrence and count range-wide and highlighted other important environmental predictors, such as forest cover, herbaceous plant cover, and water bodies such as lakes and oceans. ALAN was the most important environmental predictor of kestrel occurrence range-wide, indicating that kestrels may use resources provided in urban areas (i.e. nesting and foraging sites) and show some adaptability to urbanisation. However, all three kestrel species modelled displayed a significantly negative response profile to ALAN (i.e. urban avoidant), but the magnitude of this response was relatively small. This result suggests that whilst kestrels may choose to avoid urban areas range-wide, some populations may be tolerant to urban ecosystems. We also gained novel insights into the urban green space use of urban kestrels, and the compositional factors at the landscape level that influence their occupancy. Urban green space positively influenced occupancy of Nankeen Kestrels, American Kestrels and Eurasian Kestrels in cities, emphasising its importance for species living in urban areas, and the composition and configuration of landscape types such as grassland and cropland were highly influential for kestrel occupancy. Our results affirm the notion that urbanisation is a key driver in shaping species distributions worldwide (Sun et al., 2022, Sol et al., 2014, Start et al., 2020), including avian predators like kestrels.

For two of the three kestrel species modelled in this study, the American Kestrel and the Eurasian Kestrel, ALAN, used as a proxy for urban development, was in the top two predictors of occurrence and count. Artificial light at night also ranked highly for the Nankeen Kestrel, ranking fourth in the occurrence model and third in the count model. Such frequent sightings of kestrels in urban areas suggests that they may provide resources pertaining to their survival. Kestrels are known to exploit anthropogenic structures that are analogous to cliffs to nest on, such as ledges and building cavities, and respond positively to the provisioning of nest boxes, much like the related Peregrine Falcon (Mak et al., 2021a, Kettel et al., 2018b, Gahbauer et al., 2015, Sumasgutner et al., 2020). Lesser Kestrels in Sevilla, Spain, nest in holes in urban buildings and churches (Tella et al., 1996, Negro and Hiraldo, 1993), while Eurasian Kestrels across Israel mainly use flowerpots on windowsills, windowsill ledges and utility porches (Charter et al., 2007). Urban areas can also provide illumination from streetlights and buildings that can serve as hotspots for prey to congregate and kestrels to forage (Negro et al., 2000, Sumasgutner et al., 2013). Lesser Kestrels in Sevilla, Spain, forage for insects above the main town cathedral where they nest, using the light illuminating the cathedral at night (Negro et al., 2000). It is thought that this foraging period from sunset until midnight (when the lights are turned off) is used to feed themselves, as low provisioning rates to chicks were observed, which may facilitate better body conditioning (Negro et al., 2000). Although there are no published studies documenting this behaviour in the Nankeen Kestrel or the American Kestrel, (but see Sumasgutner et al. 2013), similar behaviours have been observed in other Falcon species, such as Peregrine Falcons (Kettel et al., 2016) and Eleonora’s Falcon (Buij and Gschweng, 2017), suggesting that kestrel species may also use ALAN to extend their foraging hours.

The limiting factor of ALAN in this study is that the responses of kestrels to urbanisation is likely to be different across regions. Therefore, the importance of ALAN derived from the eBird Status and Trends models and the species urban tolerance from the GAMs are to be interpreted in the context of the species range (i.e. broad scale) rather than at finer scales. It is also important to note that random forest models assign weights to model variables that have high explanatory power in conjunction with other variables, and therefore whilst ALAN is an important land cover predictor in the models, effort variables (such as survey duration and survey effort) are usually the most important predictors for these models. Future analyses of the influence of urbanisation on species at the broad scale could focus on modelling that splits detection bias from ecological patterns, such as occupancy modelling using spatially varying coefficients to account for differing levels of urbanisation across large scales (Doser et al., 2025).

Urban tolerance analysis revealed that all three kestrel species displayed a negative response profile to urbanisation, or were urban avoidant. In combination with the predictor importance results, this uncovers that, whilst kestrels are frequently sighted in urban areas where they may nest and forage, their response is generally to avoid urban settings. These results provide new insights into kestrel urban tolerance across each species range. Whilst urban populations of kestrels may exist in cities, such as Vienna (Huchler et al., 2020, Sumasgutner et al., 2014a, Sumasgutner et al., 2014b) and Berlin (Kübler et al., 2005), where they appear to be more urban tolerant, these observations reflect a pattern at a finer, local scale, whilst our results reflect broader, large-scale trends. It is also important to note that whilst our results indicate a level of urban avoidance, the magnitude of this response appears to be low, which may explain the presence of urban tolerant kestrel populations at the finer spatial scale. The Nankeen Kestrel may have a lower tolerance to urbanisation compared to the Eurasian and American Kestrels given that rapid urbanisation in Australia is a relatively recent phenomenon (Coffee et al., 2016), whereas Europe and the Americas have a much longer history of urbanisation. Therefore, the period of time for which the American and Eurasian Kestrels have been able to adapt to anthropogenic disturbance is much greater than that for the Nankeen Kestrel. The Eurasian Kestrel, in particular, has likely nested in cavities in buildings, along with the similar Lesser Kestrel, for hundreds of years (Negro et al., 2020), which explains their urban affinity in some regions.

The Eurasian Kestrel, and to a lesser extent the American Kestrel, which are migratory species, display seasonal use of urban environments (Huchler et al., 2020, Sumasgutner et al., 2014a, Smallwood and Bird, 2020). Across the full annual cycle, the population of Eurasian Kestrels studied in Vienna inhabit the city from approximately February to August and migrate elsewhere after the breeding season (Huchler et al., 2020, Sumasgutner et al., 2014a, Sumasgutner et al., 2014b). This seasonal pattern might also influence the urban tolerance index, as the species intensive use of anthropogenic structures is limited to the breeding season. However, the intensive use of urban areas does not always equate to population viability. For example, kestrels in Vienna experienced higher nesting failure, lower hatching rates and smaller fledged brood sizes due to low prey availability (Sumasgutner et al., 2014a). Thus, when interpreting model results for migratory species, it is important to consider aspects of the species ecology such as the full annual cycle. This study focussed on general habitat associations across a broad (i.e., a species range) and temporal (i.e., whole year) scale, but further investigations for habitat associations throughout the breeding and non-breeding seasons and the importance of urban environments in shaping such seasonal distributions for kestrels are needed.

Forest land cover predictors, particularly open forest and sparse forest were highly important in predicting kestrel occurrence. However, kestrels generally avoid areas such as these, and are usually associated with open and semi-open land cover types, particularly agricultural areas, where they can hover hunt (Costantini and Dell'Omo, 2020). This predominant hunting style might explain the high importance of dense herbaceous plant cover and herbaceous cropland within the models. But alternative hunting styles, such as hunting from perches or in pursuit, are often associated with forest edges. Tracking of three common raptor species (Northern Goshawk (*Accipiter gentilis*), Common Buzzard (*Buteo buteo*), Lesser Spotted Eagle (*Clanga pomarina*)) northwest of Tartu, Estonia, revealed that these three species perched on forested edges, tree lines and small woods preferentially over other landscape features within an agricultural area (Mirski and Väli, 2021). Many kestrel species are commonly seen perched on powerlines adjacent roads or trees on roadside verges (Costantini and Dell'Omo, 2020, Debus, 2019, Dean and Milton, 2009). Foraging at the forest edge may be preferential for kestrel species and raptors alike, as edge habitat is strongly associated with prey abundance (Šálek et al., 2010, Batáry et al., 2014) and diversity (Andrén, 1995, Tews et al., 2004), rendering them prey hotspots. Therefore, protecting these highly productive verges, as well as forest patches and edge habitat to provide important resources for foraging and nesting for kestrels, is vital as urbanisation continues to sprawl into natural areas.

At the fine scale, we found that the habitat use of Nankeen, Eurasian and American Kestrels in urban environments was positively influenced by urban green space, which is consistent with findings from species and city-specific previous studies (Sumasgutner et al., 2014a, Hogg and Nilon, 2015). Eurasian Kestrels in Vienna, Austria, forage in large open green spaces, such as parks and green courtyards that are located next to nest sites in buildings (Sumasgutner et al., 2014a), and grassland cover had a positive effect on occupancy of American Kestrels inhabiting St. Louis, Missouri (Hogg and Nilon, 2015). Similarly, a pair of urban breeding Nankeen Kestrels in Adelaide, Australia, use grassland adjacent to the airport runway to forage proportionately more than other available land cover types (Headland, personal observation). Our results showed that these three kestrel species generally avoided tree cover, illustrating that the type of urban green space is important in where kestrels are encountered, which has not previously been documented in detail. Differences in occupancy between cities, in the same region, and across regions, could be due to different habitat configurations within cities. The amount and spatial configuration of urban green space may vary depending on how a city was developed and the priority given to incorporating green areas, potentially influencing the extent to which such environments are suitable or attractive for kestrel occupancy. However, it is important to note that urban green spaces such as parks and botanical gardens are popular birdwatching sites as they are hotspots for urban wildlife (Callaghan et al., 2019a, Backstrom et al., 2024a, Threlfall et al., 2017). This might give urban green space a higher weight due to an observer bias. Clustered detectability of kestrels may be apparent due to known roost sites. In combination with observers (e.g., birders) who are eager to tick off a target species, this can lead to overrepresentation of a single individual in an area (Callaghan et al., 2018). But the systematic sampling bias that the kestrel species in this study are subject to is likely the same, as raptors as taxa are observed using similar methods, and the observations are biased in the same way.

Across cities, urban green space configuration and composition was influential in determining how strongly kestrels used specific land cover types, as we predicted. Edge density, a measure of landscape configuration and fragmentation, was a significant predictor of occupancy for grassland and cropland land cover types across the cities analysed. Cities with a higher edge density of grassland, or grassland that is more fragmented throughout the landscape, had a stronger coefficient value than cities with less fragmented grassland while cities with a lower edge density of cropland, or larger, continuous patches of cropland, had a stronger coefficient value than cities with more fragmented cropland. We also found that percent landcover, a metric describing the composition of a landscape, was a significant predictor of occupancy for grassland, as cities containing a higher percentage of grassland had stronger coefficient values than cities with a lower percentage of grassland. These results provide critical new knowledge, indicating that grassland that is frequently dispersed throughout the city is important to sustain their occupancy, as well as large cropland patches. The fragmentation of urban green space due to urbanisation can lead to habitat and resource loss, which in turn causes declines in species richness, and in some cases, localised extinctions (McKinney, 2008, Sol et al., 2014). These remaining green spaces are often refugia for urban wildlife (Aronson et al., 2017, Gentili et al., 2023, Steven and Newsome, 2025), which likely serve as important prey hotspots for kestrels. Therefore, it is vitally important to maintain existing urban green spaces and to continue creating structurally diverse connected green spaces for raptors to forage and breed.

Small, cavity nesting raptors such as kestrels, take to natural nest analogues such as nest boxes, which may influence their association to urbanisation. There are many studies documenting kestrels taking to nest boxes in rural regions across Europe (Fargallo et al., 2001, Valkama and Korpimäki, 1999, Aviles et al., 2001) and North America (Katzner et al., 2005, Rohrbaugh Jr and Yahner, 1997, Butler et al., 2009), but dedicated nest box programs appear to be less common in cities. In our study regions, Berlin (Kübler et al., 2005) and Rome (Dell'Omo et al., 2008) have nest box programs for Eurasian Kestrels, and the American Kestrel Partnership, which has now merged with Project Nestwatch (Evans et al., 2005), has prominent nest box monitoring programs in New York and Denver (Project Nestwatch, Cornell Lab of Ornithology). There are no known nest box programs targeting urban kestrels in Australia, likely because of the relatively few records of urban breeding (McCrie and Noske, 2015, Debus, 2022). Among the cities modelled, urban land cover had a significant positive influence on occupancy in Berlin, Phoenix, and Miami. The long running nest box program in Berlin may explain some of the positive association to urbanisation, however in-depth investigations into the mechanisms driving a positive association to urban land cover are still needed. Nest boxes have been demonstrated to drive population growth in urban raptor populations (James Reynolds et al., 2019), particularly for kestrels (Village, 1983, Bortolotti, 1994), where they have the potential to provide nesting sites for kestrels that frequently use urban areas. But, if fitness consequences are not considered, it can lead to an ecological trap, where nesting site quality is high while preferred prey availability might be low, leading to reduced breeding success (Sumasgutner et al., 2014a) and nestling condition (Sumasgutner et al., 2018).

Conclusion

We used community science observations of kestrel species at a global scale to investigate the importance of urbanisation in predicting the occurrence, as well as the urban tolerance and urban green space use of three kestrel species across their range. We provided new insights into kestrel urban affinity for three common kestrel species, revealing crucial insight into the spatial nature of urban tolerance. Artificial light at night, as a proxy for urbanisation, was an important predictor of kestrel occurrence and count for all three species across their range, which demonstrates that urbanisation is a major driving force shaping kestrel distributions across the globe. While we acknowledge the limitations of the use of artificial light at night as a proxy for urban development, as it has the potential to misclassify areas of low urban infrastructure that are well-lit, such as ports and mines, as well as low-lit areas that have high human densities such as informal settlements, this is unlikely to be an issue at the finer scale, and therefore we are confident that the results from our study reflect the urban tolerance at the broad scale. Urbanisation is known to dramatically transform natural landscapes, altering ecological processes, and shaping species assemblages and resource availability across large spatial scales (McKinney, 2002, Shochat et al., 2010). Urban tolerance analysis sheds light on species-specific urban tolerances profiles for kestrel species, which may help shape conservation action for lesser-known kestrel species located in developing areas (e.g. Africa). We also provided novel insights into kestrel urban space use at the fine scale, discovering that land cover type and urban landscape composition was an important determinant of habitat use, a first for these species. Within cities, urban green spaces provide critical resources for urban kestrels in the form of foraging and perching areas. Protecting remaining suitable natural habitat, as well as continuing to restore degraded habitat and creating new urban green spaces is essential for the persistence of kestrel in urban and rural areas, particularly as urban areas expand, and natural land is transformed into low quality habitat for wildlife.

Acknowledgements

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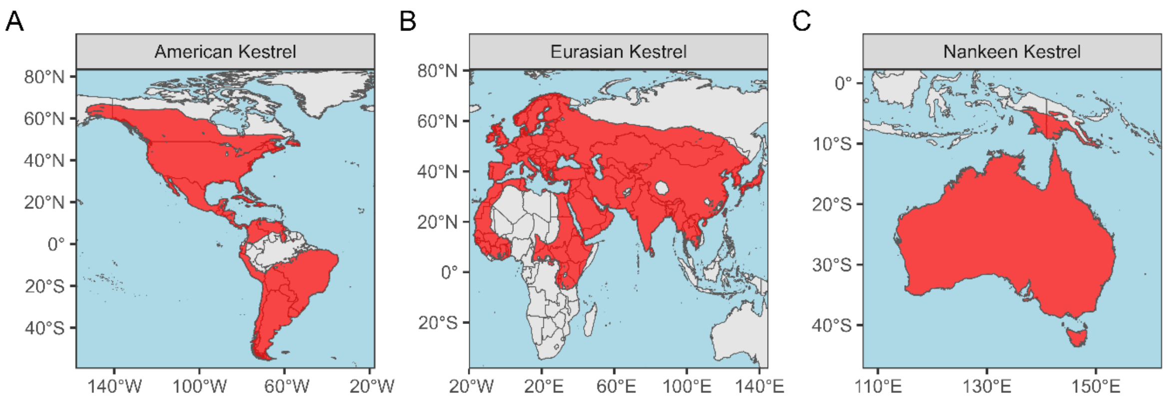

Figure 2.1 The individual distributions of all 14 Kestrel species present in the analysis. The red areas represent the distribution of each species. Species distributions are reproduced from shapefiles from the eBird Status and Trends dataset.

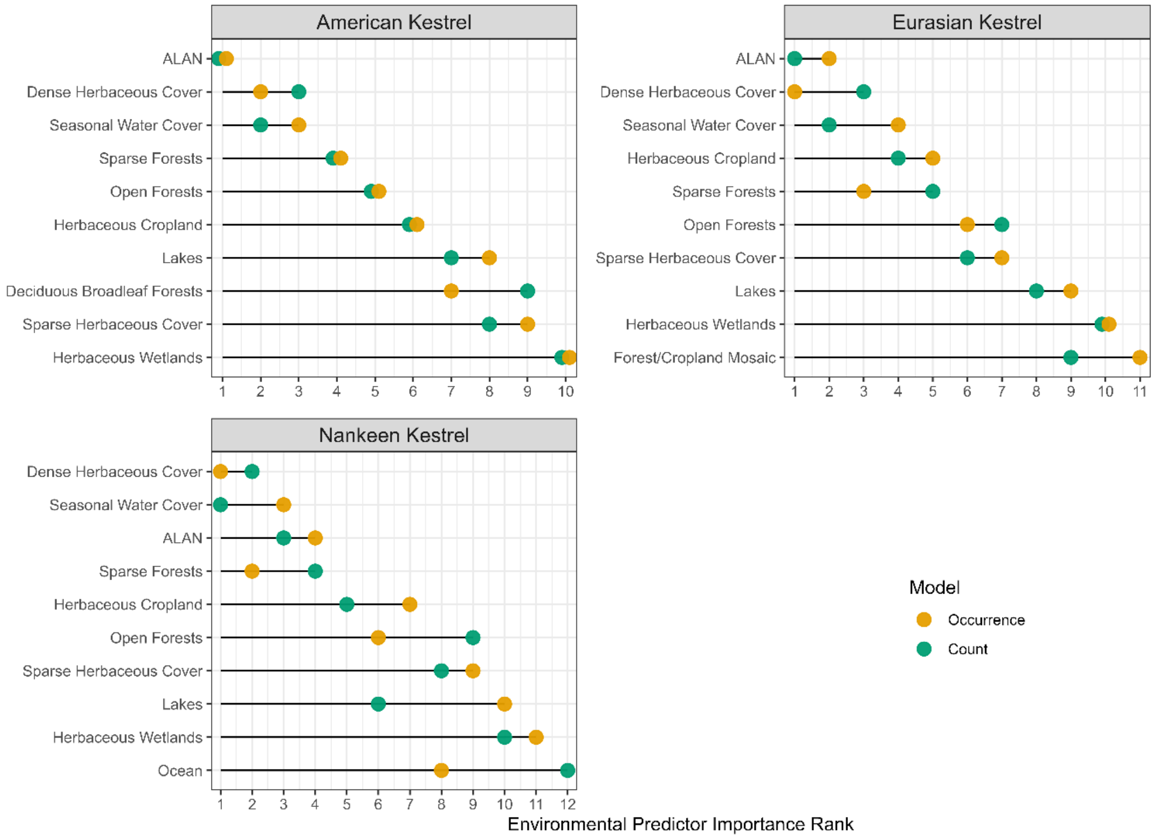

Figure 2.2 The environmental predictor importance ranking derived from the random forest occurrence and count models from the eBird status and trend dataset.

Predictors that were ranked within the top 10 most important in explaining kestrel occurrence are displayed. Yellow circles denote the environmental predictor importance rank from the occurrence model, while green circles denote the environmental predictor importance rank from the count model. Overlapping circles indicate that the predictor held the same rank in both the occurrence and count model.

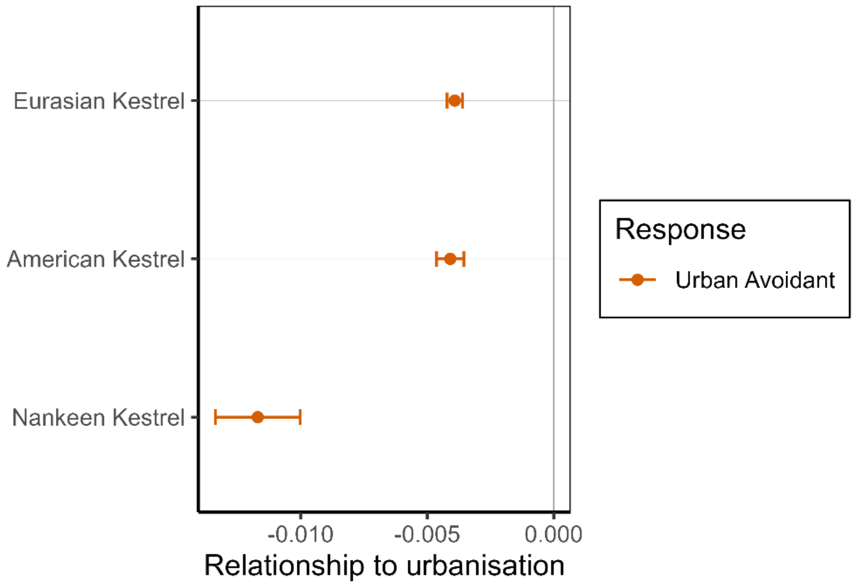

Figure 2.3 The Urban tolerance index for the three kestrel species, ranked by the coefficient estimate from general additive models. Negative values indicate a negative response to urbanisation (‘Urban Avoidant’, in orange). Error bars represent the 95% confidence intervals.

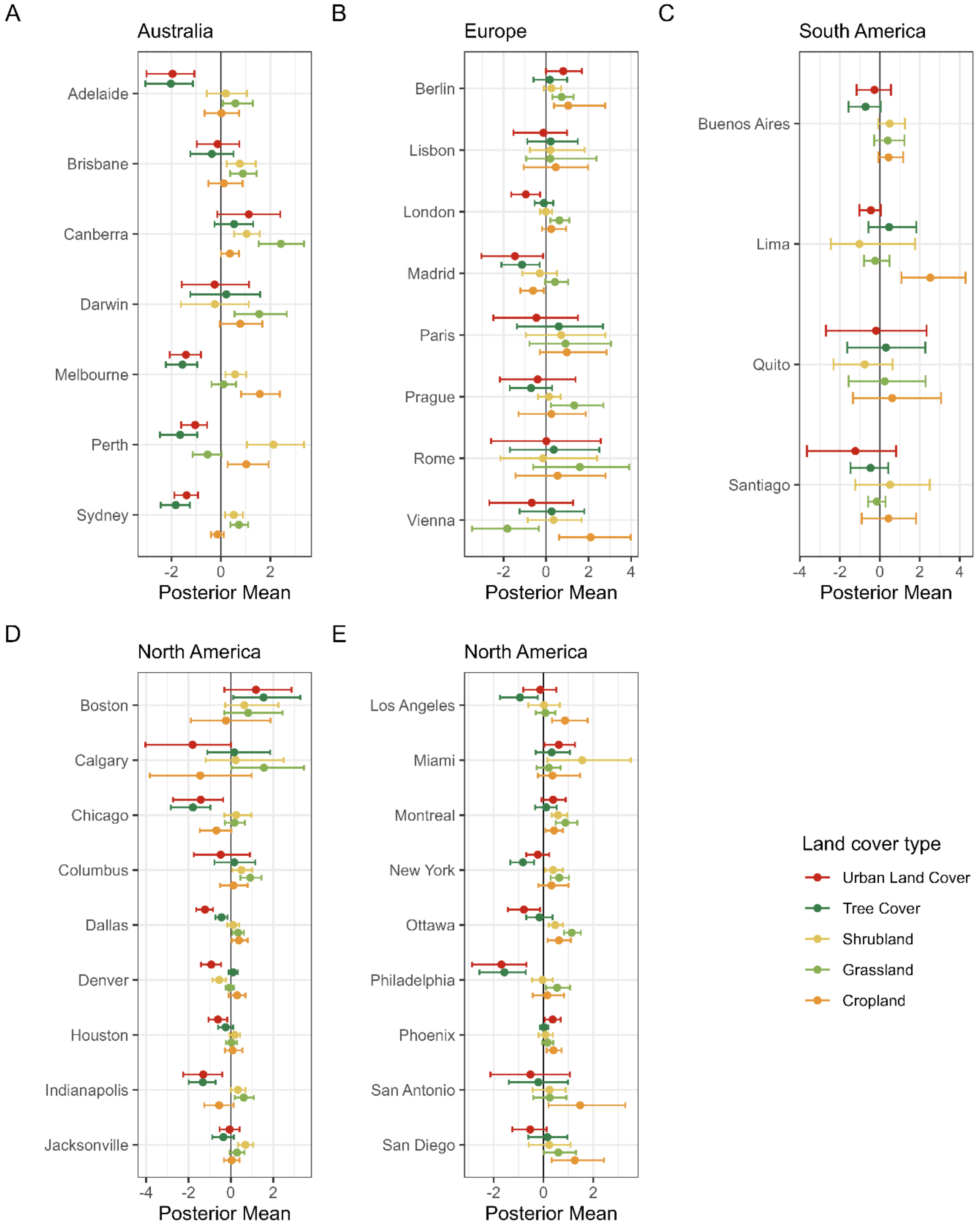

Figure 2.4 The posterior mean estimates of the effect of land cover type on the probability of Kestrel occupancy. Nankeen Kestrel occupancy was modelled in cities across Australia (A), Eurasian Kestrel Occupancy was modelled in cities across Europe (B), and American Kestrel occupancy was modelled across cities across South and North America (C-E). the error bars represent the 95% credible intervals.

Effects were interpreted as being significant if their credible intervals did not cross zero.

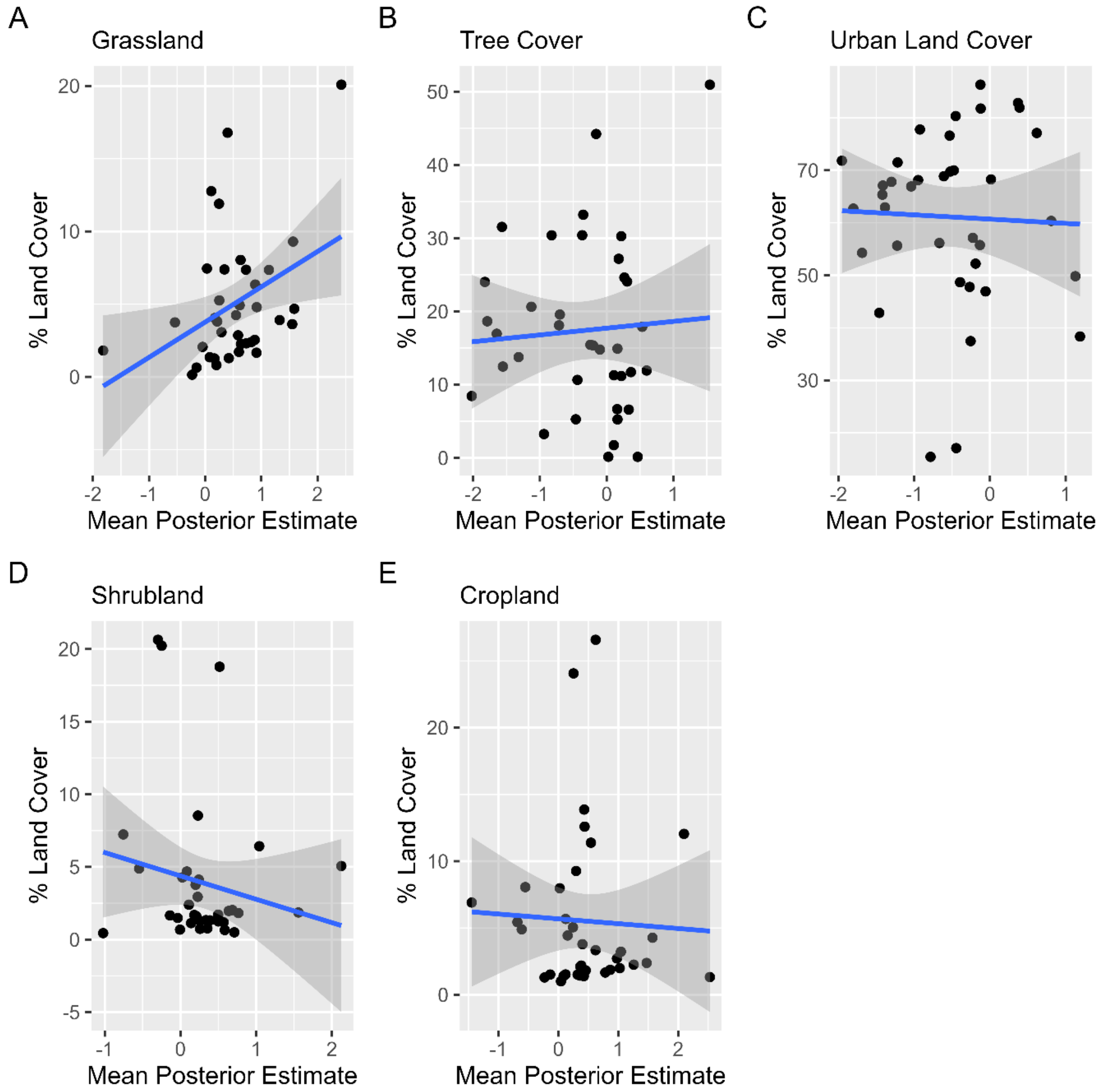

Figure 2.5 The relationship between species occupancy and the percent land cover of habitat types present in the modelled cities. Scatter plots depict the relationship between occupancy and (A) Grassland, (B) Tree Cover, (C), Urban Land Cover, (D) Shrubland and (E) Cropland. The black points represent the values of variables of

interest, the grey shaded area represents the 95% confidence interval, and the blue line represent the estimate of the conditional mean.

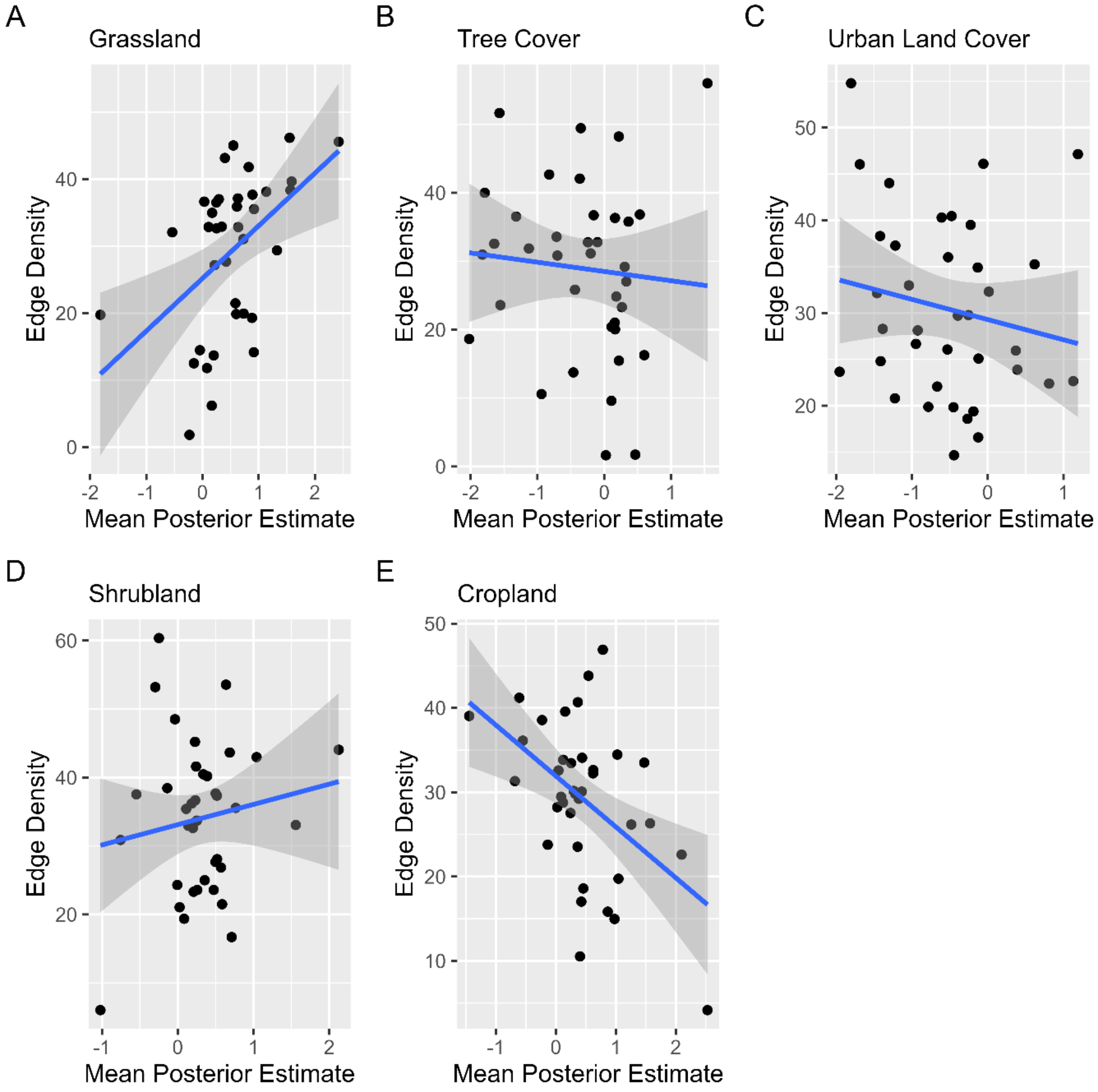

Figure 2.6 The relationship between species occupancy and the edge density of habitat types present in the modelled cities. Scatter plots depict the relationship between occupancy and (A) Grassland, (B) Tree Cover, (C), Urban Land Cover, (D) Shrubland and (E) Cropland. The black points represent the values of variables of

interest, the grey shaded area represents the 95% confidence interval, and the blue line represent the estimate of the conditional mean.

Table 2.1 Model summaries of the association between the percentage of land cover of the land cover classes present in the analysis and kestrel occupancy for linear regression modelling, including the estimate, the standard error (SE), the test statistic, the lower and upper confidence limits and the p-value. The p-values in bold denote significant relationships.

Class	**Estimate**	**SE**	**Statistic**	**95% CI**	**p-value**
Grassland					
(Intercept)	0.21	0.165	1.28	-0.12, 0.55	0.2
Percent Land Cover	0.06	0.025	2.47	0.01, 0.11	**0.019**
Tree Cover					
(Intercept)	-0.42	0.246	-1.70	-0.92, 0.08	0.10
Percent Land Cover	0.00	0.012	0.383	-0.02, 0.03	0.7
Urban Land Cover					
(Intercept)	-0.42	0.502	-0.834	-1.4, 0.60	0.4
Percent Land Cover	0.00	0.008	-0.226	-0.02, 0.01	0.8
Shrubland					
(Intercept)	0.38	0.116	3.29	0.15, 0.62	**0.002**
Percent Land Cover	-0.02	0.018	-1.04	-0.06, 0.02	0.3
Cropland					
(Intercept)	0.48	0.170	2.83	0.14, 0.83	**0.008**
Percent Land Cover	-0.01	0.021	-0.267	-0.05, 0.04	0.8

SE = Standard Error, CI = Confidence Interval

Table 2.2 Model summaries of the association between edge density of the land cover classes present in the analysis and kestrel occupancy for linear regression modelling, including the estimate, the standard error (SE), the test statistic, the lower and upper confidence limits and the p-value. The p-values in bold denote significant relationships.

Class	**Estimate**	**SE**	**Statistic**	**95% CI**	**p-value**
Grassland					
(Intercept)	-0.33	0.283	-1.15	-0.90, 0.25	0.3
Edge Density	0.03	0.009	3.20	0.01, 0.05	**0.003**
Tree Cover					
(Intercept)	-0.18	0.337	-0.548	-0.87, 0.50	0.6
Edge Density	-0.01	0.011	-0.507	-0.03, 0.02	0.6
Urban Land Cover					
(Intercept)	-0.10	0.427	-0.233	-0.97, 0.77	0.8
Edge Density	-0.01	0.013	-1.05	-0.04, 0.01	0.3
Shrubland					
(Intercept)	0.06	0.299	0.187	-0.55, 0.66	0.9
Edge Density	0.01	0.008	0.886	-0.01, 0.02	0.4
Cropland					
(Intercept)	1.6	0.363	4.36	0.85, 2.3	**<0.001**
Edge Density	-0.04	0.012	-3.27	-0.06, -0.01	**0.002**

SE = Standard Error, CI = Confidence Interval

Table S2.1 The predictor variables extracted from the eBird Status and Trends occurrence models, as well as the product source, and the spatial and temporal resolution.

Variable	Source	Spatial Resolution	Temporal Resolution
Barren Land	MODIS	500 m	1-yr
Permanent Snow and Ice	MODIS	500 m	1-yr
Evergreen Needleleaf Forests	MODIS	500 m	1-yr
Evergreen Broadleaf Forests	MODIS	500 m	1-yr
Deciduous Needleleaf Forests	MODIS	500 m	1-yr
Deciduous Broadleaf Forests	MODIS	500 m	1-yr
Mixed Broadleaf/Needleleaf Forests	MODIS	500 m	1-yr
Mixed Broadleaf Evergreen/Deciduous Forests	MODIS	500 m	1-yr
Open Forests	MODIS	500 m	1-yr
Sparse Forests	MODIS	500 m	1-yr
Dense Herbaceous Cover	MODIS	500 m	1-yr
Sparse Herbaceous Cover	MODIS	500 m	1-yr
Dense Shrublands	MODIS	500 m	1-yr
Shrubland/Grassland Mosaics	MODIS	500 m	1-yr
Sparse Shrublands	MODIS	500 m	1-yr
Forest/Cropland Mosaics	MODIS	500 m	1-yr
Natural Herbaceous/Cropland Mosaics	MODIS	500 m	1-yr
Herbaceous Croplands	MODIS	500 m	1-yr
Woody Wetlands	MODIS	500 m	1-yr

Herbaceous Wetlands	MODIS	500 m	1-yr
Tundra	MODIS	500 m	1-yr
Oceans	Terra ASTER	30 m	1-yr
Rivers	Terra ASTER	30 m	1-yr
Lakes	Terra ASTER	30 m	1-yr
Nighttime Lights Mean	NOAA VIIRS	1 km	1-yr
Seasonal Water Cover	JRC GLOBAL SURFACE WATER	30 m	1-yr

Table S2.2 The cities included in the occupancy modelling analysis and the source of the city extent shapefile.

City	Region	Shapefile source
Adelaide	Australia	https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/significant-urban-areas-urban-centres-and-localities-section-state/urban-centres-and-localities
Perth	Australia	https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/significant-urban-areas-urban-centres-and-localities-section-state/urban-centres-and-localities
Darwin	Australia	https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/significant-urban-areas-urban-centres-and-localities-section-state/urban-centres-and-localities
Brisbane	Australia	https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/significant-urban-areas-urban-centres-and-localities-section-state/urban-centres-and-localities
Sydney	Australia	https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/significant-urban-areas-urban-centres-and-localities-section-state/urban-centres-and-localities
Canberra	Australia	https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/significant-urban-areas-urban-centres-and-localities-section-state/urban-centres-and-localities
Melbourne	Australia	https://www.abs.gov.au/statistics/standards/australian-statistical-geography-standard-asgs-edition-3/jul2021-jun2026/significant-urban-areas-urban-centres-and-localities-section-state/urban-centres-and-localities
Berlin	Europe	GADM
Lisbon	Europe	GADM

London	Europe	GADM
Madrid	Europe	GADM
Paris	Europe	GADM
Prague	Europe	GADM
Rome	Europe	Modified from GADM
Vienna	Europe	GADM
Boston	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Calgary	North America	GADM
Chicago	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Columbus	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Dallas	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Denver	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Houston	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Indianapolis	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Jacksonville	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Los Angeles	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Miami	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Montreal	North America	https://jmacman12.carto.com/tables/montreal_shapefile/public
New York	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Ottawa	North America	GADM
Philadelphia	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Phoenix	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
San Antonio	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
San Diego	North America	https://catalog.data.gov/dataset/tiger-line-shapefile-2020-nation-u-s-2020-census-urban-area
Buenos Aires	South America	https://data.world/vazquez-brust/regin-metropolitana-de-buenos-aires
Quito	South America	GADM
Lima	South America	GADM

Santiago	South America	GADM

Table S2.3 Predictive performance metrics (PPMs) from the random forest models produced by the eBird status and trends team. An explanation for each of the PPMs can be found here: https://ebird.github.io/ebirdst/articles/status.html#predictive-performance-metrics-ppms

Species	PPM Category	PPM	Value
American Kestrel	Binary	F1-Score	0.2972846
		MCC	0.2708966
		Prevalence	0.07152908
	Occurrence	Bernoulli deviance	0.03561757
		Spearman’s rank correlation binned	0.4571102
		Brier Score	0.5443397
		PR-AUC	0.3871397
		PR-AUC greater than prevalence	0.9993548
		PR-AUC normalised	0.3670245
	Count	Log Pearson correlation coefficient	0.2788844
		MAE	0.9439668
		Poisson deviance	-1.098634
		RMSE	1.729188
		Spearman rank correlation coefficient	0.2442959
Eurasian Kestrel	Binary	F1-Score	0.3660593
		MCC	0.2972136
		Prevalence	0.1150102
	Occurrence	Bernoulli deviance	0.0449054

		Spearman's rank correlation binned	0.4596008
		Brier Score	0.4663394
		PR-AUC	0.4764098
		PR-AUC greater than prevalence	0.9995273
		PR-AUC normalised	0.4479052
	Count	Log Pearson correlation coefficient	0.3621318
		MAE	0.9284665
		Poisson deviance	0.1133047
		RMSE	1.599498
		Spearman rank correlation coefficient	0.3125563
Nankeen Kestrel	Binary	F1-Score	0.3059214
		MCC	0.2519764
		Prevalence	0.08651961
	Occurrence	Bernoulli deviance	0.03855556
		Spearman's rank correlation binned	0.418754
		Brier Score	0.5234401
		PR-AUC	0.3700425
		PR-AUC greater than prevalence	1
		PR-AUC normalised	0.3469027
	Count	Log Pearson correlation coefficient	0.2713441
		MAE	0.4642433
		Poisson deviance	0.04128181
		RMSE	0.690374

		Spearman rank correlation coefficient	0.2319285

Table S2.4 Occupancy model diagnostics including the number of chains, the number of burn in samples and the thinning rate used in the models.

City	Location	Species	Number of chains	Chain length	Number of burn-in samples	Thinning rate
Adelaide	Australia	Nankeen Kestrel	3	30000	15000	5
Perth	Australia	Nankeen Kestrel	3	30000	15000	5
Darwin	Australia	Nankeen Kestrel	3	30000	15000	5
Brisbane	Australia	Nankeen Kestrel	3	75000	50000	8
Sydney	Australia	Nankeen Kestrel	3	30000	15000	5
Canberra	Australia	Nankeen Kestrel	3	30000	15000	5
Melbourne	Australia	Nankeen Kestrel	3	30000	15000	5
Berlin	Europe	Eurasian Kestrel	3	30000	15000	5
Lisbon	Europe	Eurasian Kestrel	3	25000	10000	5
London	Europe	Eurasian Kestrel	3	30000	15000	5
Madrid	Europe	Eurasian Kestrel	3	25000	10000	5
Paris	Europe	Eurasian Kestrel	3	25000	10000	5
Prague	Europe	Eurasian Kestrel	3	25000	10000	5
Rome	Europe	Eurasian Kestrel	3	25000	10000	5
Vienna	Europe	Eurasian Kestrel	3	25000	10000	5
Boston	North America	American Kestrel	3	10000	60000	10
Calgary	North America	American Kestrel	3	75000	30000	8
Chicago	North America	American Kestrel	3	100000	60000	10
Columbus	North America	American Kestrel	3	50000	30000	5
Dallas	North America	American Kestrel	3	50000	30000	5

Denver	North America	American Kestrel	3	50000	30000	5
Houston	North America	American Kestrel	3	50000	30000	5
Indianapolis	North America	American Kestrel	3	30000	15000	5
Jacksonville	North America	American Kestrel	3	30000	15000	5
Los Angeles	North America	American Kestrel	3	50000	30000	5
Miami	North America	American Kestrel	3	50000	30000	5
Montreal	North America	American Kestrel	3	50000	30000	5
New York	North America	American Kestrel	3	50000	30000	5
Ottawa	North America	American Kestrel	3	50000	30000	5
Philadelphia	North America	American Kestrel	3	50000	30000	5
Phoenix	North America	American Kestrel	3	50000	30000	5
San Antonio	North America	American Kestrel	3	30000	15000	5
San Diego	North America	American Kestrel	3	50000	30000	5
Buenos Aires	South America	American Kestrel	3	50000	30000	5
Quito	South America	American Kestrel	3	30000	15000	5
Lima	South America	American Kestrel	3	30000	15000	5
Santiago	South America	American Kestrel	3	30000	15000	5

Table S2.5 Model output from the kestrel occupancy modelling, including the region and city the analyses was undertaken, the species modelled, the land cover covariates included in the model, and the posterior mean, the lower confidence interval (LCI) and upper confidence interval (UCI) of the land cover covariates.

Region	City	Species	Land Cover Type	Posterior Mean	LCI	UCI
Australia	Adelaide	Nankeen Kestrel	Urban Land Cover	-1.9547	-3.0053	-1.071
			Tree Cover	-2.0224	-3.0539	-1.135
			Shrubland	0.1996	-0.5734	1.0532
			Grassland	0.5856	0.0847	1.2967
			Cropland	0.0239	-0.6579	0.7365
	Brisbane		Urban Land Cover	-0.1325	-0.9723	0.7469
			Tree Cover	-0.3662	-1.2355	0.5089
			Shrubland	0.765	0.2358	1.4101
			Grassland	0.89	0.3708	1.4469
			Cropland	0.1209	-0.5043	0.8803
	Canberra		Urban Land Cover	1.1282	-0.146	2.3985
			Tree Cover	0.5333	-0.2606	1.3066
			Shrubland	1.0407	0.5346	1.5687
			Grassland	2.4239	1.5334	3.3614
			Cropland	0.3665	0.0029	0.7285
	Darwin		Urban Land Cover	-0.2545	-1.585	1.1341
			Tree Cover	0.2188	-1.2389	1.5827
			Shrubland	-0.248	-1.6211	1.1271
			Grassland	1.5497	0.5473	2.6641
			Cropland	0.7836	-0.0463	1.6772
	Melbourne		Urban Land Cover	-1.4136	-2.07	-0.8056
			Tree Cover	-1.5554	-2.2258	-0.9557
			Shrubland	0.5707	0.1849	1.017
			Grassland	0.1084	-0.3797	0.6093
			Cropland	1.5723	0.8204	2.3806

	Perth		Urban Land Cover	-1.04	-1.6043	-0.5558
			Tree Cover	-1.6476	-2.4637	-0.95
			Shrubland	2.1243	1.0518	3.355
			Grassland	-0.5381	-1.1422	0.0308
			Cropland	1.0258	0.273	1.9245
	Sydney		Urban Land Cover	-1.386	-1.8841	-0.927
			Tree Cover	-1.8248	-2.4359	-1.2585
			Shrubland	0.5197	0.1725	0.8938
			Grassland	0.7272	0.3845	1.1017
			Cropland	-0.1357	-0.4004	0.1172
Europe	Berlin	Eurasian Kestrel	Urban Land Cover	0.8095	-0.0003	1.6867
			Tree Cover	0.1808	-0.591	0.994
			Shrubland	0.2583	-0.1082	0.7087
			Grassland	0.7317	0.2954	1.2918
			Cropland	1.0443	0.3696	2.7834
	Lisbon		Urban Land Cover	-0.122	-1.5318	0.9833
			Tree Cover	0.2204	-0.8821	1.4916
			Shrubland	0.2095	-0.7534	1.8075
			Grassland	0.1999	-0.9359	2.3739
			Cropland	0.4576	-1.0541	1.9734
	London		Urban Land Cover	-0.948	-1.6349	-0.2762
			Tree Cover	-0.1011	-0.5363	0.3381
			Shrubland	-0.006	-0.2742	0.2834
			Grassland	0.6298	0.1939	1.1051
			Cropland	0.2445	-0.1887	0.9413
	Madrid		Urban Land Cover	-1.4613	-3.0375	-0.1347
			Tree Cover	-1.1283	-2.1021	-0.2976
			Shrubland	-0.2966	-1.1171	0.5166
			Grassland	0.4205	-0.041	1.0407
			Cropland	-0.6114	-1.2064	-0.1059
	Paris		Urban Land Cover	-0.4522	-2.4796	1.4981

			Tree Cover	0.5998	-1.3662	2.6778
Europe			Shrubland	0.7114	-0.946	2.7914
			Grassland	0.9132	-0.7778	3.0605
			Cropland	0.9786	-0.2929	2.8398
	Prague		Urban Land Cover	-0.3945	-2.163	1.3879
			Tree Cover	-0.7008	-1.7019	0.2859
			Shrubland	0.14	-0.373	0.6924
			Grassland	1.326	0.2268	2.6938
			Cropland	0.2539	-1.2945	1.8679
	Rome		Urban Land Cover	0.0143	-2.5819	2.5713
			Tree Cover	0.3641	-1.6976	2.506
			Shrubland	-0.1383	-2.1505	2.3995
			Grassland	1.5857	-0.6032	3.9058
			Cropland	0.5445	-1.4331	2.7996
	Vienna		Urban Land Cover	-0.6674	-2.6653	1.275
			Tree Cover	0.2651	-1.2454	1.7993
			Shrubland	0.356	-0.8632	1.6644
			Grassland	-1.8168	-3.4784	-0.3367
			Cropland	2.097	0.6105	3.9782
South America	Buenos Aires	American Kestrel	Urban Land Cover	-0.2681	-1.155	0.5615
			Tree Cover	-0.7137	-1.5708	0.0392
			Shrubland	0.4982	-0.079	1.2576
			Grassland	0.3986	-0.28	1.2336
			Cropland	0.4387	-0.063	1.1682
	Lima		Urban Land Cover	-0.4451	-1.0214	0.0568
			Tree Cover	0.4653	-0.5636	1.8282
			Shrubland	-1.0203	-2.4513	1.7613
			Grassland	-0.2329	-0.7871	0.4808
			Cropland	2.5289	1.087	4.2938
	Quito		Urban Land Cover	-0.1893	-2.6939	2.3411

			Tree Cover	0.3071	-1.6258	2.2791
			Shrubland	-0.7549	-2.3166	0.6447
			Grassland	0.2464	-1.5554	2.2953
			Cropland	0.622	-1.3456	3.0726
	Santiago		Urban Land Cover	-1.225	-3.6499	0.8134
			Tree Cover	-0.4621	-1.4668	0.4263
			Shrubland	0.517	-1.2215	2.4951
			Grassland	-0.1539	-0.5864	0.2853
			Cropland	0.432	-0.9048	1.8177
North America	Boston		Urban Land Cover	1.1895	-0.3025	2.8654
			Tree Cover	1.5471	0.116	3.2826
			Shrubland	0.6378	-0.2699	2.2468
			Grassland	0.8216	-0.303	2.4451
			Cropland	-0.2301	-1.8842	1.879
	Calgary		Urban Land Cover	-1.8037	-4.0364	0.0121
			Tree Cover	0.1629	-1.1128	1.8575
			Shrubland	0.2279	-1.1868	2.4848
			Grassland	1.5649	0.0281	3.4582
			Cropland	-1.4452	-3.8323	0.9858
	Chicago		Urban Land Cover	-1.4205	-2.7302	-0.3612
			Tree Cover	-1.7895	-2.8374	-0.9686
			Shrubland	0.2519	-0.3109	0.9781
			Grassland	0.172	-0.2831	0.6654
			Cropland	-0.6829	-1.4648	0.0273
	Columbus		Urban Land Cover	-0.4773	-1.7461	0.9006
			Tree Cover	0.1621	-0.7761	1.1567
			Shrubland	0.5003	0.0611	1.0074
			Grassland	0.9174	0.4573	1.4444
			Cropland	0.1225	-0.5061	0.7923

	Dallas		Urban Land Cover	-1.2191	-1.6375	-0.8417
			Tree Cover	-0.4379	-0.7311	-0.1561
			Shrubland	0.1115	-0.1717	0.399
			Grassland	0.3427	0.0755	0.6144
			Cropland	0.3824	0.0455	0.8023
	Denver		Urban Land Cover	-0.9241	-1.4054	-0.4604
			Tree Cover	0.1076	-0.1056	0.3319
			Shrubland	-0.546	-0.871	-0.2282
			Grassland	-0.0461	-0.2343	0.1437
			Cropland	0.2964	-0.0941	0.6958
	Houston		Urban Land Cover	-0.6085	-1.0524	-0.167
			Tree Cover	-0.2441	-0.6036	0.1085
			Shrubland	0.1835	-0.0552	0.437
			Grassland	0.0312	-0.2271	0.2897
			Cropland	0.0876	-0.278	0.5457
	Indianapolis		Urban Land Cover	-1.3002	-2.2517	-0.4013
			Tree Cover	-1.3202	-1.9861	-0.7217
			Shrubland	0.3375	-0.0024	0.688
			Grassland	0.613	0.1872	1.0902
			Cropland	-0.5509	-1.2574	0.1294
	Jacksonville		Urban Land Cover	-0.0575	-0.5322	0.4097
			Tree Cover	-0.3511	-0.8788	0.141
			Shrubland	0.6862	0.3409	1.0622
			Grassland	0.2907	-0.054	0.6475
			Cropland	0.0443	-0.3231	0.4081
	Los Angeles		Urban Land Cover	-0.1257	-0.813	0.5197
			Tree Cover	-0.9392	-1.7409	-0.2299
			Shrubland	0.0247	-0.6081	0.6586
			Grassland	0.0793	-0.305	0.476
			Cropland	0.8659	0.3447	1.7728

	Miami		Urban Land Cover	0.6177	0.0353	1.2656
			Tree Cover	0.3317	-0.3155	1.0639
			Shrubland	1.5578	0.1577	3.5038
			Grassland	0.2142	-0.273	0.6956
			Cropland	0.3624	-0.2199	1.4739
	Montreal		Urban Land Cover	0.3903	-0.0859	0.8968
			Tree Cover	0.1092	-0.3315	0.5316
			Shrubland	0.5859	0.3371	0.9561
			Grassland	0.8817	0.4933	1.3592
			Cropland	0.4251	0.0841	0.7777
	New York		Urban Land Cover	-0.2262	-0.6915	0.2332
			Tree Cover	-0.8245	-1.3291	-0.3774
			Shrubland	0.3881	0.0652	0.7823
			Grassland	0.6359	0.288	1.0272
			Cropland	0.3215	-0.2082	1.0047
	Ottawa		Urban Land Cover	-0.7842	-1.4309	-0.1393
			Tree Cover	-0.1576	-0.691	0.3695
			Shrubland	0.4747	0.2116	0.7848
			Grassland	1.1355	0.8264	1.4993
			Cropland	0.6231	0.1705	1.0973
	Philadelphia		Urban Land Cover	-1.6879	-2.8693	-0.6835
			Tree Cover	-1.5693	-2.5762	-0.7083
			Shrubland	-0.0362	-0.4518	0.3751
			Grassland	0.5484	0.1017	1.0689
			Cropland	0.1554	-0.4333	0.8258
	Phoenix		Urban Land Cover	0.3704	0.0544	0.6963
			Tree Cover	0.0252	-0.1429	0.1988
			Shrubland	0.0843	-0.1914	0.3792
			Grassland	0.1646	-0.0455	0.3918
			Cropland	0.4027	0.1334	0.7297
	San Antonio		Urban Land Cover	-0.5232	-2.1293	1.0618
			Tree Cover	-0.203	-1.3869	0.9867

			Shrubland	0.2417	-0.4347	0.8947
			Grassland	0.2506	-0.4083	0.9186
			Cropland	1.4739	0.2052	3.2871
	San Diego		Urban Land Cover	-0.5324	-1.246	0.1265
			Tree Cover	0.1587	-0.614	0.9604
			Shrubland	0.231	-0.5928	1.0891
			Grassland	0.6002	0.0197	1.3095
			Cropland	1.2586	0.3285	2.4334

Chapter 3 - Smaller Australian raptors have greater urban tolerance

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Abstract

Urbanisation is occurring around the world at a rapid rate and is generally associated with negative impacts on biodiversity at local, regional, and global scales. Examining the behavioural response profiles of wildlife to urbanisation helps differentiate between species that do or do not show adaptive responses to changing landscapes and hence are more or less likely to persist in such environments. Species-specific responses to urbanisation are poorly understood in the Southern Hemisphere compared to the Northern Hemisphere, where most of the published literature is focussed. This is also true for raptors, despite their high diversity and comparably high conservation concern in the Southern Hemisphere, and their critical role within ecosystems as bioindicators of environmental health. Here, we explore this knowledge gap using community science data sourced from eBird to investigate the urban tolerance of 24 Australian raptor species at a continental scale. We integrated eBird data with a global continuous measure of urbanisation, artificial light at night

(ALAN), to derive an urban tolerance index, ranking species from positive to negative responses according to their tolerance of urban environments. We then gathered trait data from the published literature to assess whether certain traits (body mass, nest substrate, habitat type, feeding guild, and migratory status) were associated with urban tolerance. Body size was negatively associated with urban tolerance, as smaller raptors had greater urban tolerance than larger raptors. Out of the 24 species analysed, 13 species showed tolerance profiles for urban environments (positive response), and 11 species showed avoidance profiles for urban environments (negative response). The results of this study provide impetus to conserve native habitat and improve urban conditions for larger-bodied raptor species to conserve Australian raptor diversity in an increasingly urbanised world.

Introduction

Urban landscapes act as a trait-based filter for wildlife, and responses to changes in environmental conditions may be influenced by species-specific phenotypic and behavioural traits (Grimm et al., 2008, Aronson et al., 2016, Shochat et al., 2010). Traits that generally promote positive responses to urbanisation include high fecundity, strong dispersal ability, behavioural flexibility, and increased tolerance and/or habituation to human presence (Sih et al., 2011, Lowry et al., 2013, Vrbanec et al., 2021, Croci et al., 2008, Murray et al., 2018, Møller, 2009, Rodewald and Gehrt, 2014), but it is usually species dependent as to which traits are the most favourable (French et al., 2018, Mazza et al., 2020). Recently published literature shows that diet generalists tend to exhibit a positive response more often than diet specialist species in urban ecosystems (Callaghan et al., 2019b, Ducatez et al., 2018), as generalist species occupy broader niches that allow them to tolerate a wider array of landscapes (Liang et al., 2020, Palacio, 2019, Bonier et al., 2007) and to explore a variety of different food resources (Coogan et al., 2018, Murray et al., 2018). As the world continues to urbanise (Seto et al., 2011, Liu et al., 2020), understanding the species-specific traits that allow wildlife to survive within urban habitat is vital to maintain wildlife biodiversity.

Mechanistic responses, specifically of species in high trophic levels that fulfil a stabilising function in ecosystems such as raptors, have been largely overlooked. Raptors (species from the orders Accipitriformes, Cathartiformes, Strigiformes and Falconiformes) are apex predators that showcase archetypal examples of urban avoiders, adapters, and exploiters across the urban/rural gradient. Successful urban raptor species are traditionally bird specialist feeders (Kettel et al., 2018a, Gahbauer et al., 2015, Cade et al., 1994, Estes and Mannan, 2003) due to the plentiful supply of food available for them in cities and towns, which allows them to be successful despite not fulfilling a generalist feeding niche that is usually associated with greater urban affinity (Callaghan et al., 2019b). Urban green spaces, such as parks, cemeteries and golf courses provide the habitat necessary for forest and woodland birds to forage, and raptors, such as the Peregrine Falcon (*Falco peregrinus,* pan-global), Cooper's Hawk (*Accipiter cooperii,* America), Black Sparrowhawk (*Accipiter melanoleucus,* Southern Africa) and Eurasian Sparrowhawk (*Accipiter nisus,* Europe), take advantage of these conditions (Panter and Amar, 2021, Drewitt and Dixon, 2008, Estes and Mannan, 2003, Suri et al., 2017). Rodent specialist hunters and scavenging raptors are not uncommon within urban areas; however, their occurrence depends heavily upon prey availability (Hindmarch and Elliott, 2014, Rullman and Marzluff, 2014, Thomson et al., 2016, Patankar et al., 2021, Chamberlain et al., 2017, Sumasgutner et al., 2014a). As raptors are vital for ecosystem functioning through controlling prey populations and nutrient cycling (Donázar et al., 2016), prioritising feeding and breeding habitat for urban-tolerant raptor species is essential to enable biodiverse urban landscapes.

Urban raptors possess certain behavioural and phenotypic traits that enable successful breeding and foraging in urban ecosystems. Raptor home ranges encompass large areas, and urban centres may only be used to fulfil part of their ecological requirements (i.e., using urban areas for hunting, but more natural habitat for breeding or *vice versa*). Examples include Ospreys (*Pandion haliaetus*) that regularly use man-made structures (e.g. barges and platforms) for breeding, but feed almost exclusively on fish in neighbouring water bodies (e.g. rivers, estuaries, oceans, urban lakes and ponds) (Chace and Walsh, 2006), or Peregrine Falcons that breed on the cliffs of Table Mountain, South Africa, but use inner-city districts to prey on pigeons, doves and starlings (Altwegg et al., 2014). The movement patterns of raptors are diverse, as some migrate thousands of kilometres to other continents (Phipps et al., 2019, Mellone et al., 2011), while others are partially migratory (Holte et al., 2016, Holte et al., 2017), or sedentary (Chakarov et al., 2013, Balza et al., 2020). It is not clear how home range and movement patterns impact raptor urban tolerance, but sedentary birds show overall increased behavioural plasticity as opposed to migratory species (Morelli et al., 2022). Raptors that are capable of nesting on a variety of structures (e.g. trees and buildings) and raptors that exhibit flexible foraging techniques, such as perch hunting, pursuit and swoops (Kübler et al., 2005, Mak et al., 2021b, Mikula et al., 2013) or hunting under artificial light at night (ALAN) (Negro et al., 2000, Kettel et al., 2016, Rutz, 2006), demonstrate adaptations that allow them to successfully survive in urban habitat by taking advantage of anthropogenic change (Willmott et al., 2022). Eurasian kestrels *(Falco tinnunculus)* in Slovakia have adopted a novel perch hunting technique that involves waiting above ventilation shafts to catch bats and common swifts (*Apus apus*) (Fleming and Bateman, 2018), while Eleonora's falcons *(Falco eleonorae)* in Morocco are known to hunt migratory species disorientated by street lights at night (Buij and Gschweng, 2017). The use of ALAN by raptor species in urban areas (Kettel et al., 2016, Rodríguez et al., 2021) demonstrates that VIIRS night-time lights data are an appropriate proxy to study urbanisation patterns in bird species. Body size also plays a role in urban tolerance, as very small and very large raptors generally become extirpated from the urban environment (Cooper et al., 2022, Cooper et al., 2020). This is likely due to a mixture of factors, namely tolerance to anthropogenic disturbance and suitability of the urban habitat for foraging and nesting (Boal, 2018). However, there are exceptions to this, as very large scavengers (e.g. vultures) exist in urban areas where food availability is high and persecution is low due to socioeconomic, climatic, and biogeographic factors (Chamberlain et al., 2017).

Raptors continue to be understudied in urban areas, in part due to their sharp global decline (McClure et al., 2018, Buechley et al., 2019) and their general low population densities (Donázar et al., 2016), and thus high effort is required to conduct comprehensive studies. Community science is therefore an effective tool to assess raptor responses to urbanisation as it allows data collection over large spatial and temporal scales, utilising volunteers of differing skill levels to gather data across a variety of projects (Theobald et al., 2015). Projects such as eBird (Sullivan et al., 2014, Sullivan et al., 2009) and iNaturalist (Unger et al., 2021) amass millions of observations each year, and the data collected contribute to scientific publications or are used by various stakeholders, such as Government agencies and industry organisations (Pocock et al., 2019, Vann-Sander et al., 2016). Data from community science projects are invaluable in terms of time and effort, as these are generally the major limiting factors restricting researchers from collecting large amounts of data themselves (Dickinson et al., 2010, Frigerio et al., 2018). Large datasets can also be challenging and time-consuming to analyse, often requiring copious amounts of data cleaning before analysis can commence (Chu et al., 2016). Despite these limitations, data from community science projects continue to be a driving force behind scientific discovery, and growth in this sphere will exist as public awareness increases, programs expand, and technology advances (Kobori et al., 2015, Adler et al., 2020, McClure et al., 2020).

In this study, we used species occurrence data collected via eBird (Sullivan et al., 2014, Sullivan et al., 2009), a global community science initiative documenting avian distributions worldwide, to assess the urban tolerance of 24 Australian raptor species and investigate whether specific phenotypic and behavioural traits, namely body mass, nest substrate breadth, habitat breadth, feeding guild, and migratory status, may explain species-specific responses to urbanisation. We predicted that species adapted to urbanisation (i.e. those with a positive urban tolerance index score) would be bird specialist or generalist feeders (e.g. feed on a variety of food types) rather than mammal specialist feeders, and nest on a variety of substrates allowing for more breeding opportunities (Kettel et al., 2018a). We also predicted that urban adapters would be habitat-generalists and have a smaller to moderate body mass, as opposed to habitat specialists with a very large or very small body mass, as this pattern was previously found for raptors globally (Cooper et al., 2022). Our final prediction was that urban tolerant species would be sedentary species rather than migratory, as previous studies indicated that urban-adapted birds showed higher levels of sedentism, and some Australian species of raptors (e.g. Peregrine Falcon) are sedentary in Australia but migratory elsewhere (Croci et al., 2008, Kark et al., 2007, Dingle, 2008, Marchant and Higgins, 1993). As raptor research is largely biased towards a very small portion of the 557 raptor species, and the species with the highest number of publications (>500) either have a pan-global distribution or are based in the Northern hemisphere, raising the profile of the conservation concern of Southern hemisphere raptors is a priority (Buechley et al., 2019). Based on the research and conservation prioritization index from (Buechley et al., 2019), Australia falls within the medium and high categories of the index within certain areas. Therefore, we tested these hypotheses in Australia, located in the Southern Hemisphere, to challenge current theories and assumptions that are largely based on raptor research conducted in the Northern Hemisphere (Boggie and Mannan, 2014, Cooper et al., 2022).

Methods and Materials

Raptor observation data

We used observations of raptors across continental Australia from eBird (Sullivan et al., 2014, Sullivan et al., 2009), a long-running community science project spanning the globe. Checklists of birds seen and heard are submitted by volunteer birdwatchers, along with user effort variables, such as survey duration, distance travelled, and spatiotemporal information, which are all recorded manually or by a phone application (Wood et al., 2011). Since eBird began in 2002, users have submitted over 89 million checklists, amounting to over 1.2 billion observations of birds worldwide, making it one of the largest and most successful community science projects to date.

The eBird basic dataset for Australia (ver. ebd_rel_AU_Jun-2021; available at: <https://ebird. org/data/download>) was downloaded and all observations of raptors between 1 January 2010 and 30 June 2021 were used, as the vast majority of submitted checklists lie within this period (> 95%). As the aim of this study was to identify Australian raptor tolerance to urban environments at a broad temporal and spatial scale rather than examining changes between years, pooling the data over many years to include the largest amount possible was necessary to achieve this outcome. Checklists were filtered according to the eBird best practices guide recommendations (Strimas-Mackey et al., 2023) to minimise the bias often present in community science datasets (Bird et al., 2014). We filtered the data to include only 'complete' checklists – a case where the user had submitted a checklist of all the bird species they had seen/heard. Checklists that were 'Stationary' or 'Travelling' or followed Birdlife Australia survey protocols such as 'Birdlife Australia 20min-2ha survey', 'Birdlife Australia 500m radius search' or 'Birdlife Australia 5 km radius search' were included, while checklists where the observer travelled for greater than 5 hours or over 5 kilometres were removed to reduce observer variation effort (Johnston et al., 2021).

Ecological traits

Ecological traits were selected from the existing literature that may influence avian tolerance to urban environments (Cooper et al., 2022, Boal, 2018). Data for body mass, nest substrate, habitat type, feeding guild, and migratory status were compiled from information found in the dataset ‘Biological, ecological, conservation and legal information for all species and subspecies of Australian bird’ (Garnett et al., 2015), the books ‘*Birds of Prey of Australia: a field guide (3rd edition)*’ (Debus, 2019) and ‘Australasian Eagles and Eagle-like birds’ (Debus, 2017), and the online database ‘Birds of the World’ provided by the Cornell Lab of Ornithology (Billerman S. M. et al., 2022). Average body mass was used as a proxy for body size, and when possible, morphometric measures stemming directly from the Australian subspecies (e.g. Eastern Osprey) of a raptor were preferred from (Garnett et al., 2015) over other published material. Nesting substrate breadth categories were determined by searching the literature for all possible nesting structures that the birds may use and dividing them into six categories: building, other artificial structure (e.g. pole, barge, telecommunications tower), cliff, tree, water and ground. These values were then added to a total number of nesting substrate types recorded for each species. Habitat breadth values were calculated from (Garnett et al., 2015) by adding the total number of habitat types recorded for each species (Methodology S3.1). Feeding guilds were determined by examining the literature on species’ core diet and separating them based on four main categories: generalist (consumes a variety of food types), bird specialist, mammal specialist or fish specialist. Migratory status was classified as local dispersal or partially migrant, as there are no fully migratory raptor species in Australia (Chan, 2001, Garnett et al., 2015). We used the definition of local dispersal and partially migrant from (Garnett et al., 2015), and these definitions can be found in table 3.1 in the ‘migratory status’ section.

Measure of urbanisation

To quantify the relationship between species occurrence and the urban environment, we used Visible Infrared Imaging Radiometer Suite (VIIRS) night-time lights (Elvidge et al., 2017) data as a proxy for urban areas. It is a continuous measure readily available for download through Google Earth Engine (Gorelick et al., 2017) that correlates positively with human population density (Cox et al., 2020, Li and Zhou, 2017) and that is frequently used as a measure of urbanisation in ecological studies (Callaghan et al., 2020, Callaghan et al., 2019b, Wolf et al., 2022, Fanelli et al., 2022). Whilst other measures of urbanisation exist (Hahs and McDonnell, 2006, Falchi et al., 2016) (e.g. impervious surface cover, skyglow), we chose this method due to its ability to produce a continuous estimate that can individually rank species rather than placing species into arbitrary categories. Our choice was also driven by the fact that the available data existed mostly within the timeframe of this study at the appropriate spatial grain. The data product comes pre-filtered from sources of background noise such as degraded data, fires, and light source contamination for maximum precision. To obtain the median radiance value for each checklist, monthly rasters of the VIIRS night-time lights were combined from 1 January 2014 to 31 December 2020 to create a single raster in Google Earth Engine. This raster was imported into R(R Core Team, 2023), where the median radiance was extracted within a 5-kilometre buffer of each checklist. The ALAN median radiance values were condensed between 2014-2020 into a single value as exploratory analysis showed there were no large differences between years of a random sample of 1,000 distinct localities.

Statistical analysis

Analyses were conducted using the statistical software R (v4.2) in the integrated RStudio environment (R Core Team, 2023). The *tidyverse* workflow was used for data manipulation(Wickham et al., 2019), and the *ggplot2* package(Wickham, 2011) was used for figure plotting. To eliminate records where the birds were unlikely to occur and remove any unusual records, species checklists were cropped to the extent of their known ranges using shapefiles from the 'Birds of the World' dataset from Birdlife International (2021) using the *sf* package (Pebesma, 2018), which is a common technique used within ecological studies (Liu et al., 2021, Callaghan et al., 2021a). Hexagonal grids of 5km width were generated across mainland Australia using the *dggridR* package (Barnes et al., 2017) to facilitate spatiotemporal sub-sampling, a commonly used technique to remove potential spatial and temporal bias, as well as class imbalance (more non-detections than detections of focal species), within community science data (Boakes et al., 2010, Johnston et al., 2021). Prior to modelling, one checklist was sampled from each grid cell from every week of the year across all available years (2010-2021) to remove any spatiotemporal bias, and detection and non-detection were sampled independently to deal with any class imbalance and ensure that not too many detections were lost. Exploratory modelling was then undertaken on all species; species under 1000 checklists with at least 1 observation produced large confidence intervals of their urban tolerance profile relative to the other species and were therefore excluded from the analysis. This reduced the initial set of 34 mainland Australian raptors to the final set of 24 candidate species for modelling (table S3.1).

To examine urban tolerance in Australian raptors, generalised additive models (GAMs) were used with a negative binomial error structure to account for over-dispersion within the data. The eBird best practices guide (Strimas-Mackey et al., 2023) was used as guidance for model preparation and fitting. The response variable for each model was the estimated abundance of each species within the checklist, while the predictor variable was the median VIIRS night-time lights value assigned to each checklist. Smoothing functions were applied to variables that were likely to influence the detection of a species on a checklist: number of observers, latitude and longitude, duration (min), day of year, effort distance (km) and ‘time observations started’. Thin plate regression splines were used for the variables: number of observers, latitude and longitude, duration (min), day of year, effort distance (km) with four degrees of freedom, and a cyclic cubic regression spline was used for ‘time observation started’ with 5 degrees of freedom. For each species’ model, the parameter estimate for night-time lights was obtained, indicating the relationship each species had with urbanisation (i.e. positive or negative) and the magnitude of that relationship. To reduce the uncertainty of the measure of urban tolerance due to the random sampling of eBird checklists within a grid cell, we ran our analysis 100 times for each species to obtain an average parameter estimate.

Multiple linear regression (i.e., all variables included in one model simultaneously) was used to investigate which ecological traits were associated with the species’ response to urbanisation, accounting for all other traits. The response variable was the species response to urbanisation (i.e. parameter estimate) extracted from the GAMs, while the predictor variable was the value of the five traits for each raptor (body mass, nest substrate breadth, habitat breadth, feeding guild, and migratory status) (Table 1). All quantitative predictor variables were scaled and centred prior to linear regression modelling, and visual inspection of residuals for model validation was undertaken.

Results

A total of 840,918 eBird checklists were analysed, using 364,074 observations from 24 species prior to spatiotemporal subsampling, where one checklist was sampled across each 5x5 km grid from a species distribution range per week (Figure 3.1). Spatio-temporal subsampling reduced the total number of species observations to 276,674. The Whistling Kite (*Haliastur sphenurus*) was detected the most of any raptor in the study, amassing 45,787 observations, while the Eastern Barn Owl (*Tyto alba*) was observed the fewest times, recorded on 1,051 occasions across checklists (table S3.1). Detection rates across sampled grids and the respective distributions of the study species can be found in table S3.2.

The raptors observed in the area with the highest median radiance, or the brightest area across the study region, were the Brown Goshawk (*Accipiter fasciatus*) and Southern Boobook (*Ninox boobook*) (103.107 nW cm^{-2} sr^{-1}) in Docklands Park, adjacent to the Yarra River in central Melbourne, Victoria. A Whistling Kite was sighted in the area with the lowest median radiance (0.062 nW cm^{-2} sr^{-1}), or the darkest area across the study region, which was at Lagoon Island, Lake Argyle, in north-eastern Western Australia.

From the 24 species included in the analysis, 13 species displayed a positive response and 11 species showed a negative response to urbanisation. The species with the highest tolerance to urbanisation were the Brahminy Kite (*Haliastur indus*) and the Peregrine Falcon, while the Brown Falcon (*Falco berigora*) and the Wedge-tailed Eagle (*Aquila audax*) were the least tolerant raptor species to urban areas (Figure 3.2).

A significantly negative relationship between raptor response to urbanisation and body mass was observed (Table 2), indicating that raptors with a smaller body mass (g) were more urban tolerant than larger-bodied raptors (F = 9.449, P = 0.007; Figure 3.3A). No significant relationship was detected between the other variables and urban tolerance; nest substrate breadth (F = 0.559, P = 0.465; Figure 3.3B), habitat breadth (F = 0.010, P = 0.920; Figure 3.3C), feeding guild (F = 0.110, P = 0.953; Figure 3.3D) and migratory status (F = 1.751, P = 0.204; Figure 3.3E).

Discussion

We assessed the urban tolerance of 24 Australian raptor species, whereby 13 showed a positive response to artificial light at night and 11 species showed a negative response. This finding highlights species-specific differences in urban tolerance across the Australian continent (Callaghan et al., 2019b), with some raptors showing tolerance response profiles in urban areas and others showing avoidance response profiles. Furthermore, body size was the main trait explaining the species-specific urban tolerance score, as smaller raptors were more likely to have greater urban tolerance index scores than larger raptors. Our results show the wide range in raptor tolerance response to urban environments, measured here using artificial light at night. Given that urban sprawl continues to develop across Australia, understanding the tolerance profiles of different raptor species to environmental change is vital information to inform conservation strategies for human-modified landscapes.

The Brahminy Kite (*Haliastur indus*) was found to be the most tolerant Australian raptor to urbanisation. Brahminy Kites are a coastal raptor, commonly seen soaring along the shoreline, as well as scavenging for food on beaches and jetties (Debus, 2019). Records exist of Brahminy Kites breeding in urban areas, namely Darwin (Riddell, 2017), Northern Territory, and Port Macquarie (Rourke and Debus, 2016) and Port Stephens (Wooding, 2019), New South Wales, where there was varied breeding success across the study locations depending upon the level of human disturbance. A few factors may interplay to explain the tolerance Brahminy Kites to urbanisation, in particular its ability to breed on more than one substrate, its flexible diet and tolerance of human disturbance. Brahminy Kites are flexible in their breeding substrates, opting to use either large trees within mangroves or cities such as the African Mahogany (*Khaya senegalensis*) in Darwin (Riddell, 2017), or common artificial structures such as light towers (Debus, 2019). Additionally, they also showcase a generalist diet which comprises of fish, birds, reptiles, crustaceans, amphibians, mammals, insects and offal (Debus, 2019, Riddell, 2017), which allows it to exist within a wide variety of different environmental conditions. The ability of Brahminy Kites to breed within urban areas highlights their capacity to tolerate human disturbance, but with increasing levels of urbanisation on the coast of Australia, there is an increased risk of poisoning from feral animal control and ingestion and entanglement from fishing equipment (Rourke and Debus, 2016). At the other end of the urban tolerance spectrum is the Wedge-tailed Eagle, the raptor with the lowest urban tolerance score. The species is known to be highly sensitive to human disturbance (Mooney and Holdsworth, 1991) and to avoid urban landscapes. For example, human activity from mountain bikers, off-road vehicles and bushwalkers has the potential to impact breeding success in Wedge-tailed Eagles that are located close to urban areas in Perth, Western Australia (Cherriman et al., 2022). Wedge-tailed Eagles will retreat from urban expansion (Debus, 2008), however, some individual pairs show a higher disturbance tolerance to human activity when breeding inside protected reserves (Hatton et al., 2014).

The finding that larger raptors have lower urban tolerance than smaller species is consistent with findings from other studies investigating urban raptor occurrence (Cooper et al., 2022, Cooper et al., 2020). One particular study undertaken in Reno-sparks, Nevada, USA, showed that Golden Eagles (*Aquila chrysaetos*) breed the furthest away from urban development when compared to other smaller species, and the authors concluded that habitat requirements (e.g. large, open terrain) and life history traits (e.g. small clutch sizes, long-post-fledging dependency) likely explained this result (White et al., 2018). In our study, Australia’s largest birds of prey, the Wedge-tailed Eagle, and White-bellied Sea-Eagle (*Haliaeetus leucogaster*), were both found to avoid urban areas. Given that body size usually correlates with life history ‘speed’ (Roff, 1986), this negative correlation between urbanisation and eagle occurrence might have a similar explanation to the one reported for Golden Eagles (Hatton et al., 2014, Dennis et al., 2011). Wedge-tailed Eagles usually nest several kilometres away from human developments (Debus et al., 2007, Mooney and Holdsworth, 1991, Hatton et al., 2014), while White-bellied Sea-Eagles can occasionally nest within urban green space (O'Meara and Darcovich, 2015) using forested zones scattered throughout the metropolitan area (Spencer and Lynch, 2005). However, from a global perspective, larger raptors are not always urban avoiders: in South Africa, for example, Crowned Eagles (*Stephanoaetus coronatus*) feed on urban exploiters such as the Rock Hyrax (*Procavia capensis*), Hadeda Ibis (*Bostricia hagedash*) nestlings, and Vervet Monkeys (*Chlorocebus pygerythrus*) which support a large urban breeding population of Crowned Eagles in Durban and Pietermaritzberg (McPherson et al., 2016b). In Vancouver, Canada, Bald Eagles (*Haliaeetus leucocephalus*) feed on a variety of birds and fish, and commonly nest in tall Black Cottonwood (*Populus trichocarpa*) and Douglas Fir (*Pseudotsuga menziesii*) trees, occasionally choosing to nest on transmission towers (Goulet et al., 2021). A metanalysis of 172 threatened and near threatened raptors around the world identified body size as the strongest predictor for their conservation status (O’Bryan et al., 2022), whereby the larger the species, the higher the potential for exposure to anthropogenic threats and conservation concern. This is because larger raptor species generally have slower life histories and are more sensitive to anthropogenic disturbance, and fecundity levels cannot counteract high mortality rates due to poisoning, shooting, habitat clearance, electrocution and climate change impacts (Buechley and Şekercioğlu, 2016, McClure et al., 2018). This association between body size and conservation status highlights the need to safeguard suitable habitat outside of cities to meet the requirements for large raptor species in the future.

In Australia, raptors with smaller body mass (172g to 370g) were generally tolerant of urbanisation, while medium-sized raptors (548g to 847g) displayed a variable response (e.g. tolerant or avoidant) to urbanisation. A potential driver of this trend may be the distribution of suitable prey residing within and outside urban areas, which can be linked to body size. Avian specialists are known to thrive in urban areas (Kettel et al., 2018a), as they profit from an increased density of avian prey attracted to supplementary food sources such as bird feeders (Schütz and Schulze, 2018, Fuller et al., 2008), which are a common feature amongst Australian Gardens (Reynolds et al., 2017, Gillanders et al., 2017), and large numbers all-year-round of starlings, doves and pigeons (Chace and Walsh, 2006). Many of Australia’s bird specialist feeders have a smaller body mass [e.g. Australian Hobby, Peregrine Falcon and Collared Sparrowhawk (*Accipiter cirrocephalus*)], enabling swift pursuits of their avian prey. Australian cities include a mosaic of vegetation that is likely to attract birds (White et al., 2005, Threlfall et al., 2016). This includes *Eucalyptus* spp. that are suitable nesting trees for both large and small raptors in Australia (Olsen, 2014, Debus, 2017), and urban remnant bushland (Davis and Wilcox, 2013, Sewell and Catterall, 1998), as well as exotic shrubs and flowers planted in gardens (Daniels and Kirkpatrick, 2006), that can provide nectar all year round (French et al., 2005) for species such as honeyeaters and parrots (Parsons et al., 2003) upon which raptors can feed. Many of the raptors with a moderate body mass are diet generalists, such as the Brahminy Kite and Spotted Harrier (*Circus assimilis*). These species displayed markedly different urban tolerance profiles, which could be a function of the distribution of their prey existing either inside or outside of urban habitat. However, habitat preferences may also play a role in this phenomenon, and therefore further research is needed to clarify the link between Australian raptors of medium body size and urban tolerance and the underlying mechanisms driving the pattern.

Partially migrant and sedentary species had similar urban tolerance profiles, which is consistent with the findings from recent studies focussing on raptors across the globe (Cooper et al., 2022) and in Argentina (Leveau et al., 2022). Little Eagles (*Hieraaetus morphnoides*) are partially migratory, usually migrating from Southern Australia to Northern Australia during the winter months (Brawata et al., 2018). Ongoing GPS tracking studies have confirmed that the habitats used by breeding Little Eagles in Canberra were similar to those used during migration (woodland, grassland, forested areas, open urban land), and they appear to be tolerant of human activity and urban landscapes regardless of their breeding or migration state (Rae et al., 2018). Booted Eagles (*H. pennatus*), a close relative of the Little Eagle, also showed positive responses to urban landscapes, as a population increase in western Europe was observed due to an increase in suitable prey (Palomino and Carrascal, 2007). Ongoing monitoring of raptor migration will be important to locate key areas used by urban-adapted species, potentially also as suitable stop-over spots during migration, to ensure their conservation.

Study limitations

While large-scale data collection by community scientists can facilitate continental-wide data, we acknowledge that such data face several limitations. For example, owls are nocturnal hunters, well camouflaged and cryptic in nature, which results in a lower detectability that often relies on identification by call rather than a visual observation. Sightings of owls may be more biased towards brighter urban areas, as artificial light sources such as streetlights and industrial lighting could enable easier observation. A clustered detectability may be apparent because of known roost sites, and in combination with some observers (i.e. birders) keen to take advantage of ticking off a target species, can lead to an over-representation of one single individual in an area (Callaghan et al., 2018). Additionally, we also recognize that most of the Australian population lives coastally, and therefore checklists are heavily biased towards these areas and along main highways connecting inhabited regions. Even though spatiotemporal sub-sampling was used to mitigate such biases, such clustering of observations still occurred, especially in data rich areas. But, as raptors were the only taxa investigated in this study, which are usually detected using the same methods and the observations are subject to the same biases, it is probable that the systematic sampling bias is analogous for all species observed in this study (Callaghan et al., 2019b, Phillips et al., 2009).

ALAN was used as a continuous metric of urbanisation within this study, and whilst this measure of urbanisation correlates positively with human population density and impervious surface cover (Zhang and Seto, 2013, Pandey et al., 2013), urbanisation occurs across large spatial scales, from the landscape to the local level (Piano et al., 2020). Therefore, it is likely that across these scales species responses to urbanisation may differ (Merckx et al., 2019), and the results from this study reflect Australian raptor responses to urbanisation at a broad scale rather than a fine scale, with the limitation that ALAN was used as a proxy for urbanisation. However, while ALAN is a proxy for urbanisation, it could also serve as a sensory pollutant for raptors, impacting the biological clocks of raptors and their prey. For example, owl species in this study could use night-time lighting as artificial hunting hot spots where prey may congregate to the lights, whereas larger species such as eagles may avoid well-lit areas due to their sensitivity to anthropogenic disturbance. To assess urban tolerance more accurately at finer scales, rather than the broad-scale approach that we have used here, data from GPS-tracked birds or survey data assessing the occupancy of birds in urban areas in conjunction with high-resolution landcover data would be a more suitable approach. Further, the results showed that body mass was the only trait that significantly influenced urban tolerance in Australian raptors, and no other traits influenced urban tolerance. The non-significance of the other traits may have been because of the coarse resolution that the traits were selected at (e.g. continental Australia). To be reliable, generally functional traits need to be location and individual specific (Kohli et al., 2021), however when working at the macroecological scale and assessing interspecific differences, coarser trait resolution is suitable (Palacio et al., 2022). As we were assessing tolerance at the landscape level, we chose to select traits at a coarse scale as it was the most useful resolution for this study, but we acknowledge that the reliability of these traits across time and space for some species may be significantly decreased. ALAN also has the potential to misclassify urban areas, as industrial areas such as ports, mines and highways can be brightly lit but contain little urban infrastructure, while dimly light areas can contain high human population densities. This may have occurred in our study, however we are confident that the general trends that are reported are true of nature.

Future areas of study

The eBird checklist numbers in Australia are growing more numerous each year, and therefore investigations into the urban tolerance of raptor species that occur at lower densities (e.g. Red Goshawk *Erythrotriorchis radiatus*) may become feasible in the future, most likely in conjunction with targeted surveys from conservation related organisations. Population level studies of urban raptors will aid in unravelling their viability and determine metrics such as population turnover and mortality rates.Also, a more granular examination of habitat use within urban areas of urban tolerant raptors, along with concurrent diet studies, will be an important area of future research to conserve important foraging and breeding areas and determine urban prey items and diet composition. Such approaches will help identify which raptor species are occupying urban areas during the breeding season, and those that only visit to forage or roost.

Conclusion

In summary, this research used a large continent-wide raptor data set collected by community scientists and professional birders across Australia to generate valuable insights into the urban tolerance index scores of 24 Australian raptor species. The finding that the 13 species with greater urban tolerance also had, on average, smaller body size, sheds light on mechanistic pathways that may be driving urban tolerance response profiles. Smaller-bodied species tend to have faster life histories and higher metabolic rates, producing larger clutches earlier in life that are frequently provisioned with prey. The abundance and commonality of nocturnal and diurnal prey including small mammals, rodents, pigeons, doves, and passerines, in conjunction with the diet speciality of many small Australian raptors, may favour the persistence and survival of smaller-bodied raptors in urban environments. Conservation management initiatives, particularly those that focus on habitat preservation and restoration (e.g. wilderness area protection), are needed with a special focus on protecting larger-bodied raptor species given urban expansion and an avoidance response of larger raptor species to urban areas.

Acknowledgements

We thank Southern Launch and the Birdlife Australia Raptor Group for funding. We thank Steve Debus for helpful information regarding Australian raptor traits, and the Australian eBird community who submitted the observations to make this study possible. The idea for this study developed from engaging in discussions with Barbara Helm and Davide Dominoni.

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Figure 3.1 Map depicting the distribution of eBird checklists and their associated median VIIRS night-time lights value (log-transformed). Individual checklists are characterised by a coloured point, with purple and blue representing lower values and orange and red representing higher values.

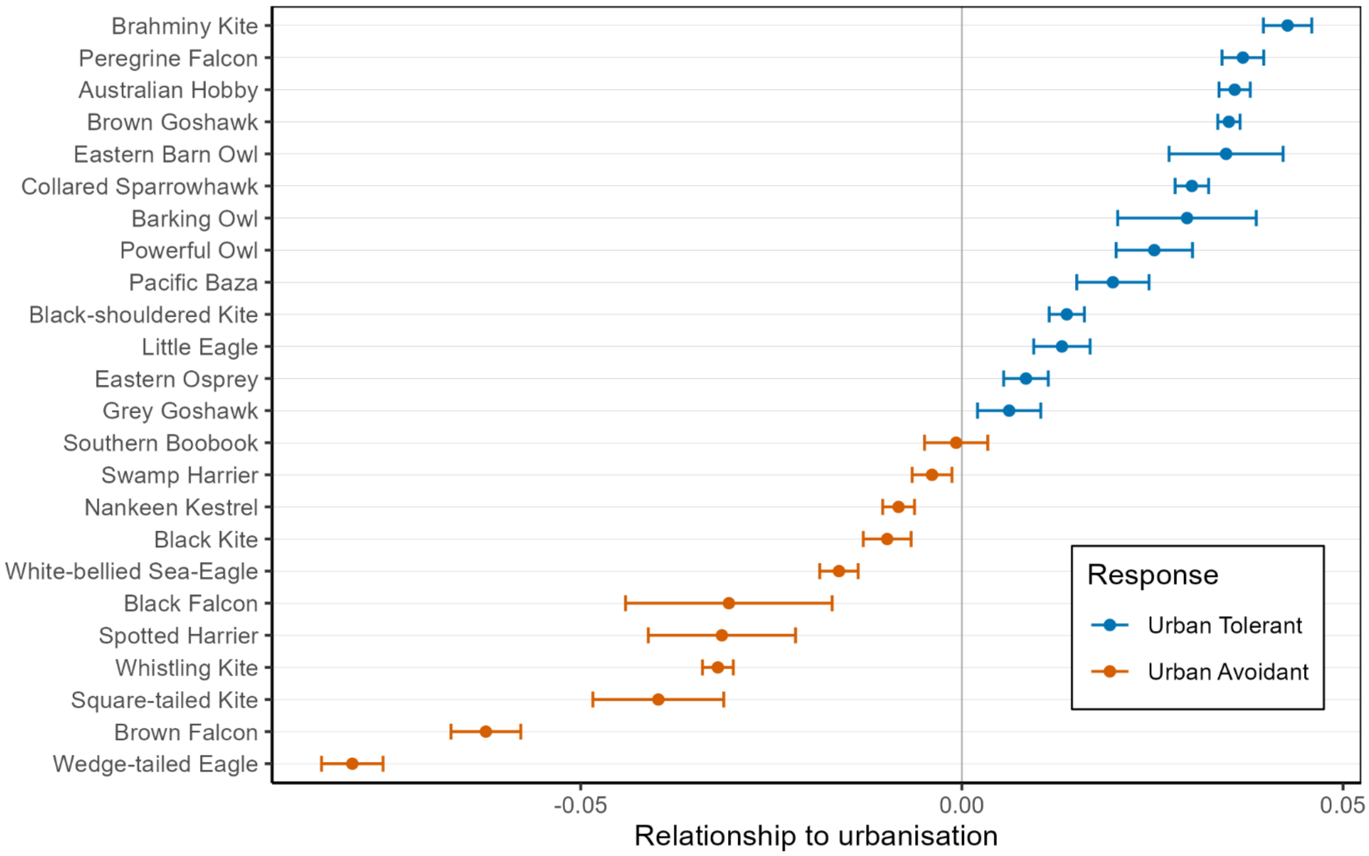

Figure 3.2 Urban tolerance index for the 24 Australian raptor species, ranked by the coefficient estimate from the generalised additive models. Larger positive values signify an increased effect of the predictor variable (ALAN), which indicates a positive response to urbanisation ('Urban Tolerant', in blue), while smaller negative values signify a decreased effect of the predictor variable, which indicates a negative response to urbanisation ('Urban Avoidant', in orange). The error bars represent the 95% confidence interval (of all 100 parameter estimates).

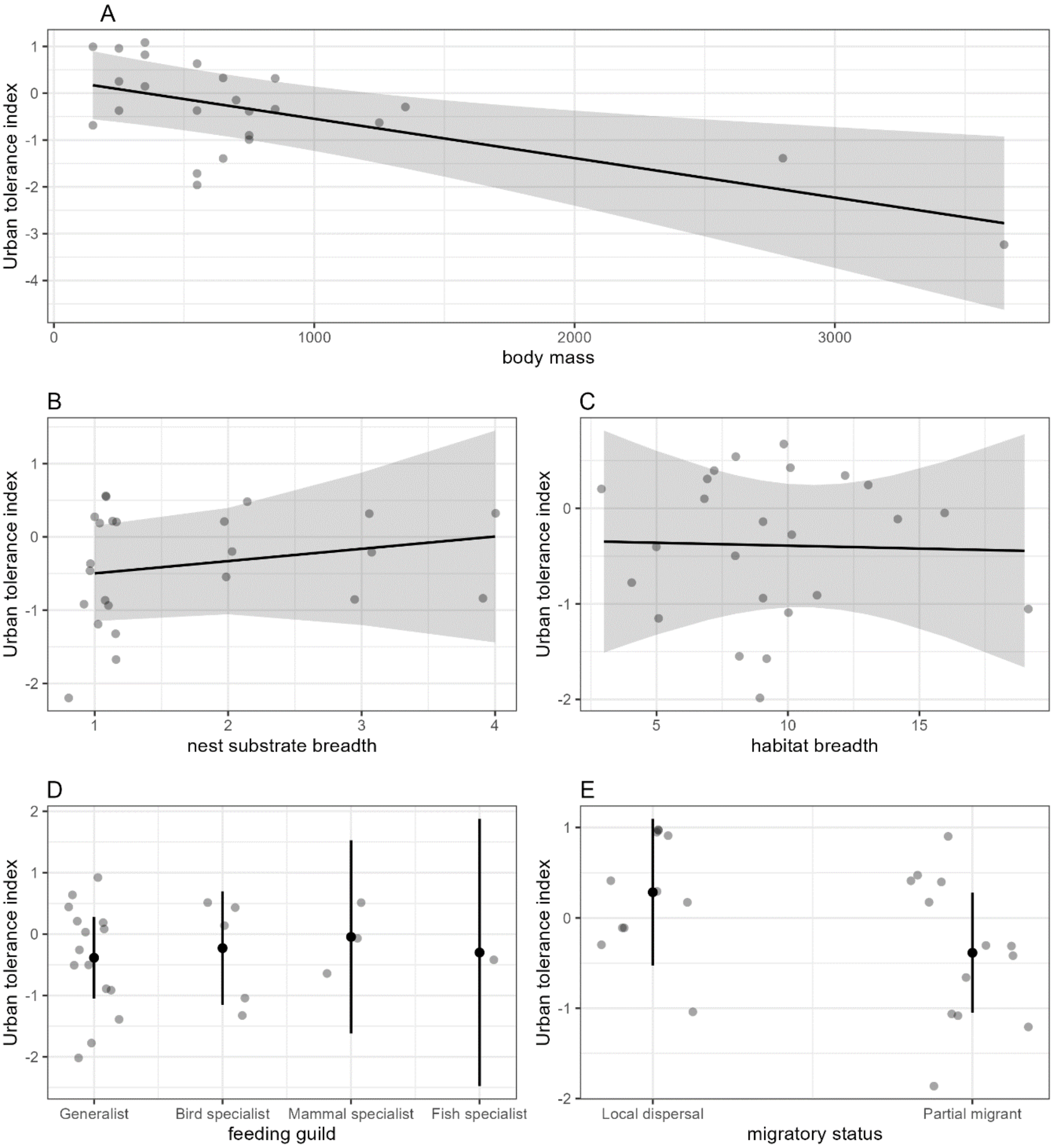

Figure 3.3 The Relationship between the urban tolerance index and ecological traits. Marginal effects plots depict the relationship between urban tolerance and (A) body size, (B) nest substrate breadth, (C) habitat breadth, (D) feeding guild and (E) migratory status, accounting for all predictors. The grey points represent the partial residuals and the grey shaded area for (A), (B) and (C), and the black lines for (D) and (E) represent the 95% confidence interval.

Table 3.1 The traits used in the linear modelling analysis to investigate the association between traits and the urban tolerance index for each species.

Trait	Description	Source
Body mass	The average body mass of the species. The value for the Australian subspecies was used where applicable.	Garnett et. al 2015
Nest substrate breadth	Derived from 6 nesting substrates: building, other artificial structure (e.g. pole, telecommunications tower), cliff, tree, water, ground.	Debus 2019, Debus 2017, Billerman 2022
Habitat breadth	Derived from 30 different habitat categories where species are known to feed; details provided in Methodology S3.1.	Garnett et al., 2015
Feeding guild	Determined from primary food sources: generalist (consumes a variety of food types), bird specialist, mammal specialist or fish specialist.	Debus 2019, Debus 2017, Billerman et al. 2022
Migratory status	Local dispersal – taxa that are largely sedentary with dispersal by juveniles over small distances. Partial migrant – taxa in which some individuals regularly move away from breeding areas after nesting but some remain behind all year.	Garnett et al. 2015

Table 3.2 Model summaries of the association between ecological traits and species urban tolerance index for multiple regression linear modelling, including estimate, standard error (SE), t-value, lower and upper confidence limits. The confidence interval is reported at the 95% level. The reference category for Feeding guild was Generalist, and the reference category for Migratory status was Local dispersal.

Term	**Estimate**	**SE**	**T-value**	**Lower Confidence Interval Limit**	**Upper Confidence Interval Limit**
Intercept	0.284	0.383	0.742	-0.528	1.096
Body Mass	-0.684	0.222	-3.074	-1.155	-0.212
Nest substrate breadth	0.169	0.226	0.748	-0.310	0.647
Habitat breadth	-0.022	0.218	-0.102	-0.485	0.440
Feeding guild: Generalist	-	-	-	-	-
Feeding guild: Bird specialist	0.157	0.485	0.325	-0.870	1.185
Feeding guild: Mammal specialist	0.340	0.677	0.502	-1.095	1.775
Feeding guild: Fish specialist	0.085	1.025	0.083	-2.088	2.258
Migratory status: Local dispersal	-	-	-	-	-
Migratory status: Partial migrant	-0.670	0.506	-1.323	-1.743	0.403

multiple r-squared – 0.4413

Methodology S3.1 Derivation of traits from Garnett et al. 2015

The dataset from Garnett et al. 2015 provides morphological, ecological and general biological information for all Australian species and subspecies of birds. Habitat breadth, migratory status and body mass were calculated from this dataset. Habitat breadth and migratory status values were used at the species level, but if body mass was available for the Australian subspecies, that was used in its place.

Below is a description on the value and the column(s) it was derived from.

Body size: Extracted from the body mass average column (99).

Habitat breadth: Extracted from columns 115-144 and summed together. We used feeding habitat as a proxy for the habitat most likely used by the species. Column 145 was ‘Feeding_habitat_urban’, and this was not used as it would have influenced our response variable, the urban tolerance index.

These columns consisted of:

- Feeding_habitat_Terrestrial_Arid_shrubland
- Feeding_habitat_Terrestrial_Chenopod_shrubland
- Feeding_habitat_Terrestrial_Heath
- Feeding_habitat_Terrestrial_Triodia_hummock_grassland
- Feeding_habitat_Terrestrial_Other_grassland
- Feeding_habitat_Terrestrial_Mallee
- Feeding_habitat_Terrestrial_Tropical_savanna_woodland

- Feeding_habitat_Terrestrial_Temperate_dry_sclerophyll_forest_and_woodland
- Feeding_habitat_Terrestrial_Temperate_wet_sclerophyll_forest_and_woodland
- Feeding_habitat_Terrestrial_Rainforest
- Feeding_habitat_Terrestrial_Mangrove_trees
- Feeding_habitat_Inland_waters_Rivers_and_streams
- Feeding_habitat_Inland_waters_Deep_open_water
- Feeding_habitat_Inland_waters_Shallow_open_water
- Feeding_habitat_Inland_waters_Reeds_and_tall_wet_grassland
- Feeding_habitat_Inland_waters_Low_marshland_and_wet_grassland
- Feeding_habitat_Coastal_Sandy
- Feeding_habitat_Coastal_Rocky
- Feeding_habitat_Coastal_Soft_mud
- Feeding_habitat_Coastal_Saltmarsh
- Feeding_habitat_Coastal_Mangrove_floor
- Feeding_habitat_Marine_Cold_pelagic
- Feeding_habitat_Marine_Temperate_pelagic
- Feeding_habitat_Marine_Warm_pelagic
- Feeding_habitat_Marine_Cold_inshore
- Feeding_habitat_Marine_Temperate_inshore
- Feeding_habitat_Marine_Warm_inshore
- Feeding_habitat_Other_non-Australian_habitat
- Feeding_habitat_Agricultural_landscapes

Migratory status – This represented migratory behaviour, either locally dispersing (column 193) or partially migrating (column 194).

These columns consisted of:

- National_movement_local_dispersal
- National_movement_Partial_migrant

Table S3.1 Number of eBird checklists for each species prior to and post spatio-temporal subsampling from January 2010-June 2021. Species with lower than 1,000 checklists with an observation count > 0 post spatio-temporal subsampling were excluded from the analyses.

Species	Number of checklists prior to spatio-temporal subsampling	Number of checklists with an observation count > 0 prior to spatio-temporal subsampling	Number of observations prior to spatio-temporal subsampling	Number of checklists post spatio-temporal subsampling	Number of checklists with an observation count > 0 post spatio-temporal subsampling	Number of observations post spatio-temporal subsampling
Eastern Osprey	608, 756	13,563	19,365	248, 631	9,428	12,792
Black-shouldered Kite	823,966	19,363	26,215	348,979	14,505	19,078
Letter-winged Kite	16,413	39	323	9,647	36	292
Square-tailed Kite	807,516	2,667	3,146	332,119	2,383	2,757
Black-breasted Buzzard	224,304	979	1,253	100,224	924	1,173
Pacific Baza	368,268	5,377	7,580	155,106	4,635	6,517
Black Kite	763,674	41,934	205,488	320,693	28,735	130,283
Whistling Kite	811,101	61,986	105,247	352,609	45,787	76,050
Brahminy Kite	348,685	11,327	15,005	148,187	8,666	11,305
White-bellied Sea-Eagle	804,569	23,780	29,927	339,243	19,651	24,432
Brown Goshawk	840,058	22,330	25,554	360,455	18,551	21,093

Collared Sparrowhawk	828,420	9,495	10,683	345,223	8,411	9,353
Grey Goshawk	738,287	5,474	6,088	290,302	4,677	5,161
Red Goshawk	236,813	86	132	98,333	78	117
Spotted Harrier	807,230	2,779	3,148	332,761	2,496	2,805
Swamp Harrier	821,241	19,405	25,729	344,117	13,520	17,576
Wedge-tailed Eagle	839,024	24,159	35,597	357,597	21,655	31,700
Little Eagle	815,574	5,578	6,333	337,854	4,929	5,574
Nankeen Kestrel	839,347	31,046	40,692	359,812	25,799	33,529
Brown Falcon	839,352	18,237	23,798	354,569	15,604	20,246
Australian Hobby	839,172	11,543	13,181	353,389	9940	11,156
Grey Falcon	235,099	207	342	112,756	185	301
Black Falcon	764,068	1,421	1,775	308, 993	1,305	1,613
Peregrine Falcon	837,301	6,691	7,942	349,365	5,954	7,003
Eastern Barn Owl	840,775	1,273	1,829	348,330	1,051	1,498
Eastern Grass Owl	254,281	235	310	103,445	184	241
Australian Masked Owl	776,041	560	654	309,436	355	413
Sooty Owl	483,370	506	952	165,237	429	542
Lesser Sooty Owl	49,376	260	314	18,628	217	259
Powerful Owl	576,952	3,488	5,603	208,419	2,172	3,287
Rufous Owl	70,579	699	1,067	28,560	429	628
Barking Owl	767,461	1,634	2,666	303,875	1353	2,208
Southern Boobook	816,501	6,724	8,970	339,370	5,477	7,316
Tasmanian Boobook	24,275	271	381	12,317	241	339

Table S3.2 Summary statistics of the total number of grids across the focal species distribution, total number of grids across a species distribution with at least one checklist containing an observation of the focal species, the percentage of grids across the focal species distribution containing an observation of the focal species, and the size of the species distribution (km^2). All of these figures are post spatiotemporal subsampling.

Species	Total number of grids across the focal species distribution	Total number of grids across a species distribution with at least one checklist containing an observation of the focal species	Percentage of grids across the focal species distribution containing an observation of the focal species	Size of species distribution (km^2)
Eastern Osprey	11,273	965	8.56	1,844,506
Black-shouldered Kite	23,976	3045	12.70	7,657,212
Letter-winged Kite	1,369	18	1.31	729,216
Square-tailed Kite	22,281	918	4.12	5,957,136
Black-breasted Buzzard	9,952	515	5.17	5,305,882
Pacific Baza	6,373	872	13.68	843,946
Black Kite	20,329	4523	22.25	5,884,718
Whistling Kite	22,097	6291	28.47	5,125,443
Brahminy Kite	5966	902	15.12	1,160,739
White-bellied Sea-Eagle	19,992	2,923	14.62	3,647,386

Brown Goshawk	24,414	3,623	14.85	7,621,370
Collared Sparrowhawk	22,270	2450	11.00	4,733,161
Grey Goshawk	14,952	1,079	7.22	1,805,514
Red Goshawk	4,546	35	0.77	1,075,919
Spotted Harrier	23,158	1294	5.59	7,599,947
Swamp Harrier	22,051	1923	8.72	4,714,167
Wedge-tailed Eagle	24328	6514	26.78	7,686,046
Little Eagle	23,222	1735	7.47	7,271,813
Nankeen Kestrel	24,369	6480	26.59	7,685,869
Brown Falcon	24,336	4950	20.34	7,678,186
Australian Hobby	24,298	2732	11.24	7,676,401
Grey Falcon	11639	98	0.84	5,374,709
Black Falcon	20,042	710	3.54	5,918,750
Peregrine Falcon	23,758	1907	8.03	6,569,133
Eastern Barn Owl	24,448	556	2.27	7,692,945
Eastern Grass Owl	4028	39	0.97	483,699
Australian Masked Owl	18,402	134	0.73	3,138,625
Sooty Owl	5442	132	2.43	338,441
Lesser Sooty Owl	520	35	6.73	55,342
Powerful Owl	8252	307	3.72	573,071
Rufous Owl	932	60	6.44	159,509
Barking Owl	16,525	358	2.17	2,507,900
Southern Boobook	23,455	1941	8.28	7,625,275
Tasmanian Boobook	989	97	9.81	67,371

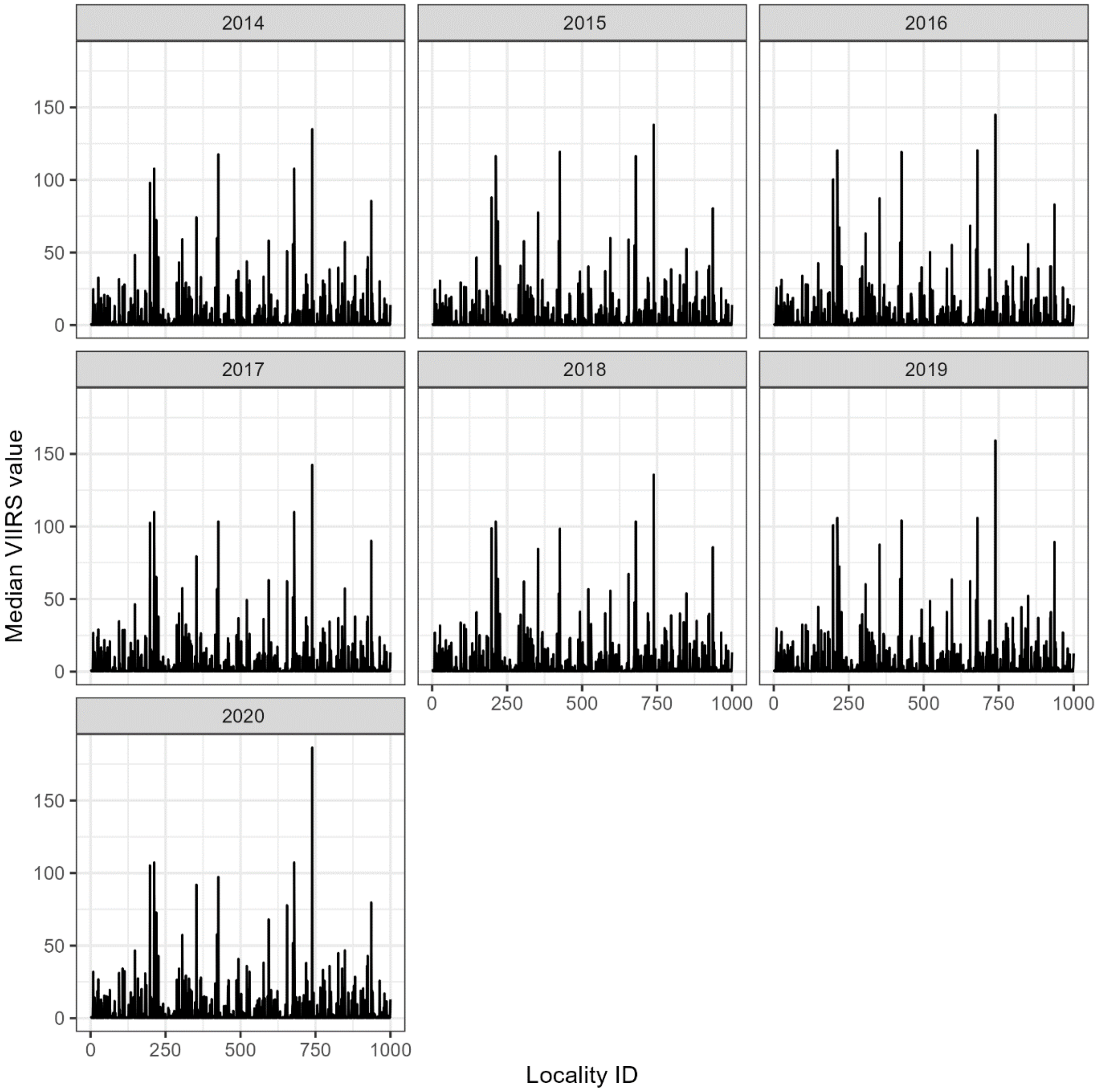

Figure S3.1 The median VIIRS values from 1000 random localities in the study region across the years 2014 to 2020.

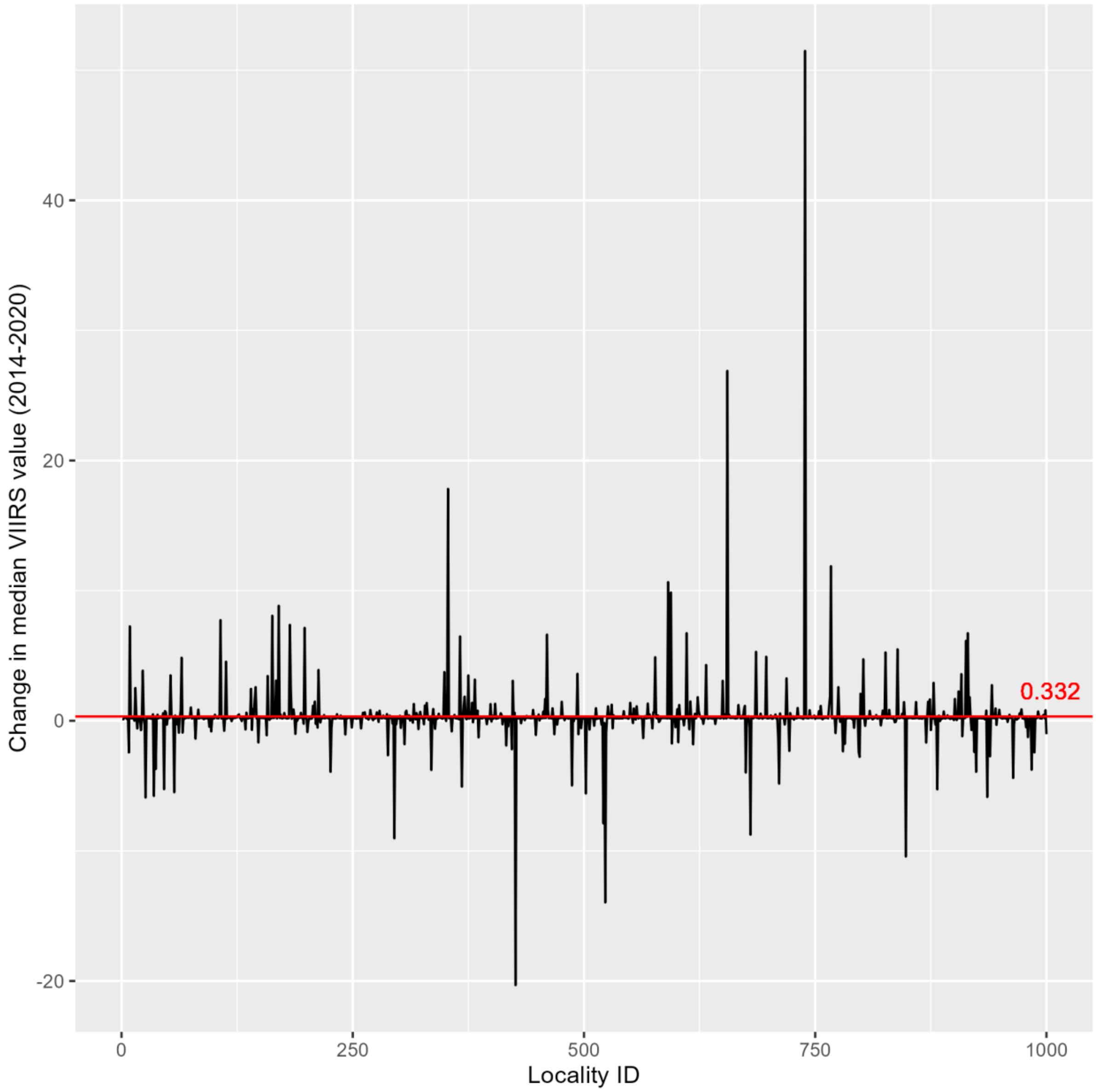

Figure S3.2 The change in median VIIRS values from 2014 to 2020 from 1000 random localities. The red line denotes the mean change in the median VIIRS values from 2014 to 2020 for all localities (0.332).

Chapter 4 – Low urbanisation levels and their impact on raptor richness and diversity

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Abstract

Urbanisation has pervasive effects on biodiversity, and factors such as species' ecological and morphological traits, as well as habitat and dietary preferences, can shape whether species respond positively or negatively to landscape level change. Understanding how urban expansion impacts species richness and diversity is critical for identifying the mechanisms driving changes in community composition and determining which species are most affected. Raptors, as apex predators and bio-indicators of ecosystem health, are particularly vulnerable to anthropogenic change due to their slow life histories. This vulnerability is especially pronounced in the southern hemisphere, where rapid urbanisation coincides with high raptor species richness, and limited research effort compared to the northern hemisphere. We investigated the species richness and diversity of raptors across an urban gradient in eight localities (cities and towns) in South Australia, Australia, using road transect surveys. We then assessed whether ecological traits – habitat breadth, diet breadth and body mass – could predict raptor occurrence along the urban gradient. Raptor species richness was greater in towns compared to cities, but there was no significant difference in raptor diversity. Across the urban gradient, we found a greater richness of raptors in the rural zone compared to the urban zone of cities, but not for towns. There was no significant difference in raptor diversity across the urban gradient of cities or towns. Body mass, diet breadth and habitat breadth did not influence where raptors were observed across the urban gradient or locality types. Raptor community composition was significantly different between locality types, and between the urban and rural gradient, such that towns had a greater variability in community composition than cities, and the rural zone had a greater variability in community composition than the urban zone. Indicator species analysis revealed that Nankeen Kestrels and Wedge-tailed Eagles were indicator species of peri-urban and rural environments, and Brown Falcons and Australian Hobbies were indicator species of towns. Our findings highlight the strong filtering effect of urbanisation on raptor community composition in urban areas, even under moderate to low levels of urbanisation. These results underscore the importance of conserving foraging resources and nesting habitats across urban gradients to support raptor populations in rapidly urbanising regions.

Introduction

The transformation of natural landscapes into artificial urban environments significantly alters ecosystem functioning and biodiversity at multiple scales (Concepción et al., 2015, Newbold et al., 2015, Grimm et al., 2008). This anthropogenic land transformation leads to habitat loss, degradation and fragmentation (Jaureguiberry et al., 2022, Gaston, 2010, Theobald et al., 2020), and more broadly alters microclimates (i.e. urban heat island effect; Sumasgutner et al., 2023), increases pollution (Grimm et al., 2008, Johnson and Munshi-South, 2017), and intensifies human disturbance (Faeth et al., 2011, Gaynor et al., 2018), all of which reduce the richness and diversity of wildlife in urban ecosystems (Sol et al., 2014, McKinney, 2008). Shifts in wildlife presence can disrupt ecosystem functions, particularly predator-prey interactions (Rocha and Fellowes, 2020, Roquero et al., 2024), resource availability (Bradsworth et al., 2021, Sumasgutner et al., 2013), and intra- and inter-specific competition (Santicchia et al., 2024, Shochat et al., 2010). Understanding the impacts of urbanisation on wildlife and the drivers of biodiversity loss is therefore crucial for effective conservation planning, such as diversifying urban green spaces to attract wildlife (Threlfall et al., 2017).

Raptors (species belonging to the orders Strigiformes, Falconiformes, Accipitriformes and Cathartiformes) (McClure et al., 2019), also known as birds of prey, are apex predators that inhabit urban areas and play critical roles in ecosystem functioning (Reynolds et al., 2021, Boal and Dykstra, 2018, Donázar et al., 2016). Raptors are important bio-indicators of environmental health because they sit at the top of the food web and reflect changes in biodiversity (Donázar et al., 2016, Sergio et al., 2005). Observing raptors and how their behaviour and ecology change over time can aid in our understanding of ecological processes, such as how urbanisation impacts wildlife and how different species can adapt to it (Muller et al., 2020, Sumasgutner et al., 2014a, Headland et al., 2023). The diverse ecological needs of raptors, as well as their different spatial, habitat, and dietary requirements, influence their response to urbanisation, which is species specific (Headland et al., 2023, Kettel et al., 2018a). Some raptors, like the Peregrine Falcon (*Falco peregrinus*), thrive in urban areas, nesting on building ledges in cities around the world and hunting invasive prey such as the Rock Dove (*Columba livia*) and the Common Starling (*Sturnus vulgaris*) (Mak et al., 2023, Mak et al., 2021a, Altwegg et al., 2014). Other examples include the Eurasian Sparrowhawk (*Accipiter Nisus*) across Eurasia (Schütz and Schulze, 2018, Thornton et al., 2017), and the Black Sparrowhawk (*Astur melanoleucus*) in Southern Africa (Martin et al., 2014, Suri et al., 2017). However, some species, such as the Golden Eagle (*Aquila chrysaetos*) (White et al., 2018, Domenech, 2015) and the White-Bellied Sea-Eagle (*Icthyophaga leucogaster*) (Dennis et al., 2011, Debus et al., 2014) avoid urban areas due their sensitivity to anthropogenic disturbance and a long history of persecution. As urbanisation poses a global threat to raptor populations (O'Bryan et al., 2022), investigating species-specific responses to anthropogenic land use changes is critical for their conservation and to ensure biodiverse ecosystems.

Raptors' responses to urbanisation vary based on phenotypic, ecological, and behavioural traits (Headland et al., 2023, Cooper et al., 2022). One key factor influencing urban tolerance in raptors is body size (Headland et al., 2023, Cooper et al., 2022). Smaller raptor species have higher thresholds for anthropogenic disturbance (Shaw et al., 2024, Headland et al., 2023) and smaller spatial requirements (Peery, 2000), which aids in their success in urban environments. Another fundamental trait is habitat generalism (Cooper et al., 2022, Boal, 2018), the ability to adapt and thrive in a wider variety of environmental conditions (Kettel et al., 2018a). However, not all studies have found this trait to be a strong predictor of urban tolerance (Leveau et al., 2022, Headland et al., 2023), suggesting that the underlying mechanisms driving urban tolerance are complex and can vary geographically (Callaghan et al., 2023, Neate-Clegg et al., 2023). Diet breadth appears to be another important trait driving urban tolerance, but similarly to habitat breadth, studies have found inconsistent results on whether diet specialism is a strong predictor of urban tolerance in raptors (Cooper et al., 2022, Headland et al., 2023, Leveau et al., 2022, Kettel et al., 2018a).

Raptors located in the southern hemisphere are vulnerable to the impacts of urbanisation (Buechley et al., 2019, O'Bryan et al., 2022). Australia is home to both urban-tolerant raptor species and species that avoid urban areas and may be more vulnerable to the effects of urbanisation (Headland et al., 2023). Australia is home to 36 species of raptors, 34 of which are located on mainland Australia (Christie et al., 2001). Out of these 36 species, one species and two subspecies are vulnerable (Grey Falcon, *Falco hypoleucos*; Tasmanian Masked Owl, *Tyto novaehollandiae castanops*; Northern Masked Owl, *Tyto novaehollandiae kimberli*), while two species and one subspecies are endangered at the national level (Christmas Island Goshawk, *Tachyspiza fasciata natalis*; Red Goshawk, *Erythrotriorchis radiatus*; Tasmanian Wedge-tailed Eagle *Aquila audax fleayi*) (Garnett and Baker, 2021). Australia ranks medium to high in the Research and Conservation Prioritisation Index (RCPI) for all Australian raptor species, as developed by Buechley et al. (2019). This index evaluates species conservation priority based on the number of scientific publications and their IUCN status. These findings underscore the critical need to advance raptor research in Australia, particularly for species vulnerable to anthropogenic land clearance, like the Red Goshawk (*Erythrotriorchis radiatus*) (MacColl et al., 2023).

In this study, we used road transect surveys to investigate how raptor richness (the number of species present in a given area) and diversity (the number of species and their relative abundance in a given area) varied across different locality types (i.e. cities and towns) and along an urban gradient (i.e. urban, peri-urban and rural zones). We then determined whether phenotypic and ecological traits, specifically diet breadth, habitat breadth, and body mass, could predict raptor distribution patterns observed during the transect surveys. To do this, we conducted 108 road transect surveys across eight localities during a two-year period. We predicted that species richness and diversity would be higher in towns compared to cities, and lowest within the urban core of all sampled locations. Conversely, we expect species richness and diversity to be higher in the peri-urban and rural zones, consistent with the well-documented decline in biodiversity as urban intensity increases across the urban-rural gradient (McKinney, 2006, McKinney, 2008). In relation to species traits, we predicted that species observed in cities would exhibit a narrower diet breadth, reflecting a global trend where raptors with a specialist diet, especially avian specialists, tend to thrive in urban environments (Kettel et al., 2018a, Headland et al., 2023). We also predicted that species observed in cities would more likely be habitat generalists as opposed to habitat specialists, enabling them to adapt to diverse and modified environments. Additionally, we expected urban-dwelling species to exhibit a smaller body mass, a pattern previously found for Australian raptors and globally for *Accipiter* species, where smaller body size confers advantages in navigating urban landscapes (Headland et al., 2023, Cooper et al., 2022). Finally, we predicted that species observed in the urban zone of cities and towns as opposed to those in the peri-urban and rural zones would predominantly be smaller-bodied, specialist feeders that tolerate a broad range of habitats. This combination of traits likely facilitates resilience to anthropogenic disturbances and enhances survival in human-modified habitats (Cooper et al., 2022, Kettel et al., 2018a, Headland et al., 2023). In relation to raptor composition, we predicted that there would be distinct raptor assemblages between locality types (city, town) and zones (urban, peri-urban and rural) because urbanisation acts as a filter of species composition (Croci et al., 2008, Aronson et al., 2016).

Methods

Study area

This study was conducted across eight localities in South Australia, Australia (Figure 4.1). Road transect surveys were undertaken in two different locality types: cities (Adelaide, Victor Harbour, Port Augusta and Port Lincoln) and towns (Strathalbyn, Clare, Tumby Bay, Nuriootpa). We adapted our definitions of cities and towns from the report 'Cities in the World: A New Perspective on Urbanisation' (Commission, 2020), and we defined localities with a population greater than 10,000 people as cities, and localities with a population between 1000-10,000 people as towns (table S4.1). South Australia has a small population (1.89 million) compared to that of other states, particularly on the east coast of Australia (Victoria – 7.01 million, New South Wales – 8.54 million, Queensland – 5.61 million) (ABS, 2025a). Localities in South Australia are small, as most of the population resides in metropolitan Adelaide, with approximately 1.46 million residents (ABS, 2025b). Therefore, we chose the largest cities and towns possible that captured an urbanisation gradient.

To identify the urban-rural gradient (i.e. the urban, peri-urban and rural zones) used in this study, we calculated, for each of our localities, the extent of urban, suburban, and rural land within 20km from the centre of the locality. We then averaged the extent of each zone for both locality types to create three distinct distance zones for each locality type, as there was a difference in urban extent between cities and towns. To delineate between the urban, peri-urban, and rural zones, we visually inspected google earth and chose three distinct factors with clear change between the zones following the methods described in Hahs and McDonnell (2006); landscape shape, dominant land cover type and housing density as a proxy for ratio of people per unit urban land cover. For cities, we classified the urban zone as 0-3km from the city centre, peri-urban as 3-8km from the city centre, and rural as 8-20km from the city centre. For towns, we classified the urban zone as 0-2km from the town centre, peri-urban as 2-5km from the town centre, and rural as 5-20km from the town centre.

Data collection

We conducted road transect surveys in December and February (Australian summer) across two seasons, 2022-2023 and 2023-2024. Surveys were undertaken at this time as this corresponds to the breeding and post-fledging dependency period for most South Australian raptors, meaning that raptor activity is high and birds are easily spotted. Three different survey routes were driven at each locality spanning 20km from the locality centre. For smaller localities, such as Tumby Bay, some intersection of survey routes was unavoidable due to the available choice of roads to drive, but care was taken to minimise this occurrence to ensure raptor observations were independent. Adelaide was split into two different sub-localities, Adelaide South and Adelaide North, due to the size of the locality relative to the others and to ensure that an urban-rural gradient could be properly encapsulated. There was a total of 27 individual survey routes driven across the eight localities, and each route was completed twice per season, once in December and once in February. Therefore, we undertook a total of 108 transect surveys, with each route driven four times across the two survey periods.

Road transects are a suitable method of data collection for conspicuous species such as raptors that are often seen soaring (e.g. Wedge-tailed Eagle, Black Kite), hovering (e.g. Nankeen Kestrel, Black-shouldered Kite) or perching on fence posts or powerlines (e.g. Spotted Harrier, Brown Falcon), but meta-analyses have shown that large variation in methodologies between studies employing road transect surveys may hinder reliable comparisons between them (McClure et al., 2021b). Therefore, we standardized our methodology following the recommendations of McClure et al., (2021), particularly the number of observers, the distance width of the survey, the speed of the vehicle, the survey start time and the time of year the survey was conducted, all of which can significantly impact raptor observability (McClure et al., 2021b).

Three people were involved in each survey: one driver and two observers. One observer was positioned in the front passenger's seat to scan the front and left-hand side field of view, while the second observer was positioned behind the driver in the back right of the vehicle to scan the right-hand side field of view. We employed an unlimited width to the surveys, however if raptors could not be confidently identified due to distance they were discarded from the analyses. The observer located in the front recorded the observations via a phone application, while the observer positioned in the rear recorded a backup of the observations on paper in case of malfunction of the phone/application. We used the phone application developed by the Global Raptor Impact Network (GRIN) (McClure et al., 2021a), which enables users to record observations of raptors using standard raptor monitoring techniques (e.g. road transects, point counts, aerial surveys etc.). These observations are then uploaded to a cloud-based database that can be accessed via download and visually inspected. Surveys started between 07:00 and 09:30 in the morning, which aligns with peak raptor activity (Roth and Lima, 2007, Lang et al., 2018), and each survey was completed in 35 to 50 minutes, depending upon the number of raptors observed. Each survey was driven at 40 km/h to enable confident raptor identification, and all three survey routes for each locality were driven consecutively on the same day. Survey routes were uniquely labelled for each locality (i.e. route 1, 2 or 3), and we randomised the order these survey routes were driven each survey period to reduce the potential bias of spotting raptors in the same locations at similar times.

Phenotypic and ecological traits

We selected phenotypic and ecological traits from the existing literature that may influence where raptors are seen across the urban gradient (Headland et al., 2023, Cooper et al., 2022). Data for diet breadth, habitat breadth and body mass were gathered from the ‘Biological, ecological, conservation and legal information for all species and subspecies of Australian bird’ dataset (Garnett et al., 2015). We used the value pertaining to average body mass as a proxy for body size, and habitat breadth and diet breadth were calculated by adding the total number of habitat or diet types recorded for each species.

Statistical analysis

We conducted all statistical analyses in R (v4.3.1) within the Rstudio environment (R Core Team, 2023). We used packages from the *tidyverse* ecosystem (ver. 2.0) (Wickham et al., 2019) for data wrangling and cleaning, *ggplot2* (ver. 3.3.5) (Wickham, 2011) and *sf* (ver. 1.19) (Pebesma, 2018) for spatial data manipulation, and *brms* (ver. 2.22) for phylogenetically-controlled bayesian generalised linear mixed model (GLMM) fitting and evaluation.

Species richness and diversity

We used the R package *iNEXT* (ver 3.0.1) (Hsieh et al., 2016) to calculate species richness, Shannon diversity and Simpson diversity between locality types (i.e. cities and towns), and species richness and Shannon diversity across the urban gradient (i.e. urban, peri-urban and rural zone) of locality types. We could not calculate Simpson’s diversity across the urban gradient due to small sample sizes in urban areas, and therefore it was discarded from the urban gradient analysis. We chose the iNEXT package to calculate Hill numbers (as our diversity metrics), which are more statistically robust than traditional methods that can be biased by sampling effort and the inability to make comparisons between ecological communities (Chao et al., 2014). We calculated the estimated species richness, Shannon diversity and Simpson diversity using the *iNEXT* function. As our data were not normally distributed and unpaired across all three metrics, we ran two Mann-Whitney U tests to assess significance in species richness and diversity between locality types.

To calculate species richness and Shannon diversity across the urban gradient of locality types, we assigned each raptor observation to either the urban, peri-urban or rural zone based upon its spatial location. We then calculated the species richness and Shannon diversity of each zone using the *iNEXT* function. We calculated species richness and Shannon diversity for locality types separately, as the distance band for each zone was different between locality types. As the data were not normally distributed and contained more than two independent samples, we used two Kruskal-Wallis tests to assess significance in species richness and Shannon diversity across the zones of cities and towns. If a statistically significant relationship was detected, we applied the Bonferroni correction method to account for multiple comparisons.

Phenotypic and ecological traits

We used bayesian phylogenetically-controlled generalised linear mixed effects models (GLMMs) to examine whether phenotypic and ecological traits such as diet breadth (models 1, 4, habitat breadth (models 2, 5), and body mass (models 3, 6), could help predict where raptors were observed during surveys (i.e. city or town and in the urban, peri-urban or rural zone). Models 1-3 included locality type (city, town) as a fixed effect, while models 4-6 included zone (urban, peri-urban or rural) as a fixed effect, and all models included transect ID and the phylogenetic covariance matrix as a random effect. The phylogenetic covariance matrix was constructed from a phylogenetic consensus tree using 1000 trees from BirdTree (Rubolini et al., 2015). Based upon the response variables, we chose a cumulative error distribution for all models (1-6). To model body mass, we converted the values into five categories (very small, small, medium, large, very large) based upon ecological function and the natural breaks in the weights of the birds. To assess model fit and convergence, we visually inspected trace plots, checked that rhat values were <1.1 and performed posterior predictive checks using the *pp_check* function in the brms package.

Species composition analysis

To identify and visualise patterns in raptor community composition between locality types and zones, we used non-metric multidimensional scaling ordination using the *metaMDS* function in the *vegan* R package (ver. 2.7-1) (Oksanen et al., 2013). As our data was in the form of species abundance, we used the Bray-Cutris distance measure to create the ordination. To measure the ordination fit, we assessed the stress value, which was deemed to fit the model if stress < 0.2. We repeated the ordination 100 times to ensure model stability and convergence.

To quantify significant differences in raptor community composition among locality types and zones, we used permutational multivariate analysis of variance (PERMANOVA). We computed the differences using the *adonis2* function in the *vegan* package using 999 permutations and Bray-Curtis distance matrices. If a PERMANOVA test was statistically significant, we used the *pairwise.adonis2* function to compute post-hoc pairwise comparisons using the Bonferroni correction method to assess which levels of locality type or zone were statistically different from each other. We validated the results of the PERMANOVA by testing for homogeneity of multivariate dispersions using the permutation test for multivariate dispersions (PERMDISP). This was done using the *betadisper* and *permutest* functions in *vegan* and ensured that that any significant PERMANOVA tests were the result of difference in species composition, not differences in site variability.

We used the R package *indicspecies* to identify raptor species with significant associations to particular zones or locality types using the *multipatt* function with 999 permutations. We used the *IndVal.g* association function within *multipatt*, which combines species abundance and frequency to calculate indicator values. Indicator values range from 0 (no indication) to 1 (perfect indication), with values calculated as the product of specificity (relative abundance in the target group) and fidelity (relative frequency in the target group). The multilevel pattern analysis tested all possible combinations of grouping variables (i.e. city/town, urban/peri-urban/rural) to identify the most appropriate scale of association for each species.

Results

Species Abundance

Across the 108 transect surveys, we observed 16 different raptor species, totalling 305 individual birds (Figure 4.2). The most abundant species observed across the 108 transects were the Nankeen Kestrel (*Falco cenchroides*), with 143 individuals observed, followed by the Wedge-tailed Eagle (*Aquila audax*; 43 individuals), the Black-shouldered Kite (*Elanus axillaris*; 37 individuals), and the Brown Falcon (*Falco berigora*; 34 individuals observed). The least abundant species were the Black Kite (*Milvus migrans;* 3 individuals observed), and the Eastern Osprey (*Pandion haliaetus*), Brown Goshawk (*Tachyspiza fasciata*), Collared Sparrowhawk (*Tachyspiza cirrocephala*), Square-tailed Kite (*Lophoictinia isura*) and Spotted Harrier (*Circus assimilis*), all with two individuals observed, and the Black Falcon (*Falco subniger*), with one individual observed. Most species observed were dietary generalists or bird specialist feeders, with only two species (Eastern Osprey, Black-shouldered Kite) belonging to the fish specialist and mammal specialist dietary niche respectively (Table 1). Rank abundance plots depicting the most abundant species in each transect location, locality type and zone can be found in supplementary material figure S4.1, S4.2 and S4.3.

Species richness and diversity

More raptor species (species richness) were seen in towns compared to cities (Figure 4.3A: Mann-Whitney U test: Z = -2.02, p = 0.043: Cities: mean species observed = 5 ± 0.58, range = 4-6: Towns: mean species observed = 7.75 ± 0.48, range = 7-9). Around cities, species richness did not vary along the urban gradient (Figure 4.4A, Mann-Whitney U test: χ = 1.28, df = 2, p = 0.526). Around towns however species richness significantly varied along the urban gradient (Figure 4.4B, Kruskal-Wallis Rank Sum test: χ = 6.45, df = 2, p = 0.04), with more species observed in the rural zone compared to the urban zone (Figure 4.4B, Dunn test: Z = 2.54, Bonferroni corrected p-value = 0.03). No difference in raptor richness was detected between the urban and peri-urban zones (Figure 4.4B, Dunn test: Z = 1.45, Bonferroni corrected p-value = 0.441), and between the peri-urban and rural zones (Figure 4.4B, Dunn test: Z = 1.18, Bonferroni corrected p-value = 0.720).

Cities and towns did not vary in their Shannon diversity (Figure 4.3B: Mann-Whitney U test, Z = -1.44, p = 0.149) or Simpson diversity (Figure 4.3C: Mann-Whitney U test, Z = -0.29, p = 0.773) of raptor species. There was no significant difference detected in raptor diversity across the urban gradient of cities (Figure 4.4C: Kruskal-Wallis

Rank Sum test: χ = 0.18, df = 2, p = 0.912) or towns (Figure 4.4D: Kruskal-Wallis Rank Sum test: χ = 1.06, df = 2, p = 0.589)

Phenotypic and ecological traits

No significant relationship was found between diet breadth and locality type (Figure 4.5A, Table 4.2, estimate = -0.64 ± 2.49, LCI = -5.81, UCI = 4.08), habitat breadth and locality type (Figure 4.5B, Table 4.2, estimate = -0.07 ± 0.33, LCI = -0.71, UCI = 0.59), and body mass and locality type (Figure 4.5C, Table 4.2, estimate = -0.53 ± 1.80, LCI = -4.34, UCI = 2.78). The diet breadth (Figure 4.5D, Table 4.3, Peri-urban - estimate = 0.06 ± 3.09, LCI = -6.29, UCI = 6.34; Rural - estimate = -0.33 ± 2.65, LCI = -5.84, UCI = 4.93), habitat breadth (Figure 4.5D, Table 4.3, Peri-urban - estimate = -0.04 ± 0.48, LCI = -0.98, UCI = 0.90; Rural - estimate = -0.10 ± 0.44, LCI = -0.96, UCI = 0.77), and body mass (Figure 4.5D, Table 4.3, Peri-urban - estimate = -0.06 ± 0.76, LCI = -1.57, UCI = 1.43; Rural - estimate = -0.17 ± 0.69, LCI = -1.53, UCI = 1.21) of the raptor species observed did not vary along the urban gradient.

Species composition analysis

Raptor community composition differed significantly between locality type (Figure 6) and zone (Figure 6, Table 4.4, PERMANOVA, df = 2, R2 = 0.11, F = 2.79, p = 0.002). Across the urban gradient, there was a significant difference in composition between the urban and rural zones (Figure 6, Table 4.4, PERMANOVA, df = 1, R2 = 0.13, F = 4.74, p = 0.002). Raptor community composition did not differ significantly between the urban and peri-urban zones (Figure 6, Table 4.4, PERMANOVA, df = 1, R2 = 0.08, F = 2.39, p = 0.109), and the peri-urban and rural zones (Figure 6, PERMANOVA Table 4.4, df = 1, R2 = 0.03, F = 1.22, p = 0.178). The stress value of 0.125 indicates adequate NMDS model fit. Raptor community variability between sites did not significantly differ among zones (Table 4.5, PERMDISP, df = 2, F = 1.81, p = 0.181) and locality types (Table 4.5, PERMDISP, df = 1, F = 0.75, p = 0.354).

The Nankeen Kestrel (Table 4.6, Statistic = 0.829, p = 0.005) and the Wedge-tailed Eagle (Table 4.6, Statistic = 0.778, p = 0.002) were strong indicator species of peri-urban and rural zones. The Brown Falcon (Table 4.6, Statistic = 0.608, p = 0.011) and Australian Hobby (Table 4.6, Statistic = 0.480, p = 0.026) were strong indicator species of towns.

Discussion

In this study, we investigated the richness and diversity of Australian raptors between two different locality types (cities and towns) and their urban gradient (urban, peri-urban and rural zones). We found that more raptor species were observed in towns compared to cities but found no difference in Shannon or Simpson diversity. We also found a significant difference in raptor community composition across different levels of urbanisation (locality type, urban and rural zone of localities), which supports the idea that greater urban intensity can cause filtering of raptor communities (Cooper et al., 2022, Cooper et al., 2020). Neither raptor richness nor diversity varied along the cities' urban gradient. Around towns, however, we found a greater richness in the rural zone compared to the urban zone. This highlights the impacts that urbanisation can have on the spatial distribution of wildlife and where they are observed, linking strongly with urban tolerance and resource availability (Headland et al., 2023, Curti et al., 2024). Body size, habitat breadth and diet breadth did not influence where raptors were seen across locality type or the urban gradient, which is consistent with another southern hemisphere study investigating raptor traits and urban occurrence whilst controlling for phylogeny (Leveau et al., 2022). Nankeen Kestrels (urban avoider) and Wedge-tailed Eagles (urban avoider) were indicator species of peri-urban and rural environments, while Browns Falcons (urban avoider) and Australian Hobbies (urban adapter) were indicators of towns, which closely aligns with their ability to tolerate human disturbance (Headland et al., 2023). These findings reflect how landscape modification and human disturbance can alter species distributions and community structure across urban gradients.

We found a significant decline in raptor richness across locality type and along their urban gradient, which is consistent with other raptor studies and our hypotheses (Carrete et al., 2009, Kumar et al., 2022, San Martín-Cruz et al., 2024). However, we did not observe a difference in Shannon or Simpson diversity across locality, or Shannon diversity across the urban gradient of cities or towns. This may be due to the dominance of a few species that were observed regularly (i.e. Nankeen Kestrel, Black-shouldered Kite, Wedge-tailed Eagle, Brown Falcon), but combined with other species that were observed infrequently (Figure 4.2), resulting in low species evenness. The decline in species richness observed in our study in response to increasing urbanisation appears to follow a more consistent, linear pattern (Batáry et al., 2018, Thaweepworadej and Evans, 2022, Leveau et al., 2017, Evans et al., 2018), which may be due to the sensitivity of raptors to anthropogenic disturbance, even at low to intermediate levels (Cherriman et al., 2022). Species richness decline is associated with anthropogenic-induced landscape change (McKinney, 2008), characterised by increased impervious surface cover, noise, chemical and light pollution, and reduced vegetation cover (Grimm et al., 2008). This is likely the cause for reduced species richness at increasing levels of urban intensity in our study, particularly the difference in species richness across the urban and rural zone of towns but not cities. However, other studies indicate that heterogeneous landscapes can buffer the impacts of urbanisation on raptor richness (Kumar et al., 2022). For example, near Seattle, USA, diverse land cover types supported both generalist and specialist raptor species, maintaining consistent species richness across urban gradients (Rullman and Marzluff, 2014). To preserve raptor diversity in urban areas, it is critical to create and manage heterogeneous landscapes that support healthy ecosystems.

Raptor community composition differed significantly with increasing levels of urbanisation (e.g. locality type and zone), which aligns with our hypothesis and previous literature (White et al., 2018, Kumar et al., 2022). We observed a significant difference between the urban and rural zones, but not between the peri-urban and rural, or the peri-urban and urban zones, possibly due to the peri-urban zone acting as a filtering zone (Kale et al., 2018). This is demonstrated in our study where both species sensitive to urbanisation, or urban avoiders (e.g. Wedge-tailed Eagle, Brown Falcon), and species tolerant to urbanisation, or urban adapters and exploiters (e.g. Peregrine Falcon, Black-shouldered Kite) were observed in the peri-urban zone, but not necessarily in the urban zone. However, the most aggressive filtering occurred in the urban zone, whereby the species observed in the urban zone, apart from the Brown Falcon, were all urban tolerant species (Headland et al., 2023). Results from the indicator species analysis also largely aligned with previous analysis of urban tolerance and where species may be observed across the gradient (Headland et al., 2023), whereby the Wedge-tailed Eagle and Nankeen Kestrel, which are urban avoidant, were indicators of the peri-urban and rural zones, and the Australian Hobby, an urban-adapted species, was an indicator of towns. Surprisingly, the Brown Falcon, a highly urban avoidant species, was an indicator of towns. This may be due to the towns in our study area having favourable habitat and prey to consume, whilst also being relatively small and less urbanised. These results confirm the ability of continental scale urban tolerance to generally translate to the local scale (Callaghan et al., 2020), whilst highlighting the need to arrest rapid anthropogenic change to combat raptor assemblage simplification.

Body Mass, habitat breadth and diet breadth did not predict where raptors were observed after controlling for phylogeny as found in previous studies examining factors that predict urban raptor presence/absence (Headland et al., 2023, Leveau et al., 2022). This goes against our hypotheses, and there may be a few reasons for this. Firstly, commonly observed raptors were both diet and habitat generalist and specialist species. Secondly, larger raptors in our study could have become more tolerant of urban areas of the size and extent found in our study area over time, as their sightings occurred in both cities and towns, as well as the urban and peri-urban zones (see Figure 4.2 and Figure S4.1, S4.2). Therefore, both large and small raptor were observed across locality type and gradient, not just smaller raptors. This finding challenges the general assumption that generalist species dominate urban areas (Callaghan et al., 2019b, Neate-Clegg et al., 2023, Callaghan et al., 2021a). Amongst raptor species it is usually the smaller avian specialist feeders that tend to exploit urban areas (Kettel et al., 2018a, McCabe et al., 2018), but in this study, both generalists (e.g. Nankeen Kestrel, Black Kite) and specialists (e.g. Peregrine Falcon, Eastern Osprey) were observed across urban gradients, suggesting urban areas may provide sufficient prey resources to support diverse foraging strategies (Rullman and Marzluff, 2014, Mak et al., 2021b). Broader analyses across regions are essential to assess whether this pattern holds across spatial scales.

The number of observations for each species across the urban gradient generally reflects their urban tolerance profiles as demonstrated in previous analyses (Headland et al., 2023), albeit with some differences. For example, Nankeen Kestrels and Black-shouldered Kites were the most observed raptors, consistent with their urban adaptability (Headland et al., 2023, Debus, 2019). In contrast, species like the Square-tailed Kite and Spotted Harrier, which are urban avoidant (Headland et al., 2023), were rarely sighted. This aligns with their low densities and specialist habitat requirements (Debus, 2019). Surprisingly, Wedge-tailed Eagles were sighted frequently in the peri-urban zone of cities and towns despite being highly urban avoidant (Headland et al., 2023). This is likely explained by the high number of eagle sightings occurring around Victor Harbour, where a stable population of Wedge-tailed Eagles occur despite increasing urban development (Rowe et al., 2018). This highlights how urban tolerance varies across spatial scales due to resource availability (Callaghan et al., 2023), and therefore careful attention should be applied when interpreting model trends, as our results may not reflect species-specific trends in other locations.

Our results demonstrate an impact on raptor richness and diversity at relatively low levels of urbanisation, which has conservation implications for raptors in Australia as urban expansion continues (Calderón-Loor et al., 2021). Urbanisation exerts a selective pressure on raptors, filtering species and potentially simplifying assemblages (San Martín-Cruz et al., 2024, Shaw et al., 2024, Carrete et al., 2009). Given the critical ecosystem services provided by raptors, such as carcass removal (O'Bryan et al., 2018, Bonetti et al., 2024) and maintaining trophic balance (Reynolds et al., 2021), it is essential to mitigate the impacts of urbanisation to maintain healthy ecosystem structure and function. Strategies include enhancing urban green spaces (Threlfall et al., 2017), preserving heterogeneity in land use (Callaghan et al., 2019a, Harlio et al., 2019), and restoring rural habitats to ensure viable populations of urban-sensitive species (Munro et al., 2011, Bennett et al., 2022).

Study limitations

Whilst road transect surveys are an appropriate method for observing raptors (Tiwari et al., 2021), we acknowledge several limitations associated with this approach, including potential biases towards conspicuous species (McClure et al., 2021b). Species such as the Nankeen Kestrel and Black-shouldered Kite are frequently observed because they regularly use powerlines and fenceposts for foraging along roadsides (Debus, 2022, Debus, 2019). Edge habitats provide an abundance of prey for these species (Rullman and Marzluff, 2014, Sánchez-Zapata and Calvo, 1999), attracting them to these hotspots, as is the case for similar species (Dean and Milton, 2009, Meunier et al., 2000). Additionally, raptors like the Wedge-tailed Eagle and Little Eagle, which regularly soar, are highly visible during surveys. In contrast, cryptic species, such as the Brown Goshawk and the Collared Sparrowhawk, which employ sit-and-wait hunting strategies in dense canopy cover, are more challenging to detect. This disparity likely contributes to the large variation in species observation. We also acknowledge the limited spatial and temporal scale of this study, which could potentially influence the results due to environmental variability across years. Such variability can affect species assemblages and compositions across survey periods (Si et al., 2018). Furthermore, the localities in our study area are relatively small, which is an artefact of the small population density in South Australia. Because of the low to moderate levels of urbanisation, and the large home ranges of some species (e.g. Wedge-tailed Eagle, Little Eagle), the birds that were detected may not necessarily be residents of the zones or localities but from the regional species assemblage. This may explain the lack of trends in our trait models. Despite these limitations, our results align with trends reported in previous long-term studies, providing confidence in the observed patterns. However, extended monitoring at the study site, as well as across other location in Australia that encompass a broader urban gradient would be valuable. Such efforts would help capture temporal and spatial variations, identify trends across scales and biomes, and further validate our conclusions.

Conclusion

In conclusion, our study adds to the growing body of literature investigating the responses of raptors to an urban gradient (Kumar et al., 2022, San Martín-Cruz et al., 2024, Carrete et al., 2009), and the traits that may predict their spatial distribution. Raptors are sensitive to anthropogenic change (McClure et al., 2018, Boal and Dykstra, 2018), and we found that moderate to low levels of urbanisation had a significant impact on where raptors were observed. This is pertinent, particularly as Australia's population and urban extent are projected to continue to increase (Calderón-Loor et al., 2021, Wilson and Temple, 2022). However, we found no significant difference in raptor richness and diversity in cities compared to towns, likely due to urban areas acting as strong filters, excluding raptor species with low urban tolerance, the high dominance of some species, and the low frequency of observations of most species; all contributing to low evenness in the community. Special consideration should be made by town planners and developers to conserve raptor foraging and breeding habitat due to their ecological importance in providing ecosystem services and stabilising food webs. For instance, Australia has a paucity of apex predators to control feral mesopredator populations such as cats, rabbits and foxes, and therefore the persistence of raptors is crucial in all ecosystems to control them. Our research also highlights the importance of documenting species observations, and the utility of technology in doing so. We suggest that continued efforts are made to upload raptor observations to platforms such as GRIN (McClure et al., 2021a), eBird (Sullivan et al., 2014, Sullivan et al., 2009, Wood et al., 2011) and iNaturalist (Unger et al., 2021, Mesaglio and Callaghan, 2021) to further document how raptor communities change in response to anthropogenic activity in Australia and across the world.

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Figure 4.1 Locations of the eight road transect areas used in this study to quantify raptor abundance in South Australia, Australia. Circles denote cities (population greater than 10,000 people) and triangles denote towns (population between 1000-10,000 people). The red shading represents human population density (individuals per square kilometre; based on the Gridded Population of the World v4 dataset).

Major urban centres and their relationship to transect locations are highlighted to contextualise sampling within human-modified landscapes.

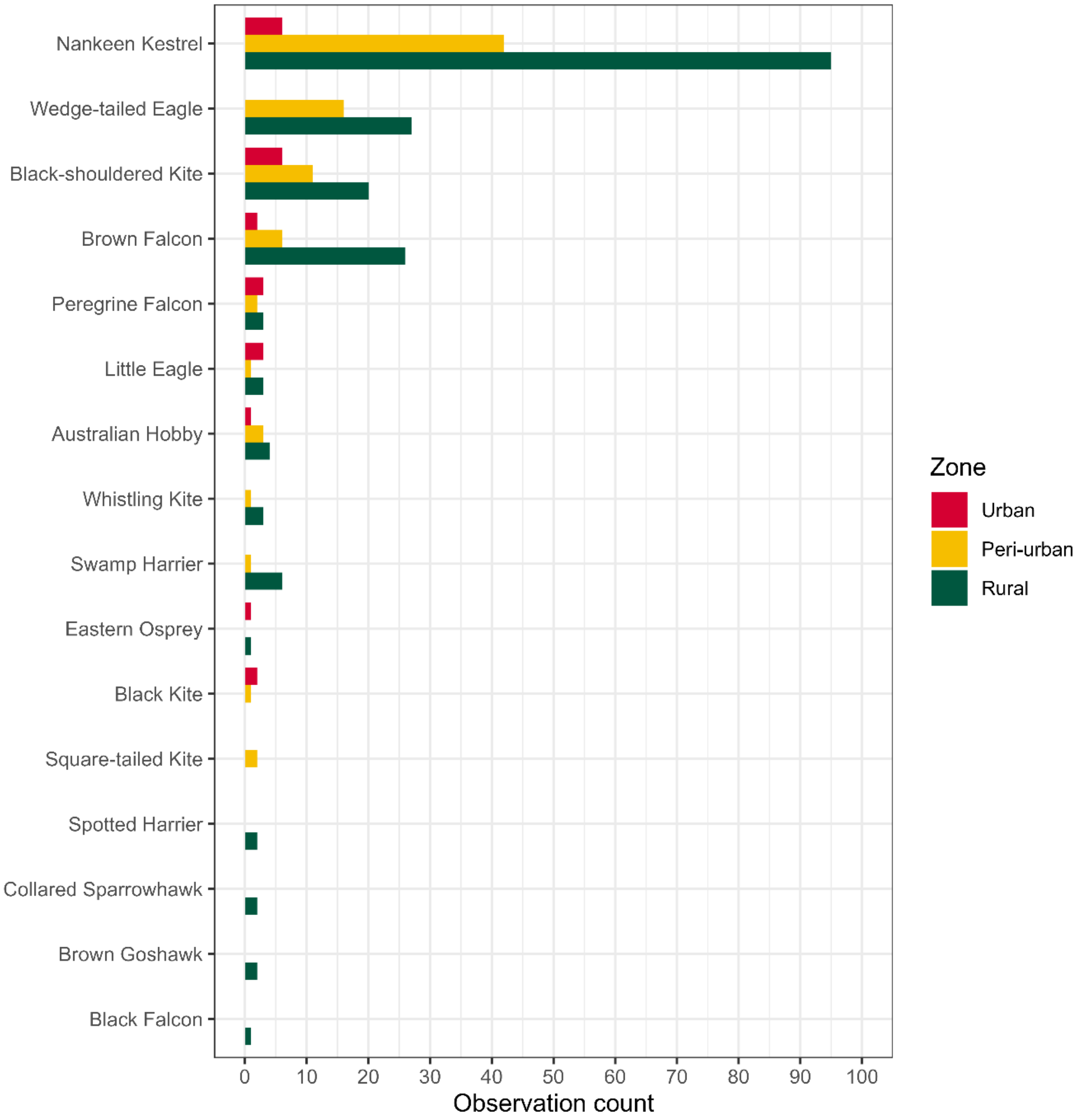

Figure 4.2 Raptor species observed during road transect surveys in South Australia, ranked from most seen to least frequently seen species (abundance). Bar colour indicates the zone(s) where each species was recorded: urban (red), peri-urban (yellow) or rural (green).

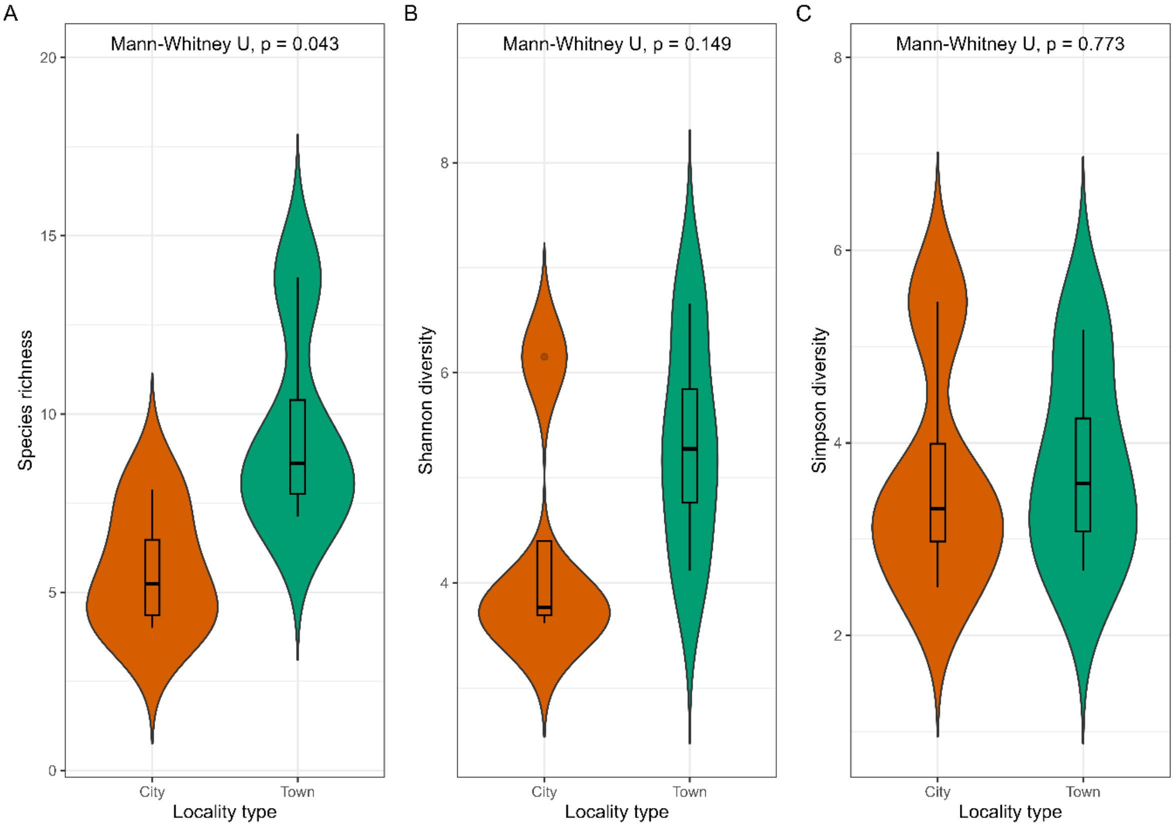

Figure 4.3 Box plots, overlayed with violin plots, displaying the relationship between (A) raptor species richness, (B) Shannon diversity, and (C) Simpson diversity across locality types (i.e. City or Town).

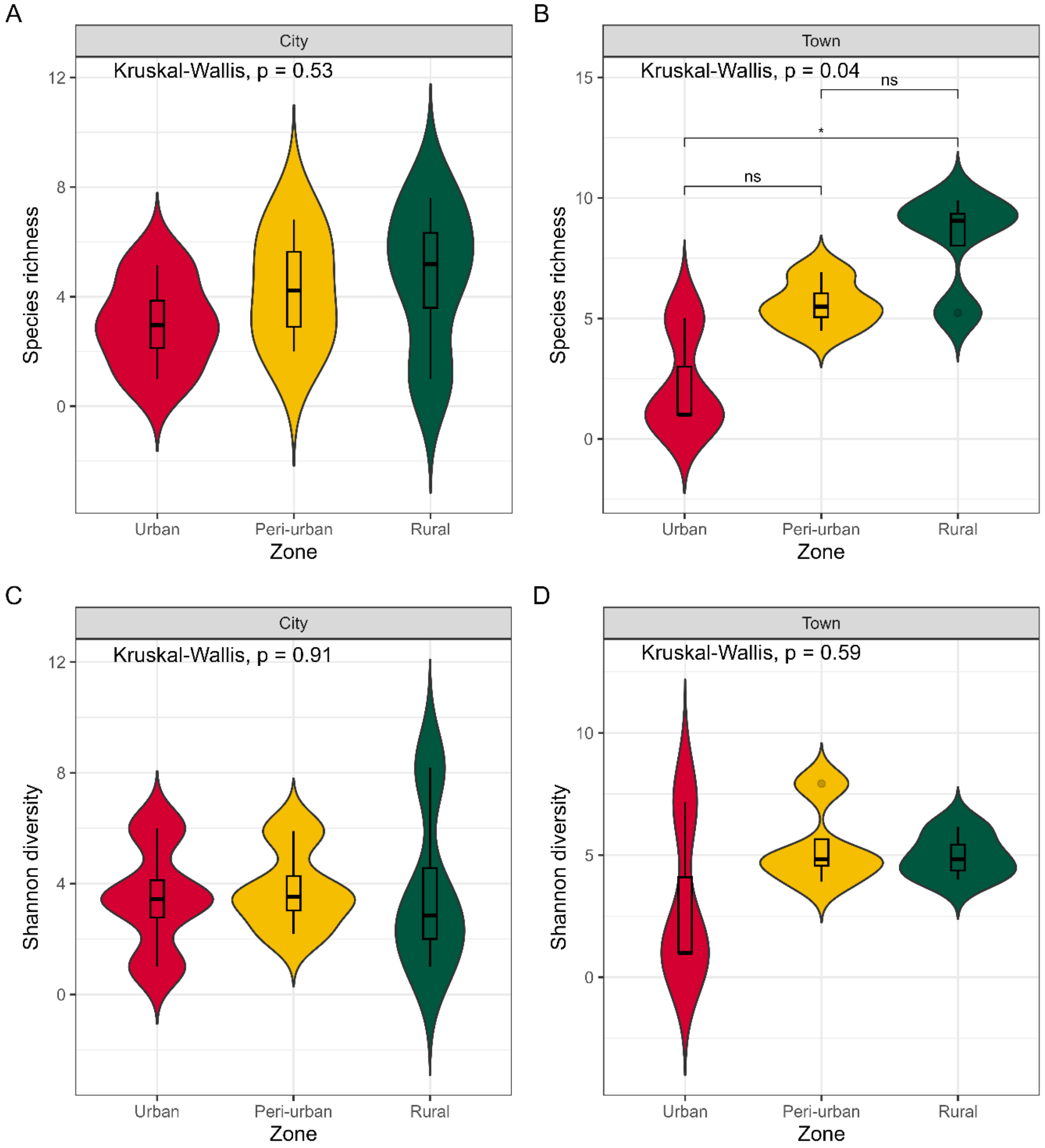

Figure 4.4 Box plots, overlayed with violin plots, displaying the relationship between raptor species richness in (A) Cities and (B) Towns, as well as Shannon diversity in (C) Cities and (D) Towns according to their urban zone (i.e. urban, peri-urban or rural). Stars (* = $p < 0.05$) denote a significant relationship between the zones, and n.s. denotes a non-significant relationship.

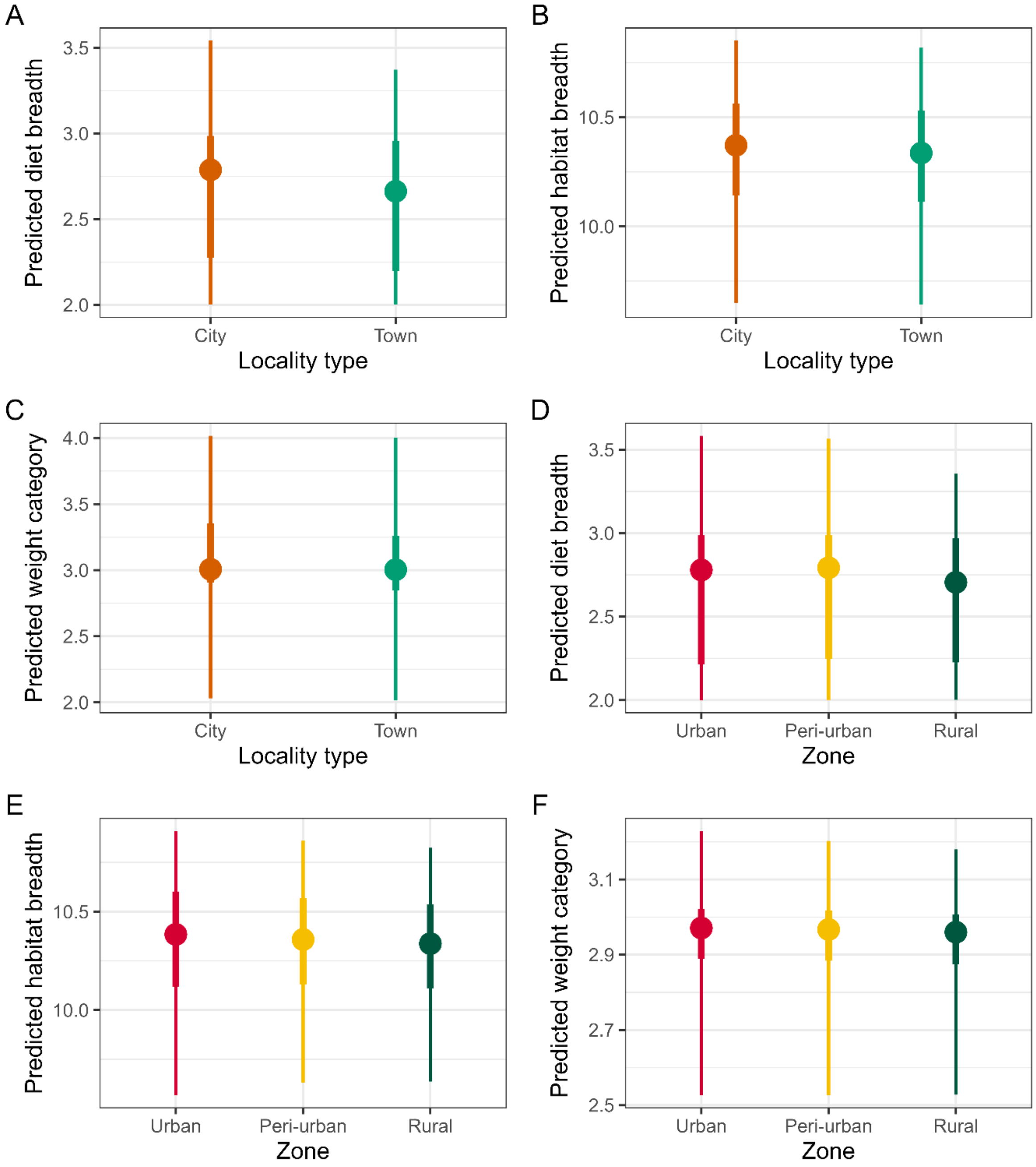

Figure 4.5 Predicted trait values for raptor species across locality type (A–C) and zone (D–F). Traits include diet breadth (A, D), habitat breadth (B, E), and body mass, converted to weight category (C, F). Points represent posterior medians from bayesian ordinal regression models, and vertical bars indicate 50% (thick line) and 95% (thin line) credible intervals.

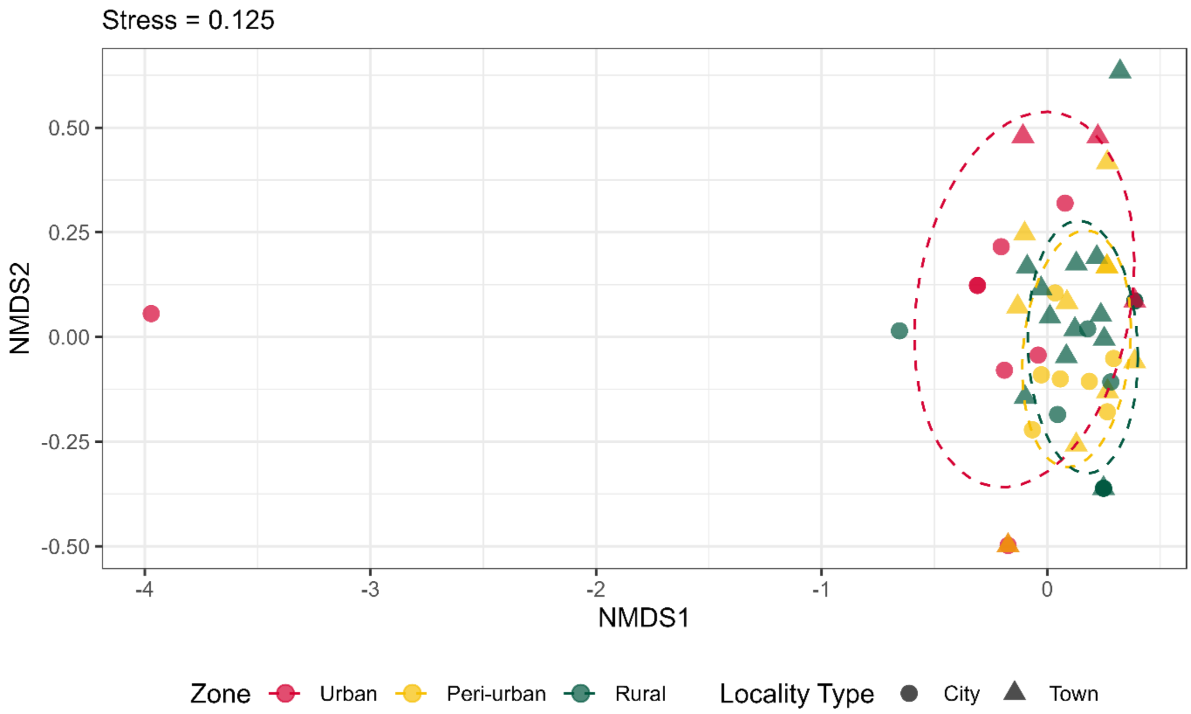

Figure 4.6 Non-metric multidimensional scaling (NMDS) ordination plot (stress = 0.125) based on Bray-Curtis dissimilarities of raptor community composition. Each point represents a sampling site, each colour a zone (Urban = red, Peri-urban = yellow, Rural = green) and each shape a locality type (City = circle, Town = triangle). Ellipses represent 95% confidence intervals for groupings by Zone. The NMDS was performed using two dimensions with a maximum of 100 iterations.

Table 4.1 Raptor species observed in this study, their dietary niche and count of observations.

Species	Dietary niche	Observation count
Australian Hobby (*Falco longipennis*)	Bird specialist	8
Black Falcon (*Falco subniger*)	Bird specialist	1
Black Kite (*Milvus migrans*)	Generalist	3
Black-shouldered Kite (*Elanus axillaris*)	Mammal specialist	37
Brown Falcon (*Falco berigora*)	Generalist	34
Brown Goshawk (*Tachyspiza fasciata*)	Generalist	2
Collared Sparrowhawk (*Tachyspiza cirrocephala*)	Bird specialist	2
Eastern Osprey (*Pandion haliaetus cristatus*)	Fish specialist	2
Little Eagle (*Hieraaetus morphnoides*)	Generalist	7
Nankeen Kestrel (*Falco cenchroides*)	Generalist	143
Peregrine Falcon (*Falco peregrinus*)	Bird specialist	8

Spotted Harrier (*Circus assimilis*)	Generalist	2
Square-tailed Kite (*Lophoictinia isura*)	Bird specialist	2
Swamp Harrier (*Circus approximans*)	Generalist	7
Wedge-tailed Eagle (Aquila audax)	Generalist	43
Whistling Kite (Haliastur sphenurus)	Generalist	4

Table 4.2 Outputs from the Bayesian generalised linear mixed models examining the relationship between locality type (towns, cities) and diet breadth (model 1), diet breadth (model 2) and body mass (weight category) (model 3) of the raptors observed during the road transects conducted in 2022-23 and 2023-24. The reference category for the locality type was ‘City’.

Trait	Estimate	SE	95% CI
Diet Breadth			
(Intercept)[1]	-28.142	12.048	-57.039, -12.155
(Intercept)[2]	-1.418	4.117	-10.199, 6.094
(Intercept)[3]	9.587	6.865	-0.181, 26.344
Locality type - Town	-0.635	2.485	-5.809, 4.076
Scientific Name SD (Intercept)	21.569	9.162	10.209, 44.906
Transect ID SD (Intercept)	0.773	0.645	0.030, 2.410
Habitat Breadth			
(Intercept)[1]	-9.694	0.966	-11.686, -7.925
(Intercept)[2]	-9.080	0.835	-10.783, -7.469
(Intercept)[3]	-8.760	0.798	-10.349, -7.247
(Intercept)[4]	-8.533	0.783	-10.091, -7.016
(Intercept)[5]	-8.361	0.772	-9.876, -6.863
(Intercept)[6]	-4.805	0.716	-6.177, -3.422
(Intercept)[7]	-4.685	0.716	-6.078, -3.304
(Intercept)[8]	-4.358	0.713	-5.774, -2.970
(Intercept)[9]	-1.191	0.698	-2.548, 0.201
(Intercept)[10]	-0.451	0.693	-1.838, 0.927
(Intercept)[11]	5.074	0.696	3.708, 6.453
(Intercept)[12]	5.166	0.694	3.799, 6.540
(Intercept)[13]	5.369	0.694	4.001, 6.743
(Intercept)[14]	5.481	0.699	4.111, 6.856
(Intercept)[15]	6.684	0.738	5.240, 8.131
(Intercept)[16]	6.872	0.747	5.437, 8.339
(Intercept)[17]	7.578	0.799	6.033, 9.171
(Intercept)[18]	7.905	0.834	6.290, 9.591
(Intercept)[19]	8.483	0.960	6.707, 10.551
Locality type - Town	-0.070	0.332	-0.714, 0.587
Scientific Name SD (Intercept)	7.177	1.257	5.121, 10.042
Transect ID SD (Intercept)	0.126	0.103	0.004, 0.383

Trait	Estimate	SE	95% CI
Body Mass			
(Intercept)[1]	-22.353	10.277	-45.783, -7.049
(Intercept)[2]	-8.253	7.581	-24.593, 3.375
(Intercept)[3]	6.269	7.705	-4.545, 24.382
(Intercept)[4]	17.206	10.652	2.775, 43.165
Locality type - Town	-0.533	1.796	-4.337, 2.783
Scientific Name SD (Intercept)	22.931	7.611	12.603, 41.868

Abbreviations: CI = Credible Interval, SE = Standard Error

Table 4.3 Outputs from the Bayesian phylogenetically controlled generalised linear mixed models examining the relationship between the zone (urban, peri-urban and rural) and diet breadth (model 4), habitat breadth (model 5) and body mass (model) of the raptors observed during the road transects conducted in 2022-23 and 2023-24. The reference category for the zone was 'Urban'.

Trait	**Estimate**	**SE**	**95% CI**
Diet Breadth			
(Intercept)[1]	-30.305	14.313	-65.723, -12.061
(Intercept)[2]	-1.485	4.748	-11.599, 6.873
(Intercept)[3]	10.374	7.517	-0.339, 28.389
Zone – Peri-urban	0.063	3.085	-6.292, 6.338
Zone - Rural	-0.326	2.654	-5.843, 4.925
Scientific Name SD (Intercept)	23.591	10.834	10.791, 49.541
Transect ID SD (Intercept)	0.805	0.680	0.030, 2.583
Habitat Breadth			
(Intercept)[1]	-9.739	1.057	-11.965, -7.782
(Intercept)[2]	-9.130	0.905	-10.958, -7.360
(Intercept)[3]	-8.807	0.867	-10.513, -7.108
(Intercept)[4]	-8.580	0.845	-10.245, -6.920
(Intercept)[5]	-8.406	0.839	-10.062, -6.759
(Intercept)[6]	-4.845	0.795	-6.408, -3.299
(Intercept)[7]	-4.722	0.793	-6.299, -3.170
(Intercept)[8]	-4.397	0.789	-5.943, -2.857
(Intercept)[9]	-1.219	0.786	-2.757, 0.320
(Intercept)[10]	-0.477	0.785	-2.026, 1.070
(Intercept)[11]	5.052	0.786	3.505, 6.575
(Intercept)[12]	5.144	0.785	3.600, 6.662
(Intercept)[13]	5.344	0.784	3.822, 6.847
(Intercept)[14]	5.456	0.787	3.940, 7.003
(Intercept)[15]	6.653	0.815	5.068, 8.268
(Intercept)[16]	6.839	0.817	5.252, 8.470
(Intercept)[17]	7.542	0.867	5.878, 9.280
(Intercept)[18]	7.874	0.908	6.159, 9.719
(Intercept)[19]	8.450	1.034	6.537, 10.628
Zone – Peri-urban	-0.043	0.475	-0.981, 0.895
Zone - Rural	-0.097	0.443	-0.959, 0.769

Trait	Estimate	SE	95% CI
Scientific Name SD (Intercept)	7.199	1.268	5.063, 9.960
Transect ID SD (Intercept)	0.126	0.100	0.005, 0.375
Body Mass			
(Intercept)[1]	-9.576	1.615	-12.832, -6.501
(Intercept)[2]	-2.926	1.447	-5.805, -0.098
(Intercept)[3]	4.009	1.445	1.225, 6.848
(Intercept)[4]	8.008	1.599	4.983, 11.152
Zone – Peri-urban	-0.058	0.763	-1.565, 1.431
Zone - Rural	-0.166	0.693	-1.529, 1.211
Scientific Name SD (Intercept)	9.165	1.529	6.543, 12.442
Transect ID SD (Intercept)	0.246	0.201	0.009, 0.753

Abbreviations: CI = Credible Interval, SE = Standard Error

Table 4.4 Model output from the permutational multivariate analysis of variance (PERMANOVA) testing for differences in raptor community composition among Locality type and Zone. The analysis was based on Bray–Curtis dissimilarities with 999 unrestricted permutations.

Model	df	R2	F	p.value
Locality type				
Urban vs Peri-urban	1	0.08	2.39	0.109
Urban vs Rural	1	0.13	4.74	0.002
Peri-urban vs Rural	1	0.03	1.22	0.178
Zone				
Urban vs Rural	2	0.11	2.79	0.002

Table 4.5 Model output from the permutational analysis of multivariate dispersions (PERMDISP) test used to measure homogeneity of multivariate dispersion among locality type and zone.

Model	df	F	p.value
Locality type	2	0.75	0.354
Zone	2	1.81	0.181

Table 4.6 Model output from the multilevel pattern analysis to assess species associations with locality type (City, Town) and zone (Urban, Peri-urban, Rural).

Group	Species	Statistic	p.value
Locality type			
City	Black Kite	0.289	0.248
	Eastern Osprey	0.289	0.253
	Whistling Kite	0.289	0.239
Town	Brown Falcon	0.608	0.013
	Australian Hobby	0.480	0.027
	Swamp Harrier	0.392	0.105
	Brown Goshawk	0.277	0.494
	Spotted Harrier	0.277	0.494
	Black Falcon	0.196	1.000
	Collared Sparrowhawk	0.196	1.000
	Square-tailed Kite	0.196	1.000
Zone			
Urban	Little Eagle	0.372	0.441
Peri-urban	Square-tailed Kite	0.243	0.594
Rural	Swamp Harrier	0.344	0.452
	Brown Goshawk	0.309	0.337
	Spotted Harrier	0.309	0.330
	Black Falcon	0.218	1.000
	Collard Sparrowhawk	0.218	1.000
Urban + Peri-urban	Black Kite	0.263	0.478
Urban + Rural	Eastern Osprey	0.246	0.697

Peri-urban + Rural	Nankeen Kestrel	0.829	0.002
	Wedge-tailed Eagle	0.778	0.002
	Brown Falcon	0.535	0.331
	Whistling Kite	0.229	1.000

Table S4.1 Localities surveyed in this study, including their locality type (city vs town), GPS coordinates and population size. The population size for each locality was gathered from the Australian Bureau of Statistics 2021 census data (https://www.abs.gov.au/census/find-census-data).

Locality	Locality type	GPS coordinates	Population size
Adelaide	City	-34.929, 138.600	1,269,473
Victor Harbour	City	-35.556, 138.623	16,139
Port Lincoln	City	-34.723, 135.860	14,404
Port Augusta	City	-32.487, 137.765	13,829
Strathalbyn	Town	-35.259, 138.893	7,871
Nuriootpa	Town	-34.469, 138.991	7,157
Clare	Town	-33.834, 138.613	3,238
Tumby Bay	Town	-34.375, 136.101	1,781

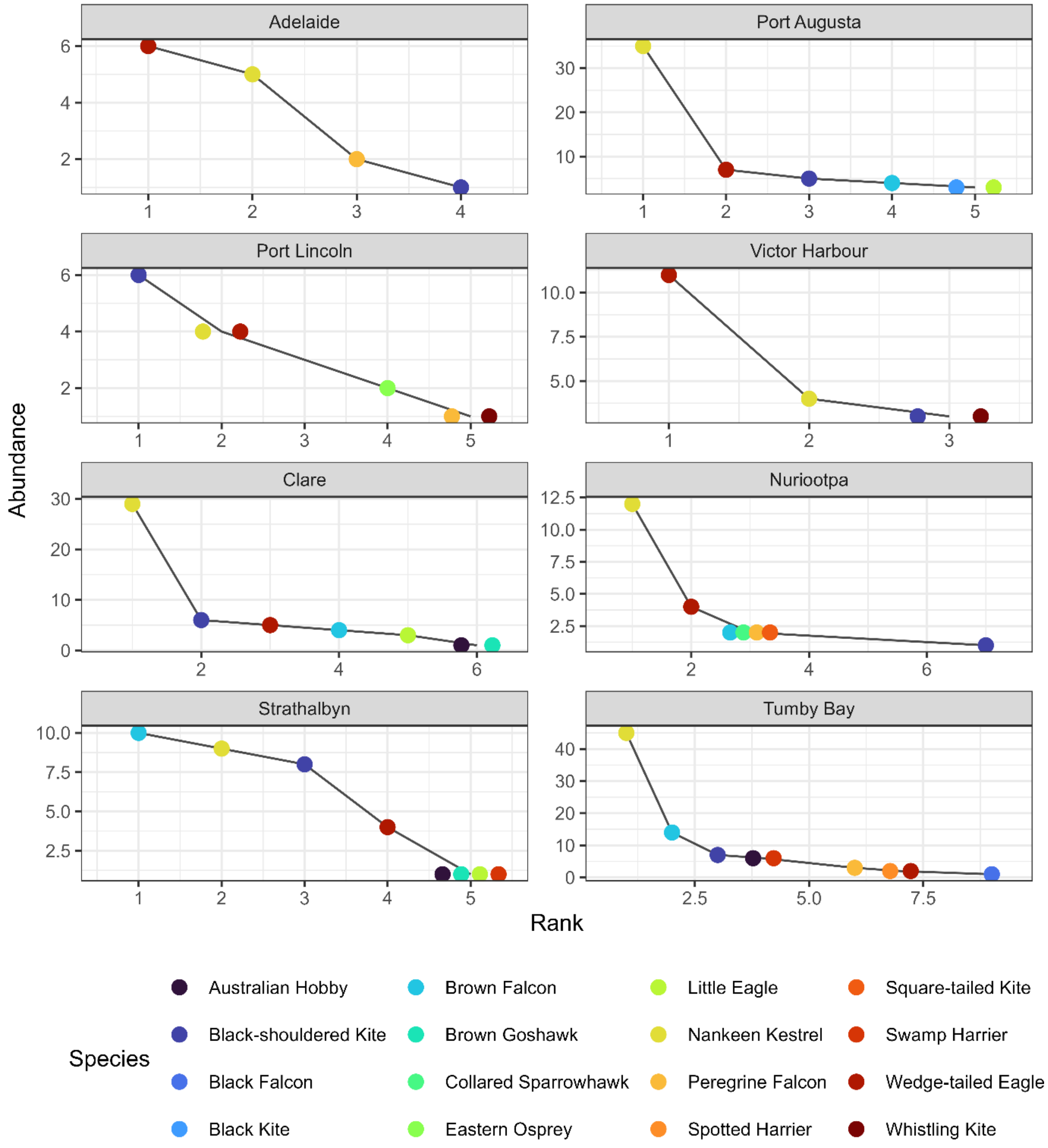

Figure S4.1 Rank abundance plots depicting the abundance of each species according to transect location. Jittered points represent species having the same abundance.

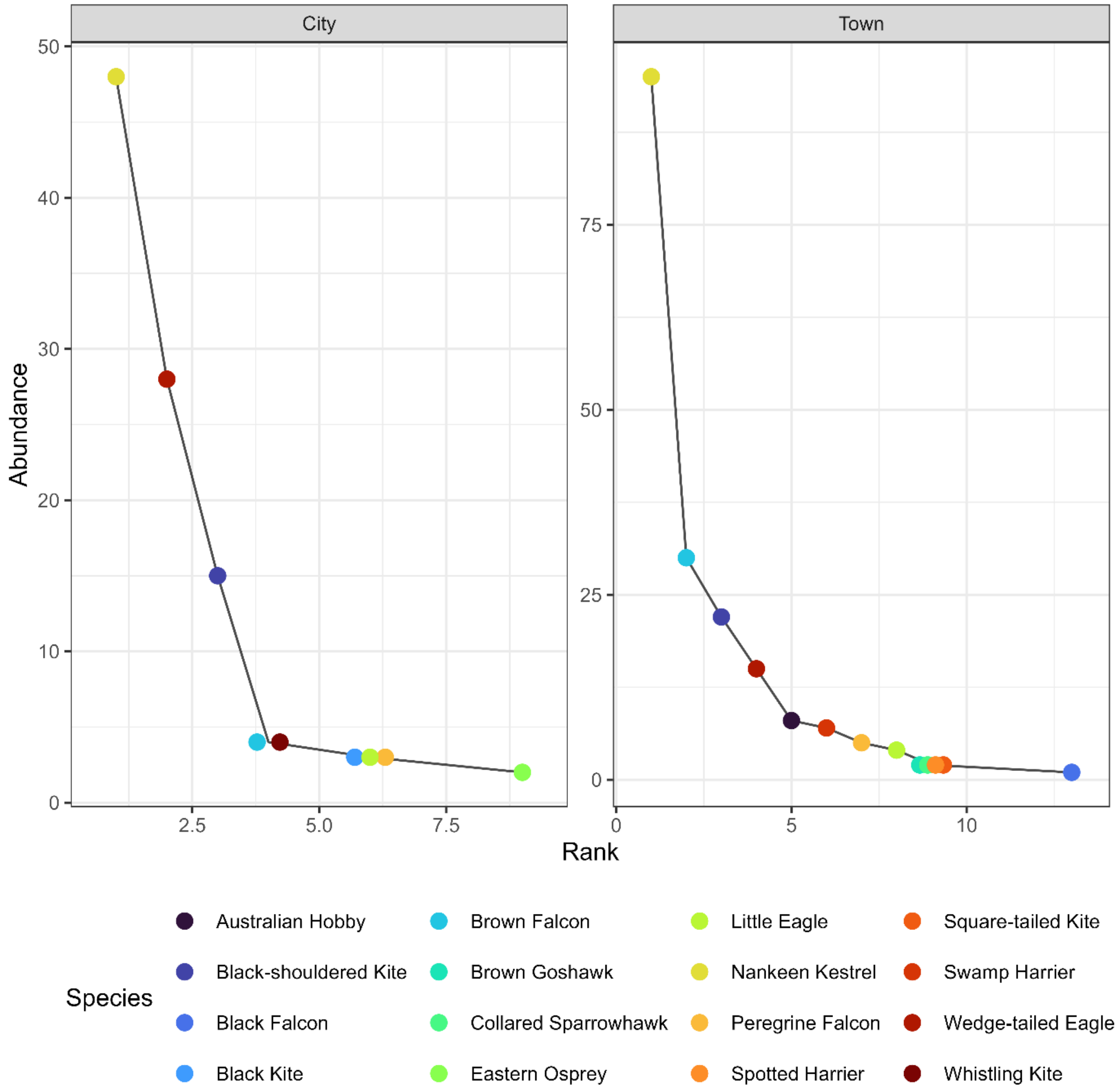

Figure S4.2 Rank abundance plots depicting the abundance of each species according to locality type (City, Town). Jittered points represent species having the same abundance.

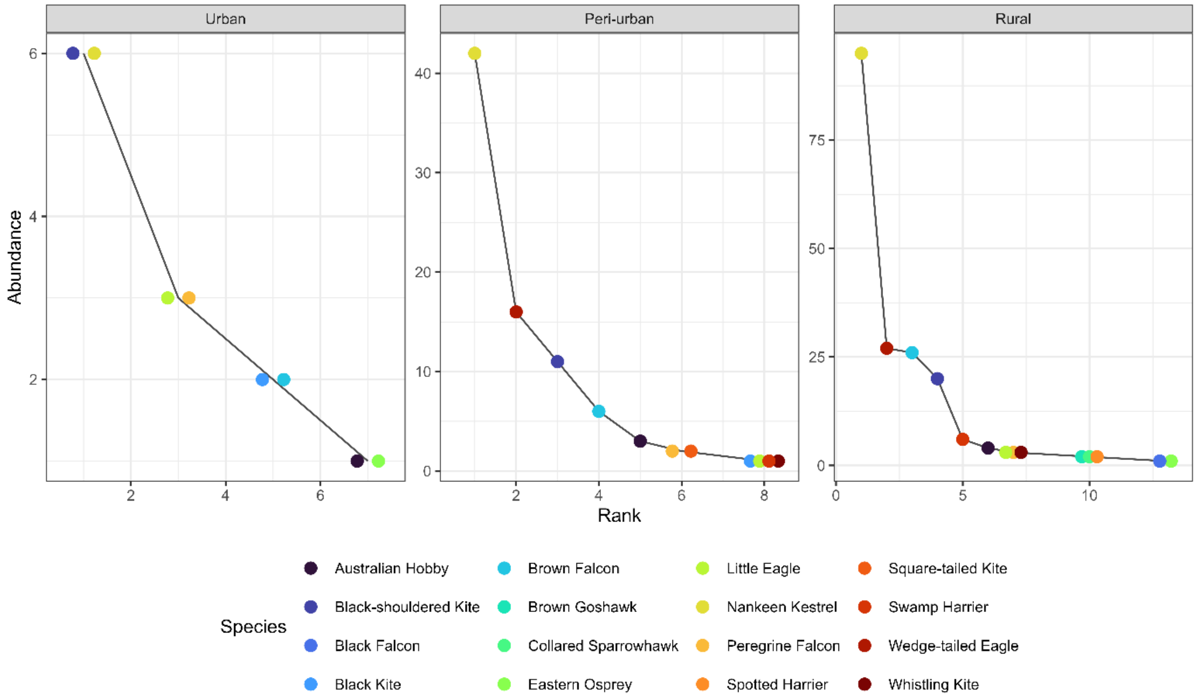

Figure S4.3 Rank abundance plots depicting the abundance of each species according to zone (Urban, Peri-urban, Rural). Jittered points represent species having the same abundance.

Chapter 5 - Discussion

Synthesis of findings

Urban expansion, due to increasing human population growth, is a principal cause of biodiversity decline worldwide (McKinney, 2002, Aronson et al., 2014, Li et al., 2022). Species lose critical foraging and breeding habitat during this landscape transformation, but some fragmented habitats remain scattered across cities in the form of urban green space (Aronson et al., 2017, Lepczyk et al., 2017). These spaces, which are either remnant, natural, or artificially created, can be biodiversity hotspots within urban ecosystems due to the range of resources they provide (Threlfall et al., 2017). Apex predators, such as raptors, tend to be particularly threatened by urbanisation and large-scale land transformation due to their sensitivity to environmental change (Sergio et al., 2008, Sergio et al., 2006). Regardless, some species have shown adaptability to urbanisation and exploit available resources, in some cases enabling them to thrive in urban ecosystems (McPherson et al., 2021, McPherson et al., 2016b, Suri et al., 2017). Overall, this thesis provides an insight into how raptor species respond to urbanisation at the global, regional and local spatial scales.

Pertinent questions for raptor biodiversity management involve how urban adapted raptors respond to urban expansion at scale, and whether patterns of urban green space use are consistent across continents. **In chapter 2**, I sought to address this question. I used three common kestrel species, the American Kestrel (*Falco sparverius*), the Eurasian Kestrel (*Falco tinnunculus*), and the Nankeen Kestrel (*Falco cenchroides*) as a model system, due to their near pan-global distribution and varying levels of tolerance towards anthropogenic stressors across scales. Artificial light at night, a proxy for urbanisation, was a top predictor of Kestrel occurrence and count globally (Chapter 2). However, urban tolerance analysis revealed that the three species had a general avoidance of urbanisation, despite some studies documenting large urban populations, particularly for the Eurasian Kestrel (Huchler et al., 2020, Sumasgutner et al., 2013, Sumasgutner et al., 2014a, Sumasgutner et al., 2014b). At the fine scale, occupancy modelling of the three kestrel species revealed an avoidance of urban land cover and tree cover as well as an association with urban green space land cover types such as grassland, cropland and shrubland. It is likely that grassland, shrubland and cropland habitats in and around urban areas are attractive to kestrels because they are open habitats that enable them to hover hunt, their preferred method of hunting, for small mammals, insects and birds, unimpeded. Whilst perch hunting has been documented in urban kestrels (Mikula et al., 2013), perch hunting in urban areas would be difficult due to the amount of obstacles required to navigate. The patterns of urban greenspace use by kestrels were varied across all three continents, and even within cities across the same continent, likely due to the different composition of the cityscapes. I built upon current knowledge of kestrel urban greenspace use (Sumasgutner et al., 2014a) by demonstrating that habitat composition and configuration is an important determination of occupancy, which aids in the management of these spaces. All three species have been documented to use anthropogenic structures, such as building ledges to breed (Debus, 2022, Sumasgutner et al., 2014a, Smallwood and Bird, 2020). However, they cannot sustain year-round presence in urban areas due to seasonal fluctuations in prey availability (Sumasgutner et al., 2014a). Eurasian Kestrels (*Falco tinnunculus*) are only present in cities during the breeding season (Huchler et al., 2020), but detrimental health impacts (Sumasgutner et al., 2018) and reduced breeding success as a result of urban living were documented in Vienna, Austria (Sumasgutner et al., 2014a). These results highlight the importance of undertaking analyses at multiple scales, as trends at the broad scale may not be visible and applicable to those at the fine scale, and vice versa.

Another core set of questions to enhance raptor biodiversity management involves an understanding of which ecological and life history traits can influence species' urban tolerance (Callaghan et al., 2019b, Neate-Clegg et al., 2023). Urban wildlife typically possesses phenotypic and behavioural traits that enable them to survive, and even thrive, within human dominated landscapes (Callaghan et al., 2021a, Callaghan et al., 2019b). Urbanisation acts as a filter, whereby species with a particular suite of traits are generally more urban tolerant (Kark et al., 2007, Evans et al., 2011). Currently it is unclear which traits enable successful urban living, as it appears to vary regionally (Cooper et al., 2022, Kettel et al., 2018a, Cooper et al., 2020, Leveau, 2022). **In chapter 3**, I examine body mass, diet and habitat generalism, nesting substrate breadth, feeding guild and migratory status (Neate-Clegg et al., 2023, Callaghan et al., 2021a, Callaghan et al., 2019b, Liu et al., 2021) to investigate which traits influence urban tolerance in Australian raptors, using community science data from eBird at the continental scale. **In chapter 4,** I examine body mass, habitat breadth and diet breadth to identify which traits influence urban tolerance at the local level using field-collected raptor sightings. As predicted, Australian raptors that were more urban tolerant generally exhibited similar trait profiles, but this varied across spatial scales. At the broad scale, smaller Australian raptors were more urban tolerant (Chapter 3), whereby species such as the

Brahminy Kite (*Haliastur indus*), Peregrine Falcon (*Falco peregrinus*), and Australian Hobby (*Falco longipennis*) were more tolerant of urbanisation, and larger species such as the Wedge-tailed Eagle (*Aquila audax*), White-Bellied Sea-Eagle (*Icthyophaga leucogaster*) and Square-tailed Kite (*Lophoictinia isura*) were more urban avoidant (Chapter 3). Many of the most urban tolerant species were characterised by either a generalist or bird specialist diet, a common trend worldwide (Kettel et al., 2018a). This is because these species can exploit available resources such as abundant avian prey or anthropogenic nesting sites such as buildings cavities or ledges.

Urbanisation is a strong selective force that significantly alters species assemblages and distributions (McKinney, 2002, Sun et al., 2022, Simkin et al., 2022), particularly for species vulnerable to anthropogenic change such as raptors (Shaw et al., 2024, MacColl et al., 2023). Urban expansion negatively impacts species richness and diversity due to a loss of resources required to survive in urban areas (Batáry et al., 2018, Thaweepworadej and Evans, 2022, Evans et al., 2018). Previous work has shown this trend in raptors in other countries (San Martín-Cruz et al., 2024, Carrete et al., 2009, Kumar et al., 2022), however, patterns in Australia may be different, as the urban gradient is usually less pronounced (Spencer et al., 2015). **In chapter 4**, I undertook road transect surveys of eight localities across an urban-rural gradient and sought to further understand which traits impact raptor distribution at the local scale. I hypothesised that species richness and diversity would be reduced across the urban gradient of cities and towns, and that species richness and diversity would be higher in towns than cities. When comparing species richness and diversity between cities and towns, I found that higher levels of urban intensity resulted in lower raptor richness, but not diversity (Chapter 4). This may be because of the dominance of a few common species, and the relative infrequency of the remaining species, resulting in low species evenness. Along the urban gradient, there was a distinct difference in raptor richness between the rural and urban zones of towns, but no difference was observed across the urban gradient in cities, likely due to the increased urbanisation levels of the cities filtering out less tolerant species, resulting in only urban tolerant species being observed in low numbers, which may explain why no signal was detected. The localities in the study area were small, and likely influenced the results, but only to a degree, as trends are still similar to those observed for raptors. The low to moderate levels of urbanisation, and the large home ranges of some species, dictate that the birds that were detected may not necessarily be residents of the zones or localities but from the regional species assemblage, potentially explaining the lack of trends in our trait models. Patterns of reduced species richness and diversity along the urban gradient have been observed previously in Argentina (Carrete et al., 2009), Mexico (San Martín-Cruz et al., 2024), and India (Kumar et al., 2022). I build on these findings by investigating which traits influence raptor spatial distribution. I further compared raptor richness and diversity between localities exhibiting different levels of urbanisation, which has not been investigated before. Most raptors were observed in the peri-urban or rural zones, but some of the urban tolerant species from chapter 3 (Peregrine Falcon, Black-shouldered Kite (*Elanus axillaris*), Little Eagle (*Hieraaetus morphnoides*), Australian Hobby) were also found in the urban zone. This supports the notion that continental urban tolerance scores can predict a species' response to urbanisation at the local scale (Callaghan et al., 2020), however, variation may exist, and therefore it is important to interpret the results with a degree of caution. These results also highlight the selective force of urbanisation, and the strong filtering of raptor communities within the zones and localities which were observed. This phenomenon was observed with *accipiter* hawks globally, as raptors in the urban core of cities were smaller, habitat generalists (Cooper et al., 2022). Urban green spaces in towns, such as parks and private gardens, provide an abundance of avian prey for raptors, which are comprised of both native and exotic plants and feeding stations for the congregation of prey (French et al., 2005, Roth et al., 2008, Gillanders et al., 2017). Urban green space composition is crucial for species richness and diversity (Threlfall et al., 2017, Threlfall et al., 2015, Callaghan et al., 2019a) as well as raptor occupancy (Chapter 2) due to the available foraging and breeding resources. While it is unknown whether urban green space size and composition differed across localities, it highlights the complex interplay of factors influencing species richness and diversity.

Research implications

The vast and human-inaccessible expanse of the Australian continent provides challenges when collecting biodiversity data. Collecting field data at scale is costly, not only in money but time, and requires significant resources to thoroughly study the species of interest. In the era of big data, community science programs such as eBird (Sullivan et al., 2014, Sullivan et al., 2009, Wood et al., 2011) and iNaturalist (Mesaglio and Callaghan, 2021, Unger et al., 2021) provide researchers with large volumes of data collected by dedicated participants. These data are subject to bias due to the unstructured and semi-structured nature of data collection (Bird et al., 2014, Backstrom et al., 2024a, La Sorte et al., 2024), but when such biases are properly accounted for, community science data can provide insights into species' ecology that would not be possible to obtain by small research teams. This thesis confirms the utility of community science for studying species distributions at both large and small scales, particularly for species that occur at low densities such as raptors. Here, I use current methods in urban tolerance species assessment and extremely fine-scale land cover data (e.g. Dynamic world dataset) to model raptor distributions in response to urbanisation, which has not been undertaken for raptor species before. An increasing number of studies have used citizen science data to investigate questions related to biodiversity in Australia (Callaghan et al., 2019b, Backstrom et al., 2024b, Lee et al., 2021b, Campbell et al., 2022), and it is likely that this avenue of research will grow into the future.

Raptor research is heavily biased towards northern hemisphere species, despite the raptors of highest conservation concern occurring in the southern hemisphere (Buechley et al., 2019, McClure et al., 2018). The human populations in Africa and Asia are the fastest growing in the world (Seto et al., 2012), and these areas represent the greatest raptor richness (Buechley et al., 2019). There is an urgent need for raptor research in these areas to prevent further species decline, and this research contributes to much needed raptor knowledge in the southern hemisphere to highlight southern hemisphere patterns. For example, the archetypal African raptor is characterised by a scavenging diet (Lee et al., 2021a, McPherson et al., 2021), something which is likely more common in Africa due to the high number of scavenging species that occur there. Although Australia is not urbanising as rapidly as other countries in the southern hemisphere, Australian raptors face similar threats, such as habitat degradation and loss, illegal shooting, poisoning from rodenticides, electrocution and vehicle strike (McClure et al., 2018, O'Bryan et al., 2022), some of which will increase as urban sprawl continues. This research highlights key factors affecting raptor occurrence in Australia and raises important questions about the potential consequences of their extirpation as urbanisation continues to expand. For example, I showed that even low levels of urbanisation led to reduced raptor species richness, which has cascading impacts on ecosystem services such as pest animal control and food web stabilisation. To plan urban centres that support raptor communities into the future in the face of ongoing urbanisation, urban green space should be prioritised and configured in such a way that they are dispersed throughout the landscape, with metrics such as edge density and percent land cover guiding configuration and composition (Chapter 2).

Apex predators are sentinel and bioindicator species because their diversity and abundance signal changes in biodiversity at the landscape level (Sergio et al., 2008, Sergio et al., 2005). They provide beneficial ecosystem services such as pest animal control, disease regulation and seed dispersal (Donázar et al., 2016, O'Bryan et al., 2018). This research highlights the importance of observing the diversity and abundance of apex predators in relation to habitat characteristics, as this can provide valuable insights into how processes like urbanisation may alter wildlife behaviour and/or ecology. For instance, the central findings in each of the chapters of this thesis support the idea that urban tolerance of raptors is species-specific, with some species showing urban tolerance profiles and some displaying urban avoidance profiles. Therefore, the conservation measures required to effectively manage each species are unique due to differing ecological requirements. This is crucial for all species, not only urban avoidant species, as urban tolerance does not guarantee against population decline (Petrenko et al., 2024). Urban expansion also increases the opportunities for human-wildlife conflict (Soulsbury and White, 2016) as species home ranges are encroached upon in natural areas, and mitigating such conflict through wilderness area protection and buffer zones around breeding areas is vital to protect both wildlife and the human population.

Future research directions

The research undertaken in this thesis addresses critical gaps in knowledge regarding raptor responses to urbanisation. There are four important next steps to be taken from this research to further our understanding of how raptors respond to urbanisation. Firstly, the assessment of species urban tolerance at the spatial level is critical to guide targeted conservation action. For example, the Wedge-tailed eagle is an urban avoidant species and is highly sensitive to anthropogenic disturbance. Understanding the landscape characteristics of areas where eagles are most observed, along with the frequency and intensity of use of these areas, can help to identify and prioritise the protection of high-use areas that may be under threat from urban landscape transformation. At a broad scale, this could be undertaken using a combination of citizen science data and field-collected observations, combined with remote sensing data such as land cover products, to elucidate patterns in raptor observations. Fine-scale patterns of use could be determined using GPS tracking technology, which would be useful to document the movement patterns of migratory species and help identify critical habitat near urban areas during the wintering period, a question that is lacking in knowledge.

Secondly, more work needs to be undertaken to understand how raptors are using urban areas at a finer scale. For some raptors, their entire home range is within an urban area (Mak et al., 2021a, Boggie and Mannan, 2014), and for others urban and rural areas are encompassed within their home range (Boal and Dykstra, 2018). Such different patterns of species distribution raise questions relating to resource use and selectivity of habitat use in urban areas, and their perceived quality relative to natural habitat. Habitat use and habitat quality issues are relevant given rapid urban expansion in the southern hemisphere (Commission, 2020), which may cause relocation of raptors living at the urban fringe. Targeted protection and enhancement of these species is possible with a greater understanding of how raptors are moving across the landscape and what habitats they select for in the urban core and fringe. This work is possible with the use of GPS tracking technology on urban raptors, which has been undertaken before (McPherson et al., 2019, Boggie and Mannan, 2014, Carter et al., 2019).

Thirdly, further research should investigate the influence of urbanisation on raptor species richness and diversity at larger spatial and temporal scales (e.g. regional and global). This will help to elucidate patterns that may be present in other parts of the world. The southern hemisphere has the highest raptor richness and diversity, yet it is also experiencing the most rapid rates of urbanisation (Seto et al., 2012, Simkin et al., 2022), so understanding how urbanisation may impact raptor populations in this area is vital. Attention should be given to the classification of the urban gradient, and a continuous measure of urbanisation could be used (e.g. artificial light at night) so that species are not placed into arbitrary zones, but instead on a scale so that peaks in species richness and diversity can be identified with greater accuracy along the gradient (Santos et al., 2024).

Finally, quantifying the breeding success of urban raptors, as well as the prey they consume, will aid in determining whether urban raptor populations are self-sustaining, and whether an urban diet enables healthy urban raptors. A meta-analysis of urban raptor breeding success (Kettel et al., 2018a), discovered that bird specialist feeders generally had a higher breeding performance and showed a positive response to urbanisation compared to mammal specialist feeders. However, across many urban breeding populations, it is unknown whether these population are self-sustaining, and whether the health of these populations will be impacted by further urbanisation. Likewise with diet, it has been shown in the Black Goshawk (*Astur melanoleucus*) that ample prey and low nutritional stress may buffer the species against potential negative health impacts from urbanisation (Suri et al., 2017), however further investigations will need to be undertaken to see whether this is the case for other raptor species.

By understanding species’ needs and preferences, we can help plan for a biodiverse world that includes raptors, even in urban environments.

Appendix

Appendix 1 – Publication version of Chapter 3 (PDF)

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Smaller Australian raptors have greater urban tolerance

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Urbanisation is occurring around the world at a rapid rate and is generally associated with negative impacts on biodiversity at local, regional, and global scales. Examining the behavioural response profiles of wildlife to urbanisation helps differentiate between species that do or do not show adaptive responses to changing landscapes and hence are more or less likely to persist in such environments. Species-specific responses to urbanisation are poorly understood in the Southern Hemisphere compared to the Northern Hemisphere, where most of the published literature is focussed. This is also true for raptors, despite their high diversity and comparably high conservation concern in the Southern Hemisphere, and their critical role within ecosystems as bioindicators of environmental health. Here, we explore this knowledge gap using community science data sourced from eBird to investigate the urban tolerance of 24 Australian raptor species at a continental scale. We integrated eBird data with a global continuous measure of urbanisation, artificial light at night (ALAN), to derive an urban tolerance index, ranking species from positive to negative responses according to their tolerance of urban environments. We then gathered trait data from the published literature to assess whether certain traits (body mass, nest substrate, habitat type, feeding guild, and migratory status) were associated with urban tolerance. Body size was negatively associated with urban tolerance, as smaller raptors had greater urban tolerance than larger raptors. Out of the 24 species analysed, 13 species showed tolerance profiles for urban environments (positive response), and 11 species showed avoidance profiles for urban environments (negative response). The results of this study provide impetus to conserve native habitat and improve urban conditions for larger-bodied raptor species to conserve Australian raptor diversity in an increasingly urbanised world.

Urban landscapes act as a trait-based filter for wildlife, and responses to changes in environmental conditions may be influenced by species-specific phenotypic and behavioural traits[1–3]. Traits that generally promote positive responses to urbanisation include high fecundity, strong dispersal ability, behavioural flexibility, and increased tolerance and/or habituation to human presence[4–10], but it is usually species dependent as to which traits are the most favourable[11,12]. Recently published literature shows that diet generalists tend to exhibit a positive response more often than diet specialist species in urban ecosystems[13,14], as generalist species occupy broader niches that allow them to tolerate a wider array of landscapes[15–17] and to explore a variety of different food resources[8,18]. As the world continues to urbanise[19,20], understanding the species-specific traits that allow wildlife to survive within urban habitat is vital to maintain wildlife biodiversity.

Mechanistic responses, specifically of species in high trophic levels that fulfil a stabilising function in ecosystems such as raptors, have been largely overlooked. Raptors (species from the orders Accipitriformes, Cathartiformes, Strigiformes and Falconiformes) are apex predators that showcase archetypal examples of urban avoiders, adapters, and exploiters across the urban/rural gradient. Successful urban raptor species are traditionally bird specialist feeders[21–24] due to the plentiful supply of food available for them in cities and towns, which allows them to be successful despite not fulfilling a generalist feeding niche that is usually associated with greater urban affinity[13]. Urban green spaces, such as parks, cemeteries and golf courses provide the habitat necessary for forest and woodland birds to forage, and raptors, such as the Peregrine Falcon (*Falco peregrinus*, pan-global), Cooper's Hawk (*Accipiter cooperii*, America), Black Sparrowhawk (*Accipiter melanoleucus*, Southern Africa) and Eurasian Sparrowhawk (*Accipiter nisus*, Europe), take advantage of these conditions[24–27]. Rodent specialist hunters and

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scavenging raptors are not uncommon within urban areas; however, their occurrence depends heavily upon prey availability[28–33]. As raptors are vital for ecosystem functioning through controlling prey populations and nutrient cycling[34], prioritising feeding and breeding habitat for urban-tolerant raptor species is essential to enable biodiverse urban landscapes.

Urban raptors possess certain behavioural and phenotypic traits that enable successful breeding and foraging in urban ecosystems. Raptor home ranges encompass large areas, and urban centres may only be used to fulfil part of their ecological requirements (i.e., using urban areas for hunting, but more natural habitat for breeding or vice versa). Examples include Ospreys (*Pandion haliaetus*) that regularly use man-made structures (e.g. barges and platforms) for breeding, but feed almost exclusively on fish in neighbouring water bodies (e.g. rivers, estuaries, oceans, urban lakes and ponds)[35], or Peregrine Falcons that breed on the cliffs of Table Mountain, South Africa, but use inner-city districts to prey on pigeons, doves and starlings[36]. The movement patterns of raptors are diverse, as some migrate thousands of kilometres to other continents[37,38], while others are partially migratory[39,40], or sedentary[41,42]. It is not clear how home range and movement patterns impact raptor urban tolerance, but sedentary birds show overall increased behavioural plasticity as opposed to migratory species[43]. Raptors that are capable of nesting on a variety of structures (e.g. trees and buildings) and raptors that exhibit flexible foraging techniques, such as perch hunting, pursuit and swoops[44–46] or hunting under artificial light at night (ALAN)[47–49], demonstrate adaptations that allow them to successfully survive in urban habitat by taking advantage of anthropogenic change[50]. Eurasian kestrels *(Falco tinnunculus)* in Slovakia have adopted a novel perch hunting technique that involves waiting above ventilation shafts to catch bats and common swifts (*Apus apus*)[51], while Eleonora's falcons *(Falco eleonorae)* in Morocco are known to hunt migratory species disorientated by street lights at night[52]. The use of ALAN by raptor species in urban areas[48,53] demonstrates that VIIRS night-time lights data are an appropriate proxy to study urbanisation patterns in bird species. Body size also plays a role in urban tolerance, as very small and very large raptors generally become extirpated from the urban environment[54,55]. This is likely due to a mixture of factors, namely tolerance to anthropogenic disturbance and suitability of the urban habitat for foraging and nesting[56]. However, there are exceptions to this, as very large scavengers (e.g. vultures) exist in urban areas where food availability is high and persecution is low due to socio-economic, climatic, and biogeographic factors[32].

Raptors continue to be understudied in urban areas, in part due to their sharp global decline[57,58] and their general low population densities[34], and thus high effort is required to conduct comprehensive studies. Community science is therefore an effective tool to assess raptor responses to urbanisation as it allows data collection over large spatial and temporal scales, utilising volunteers of differing skill levels to gather data across a variety of projects[59]. Projects such as eBird[60,61] and iNaturalist[62] amass millions of observations each year, and the data collected contributes to scientific publications or is used by various stakeholders, such as Government agencies and industry organisations[63,64]. Data from community science projects are invaluable in terms of time and effort, as these are generally the major limiting factors restricting researchers from collecting large amounts of data themselves[65,66]. Large datasets can also be challenging and time-consuming to analyse, often requiring copious amounts of data cleaning before analysis can commence[67]. Despite these limitations, data from community science projects continue to be a driving force behind scientific discovery, and growth in this sphere will exist as public awareness increases, programs expand, and technology advances[68–70].

In this study, we used species occurrence data collected via eBird[60,61], a global community science initiative documenting avian distributions worldwide, to assess the urban tolerance of 24 Australian raptor species and investigate whether specific phenotypic and behavioural traits, namely body mass, nest substrate breadth, habitat breadth, feeding guild, and migratory status, may explain species-specific responses to urbanisation. We predicted that species adapted to urbanisation (i.e. those with a positive urban tolerance index score) would be bird specialist or generalist feeders (e.g. feed on a variety of food types) rather than mammal specialist feeders, and nest on a variety of substrates allowing for more breeding opportunities[21]. We also predicted that urban adapters would be habitat-generalists and have a smaller to moderate body mass, as opposed to habitat specialists with a very large or very small body mass, as this pattern was previously found for raptors globally[54]. Our final prediction was that urban tolerant species would be sedentary species rather than migratory, as previous studies indicated that urban-adapted birds showed higher levels of sedentism, and some Australian species of raptors (e.g. Peregrine Falcon) are sedentary in Australia but migratory elsewhere[7,71–73]. As raptor research is largely biased towards a very small portion of the 557 raptor species, and the species with the highest number of publications (> 500) either have a pan-global distribution or are based in the Northern hemisphere, raising the profile of the conservation concern of Southern hemisphere raptors is a priority[58]. Based on the research and conservation prioritization index from[58], Australia falls within the medium and high categories of the index within certain areas. Therefore, we tested these hypotheses in Australia, located in the Southern Hemisphere, to challenge current theories and assumptions that are largely based on raptor research conducted in the Northern Hemisphere[54,74].

Methods and materials

Raptor observation data. We used observations of raptors across continental Australia from eBird[60,61], a long-running community science project spanning the globe. Checklists of birds seen and heard are submitted by volunteer birdwatchers, along with user effort variables, such as survey duration, distance travelled, and spatiotemporal information, which are all recorded manually or by a phone application[75]. Since eBird began in 2002, users have submitted over 89 million checklists, amounting to over 1.2 billion observations of birds worldwide, making it one of the largest and most successful community science projects to date.

The eBird basic dataset for Australia (ver. ebd_rel_AU_Jun-2021; available at: https://ebird.org/data/download) was downloaded and all observations of raptors between 1 January 2010 and 30 June 2021 were used, as the vast majority of submitted checklists lie within this period (> 95%). As the aim of this study was to identify

Australian raptor tolerance to urban environments at a broad temporal and spatial scale rather than examining changes between years, pooling the data over many years to include the largest amount possible was necessary to achieve this outcome. Checklists were filtered according to the eBird best practices guide recommendations[76] to minimise the bias often present in community science datasets[77]. We filtered the data to include only 'complete' checklists—a case where the user had submitted a checklist of all the bird species they had seen/heard. Checklists that were 'Stationary' or 'Travelling' or followed Birdlife Australia survey protocols such as 'Birdlife Australia 20 min-2 ha survey', 'Birdlife Australia 500 m radius search' or 'Birdlife Australia 5 km radius search' were included, while checklists where the observer travelled for greater than 5 h or over 5 kms were removed to reduce observer variation effort[78].

Ecological traits. Ecological traits were selected from the existing literature that may influence avian tolerance to urban environments[54,56]. Data for body mass, nest substrate, habitat type, feeding guild, and migratory status were compiled from information found in the dataset 'Biological, ecological, conservation and legal information for all species and subspecies of Australian bird'[79], the books '*Birds of Prey of Australia: a field guide (3rd edition)*'[80] and 'Australasian Eagles and Eagle-like birds'[81], and the online database 'Birds of the World' provided by the Cornell Lab of Ornithology[82]. Average body mass was used as a proxy for body size, and when possible, morphometric measures stemming directly from the Australian subspecies (e.g. Eastern Osprey) of a raptor were preferred from[79] over other published material. Nesting substrate breadth categories were determined by searching the literature for all possible nesting structures that the birds may use and dividing them into six categories: building, other artificial structure (e.g. pole, barge, telecommunications tower), cliff, tree, water and ground. These values were then added to a total number of nesting substrate types recorded for each species. Habitat breadth values were calculated from[79] by adding the total number of habitat types recorded for each species (Supplementary material A1). Feeding guilds were determined by examining the literature on species' core diet and separating them based on four main categories: generalist (consumes a variety of food types), bird specialist, mammal specialist or fish specialist. Migratory status was classified as local dispersal or partially migrant, as there are no fully migratory raptor species in Australia[79,83]. We used the definition of local dispersal and partially migrant from[79], and these definitions can be found in Table 1 in the 'migratory status' section.

Measure of urbanisation. To quantify the relationship between species occurrence and the urban environment, we used VIIRS night-time lights[84] data as a proxy for urban areas. It is a continuous measure readily available for download through Google Earth Engine[85] that correlates positively with human population density[86,87] and that is frequently used as a measure of urbanisation in ecological studies[13,88–90]. Whilst other measures of urbanisation exist[91,92] (e.g. impervious surface cover, skyglow), we chose this method due to its ability to produce a continuous estimate that can individually rank species rather than placing species into arbitrary categories. Our choice was also driven by the fact that the available data existed mostly within the timeframe of this study at the appropriate spatial grain. The data product comes pre-filtered from sources of background noise such as degraded data, fires, and light source contamination for maximum precision. To obtain the median radiance value for each checklist, monthly rasters of the VIIRS night-time lights were combined from 1 January 2014 to 31 December 2020 to create a single raster in Google Earth Engine. This raster was imported into R[93], where the median radiance was extracted within a 5-km buffer of each checklist. The ALAN median radiance values were condensed between 2014 and 2020 into a single value as exploratory analysis showed there were no large differences between years of a random sample of 1,000 distinct localities.

Statistical analysis. Analyses were conducted using the statistical software R (v4.2) in the integrated RStudio environment[93]. The *tidyverse* workflow was used for data manipulation[94], and the *ggplot2* package[95] was used for figure plotting. To eliminate records where the birds were unlikely to occur and remove any unusual records, species checklists were cropped to the extent of their known ranges using shapefiles from the 'Birds of the World' dataset from Birdlife International[96] using the *sf* package[97], which is a common technique used within ecological studies[98,99]. Hexagonal grids of 5 km width were generated across mainland Australia using the *dggridR* package[100] to facilitate spatiotemporal sub-sampling, a commonly used technique to remove potential spatial

Trait	Description	Source
Body mass	The average body mass of the species. The value for the Australian subspecies was used where applicable	Garnett et al.[79]
Nest substrate breadth	Derived from 6 nesting substrates: building, other artificial structure (e.g. pole, telecommunications tower), cliff, tree, water, ground	Debus[80,81], Billerman et al.[82]
Habitat breadth	Derived from 30 different habitat categories where species are known to feed; details provided in the supplementary material	Garnett et al.[79]
Feeding guild	Determined from primary food sources: generalist (consumes a variety of food types), bird specialist, mammal specialist or fish specialist	Debus[80,81], Billerman et al.[82]
Migratory status	Local dispersal—taxa that are largely sedentary with dispersal by juveniles over small distances Partial migrant—taxa in which some individuals regularly move away from breeding areas after nesting but some remain behind all year	Garnett et al.[79]

Table 1. The traits used in the linear modelling analysis to investigate the association between traits and the urban tolerance index for each raptor species in Australia.

and temporal bias, as well as class imbalance (more non-detections than detections of focal species), within community science data[78,101]. Prior to modelling, one checklist was sampled from each grid cell from every week of the year across all available years (2010–2021) to remove any spatiotemporal bias, and detection and non-detection were sampled independently to deal with any class imbalance and ensure that not too many detections were lost. Exploratory modelling was then undertaken on all species; species under 1000 checklists with at least 1 observation produced large confidence intervals of their urban tolerance profile relative to the other species and were therefore excluded from the analysis. This reduced the initial set of 34 mainland Australian raptors to the final set of 24 candidate species for modelling (Supplementary material A2).

To examine urban tolerance in Australian raptors, generalised additive models (GAMs) were used with a negative binomial error structure to account for over-dispersion within the data. The eBird best practices guide[76] was used as guidance for model preparation and fitting. The response variable for each model was the estimated abundance of each species within the checklist, while the predictor variable was the median VIIRS night-time lights value assigned to each checklist. Smoothing functions were applied to variables that were likely to influence the detection of a species on a checklist: number of observers, latitude and longitude, duration (min), day of year, effort distance (km) and 'time observations started'. Thin plate regression splines were used for the variables: number of observers, latitude and longitude, duration (min), day of year, effort distance (km) with four degrees of freedom, and a cyclic cubic regression spline was used for 'time observation started' with 5 degrees of freedom. For each species' model, the parameter estimate for night-time lights was obtained, indicating the relationship each species had with urbanisation (i.e. positive or negative) and the magnitude of that relationship. To reduce the uncertainty of the measure of urban tolerance due to the random sampling of eBird checklists within a grid cell, we ran our analysis 100 times for each species to obtain an average parameter estimate.

Multiple linear regression (i.e., all variables included in one model simultaneously) was used to investigate which ecological traits were associated with the species' response to urbanisation, accounting for all other traits. The response variable was the species response to urbanisation (i.e. parameter estimate) extracted from the GAMs, while the predictor variable was the value of the five traits for each raptor (body mass, nest substrate breadth, habitat breadth, feeding guild, and migratory status) (Table 1). All quantitative predictor variables were scaled and centred prior to linear regression modelling, and visual inspection of residuals for model validation was undertaken.

Results

A total of 840,918 eBird checklists were analysed, using 364,074 observations from 24 species prior to spatiotemporal subsampling, where one checklist was sampled across each 5 × 5 km grid from a species distribution range per week (Fig. 1). Spatio-temporal subsampling reduced the total number of species observations to 276,674. The Whistling Kite (*Haliastur sphenurus*) was detected the most of any raptor in the study, amassing 45,787 observations, while the Eastern Barn Owl (*Tyto alba*) was observed the fewest times, recorded on 1051 occasions across checklists (Supplementary material A2). Detection rates across sampled grids and the respective distributions of the study species can be found within the supplementary material (A3). The raptors observed in the area with the highest median radiance, or the brightest area across the study region, were the Brown Goshawk (*Accipiter fasciatus*) and Southern Boobook (*Ninox boobook*) (103.107 $\text{nW cm}^{-2}\ \text{sr}^{-1}$) in Docklands Park, adjacent the Yarra River in central Melbourne, Victoria. A Whistling Kite was sighted in the area with the lowest median radiance (0.062 $\text{nW cm}^{-2}\ \text{sr}^{-1}$), or the darkest area across the study region, which was at Lagoon Island, Lake Argyle, in north-eastern Western Australia.

From the 24 raptor species included in the analysis, 13 species displayed a positive response and 11 species showed a negative response to urbanisation. The species with the highest tolerance to urbanisation were the Eastern Barn Owl and the Australian Hobby (*Falco longipennis*), while the Brown Falcon (*Falco berigora*) and the Wedge-tailed Eagle (*Aquila audax*) were the least tolerant raptor species to urban areas (Fig. 2).

A significantly negative relationship between raptor response to urbanisation and body mass was observed (Table 2), indicating that raptors with a smaller body mass (g) were more urban tolerant than larger-bodied raptors ($F = 9.449$, $P = 0.007$; Fig. 3A). No significant relationship was detected between the other variables and urban tolerance; nest substrate breadth ($F = 0.559$, $P = 0.465$; Fig. 3B), habitat breadth ($F = 0.010$, $P = 0.920$; Fig. 3C), feeding guild ($F = 0.110$, $P = 0.953$; Fig. 3D) and migratory status ($F = 1.751$, $P = 0.204$; Fig. 3E).

Discussion

We assessed the urban tolerance of 24 Australian raptor species, whereby 13 showed a positive response to artificial light at night and 11 species showed a negative response. This finding highlights species-specific differences in urban tolerance across the Australian continent[13], with some raptors showing tolerance response profiles in urban areas and others showing avoidance response profiles. Furthermore, body size was the main trait explaining the species-specific urban tolerance score, as smaller raptors were more likely to have greater urban tolerance index scores than larger raptors. Our results show the wide range in raptor tolerance response to urban environments, measured here using artificial light at night. Given that urban sprawl continues to develop across Australia, understanding the tolerance profiles of different raptor species to environmental change is vital information to inform conservation strategies for human-modified landscapes.

The Brahminy Kite (*Haliastur indus*) was found to be the most tolerant Australian raptor to urbanisation. Brahminy Kites are a coastal raptor, commonly seen soaring along the shoreline, as well as scavenging for food on beaches and jetties[80]. Records exist of Brahminy Kites breeding in urban areas, namely Darwin[102], Northern Territory, and Port Macquarie[103] and Port Stephens[104], New South Wales, where there was varied breeding success across the study locations depending upon the level of human disturbance. A few factors may interplay to explain the tolerance Brahminy Kites to urbanisation, in particular its ability to breed on more than one substrate,

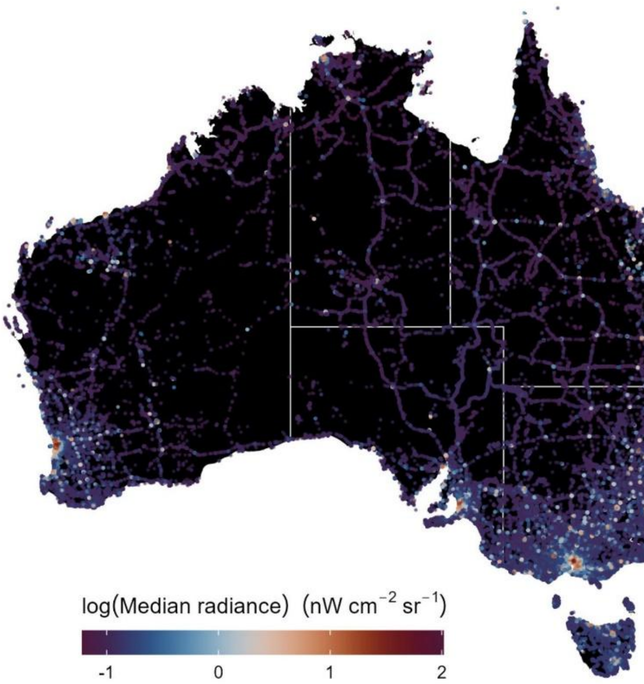

Figure 1. Map depicting the distribution of eBird checklists and their associated median VIIRS night-time lights value (log-transformed). Individual checklists are characterised by a coloured point, with purple and blue representing lower values and orange and red representing higher values.

its flexible diet and tolerance of human disturbance. Brahminy Kites are flexible in their breeding substrates, opting to use either large trees within mangroves or cities such as the African Mahogany (*Khaya senegalensis*) in Darwin[102], or common artificial structures such as light towers[80]. Additionally, they also showcase a generalist diet which comprises of fish, birds, reptiles, crustaceans, amphibians, mammals, insects and offal[80,102], which allows it to exist within a wide variety of different environmental conditions. The ability of Brahminy Kites to breed within urban areas highlights their capacity to tolerate human disturbance, but with increasing levels of urbanisation on the coast of Australia, there is an increased risk of poisoning from feral animal control and ingestion and entanglement from fishing equipment[103]. At the other end of the urban tolerance spectrum is the Wedge-tailed Eagle, the raptor with the lowest urban tolerance score. The species is known to be highly sensitive to human disturbance[105] and to avoid urban landscapes. For example, human activity from mountain bikers, off-road vehicles and bushwalkers has the potential to impact breeding success in Wedge-tailed Eagles that are located close to urban areas in Perth, Western Australia[106]. Wedge-tailed Eagles will retreat from urban expansion[107], however, some individual pairs show a higher disturbance tolerance to human activity when breeding inside protected reserves[108].

The finding that larger raptors have lower urban tolerance than smaller species is consistent with findings from other studies investigating urban raptor occurrence[54,55]. One particular study undertaken in Reno-sparks, Nevada, USA, showed that Golden Eagles (*Aquila chrysaetos*) breed the furthest away from urban development when compared to other smaller species, and the authors concluded that habitat requirements (e.g. large, open terrain) and life history traits (e.g. small clutch sizes, long-post-fledging dependency) likely explained this result[109]. In our study, Australia's largest birds of prey, the Wedge-tailed Eagle, and White-bellied Sea-Eagle (*Haliaeetus leucogaster*), were both found to avoid urban areas. Given that body size usually correlates with life history 'speed'[110], this negative correlation between urbanisation and eagle occurrence might have a similar explanation to the one reported for Golden Eagles[108,111]. Wedge-tailed Eagles usually nest several kilometres away from human developments[105,108,112], while White-bellied Sea-Eagles can occasionally nest within urban green space[113] using forested zones scattered throughout the metropolitan area[114]. However, from a global perspective, larger raptors are not always urban avoiders: in South Africa, for example, Crowned Eagles (*Stephanoaetus coronatus*) feed on urban exploiters such as the Rock Hyrax (*Procavia capensis*), Hadeda Ibis (*Bostricia hagedash*) nestlings, and Vervet Monkeys (*Chlorocebus pygerythrus*) which support a large urban breeding population of Crowned Eagles in Durban and Pietermaritzberg[115]. In Vancouver, Canada, Bald Eagles (*Haliaeetus leucocephalus*) feed

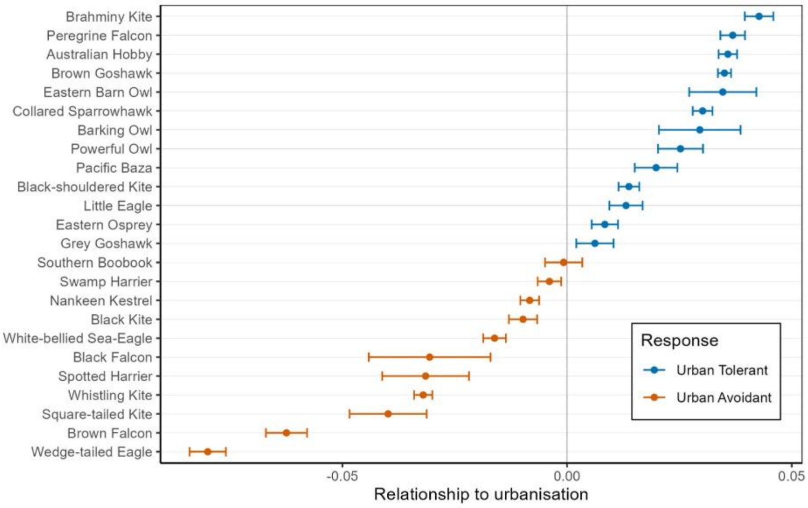

Figure 2. Urban tolerance index for the 24 Australian raptor species, ranked by the coefficient estimate from the generalised additive models. Larger positive values signify an increased effect of the predictor variable artificial light at night (ALAN), which indicates a positive response to urbanisation ('Urban Tolerant', in blue), while smaller negative values signify a decreased effect of ALAN as predictor variable, which indicates a negative response to urbanisation ('Urban Avoidant', in orange). The error bars represent the 95% confidence interval (of all 100 parameter estimates).

Term	Estimate	SE	T-value	Lower confidence interval limit	Upper confidence interval limit
Intercept	0.284	0.383	0.742	– 0.528	1.096
Body mass	– 0.684	0.222	– 3.074	– 1.155	– 0.212
Nest substrate breadth	0.169	0.226	0.748	– 0.310	0.647
Habitat breadth	– 0.022	0.218	– 0.102	– 0.485	0.440
Feeding guild: generalist	–	–	–	–	–
Feeding guild: bird specialist	0.157	0.485	0.325	– 0.870	1.185
Feeding guild: mammal specialist	0.340	0.677	0.502	– 1.095	1.775
Feeding guild: fish specialist	0.085	1.025	0.083	– 2.088	2.258
Migratory status: local dispersal	–	–	–	–	–
Migratory status: partial migrant	– 0.670	0.506	– 1.323	– 1.743	0.403

Table 2. Model summaries of the association between ecological traits of 24 Australian raptor species and their urban tolerance index for multiple regression linear modelling, including estimate, standard error (SE), t-value, lower and upper confidence limits. The confidence interval is reported at the 95% level. The reference category for feeding guild was generalist, and the reference category for migratory status was Local dispersal. Multiple r-squared—0.4413.

on a variety of birds and fish, and commonly nest in tall Black Cottonwood (*Populus trichocarpa*) and Douglas Fir (*Pseudotsuga menziesii*) trees, occasionally choosing to nest on transmission towers[116]. A metanalysis of 172 threatened and near threatened raptors around the world identified body size as the strongest predictor for their conservation status[117], whereby the larger the species, the higher the potential for exposure to anthropogenic threats and conservation concern. This association between body size and conservation status highlights the need to safeguard suitable habitat outside of cities to meet the requirements for large raptor species in the future.

In Australia, raptors with smaller body mass (172 g to 370 g) were generally tolerant of urbanisation, while medium-sized raptors (548 g to 847 g) displayed a variable response (e.g. tolerant or avoidant) to urbanisation. A potential driver of this trend may be the distribution of suitable prey residing within and outside urban areas, which can be linked to body size. Avian specialists are known to thrive in urban areas[21], as they profit from an increased density of avian prey attracted to supplementary food sources such as bird feeders[118,119], which are a

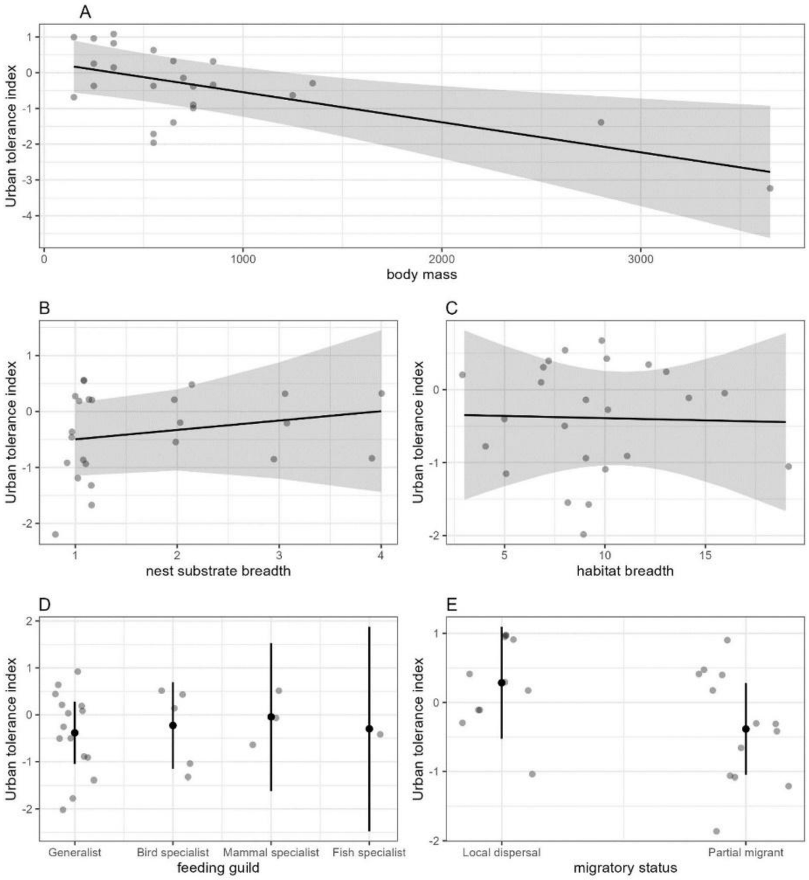

Figure 3. The Relationship between the urban tolerance index and ecological traits of 24 Australian raptor species. Marginal effects plots depict the relationship between urban tolerance and (**A**) body size, (**B**) nest substrate breadth, (**C**) habitat breadth, (**D**) feeding guild and (**E**) migratory status, accounting for all predictors. The grey points represent the partial residuals and the grey shaded area for (**A**), (**B**) and (**C**), and the black lines for (**D**) and (**E**) represent the 95% confidence interval.

common feature amongst Australian Gardens[120,121], and large numbers all-year-round of starlings, doves and pigeons[35]. Many of Australia's bird specialist feeders have a smaller body mass [e.g. Australian Hobby, Peregrine Falcon and Collared Sparrowhawk (*Accipiter cirrocephalus*)], enabling for swift pursuits of their avian prey. Australian cities include a mosaic of vegetation that is likely to attract birds[122,123]. This includes *Eucalyptus* spp. that are suitable nesting trees for both large and small raptors in Australia[81,124], and the urban remnant bushland[125,126], as well as exotic shrubs and flowers planted in gardens[127], that can provide nectar all year round[128] for species such as honeyeaters and parrots[129] upon which raptors can feed on. Many of the raptors with a moderate body mass are diet generalists, such as the Brahminy Kite and Spotted Harrier (*Circus assimilis*). These species displayed markedly different urban tolerance profiles, which could be a function of the distribution of their prey existing either inside or outside of urban habitat. However, habitat preferences may also play a role in this phenomenon, and therefore further research is needed to clarify the link between Australian raptors of medium body size and urban tolerance and the underlying mechanisms driving the pattern.

Partially migrant and sedentary species had similar urban tolerance profiles, which is consistent with the findings from recent studies focussing on raptors across the globe[54] and in Argentina[130]. Little Eagles (*Hieraaetus morphnoides*) are partially migratory, usually migrating from Southern Australia to Northern Australia during the winter months[131]. Ongoing GPS tracking studies have confirmed that the habitats used by breeding Little Eagles in Canberra were similar to those used during migration (woodland, grassland, forested areas, open urban land), and they appear to be tolerant of human activity and urban landscapes regardless of their breeding or migration state[132]. Booted Eagles (*H. pennatus*), a close relative of the Little Eagle, also showed positive responses to urban landscapes, as a population increase in western Europe was observed due to an increase in suitable prey[133]. Ongoing monitoring of raptor migration will be important to locate key areas used by urban-adapted species, potentially also as suitable stop-over spots during migration, to ensure their conservation.

Study limitations. While large-scale data collection by community scientists can facilitate continental-wide data, we acknowledge that such data face several limitations. For example, owls are nocturnal hunters, well camouflaged and cryptic in nature, which results in a lower detectability that often relies on identification by call rather than a visual confirmation. Sightings of owls may be more biased towards brighter urban areas, as artificial light sources such as streetlights and industrial lighting could enable easier observation. A clustered detectability may be apparent because of known roost sites, and in combination with some observers (i.e. birders) keen to take advantage of ticking off a target species, can lead to an over-representation of one single individual in an area[134]. We also recognize that most of the Australian population lives coastally, and therefore checklists are heavily biased towards these areas and along main highways connecting inhabited regions. Even though spatiotemporal sub-sampling was used to mitigate such biases, such clustering of observations still occurred, especially in data rich areas. But, as raptors were the only taxa investigated in this study, which are usually detected using the same methods and the observations are subject to the same biases, it is probable that the systematic sampling bias is analogous for all species observed in this study[13,135].

ALAN was used as a continuous metric of urbanisation within this study, and whilst this measure of urbanisation correlates positively with human population density and impervious surface cover[136,137], urbanisation occurs across large spatial scales, from the landscape to the local level[138]. Therefore, it is likely that across these scales species responses to urbanisation may differ[139], and the results from this study reflect Australian raptor responses to urbanisation at a broad scale rather than a fine scale, with the limitation that ALAN was used as a proxy for urbanisation. However, while ALAN is a proxy for urbanisation, it could also serve as a sensory pollutant for raptors, impacting the biological clocks of raptors and their prey. For example, owl species in this study could use night-time lighting as artificial hunting hot spots where prey may congregate to the lights, whereas larger species such as eagles may avoid well-lit areas due to their sensitivity to anthropogenic disturbance. To assess urban tolerance more accurately at finer scales, rather than the broad-scale approach like we have used here, data from GPS-tracked birds or survey data assessing the occupancy of birds in urban areas in conjunction with high-resolution landcover data would be a more suitable approach. Further, the results showed that body mass was the only trait that significantly influenced urban tolerance in Australian raptors, and no other traits influenced urban tolerance. The non-significance of the other traits may have been because of the coarse resolution that the traits were selected at (e.g. continental Australia). To be reliable, generally functional traits need to be location and individual specific[140], however when working at the macroecological scale and assessing interspecific differences, coarser trait resolution is suitable[141]. As we were assessing tolerance at the landscape level, we chose to select traits at a coarse scale as it was the most useful resolution for this study, but we acknowledge that the reliability of these traits across time and space for some species may be significantly decreased.

Future areas of study. The eBird checklist numbers in Australia are growing more numerous each year, and therefore investigations into the urban tolerance of raptor species that occur at lower densities (e.g. Red Goshawk) may become feasible in the future, most likely in conjunction with targeted surveys from conservation related organisations. Also, a more granular examination of habitat use within urban areas of urban tolerant raptors will be an important area of future research to conserve important foraging and breeding areas. Such approaches will help identify which raptor species are occupying urban areas during the breeding season, and those that only visit to forage or roost.

Conclusion

In summary, this research used a large continent-wide raptor data set collected by community scientists and professional birders across Australia to generate valuable insights into the urban tolerance of 24 Australian raptor species. The finding that the 13 species with greater urban tolerance also had, on average, smaller body size, sheds light on mechanistic pathways that may be driving urban tolerance response profiles. Smaller-bodied species tend to have faster life histories and higher metabolic rates, producing larger clutches earlier in life that are frequently provisioned with relatively small prey. The abundance and commonality of nocturnal and diurnal prey including small mammals, rodents, pigeons, doves, and passerines, in conjunction with the diet speciality of many small Australian raptors, may favour the persistence and survival of smaller-bodied raptors in urban environments. Conservation management initiatives, particularly those that focus on habitat preservation and restoration (e.g. wilderness area protection), are needed with a special focus on protecting larger-bodied raptor species given urban expansion and an avoidance response of larger raptor species to urban areas.

Data availability

The data and code to reproduce these analyses are available here: https://doi.org/10.5281/zenodo.8093060.

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Author contributions

T.H., S.K., D.C.N., C.T.C. and P.S. designed the research and T.H. wrote the first draft of the paper; T.H., C.T.C., S.C.S., P.S. extracted the data; T.H., C.T.C., P.S. statistically analysed the data; all authors developed the ideas presented in the manuscript, including edits and final approval.

Competing interests

The authors declare no competing interests.

Additional information

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Appendix 2 – Manuscript - ‘Home range sizes of urban Nankeen Kestrels in South Australia across the annual cycle’

Home range sizes of urban Nankeen Kestrels in South Australia across the annual cycle

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Abstract

Raptors are declining globally, with species in the Southern Hemisphere particularly understudied. Urban raptors are of special interest as they exhibit a unique duality: their presence in urban areas suggests adaptability and potential resilience to human disturbances, yet their proximity to human infrastructure may expose them to overlooked threats. To address these knowledge gaps, this study investigates the space use of Nankeen Kestrels (*Falco cenchroides*) across an urbanisation gradient throughout an entire annual cycle—the first such study for this species. We tagged 12 Nankeen Kestrels with high-resolution GPS loggers, obtaining fine-scale movement data for 9 individuals for home range estimates. Using kernel density estimators, we compared home range sizes relative to urbanisation levels based on artificial light at night and seasonal changes. Our results indicate no significant relationship between home range size and the degree of urbanisation. However, some individuals exhibited foray flights—long-distance exploratory movements—and males showed a slight tendency toward larger home ranges (n=7; mean 4.138 km; ranging from 0.858 km^2 to 14.577 km^2) than females (n=2; ranging from 1.074^2 km to 1.189 km^2), though this was not statistically significant. Interestingly, Nankeen Kestrels in Australia displayed

relatively large home ranges compared to similar-sized kestrels globally. This could reflect the use of advanced GPS technology and extended tracking periods, which allowed us to detect more extensive spatial behaviours, including foray flights during and outside of the breeding season. This study sheds light on the spatial ecology of a key Southern Hemisphere raptor. By understanding how these raptors navigate human-altered landscapes, we can better assess their conservation needs and guide urban planning strategies to mitigate threats such as collisions with traffic infrastructure while maintaining habitats that support viable populations.

1. Introduction

Human-induced changes to natural habitats are transforming landscapes worldwide, profoundly affecting wildlife populations (Sodhi & Ehrlich, 2010; Li et al., 2022). Raptors, as apex predators, are particularly vulnerable to these changes and are experiencing global population declines (McClure et al., 2018). However, smaller raptor species tend to show greater tolerance to urban environments compared to their larger counterparts (Cooper et al., 2022; Headland et al., 2023). Yet they often fulfil critical roles in functioning ecosystems (Reynolds et al., 2021). Their ability to inhabit urban areas suggests adaptability to human disturbances, yet their proximity to anthropogenic infrastructure poses often underestimated threats (Chace & Walsh, 2006; McPherson et al., 2021; Panter et al., 2022).

In urban settings, resource availability and landscape features strongly influence raptor success (Kettel et al., 2018; Dykstra, 2018). Adaptability, either through resource flexibility in terms of prey (Kübler et al., 2005; Solaro, 2018; Sumasgutner et al., 2013) and nesting substrate (Reynolds et al. 2019), or extended movement patterns that reach beyond the urban boundaries (Riegert et al., 2007), appears critical for urban raptors. For example, high densities of pigeons support high numbers of avian specialists, such as Peregrine Falcons (*Falco peregrinus*; Kettel et al., 2018), Black Sparrowhawks (*Accipiter melanoleucus*; Suri et al., 2017), or Northern Goshawks (*Accipiter gentilis*; Rutz, 2006), while low numbers of diurnal mammals might create an ecological trap or habitat sink for mammalian specialists like Eurasian Kestrels (*Falco tinnunculus;* Kettel et al., 2018; Sumasgutner et al., 2014). To fulfil their ecological requirements, some raptor species commute between urban breeding sites and rural hunting grounds (Riegert et al., 2007), while others exhibit partial migration

– where the urban breeding population is migratory and the rural breeding population remains largely resident (Warkentin et al., 1990; Huchler et al., 2020). These behaviours underscore the need to interrogate how urbanisation affects the spatial ecology of urban raptors throughout the annual cycle, which require longer-term tracking studies.

A ***home range*** was originally defined by Burt (1943) as “the area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional ventures outside the area, perhaps exploratory in nature, should not be considered part of the home range.” This definition highlights that a home range can only be calculated if an animal exhibits range-residency behaviour (Spencer et al., 1990), which can be assessed using tracking periods of sufficient duration. During juvenile dispersal or other exploratory periods (hereafter ‘foray flights’), the space used by an individual does not meet the criteria for a home range. Instead, the concept of a ***utilisation distribution (UD)*** is more appropriate. A UD characterises space use as a probability distribution, offering insights into resource selection and identifying core areas based on visitation frequencies (Powell & Mitchell, 2012). Integrating UD data with randomised landscape variables makes it possible to derive and generalise an animal’s habitat preferences and ecological requirements (Horne et al., 2008). When a location-time series underlying a UD becomes sufficiently long and incorporates various stages of the animal's annual or life cycle, it can fulfil the criteria for being considered a home range. However, due to technical and logistical constraints, the term "home range" is often used more broadly in the literature, frequently referring to the area an individual occupies during the specific timeframe of a GPS tracking study.

This widespread, albeit looser, application underscores the need for clarity and precision when using these terms.

Technological advances, particularly in GPS tracking, now allow precise movement data collection even for smaller raptors (Kolowski et al., 2023). Despite these advancements, there remains a paucity of studies on raptors in the Southern Hemisphere, particularly smaller urban species. Previous research has been constrained by limited tracking durations and low data resolution, often focusing only on the breeding season (Cunningham, 2013; Riegert et al., 2007). These limitations obscure comprehensive insights into space use patterns across life cycles and habitat gradients. The Nankeen Kestrel (*Falco cenchroides*) offers an ideal study system to address these research gaps. As a small, adaptable raptor widely distributed across diverse landscapes in Australia, it inhabits both suburban and rural environments (Headland et al. 2023), providing a good opportunity to explore spatial ecology under varying habitat conditions. Furthermore, its relatively small size and broad ecological niche align with the challenges faced in tracking studies of similar species, enabling insights that are broadly generalisable.

This study aims to address the aforementioned knowledge gaps by generating high-resolution GPS tracking data for Nankeen Kestrels across an urbanisation gradient in South Australia. We hypothesise that suburban Nankeen Kestrels exhibit home range sizes that are smaller or similar to their rural conspecifics, consistent with findings from studies on related kestrel species in the Northern Hemisphere. For urban raptors, home ranges are generally smaller than their rural counterparts due to the rich concentration of resources (e.g. prey, nesting and roosting sites) available in urban areas, reducing territory size and movement activity (Casagrande et al., 2008; Cunningham, 2013; Kang et al., 2015; Løken, 2009; Riegert et al., 2007). Additionally, we aim to assess the validity of using mean circular buffers to estimate population-level spatial characteristics, a method commonly applied in conservation planning (Murgatroyd et al., 2021; Venter et al., 2019; Watson et al., 2014) or to derive an urban gradient to address ecological questions in a larger study population (Sumasgutner et al., 2014 and 2020; Rose et al., 2017; Mueller et al., 2020).

Second, we investigate how utilisation distributions vary across the annual cycle, comparing breeding and non-breeding seasons, as well as between sexes. Based on behavioural traits documented in other kestrel species, we hypothesise that female Nankeen Kestrels will exhibit smaller utilisation distributions during the breeding season, while males will maintain similar utilisation distribution sizes year-round. This expectation aligns with the observed role of males as primary food providers during the breeding season, while females are largely confined to the nest during incubation and brooding (Balgooyen, 1976; Riegert et al., 2007). To test these hypotheses, we analysed high-resolution spatio-temporal GPS data collected over the course of a year, enabling a detailed examination of home range sizes, seasonal changes in utilisation distributions, and differences between sexes. By exploring these patterns, this study provides critical insights into the adaptability and conservation needs of a Southern Hemisphere raptor in urbanising landscapes.

2. Material and Methods

2.1. Challenges and limitations of home range studies

Currently, no studies have quantified the home range sizes or utilisation distributions of Nankeen Kestrels. Most available tracking studies of kestrels have relied on fewer than 100 fixed positions per individual and relatively short time frames, often focusing on portions of the breeding season (Table 1). These limitations arise from several methodological constraints: First, the power-to-weight ratio of tracking devices has historically restricted their use to larger species and shorter tracking durations (White & Garrott, 1990). However, recent advances, such as solar-powered GPS loggers, can facilitate more detailed and prolonged studies. For example, Kolowski et al. (2023) used solar-powered GPS loggers to track female American Kestrels (*Falco sparverius*) throughout their annual cycle. This approach provided insights into non-resident behaviour during the breeding season and home range shifts after the breeding season, highlighting the potential of new technology for revealing nuanced movement patterns. Second, traditional radio-tracking methods based on VHF face significant challenges in urban areas, where signal reflections from buildings and infrastructure reduce reliability and require labour-intensive visual confirmation or location estimates based on triangulation (Gerber et al., 2018; Millspaugh & Marzluff, 2001; White & Garrott, 1990). New methods, such as on-board data storage or transmission via satellite or GSM networks, are overcoming these obstacles and enable the study of smaller raptor species in urban contexts.

Several approaches are used to quantify home ranges and utilisation distributions. The ***Minimum Convex Polygon (MCP)*** method constructs a polygon encompassing a specified percentage of GPS points (e.g., 95% or 100%) but does not account for the intensity of space use and assumes independence between observations (Boyle et al., 2008; Mitchell, 2006). The ***Kernel Density Estimation (KDE)*** method estimates the density of location points and calculates the probability of an animal being in a specific area (Worton, 1989). It is commonly used to delineate home ranges (95% KDE) and core areas (50% KDE) (Powell, 2000; Mitchell, 2006). However, KDEs require regular sampling and assume independence between points, which may underestimate home range sizes if spatio-temporal autocorrelation is present (Fleming et al., 2015). Recently, the ***Autocorrelated Kernel Density Estimator (AKDE)*** has gained traction for its ability to account for spatio-temporal autocorrelation, offering more accurate home range estimates (Fleming et al., 2015).

2.2. Study System

The Nankeen Kestrel is a relatively small raptor species with a wide distribution range across Australia. This species has a diverse diet, consuming a large number of invertebrates, but vertebrates account for approximately 70% to 85% of its prey biomass, particularly during the breeding season (Fuentes et al., 2024; Olsen et al., 1978; Stewart, 2021). Birds, for example, contribute between 22% and 67% of the total prey biomass (Fuentes et al., 2024; Olsen et al., 1978). Despite its adaptability, Nankeen Kestrels show a slight displacement response to urbanisation, suggesting potential impacts of habitat modification on their space use and behaviour (Headland et al., 2023). Breeding typically begins between late September and early November, with limited variation among individuals and regions (Bollen, 1990; Mo, 2019; Paull, 1991; Stewart, 2021). The incubation period ranges from 28 to 31 days, and nestlings fledge after approximately 26 to 35 days (Olsen & Baker, 2001; Paull, 1991; Stewart, 2021). This concise timing provides a clear temporal framework for tracking their space use during critical life stages.

The study was conducted in the Adelaide area, the capital city of South Australia, with a human population of approximately 1.37 million. Twelve Nankeen Kestrels were captured using Bal-chatri traps baited with live mice in areas categorised as rural and suburban, based on a rough assessment of surrounding habitats. Both males and females were fitted with GPS loggers (Milsar Nano Tags) weighing 3.4 g, attached with a Teflon leg-loop harnesses for females and backpack harnesses for males (Supplementary Figure S1). The combined weight of the logger and harness was approximately 2.8% of body weight for females and 2.9% for males, complying with the recommended maximum of 5% (Kenward 2000) and the more modern standard of 3% (Gould et al., 2024). These loggers, powered by solar recharge, continuously recorded GPS locations throughout their deployment and allowed for data retrieval via a base station with a range of up to 500 meters in open landscapes. Monthly downloads ensured consistent data collection, with all data securely stored in the Movebank repository under Project ID 3416661275 ("Movement Ecology of Nankeen Kestrels in South Australia"). The number of recorded GPS fixes per individual ranged from 5 to 6,032 (Supplementary Table S1).

2.3. Statistical analyses

2.3.1. General workflow

The data were analysed in RStudio using R version 4.3.2 (R Core Team, 2023), with the following workflow: Home range calculations were performed using the *ctmm* package (Calabrese et al., 2016), based on weighted Autocorrelated Kernel Density Estimates (wAKDEs). The resulting wAKDE files were converted into shape files with *sf* (Pebesma, 2018; Pebesma & Bivand, 2023). Circular buffers for intersecting environmental data were also established with *sf*. The ALAN data were imported and saved as spatial raster files using the *terra* package (Hijmans, 2024). We ensured consistent spatial units – standardised to kilometres – during buffer calculations in using the *units* package (Pebesma et al., 2016) and intersected home range shape files and circular buffers with maps of artificial light at night (ALAN) with the *exactextractr* package (Baston, 2023). For visualisations involving spatial raster data, the *rcartocolor* package (Nowosad, 2018) was employed to enhance colour schemes, particularly for displaying spatial variation. Linear mixed-effects models were fitted using the *lme4* package (Bates et al., 2015) and summarised with the ANOVA function of the *car* package (Fox & Weisberg, 2019). We assessed residual plots to validate that all model assumptions were met, and predictor effects visually to aid interpretation with the *effects* package (Fox & Weisberg, 2018), while all graphical representations of spatial patterns and regression model effects were created with *ggplot2* (Wickham, 2016). Throughout the analysis, the *dplyr* package (Wickham et al., 2023) was used to manage data frames and streamline workflows.

2.3.2. Utilisation distributions

GPS data were downloaded from Movebank (www.movebank.org). We used the Autocorrelated Kernel Density Estimations (AKDEs) in *ctmm* (Fleming et al., 2015) that account for short time intervals between GPS fixes (here between 30 min and 1 h) without the need to thin the data to regular sampling intervals. This not only improves the precision of area estimates but also produces more reliable confidence intervals compared to traditional methods (Fleming & Calabrese, 2017). Prior to analysis, invalid data entries were removed from the GPS dataset, which was then uploaded to Movebank for further processing. As finer-scaled data are more prone to errors, the detection and removal of outliers becomes increasingly important (Fleming et al., 2021). Outliers were identified visually with the *outlie* function (see Supplementary Figures S2). To evaluate whether an individual exhibited range residency behaviour, we examined the variogram, which indicates whether an animal uses specific areas consistently over time. Range residency behaviour is indicated by a variogram with a horizontal asymptote (see Supplementary Figures S3 left). Note that Nankeen Kestrel Animal ID 5 did not exhibit range residency behaviour (Supplementary Figure S3 right), as the variogram asymptote had not yet stabilised. It is possible that, with a longer tracking period, range residency behaviour would have become evident. Supplementary Figures S4 provide examples of these validations, with varying confidence intervals depending on the amount of available location data. Next, the most appropriate model to describe the data and estimate an accurate home range was selected from five available movement models: Independent Identically Distributed (IID), Brownian motion (BM), Ornstein-Uhlenbeck (OU), Integrated Ornstein-Uhlenbeck (IOU), and Ornstein-Uhlenbeck foraging (OUF) (Calabrese et al., 2016). The IID model assumes independent, uncorrelated data, while OU and BM methods model a randomly searching animal within a restricted area (Fleming et al., 2014). We compared 95% AKDE outputs with the 95% weighted Autocorrelation Kernel Density Estimation (wAKDE) with confidence intervals (Fleming et al., 2018) and present the latter where weights can be applied to prioritise certain data points (e.g., accounting for temporal relevance when there were gaps in the data due to irregular download success, or the varying sampling design as some individuals showed sufficient solar recharge on a 30 min schedule, while for others the interval was reduced to 1 h or 3 fixes per day to cope with limited battery power).

2.3.3. Environmental variables to estimate urbanisation levels

To estimate the level of urbanisation within each kestrel’s home range, we intersected the shapefile polygon derived from each wAKDE with Visible Infrared Imaging Radiometer Suite (VIIRS) night-time lights data (Elvidge et al., 2017) accessed through Google Earth Engine (Gorelick et al., 2017). The resulting ALAN values, measured in nanowatts per square centimetre per steradian (nW/cm²/sr), represented the mean light intensity within each home range. Additionally, we calculated circular buffers with a radius equivalent to the mean home range size of all kestrels, centered on each nest site, and extracted ALAN values for these buffers. We generated a linear mixed model with ALAN as explanatory variable, and sex as co-variate (7 males, 2 females). To account for potential non-independence due to shared nest sites when both kestrel parents were GPS tracked, we included nest site ID as a random factor. A final linear regression analysis compared the ALAN values from the wAKDE-derived polygons with those from the circular buffers to evaluate congruence between methods.

2.3.4. Temporal changes in utilisation distributions

To assess variation in utilisation distribution sizes across the annual cycle, data were divided into monthly intervals. This approach was chosen as a balance between temporal resolution and sufficient GPS data density, with monthly periods providing adequate data for meaningful analysis. We avoided conventional seasonal classifications due to uncertainty in clutch initiation timing and instead adopted this finer-scale temporal framework. We excluded Animal ID 5 from all analyses due to the displayed foray flights. Additional exclusions affected a total of four months in the utilisation distribution calculations, again because the variogram analyses indicating non-residency behaviour and one month with insufficient GPS data (fewer than three locations). All other data were validated and incorporated into the analyses. Exact sample sizes are provided in Supplementary Table S2.

2.4 Ethics

This study was conducted under the Flinders University Ethics permit number 4788. The trapping, handling and GPS-tagging of birds was undertaken by professionals holding the appropriate permits.

3. Results

3.1. Home range size of Nankeen Kestrels

GPS data for home range analysis were successfully collected from nine out of twelve tagged Nankeen Kestrels. The optimal movement model for most home range estimates was the OU anisotropic model, apart from one female (Animal ID 12), for which the IID anisotropic model was more appropriate. Male home range sizes ranged from 0.858 km² to 14.577 km² (n = 7), while female home range sizes varied between 1.074 km² and 1.189 km² (n = 2). The mean and median 95% wAKDE estimates were 4.138 km² and 1.637 km², respectively. Further details are provided in Table 2, and a graphical representation of these results, including confidence intervals, in Figure 1.

3.2. Correlation between home range size and urbanisation

No significant correlation was observed between home range sizes and ALAN, indicating no strong association with the urbanisation gradient (model estimate 3.74 ± 2.63 SE, t = 1.42; ALAN predictor estimate -0.16 ± 0.5 SE, t = -0,31, X^2 = 0.09, p = 0.759). There was no difference between males and females (sex predictor estimate 1.71 ± 1.16 SE, t = 1.47, X^2 = 2.17, p = 0.141). The regression analysis to understand the association between ALAN values based on wAKDE polygons and ALAN values based on mean circular buffers around each nest site showed a 91% correlation (Table 2, Figure 2). This finding suggests that mean circular buffers can serve as a reasonable approximation for wAKDE polygons in terms of ALAN-derived urbanisation metrics.

3.3. Temporal patterns across the annual cycle

Monthly utilisation distributions exhibited considerable variation in size over time (Figure 3 top). Seasonal fluctuations in space use were further explored through visual representations of data from four individual kestrels spanning an entire year (Figure 3 bottom). Detailed monthly data are available in the Supplementary Table S2, providing additional context for these temporal patterns.

4. Discussion

This study provides important insights into the movement ecology of Nankeen Kestrels, a small raptor species native to Australia, tracked over a period spanning from 23rd October 2022 to 19th December 2023. The home range sizes based on 95% wAKDEs of Nankeen Kestrels ranged from 0.86 to 14.58 km², with a mean home range of 4.138 km² and a median of 1.637 km². These results suggest that Nankeen Kestrels exhibit larger home ranges than kestrel species from the Northern Hemisphere, such as the American Kestrel *(Falco sparverius;* mean 95% AKDE = 0.32 km², range 2.06-0.91 km^2, but limited to 12 females during the breeding season; (Kolowski et al., 2023)), and Eurasian Kestrel *(Falco tinnunculus;* median 95% KDE = 0.98 km², range 0.39-3.88 km^2 (Cunningham, 2013), mean 95% MCP = 1.87 km², range 0.71-3.,1 km^2

(Løken, 2009), mean 100% MCP = 0.74 km², 0.28-1.42 km^2 (Casagrande et al., 2008), and mean 100% MCP = 7.2, 0.8-25 km^2 (Riegert et al.. 2007)), whose home ranges tend to be smaller (summarised in Table 1).

The larger home range sizes of Nankeen Kestrels could be explained by several factors, including methodological differences such as the use of high-resolution tracking technology and longer tracking periods, and potentially broader ecological factors. Specifically, our study utilised advanced GPS tracking technology, which has been shown to yield more accurate and comprehensive movement data compared to historical methods with lower resolution (Morollón et al., 2022). The increased accuracy and longer tracking periods in this study likely resulted in larger home range estimates, and the capture of more extensive movement patterns including the foray flights for Animal ID 5 (Supplementary Figure S5). The study by Kolowski et al. (2023) that reported relatively smaller home range sizes for American Kestrels is methodologically comparable, however they focused on females during the breeding season and excluded longer foray flights from the home range calculations. These findings suggest that advanced GPS tracking technologies provide a more nuanced and precise understanding of raptor space use, particularly for species like the Nankeen or American Kestrels, which were previously challenging to track accurately due to weight limitations.

Our study also investigated the relationship between home range size and urbanisation, using artificial light at night (ALAN) as a proxy for urbanisation. We hypothesised that urban Nankeen Kestrels would exhibit smaller or similar home ranges compared to rural conspecifics, as observed in other raptors (Casagrande et al., 2008; Cunningham, 2013; Kang et al., 2015; Løken, 2009; Riegert et al., 2007). However, we found no significant correlation between home range size and ALAN values, suggesting that urbanisation may not have the same effect on Nankeen Kestrels as assumed for other kestrel species. This lack of a clear relationship could be due to the coarse spatial scale of the ALAN data, which might not capture the finer-scale urban features influencing kestrel space use. Other studies have found strong correlations between ALAN and urbanisation metrics (Elvidge et al., 2021; Pandey et al., 2013; Stathakis et al., 2015; Zhang & Seto, 2013), but it is possible that the ALAN measure used here was too broad to detect individual variability in urban environments. Finer-scaled measures of more detailed urban land use that directly relate to resource selection might yield a clearer understanding of urban effects on their movement ecology. Additionally, the high ALAN values associated with infrastructure such as airport runways, which were prominent in our study area, may have overestimated the degree of urbanisation, potentially compromising the results (see supplementary Figure S6).

The study also revealed seasonal differences in the utilisation distributions (UDs) of Nankeen Kestrels, with a notable increase in home range size between November and February, suggesting that some individuals engaged in foray flights. These flights, which are thought to be a strategy for locating suitable foraging or nesting sites, have been observed in other kestrel species, including the American kestrel (Kolowski et al., 2023). Nankeen Kestrels may exhibit similar foray flight behaviour during the breeding season when parental care, specifically hunting effort, intensifies. This was evident in several individuals, including Nankeen Kestrel Animal ID 7, who showed a significant expansion of its UD in November and December 2022, followed by a contraction in January 2023. This pattern is consistent with the findings of Kolowski et al. (2023), who observed that American Kestrels engage in foray flights during the nestling period. Such behaviour likely explains the large fluctuations in UDs seen during this period, particularly for individuals such as Nankeen Kestrel Animal IDs 4, 9, and 10.

The seasonal differences in UDs also highlight potential sex-based differences in space use. Our data indicate that male Nankeen Kestrels tended to have larger home ranges than females throughout the year, which is consistent with the behaviour of other raptor species, where males cover larger areas to provision females during the breeding season (Kolowski et al., 2023; Riegert et al., 2007). This pattern is particularly pronounced in October, when females are more stationary due to nesting, while males exhibit greater mobility to secure food resources. Female Nankeen Kestrels, such as Animal ID 6, showed a reduction in their utilisation distribution size during October, likely due to nesting activity, which prevented the GPS device from collecting data. A larger sample size of females in our study would be necessary to further explore these differences and increase statistical power.

In assessing the accuracy of commonly used methods for estimating urbanisation in raptors, we compared the ALAN values derived from mean circular buffers and wAKDE polygons. Our results indicated a high correlation (91%) between the two methods. This supports the use of mean circular buffers as a reasonable approximation for assessing the degree of urbanisation in individual territories, provided the buffer size is biologically relevant to the target species. However, to determine an appropriate scale, some tracking data should be available from the study system. However, we also found that mean circular buffers underestimated the actual home range sizes, particularly for non-circular home ranges, which are typical of Nankeen Kestrels and most other urban raptors (Sumasgutner et al. 2016; McPherson et al. 2019). Our comparison highlights the strength of the buffer method to derive an urban gradient but are limited in capturing more detailed spatial ecology of urban raptors.

Conclusions and future directions

This study advances our understanding of the spatial ecology of Nankeen Kestrels, providing the first high-resolution, spatiotemporal GPS data on their movement patterns. Despite some limitations, such as the pronounced sex-bias towards males and the inability to collect continuous data for certain individuals, our findings fill critical knowledge gaps in raptor movement ecology, specifically in urban areas of the Global South. The larger home ranges observed in Nankeen Kestrels compared to similar species in the Northern Hemisphere highlight potential ecological and behavioural differences, possibly influenced by resource distribution, habitat characteristics, or foray behaviour. To address methodological constraints, future research could explore dynamic models like the dynamic Brownian bridge movement model (Walter et al., 2015) to better account for nomadic or transient behaviours. Extended data collection using solar-powered GPS tags with satellite connectivity would enable the monitoring of longer time-series data without labour-intensive data download, providing deeper insights into whether observed foray behaviour is a recurring pattern or represents shifts in home range dynamics. Such advancements could refine the definition of home ranges for raptors, particularly those exhibiting complex space-use patterns.

Our study also underscores the importance of accurately assessing individual spatial requirements to inform population-level conservation strategies. Improved technology and analytical methods will enable more precise home range estimates, critical for understanding the ecological needs of raptor populations. The application of mean circular buffers as a proxy for urbanisation assessment showed promise, but further refinements are needed to align these estimates with the diverse, non-circular shapes of real home ranges. By integrating novel tracking technologies and comprehensive analytical approaches, this research not only provides new insights into the spatial behaviour of Nankeen Kestrels but also contributes valuable perspectives for the study of raptor ecology in diverse environments.

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***Table 1:** Summary of published studies on movement patterns of kestrel species with ecological similarities to the Nankeen Kestrel (Falco cenchroides), including the method used to estimate home range sizes, reported in km^2 (subject to availability: min-max, median or mean), and key ecological or behavioral findings.*

Location / Environment	Species	Male / Female	Breeding status	No. of Animals	No. of Days	No. of fixes per bird	Method used to quantify home range size in km^2	Method	References
Southeastern Norway / Boreal forest	*Falco tinnunculus*	Female	Pre-fledging	6	2-6	49-141	0.39-3.88 / median 0.72 (95% MCP) 0.48-4.69 / median 0.98 (95% KDE)	Radio tracking VHF telemetry	(Cunningham, 2013)
Southeastern Norway / Boreal forest	*Falco tinnunculus*	Male	Chicks at least 14 days old	3	13-18	32-52	0.71, 1.9, 3.01 (95% MCP of 3)	Radio tracking VHF - Homing in, then on-site confirmation of location	(Løken, 2009)
South Korea / suburban environment	*Falco tinnunculus*	Mixed	Wintering and breeding season	6 females 8 males	5-23 (in 6 months)	31-105	0.0354 - 0.3950 / mean = 0.1855 (Female 95% KDE) 0.2168–0.9902 / mean = 0.5845 (Male 95% KDE)	Visual identification with camera and natural features of the bird	(Kang et al., 2015)
North Virginia, USA / mostly agricultural and forestry area	*Falco sparverius*	Female	Breeding season (April to August)	12	39- 140	521- 2258	0.06-0.91 / mean = 0.32 (95% aKDE)	Solar powered GPS loggers with remote data download via base station	(Kolowski et al., 2023)
South of Czech Republic / mostly agricultural and ruderal areas around the city Budějovice including nests in the city	*Falco tinnunculus*	Male	Chick rearing (May to July)	34	unclear	12-38	0.8-25 / mean = 7.2 (100% MCP – calculated hunting range size, nest site in city center was excluded)	Visual verification with 7x binoculars of all locations – mostly wing tagged birds, some with Radio tracking VHF telemetry	(Riegert et al., 2007)
North of Italy / mostly grasslands and intensive agricultural fields	*Falco tinnunculus*	Male	Breeding season (starting end of March)	15	min 45h of hunting per bird	unclear	0.28-1.42 / mean = 0.74 (100% MCP)	Radio transmitter on tail feathers. Only visual confirmation included in data	(Casagrande et al., 2008)

MCP = Minimum Convex Polygon; KDE = Kerne Density Estimate; aKDE = auto-correlated Kernel Density Estimate

Table 2: *Weighted Autocorrelated Kernel Density Estimation (wAKDE) derived with the ctmm package (Calabrese et al., 2016) with estimates and lower (lCI) and upper (UCI) 95% confidence intervals for Nankeen Kestrels in Adelaide, South Australia. Artificial light at night (glmm) values were calculated using the wAKDE polygon and a circular buffer around each nest based on the mean home range size (radius =1.018 km).*

Animal ID	**Sex**	**Optimal Model**	**95% wAKDE area in km^2**			**ALAN** (nW/cm2/sr) **wAKDE polygon**	**ALAN** (nW/cm2/sr) **circular buffer**	**Habitat**
			LCI	**estimate**	**UCI**			
1	Male	OU anisotropic	1.409	1.637	1.881	0	0	Rural
3	Male	OU anisotropic	0.756	0.858	0.966	0	0.31	Rural
4	Male	OU anisotropic	3.727	3.955	4.189	0.0065	0	Rural
6	Female	OU anisotropic	1.133	1.189	1.247	0	0	Rural
7	Male	OU anisotropic	13.891	14.577	15.279	3.1513	1.52	Suburban
9	Male	OU anisotropic	7.435	8.644	9.941	0.0014	0.164	Rural
10	Male	OU anisotropic	3.637	3.870	4.109	5.4579	2.43	Suburban
11	Male	OU anisotropic	1.397	1.438	1.479	10.759	13.3	Urban
12	Female	IID anisotropic	1.024	1.074	1.125	10.053	13.3	Urban

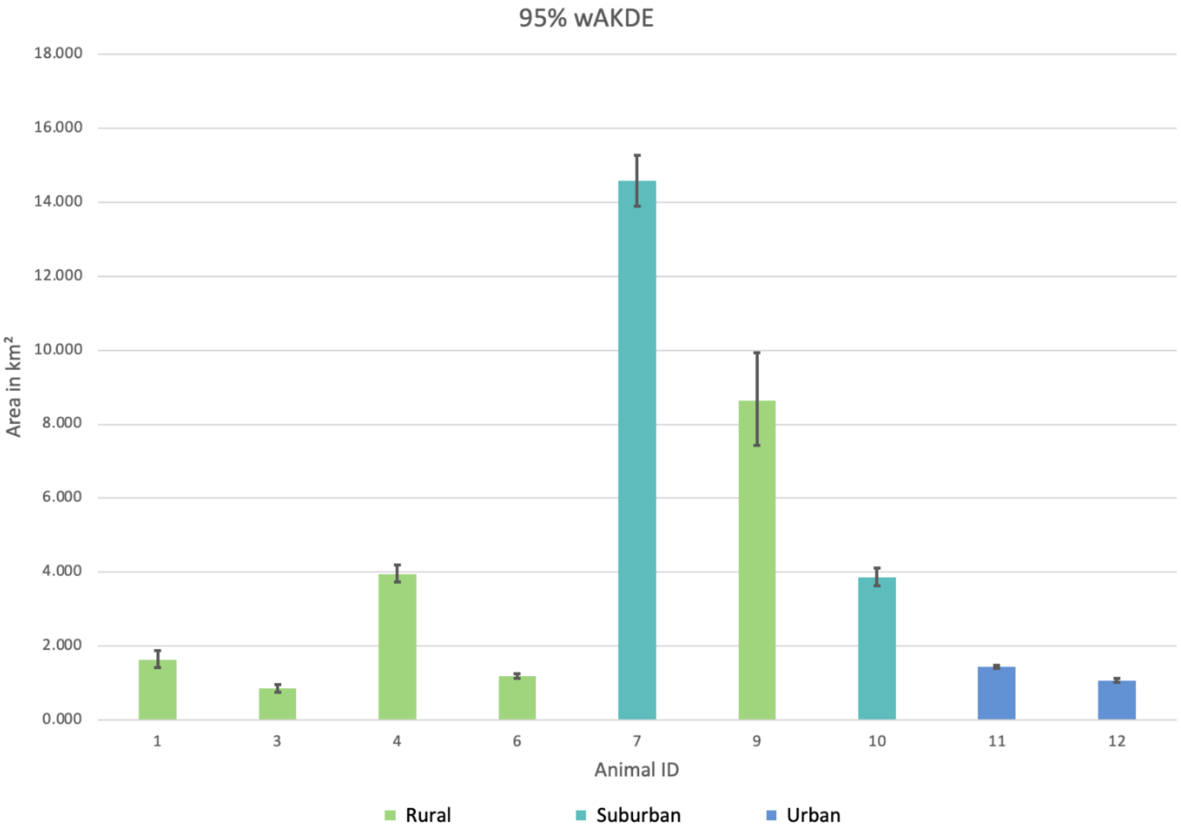


Figure 1: *Weighted Autocorrelated Kernel Density Estimation (wAKDE) derived with the ctmm package (Calabrese et al., 2016) with estimates and lower (lCI) and upper (UCI) 95% confidence intervals for Nankeen Kestrels in Adelaide, South Australia. Corresponding results are presented in Table 2.*

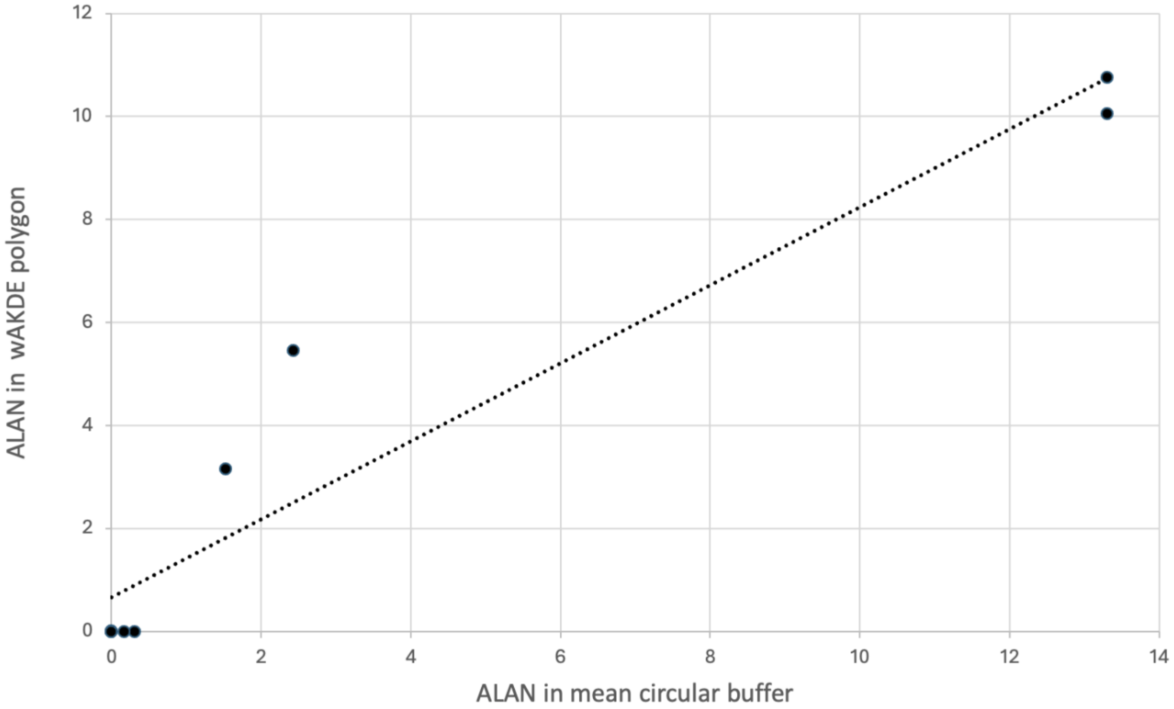
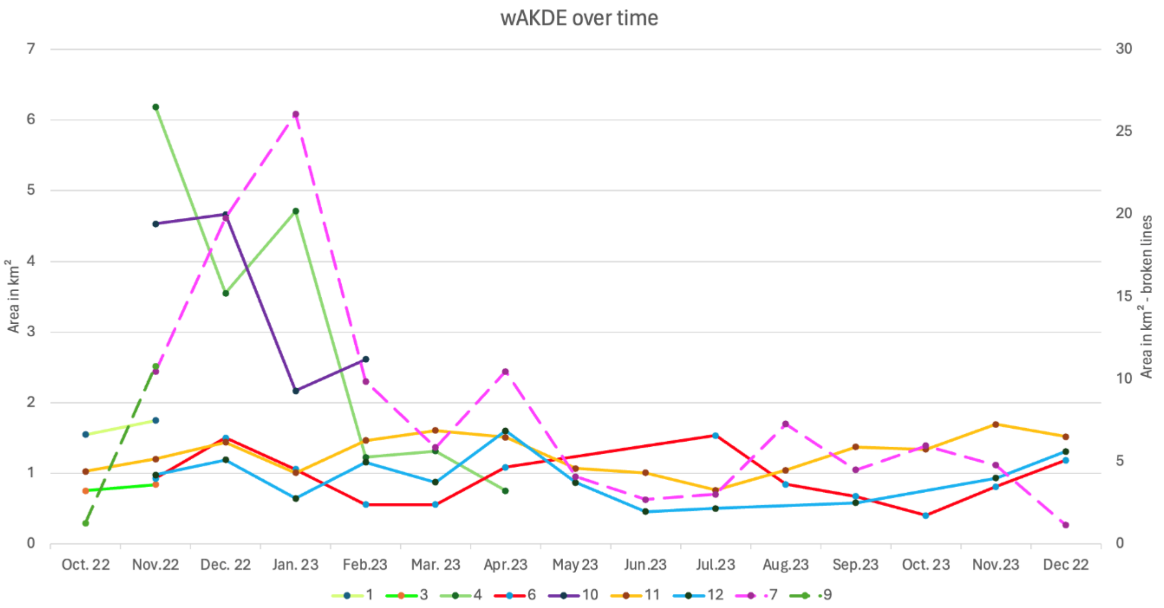


Figure 2: *Regression ($R^2 = 0.91$) between artificial light at night (ALAN [(nW/cm2/sr)]) values based on the weighted Autocorrelated Kernel Density Estimation (wAKDE) of Nankeen Kestrels in Adelaide, South Australia, and a circular buffer around each nest based calculated from the mean home range size (radius =1.018 km).*



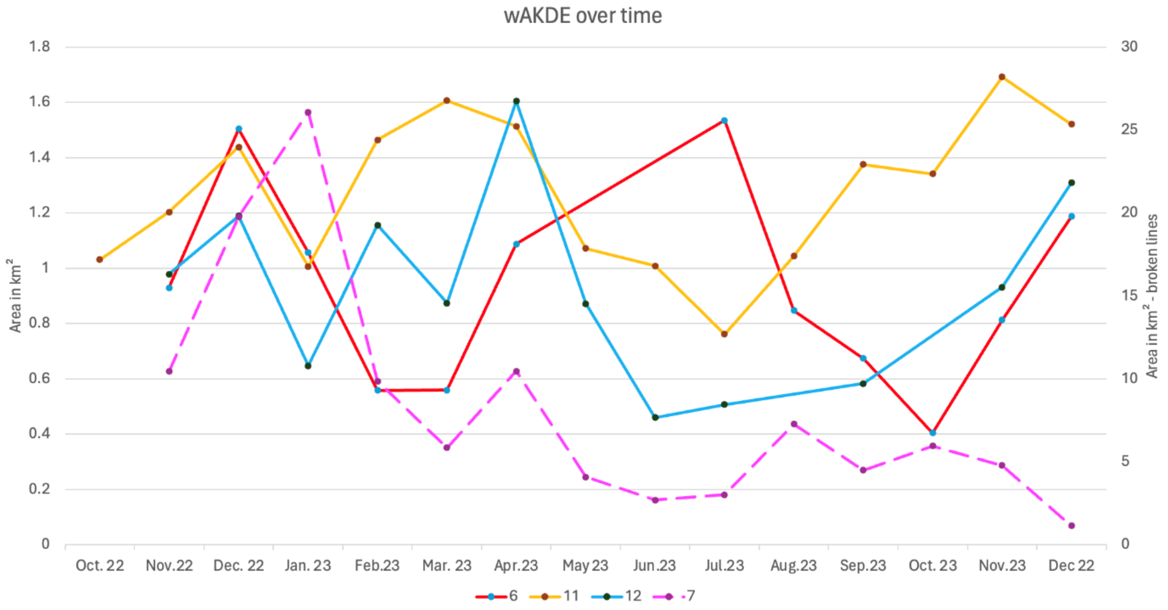


Figure 3*: (Top): Monthly utilisation distributions (UDs) for all Nankeen Kestrels tracked over the course of one year. Each line represents the UDs of an individual kestrel, with solid lines corresponding to the left axis, and broken lines corresponding to the right axis. UDs were calculated for each month, though some months were excluded from the analysis (as detailed in Supplementary Table S2) due to indications of non-resident behaviour or insufficient GPS data as reflected in the variogram analysis. (Bottom): Visualisation of monthly UDs for our kestrels were data spanned across an entire annual cycle (Animal ID 6, 11, 12 and 7).*

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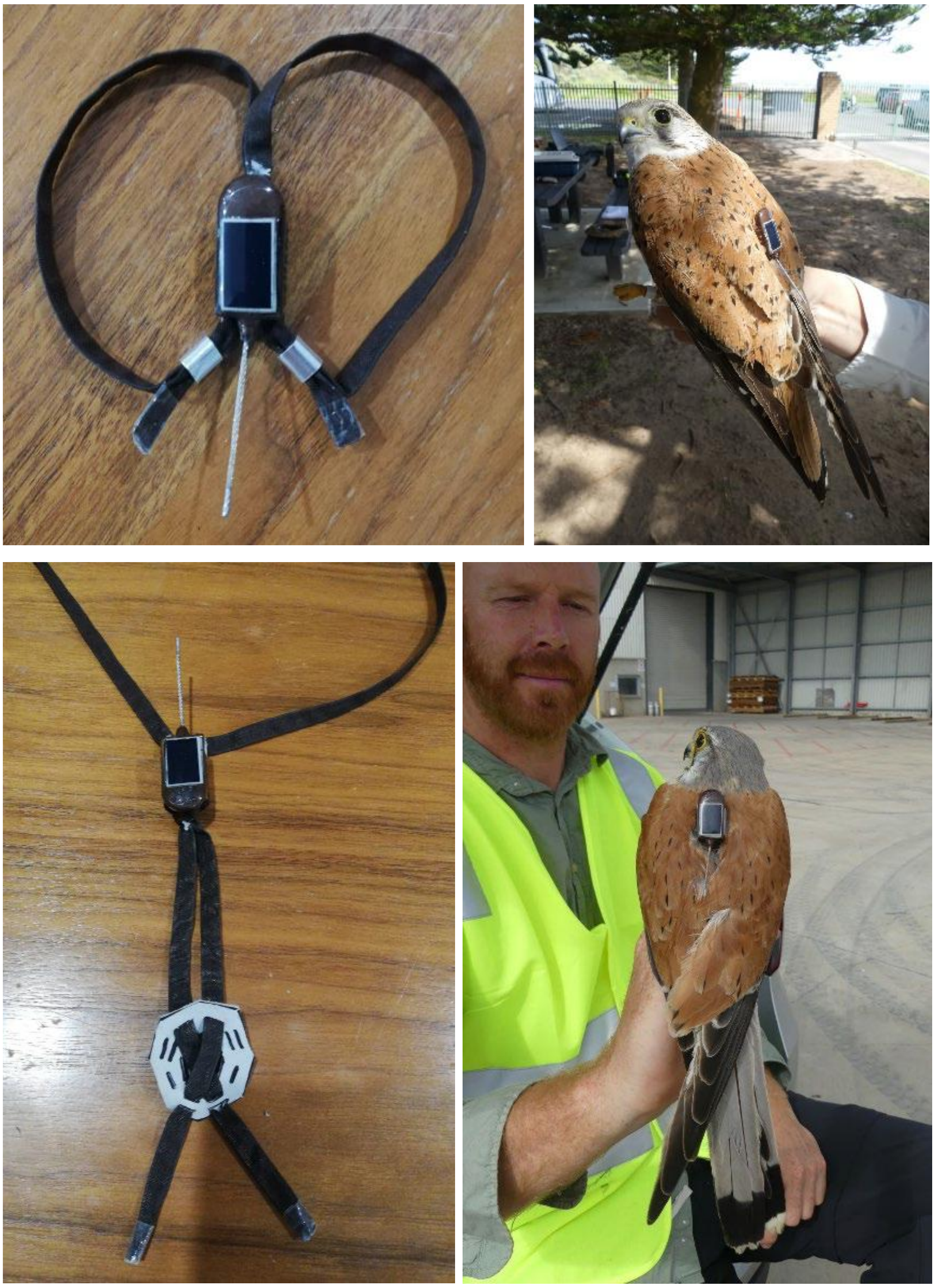
Supplementary Material

Supplementary Table S1: *Summary of the basic data collection for this study. A total of twelve Nankeen Kestrels were tagged with GPS loggers, comprising four females and eight males. The number of recorded GPS fixes per individual ranged from 5 to 6 032.*

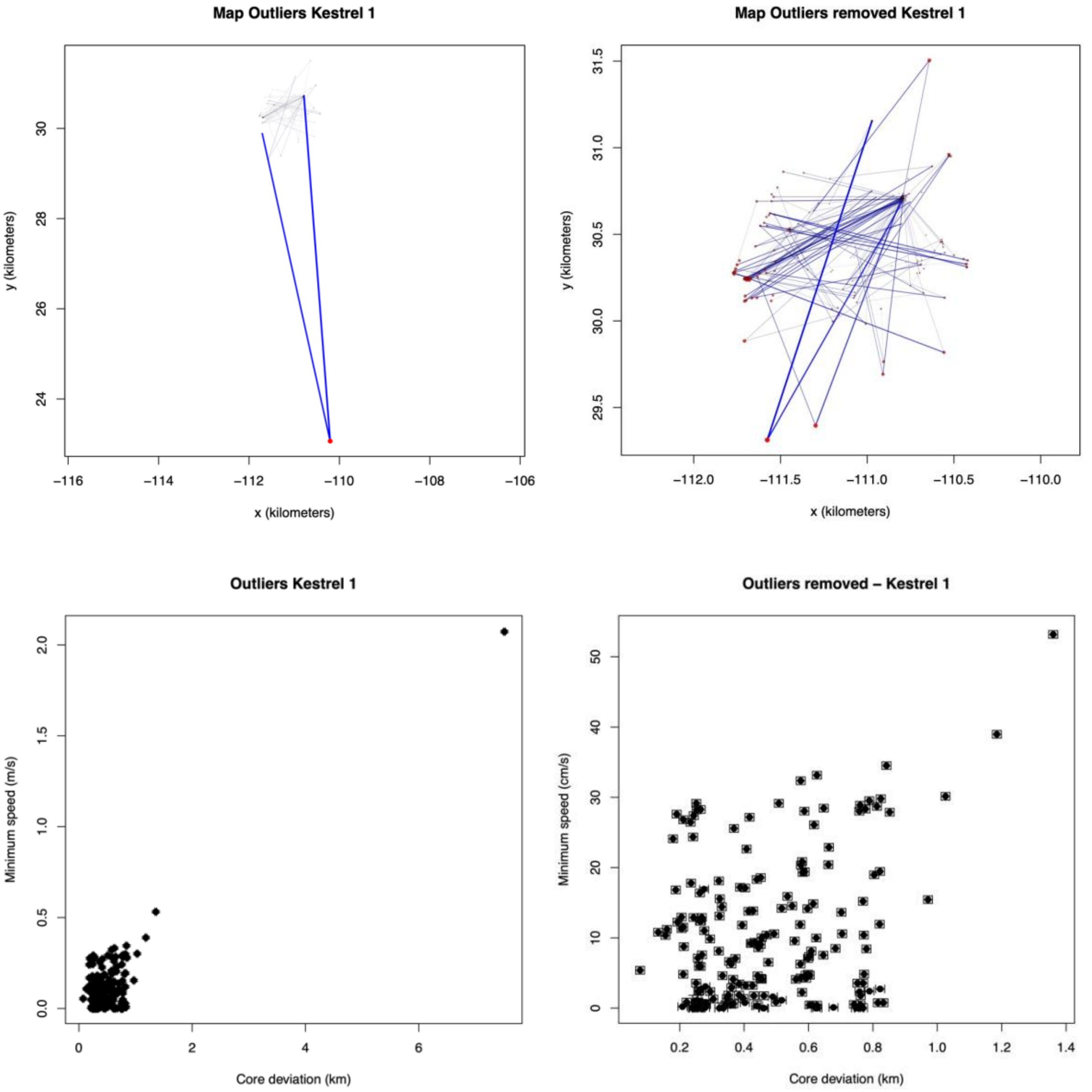
Animal ID	Sex	Habitat	Tagging date	Last GPS fix date	Number of Days tracked	Number of GPS fixes	Breeding status
1	Male	Rural	2022-10-25	2022-11-10	16	218	No data
2	Female	Rural	2022-10-23	2022-11-13	21	5 / left territory	No data
3	Male	Rural	2022-10-27	2022-11-10	14	313 / deceased	No data
4	Male	Rural	2022-11-09	2023-06-24	227	1589	No data
5	Male	Rural	2022-11-09	2023-07-10	243	4728	No data
6	Female	Rural	2022-11-02	2023-12-16	409	2710	No data
7	Male	Suburban	2022-11-04	2023-12-16	407	4968	Clutch initiation mid to late September*
8	Female	Rural	2022-10-26	no data	0	Left territory	No data
9	Male	Rural	2022-10-26	2022-11-10	15	216	No data
10	Male	Suburban	2022-11-01	2023-02-21	415	1863 / tag removed	Clutch initiation mid to late October
11	Male	Suburban	2022-10-20	2023-12-19	425	6032	Clutch initiation late September**
12	Female	Suburban	2022-11-07	2023-12-19	407	1740	Clutch initiation late September**

** Estimated from hatching date; ** back-dated based on nestling appearance (developmental age of chicks)*

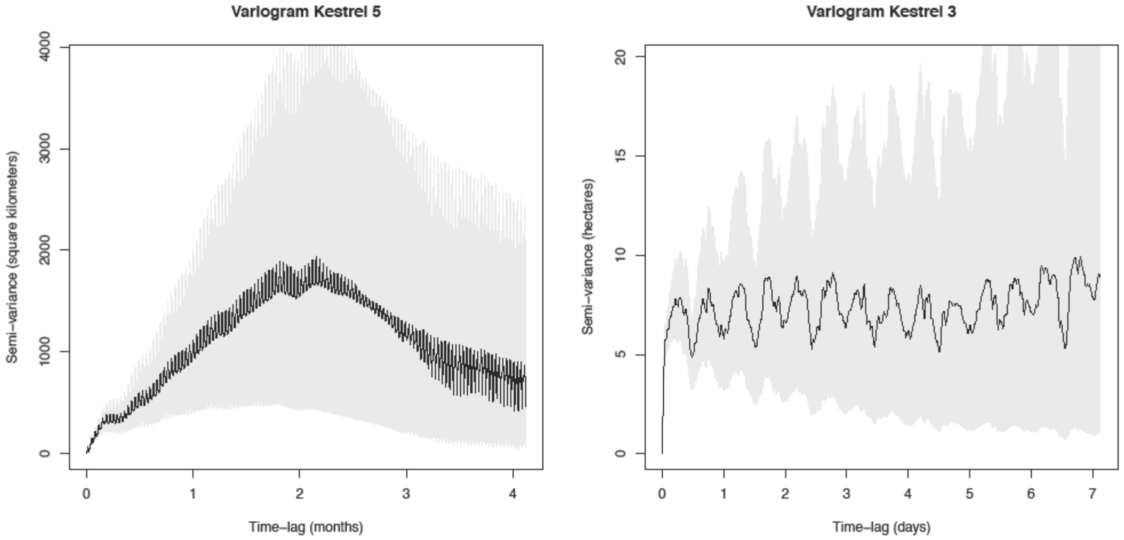
Nankeen Kestrel Animal ID 3 was struck by a car 2-weeks after the logger was mounted, and its paired female (Animal ID 2) subsequently abandoned the nest and territory. As a result, no data were collected from these individuals beyond November 13th, 2022. Similarly, Nankeen Kestrel Animal ID 8, despite being observed copulating on territory over multiple days, left the territory between the GPS tag mount and the first download cycle with the base station, resulting in a lack of usable data. Finally, Animal ID 10 was recaptured to address a malfunction in its backpack harness (one of the chest straps broke, most likely because the four straps were not stitched together properly at both points of attachment at the keel; see Bierregaard 2014), which could have posed a potential risk to the bird. To minimise stress during the sensitive nestling phase, the decision was made not to remount the logger after its removal. The male continued to provision the chicks, which eventually fledged successfully.



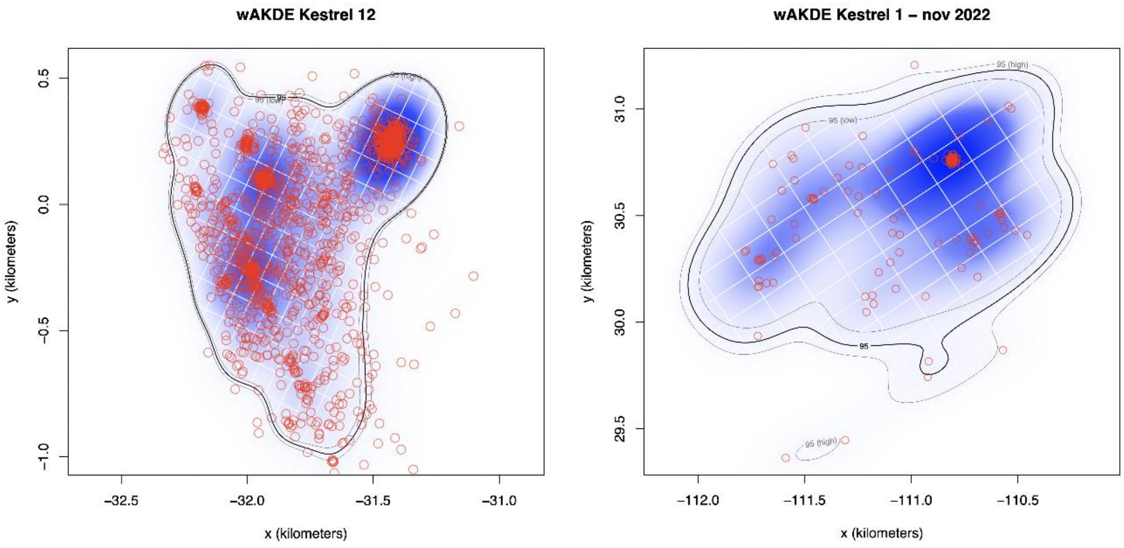
Supplementary Figure S1: *(Top): Milsar Nano Tag 3.4 g on a female (205 g; average weight: 181.5 ± 1.1 g (n=135 based on Olsen & Olsen 1987)) with leg loop harness. (Bottom): Milsar Nano Tag 3.4 g on a male (155 g; average weight: 161.1 ± 0.6 g (n=180 based on Olsen & Olsen 1987)). We worked with 6.5 mm Teflon Tube (from Bally Ribbon); fitting 6.5 mm aluminium clamps (from Ecotone) on the leg-loop; and 3 mm neoprene patch/wetsuit material to lift the GPS unit on the backpack. The kestrels were hooded during handling (fitting a tailored falconry hood following Hardy JW. 1983. The Use of Falconry Hoods in Handling Australian Kestrels). The hood was removed briefly to take photos of the head and general appearance of the bird with the fitted GPS tag before release.*



Supplementary Figure S2: *Identification of potential outliers using the outlie function of the ctmm package (Calabrese et al., 2016), applied to GPS location data for Nankeen Kestrels in Adelaide, South Australia. (Top left): Graphical representation of all GPS locations of Animal ID 1 ("Aldenhoven Road" male), highlighting an identified outlier that has been removed from subsequent analyses. The highlighted point demonstrates how the outlie function detects deviations from expected movement patterns, aiding in the refinement of data for accurate home range estimation. (Bottom left): Outliers can additionally be detected using speed (m/s) and distances travelled (km). (Top and bottom right): Control visualisation showing GPS locations without any detected outliers, providing a baseline for comparison and validation of the outlie function's results.*



Supplementary Figure S3: *Application of the variogram function from the ctmm package (Calabrese et al., 2016), which is here used to determine range residency behaviour in Nankeen Kestrels in Adelaide, South Australia. (Left): Animal ID 5 ("Finniss" male) does not display residency behaviour even after several months of tracking and was excluded from the home range analysis. (Right): Variogram illustrating range residency behaviour after a few days, confirming consistent space use patterns in Animal ID 3 ("Goolwa Barrage" male).*



Supplementary Figure S4*: Weighted autocorrelated Kernel Density Estimates (wAKDEs) generated using the ctmm package (Calabrese et al., 2016) for Nankeen Kestrels in Adelaide, South Australia. (Left): WAKDE of Nankeen kestrel Animal ID 12 (“West Torrens Depot” female), characterised by a high number of fixed GPS locations. The abundance of data results in narrow 95% confidence intervals, illustrating precise home range estimation. (Right): WAKDE of Nankeen Kestrel Animal ID 1 (“Aldenhoven Road” male) in November 2022. Due to fewer GPS locations collected within this single month, the 95% confidence intervals are considerably wider, reflecting increased uncertainty in the home range estimate.*

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Supplementary Figure S5: *Nankeen Kestrel Animal ID 5 ("Finniss" male) did not show a stabile home range size – and was thus excluded from the applied weighted Autocorrelated Kernel Density Estimates (wAKDEs). The male displayed repeated foray flights North of its breeding territory. GPS fixed in pink; direction of flights indicated by blue arrows. Map extracted from www.movebank.org.*

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Supplementary Figure S6: *Raw data of Nankeen Kestrel Animal ID (top left): 11 (male, tracked from 20th Oct 2022) and (top right): 12 (female, tracked from 07th Nov 2022). This pair at "West Torrens Depot" is breeding on a building close to the Adelaide airport, and mainly use the extended green space North of their nest site for hunting, with only occasional visits into the more urbanised areas located Southeast. Two coastal individuals Animal ID (bottom left): 7 ("Granit Island" male, tracked from 04th Nov 2022) and (bottom right): 10 ("Hallett Cove" male, tracked from 01st Nov 2022 – tag removed on 21st Feb 2023) seem to explore suburbia more extensively. The last data download for this study took place on 19th Dec 2023. Map extracted from www.movebank.org.*

Supplementary Table S2: *GPS fixes per month per individual Nankeen Kestrel in Adelaide, South Australia used to derive Weighted Autocorrelated Kernel Density Estimation (wAKDE) in ctmm (Calabrese et al., 2016). Presented as estimates and lower (lCI) and upper (UCI) 95% confidence intervals. Red and crossed out values indicate months in which the respective Nankeen kestrel did not exhibit range residency.*

Month	**Animal ID 1**				**Animal ID 3**				**Animal ID 4**				**Animal ID 6**				**Animal ID 7**			
	GPS fixes	95% wAKDE in km^2			GPS fixes	95% wAKDE in km^2			GPS fixes	95% wAKDE in km^2			GPS fixes	95% wAKDE in km^2			GPS fixes	95% wAKDE in km^2		
		LCI	Estimate	LCI		LCI	Estimate	LCI		LCI	Estimate	LCI		LCI	Estimate	LCI		LCI	Estimate	
Oct 22	-	-	-	-	63	0.567	0.756	0.970	-	-	-	-	-	-	-	-	-	-	-	-
Nov 22	87	1.207	1.551	1.938	247	0.727	0.843	0.966	318	5.298	6.187	7.143	259	0.809	0.930	1.060	494	9.403	10.449	11.549
Dec 22	130	1.438	1.748	2.088	-	-	-	-	357	3.156	3.549	3.965	251	1.296	1.504	1.729	1614	17.978	19.777	21.661
Jan 23	-	-	-	-	-	-	-	-	357	4.097	4.709	5.362	197	0.891	1.057	1.237	878	22.641	26.075	29.748
Feb 23	-	-	-	-	-	-	-	-	222	1.056	1.229	1.414	103	0.452	0.559	0.677	674	8.037	9.869	11.886
Mar 23	-	-	-	-	-	-	-	-	172	1.105	1.315	1.542	80	0.443	0.560	0.690	586	4.845	5.854	6.957
Apr 23	-	-	-	-	-	-	-	-	109	0.619	0.755	0.904	102	0.886	1.088	1.311	256	8.157	10.470	13.067
May 23	-	-	-	-	-	-	-	-	28	1.439	2.183	3.081	50	1.514	2.046	2.657	56	2.785	4.094	5.651
Jun 23	-	-	-	-	-	-	-	-	12	2.378	4.764	7.965	37	1.140	1.628	2.201	25	1.729	2.699	3.881
Jul 23	-	-	-	-	-	-	-	-	-	-	-	-	38	1.081	1.535	2.068	46	2.199	3.015	3.957
Aug 23	-	-	-	-	-	-	-	-	-	-	-	-	43	0.611	0.848	1.123	66	5.624	7.287	9.162
Sep 23	-	-	-	-	-	-	-	-	-	-	-	-	376	0.579	0.675	0.777	83	3.576	4.496	5.520
Oct 23	-	-	-	-	-	-	-	-	-	-	-	-	44	0.280	0.405	0.552	62	4.566	5.969	7.557
Nov 23	-	-	-	-	-	-	-	-	-	-	-	-	638	0.744	0.813	0.886	52	3.218	4.777	6.639
Dec 23	-	-	-	-	-	-	-	-	-	-	-	-	485	1.043	1.188	1.342	27	0.747	1.143	1.623
	Animal ID 9				**Animal ID 10**				**Animal ID 11**				**Animal ID 12**							
Oct 22	74	0.978	1.265	1.588	-	-	-	-	155	0.875	1.031	1.200	-	-	-	-				
Nov 22	141	8.991	10.792	12.755	348	4.049	4.531	5.040	805	1.116	1.204	1.295	258	0.858	0.979	1.108				
Dec 22	-	-	-	-	594	4.190	4.665	5.165	1486	1.346	1.439	1.536	572	1.077	1.189	1.308				
Jan 23	-	-	-	-	676	1.962	2.169	2.386	557	0.896	1.006	1.123	86	0.512	0.648	0.799				
Feb 23	-	-	-	-	242	2.048	2.613	3.246	484	1.282	1.465	1.660	70	0.859	1.1567	1.498				
Mar 23	-	-	-	-	-	-	-	-	583	1.442	1.606	1.779	127	0.728	0.874	1.033				
Apr 23	-	-	-	-	-	-	-	-	290	1.319	1.514	1.721	90	1.289	1.605	1.955				
May 23	-	-	-	-	-	-	-	-	79	0.840	1.072	1.332	31	0.588	0.872	1.210				
Jun 23	-	-	-	-	-	-	-	-	54	0.755	1.008	1.298	14	0.245	0.460	0.742				
Jul 23	-	-	-	-	-	-	-	-	62	0.583	0.762	0.965	17	0.290	0.509	0.784				
Aug 23	-	-	-	-	-	-	-	-	90	0.838	1.044	1.272	37	0.665	0.950	1.284				
Sep 23	-	-	-	-	-	-	-	-	268	1.215	1.375	1.545	127	0.485	0.584	0.692				
Oct 23	-	-	-	-	-	-	-	-	409	1.214	1.341	1.475	3	-	-	-				
Nov 23	-	-	-	-	-	-	-	-	429	1.535	1.693	1.857	171	0.794	0.932	1.081				

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