



Species distribution models derived from citizen science data predict the fine scale movements of owls in an urbanizing landscape

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ARTICLE INFO

Keywords:

GPS telemetry
Powerful owls
Apex predator
Model validation
Urbanization
Urban ecology
Ninox strenua

ABSTRACT

Apex predators are critical to ecological function, however their life history traits are often not conducive to survival in urban environments. While this can result in the loss of some apex predators, others are able to inhabit and utilize urban environments. Understanding predator resource requirements and the factors driving their distribution is often difficult due to their cryptic nature, however, this understanding is essential, given the current rate of urban expansion. In this research we use a threatened apex predator, the powerful owl (*Ninox strenua*) as a case study. Specifically, we aim to (1) develop a Species Distribution Model (SDM) to ascertain environmental variables driving habitat suitability across an urban gradient (2) determine fine scale spatial movements of powerful owls using GPS telemetry; (3) validate the SDM against collected GPS movement data; and (4) evaluate habitat predicted by the SDM against current reserve systems to establish whether they are adequate for the future protection of this species. We used MaxEnt and citizen science data to produce SDMs that predicted habitat suitability for powerful owls and identified the environmental variables driving habitat across the landscape. Fine-scale spatial movements for urban powerful owls, gained via GPS telemetry, were used to establish home-range sizes, validate models and assess the fit of telemetry data against SDM predictions. Rivers, vegetation (particularly dense tree cover) and distance to riparian areas were the ecological variables driving predicted habitat for powerful owls across the urban gradient. There was a strong relationship between habitat predicted by the SDM and the fine scale movements of powerful owls in urbanized environments. Home-ranges within this urban study were notably smaller than previous estimates established for forested environments. The powerful owls in our study were also shown to utilize considerable amounts of habitat outside of the reserve system. This has severe conservation implications because it is often the space outside of reserves that are at most risk from urban intensification. Conservation of the powerful owl in urban environments, therefore, needs to focus on both habitat management within existing reserves, and on establishing clear vegetation management strategies in the surrounding urban matrix.

1. Introduction

The global loss of apex predators, due largely to anthropogenic threats, is having pervasive impacts on natural ecosystems throughout the world (Cardillo et al., 2004; Estes et al., 2011; Ripple et al., 2014). Apex predators are critical in maintaining ecosystem structure and function (Wallach et al., 2015) as these typically large bodied consumers structure faunal communities by applying top-down pressure on the dominant prey and smaller predator species (Ripple et al., 2014; Sergio et al., 2014; Wallach et al., 2015). This pressure results in trophic cascades where the densities of mid-level consumers or mesopredators are suppressed, resulting in a higher abundance of basal producers and increased biodiversity (Pace et al., 1999; Estes et al., 2011). The role of

apex predators within ecosystems is often not realised until they have disappeared, at which point the capacity to restore the balance is significantly compromised (Estes et al., 2011). Apex predator populations generally exist at low densities but their density can be further reduced in disturbed urban landscapes (Sorace and Gustin, 2009).

Despite their lower abundance, some predator species are able to exist in urban environments, and others are increasingly colonizing urban landscapes (Chace and Walsh, 2006; Wang et al., 2015). Maintaining predators in urban landscapes has potentially important implications for urban species conservation as a whole. Using predators as umbrella species to provide a focus for urban conservation strategies is a useful conceptual approach (Wilcox, 1984; Lambeck, 1997; Roberge and Angelstam, 2004; Sattler et al., 2014; Sergio et al., 2014). Many

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predators have large spatial requirements and require access to habitat that supports a reasonable prey base, therefore by maintaining and enhancing populations of predators in urban environments numerous, less resource demanding species, gain conferred protection (Ripple et al., 2014). The challenge, however, with this approach is that our knowledge of predators in urban environments is extremely limited when compared to more conspicuous, higher density groups of animals. Their naturally low population densities, large home-range sizes, often nocturnal or cryptic behaviours and the difficulty in detecting or capturing predators has the potential to compromise any conservation strategies built around predators (McKinney, 2002; Cardillo et al., 2004; Santos et al., 2006). New approaches to modelling habitat suitability using presence-only datasets, increasing development of citizen science databases and significant advances in tracking technologies have the potential to revolutionise our understanding of predators in urban landscapes.

Species Distribution Models (SDMs), using presence-only datasets, are an approach that has gained popularity throughout the past decade (Guisan et al., 2013; Radosavljevic and Anderson, 2014; Ochoa-Ochoa et al., 2016). SDMs have greatly improved many aspects of conservation, including: translocation, understanding biological invasions, reserve selection and the identification and protection of critical habitat to maintain habitat connectivity (Guisan et al., 2013). Collecting presence and absence data on cryptic species such as apex predators can be labor and cost intensive due to their inherently low detection probabilities (Wintle et al., 2005). The use of presence-only data sets collected by citizen scientists, however, provides a viable alternative to presence/absence field surveys for apex predators (e.g. Santos et al., 2006; Isaac et al., 2014a; Angelieri et al., 2016). These datasets are also readily available through museums and government agencies and are an important source of public and private investment in biodiversity monitoring (Weston et al., 2006; Elith et al., 2011). This data however, may be unreliable in representing a whole population, or providing a complete coverage of their habitat use (Santos et al., 2006; Monterroso et al., 2009). Urban environments could benefit from citizen science datasets as this is where the vast majority of the human population resides, and also where many species records are reported by the public (Barrett et al., 2003). Species of public interest are also more likely to be reported by members of the public compared to common widespread species, adding value to such datasets for predators (Bonney et al., 2009; Geldmann et al., 2016).

An issue with SDM approaches is that while they may use internal validation (i.e. AUC within MaxEnt) or external statistical validation (i.e. AICc in ENMtools), they are rarely validated against independently collected spatial-use data. This is a significant issue, especially given that models are extrapolated to non-sampled areas, and wide-ranging species such as predators which often have large spatial requirements (Pinto et al., 2016). Adding to this problem is the lack of spatial-use research on predators in urban environments. This is generally associated with the difficulty of capturing predators in urban areas, and the inherent difficulty of tracking wide ranging species across urban landscapes where access to large areas of privately owned land is challenging. Significant improvements in automated tracking approaches such as the use of GPS telemetry may, in part, help to fill this substantial knowledge gap.

The powerful owl (*Ninox strenua*), Australia's largest owl, is non-migratory, maintains year-round territories (McNabb, 1996) and is of conservation interest both nationally and internationally (Appendix II CITES and IUCN (2012 IUCN Red List of Threatened Species)). The powerful owl has traditionally been perceived as a forest dependent raptor, preferring densely vegetated gullies of tall open forest (McNabb, 1996; Cooke et al., 2002a). This species does, however, persist in metropolitan reserves close to major cities such as Melbourne (Cooke et al., 2006), Sydney (Kavanagh, 2004) and Brisbane (Pavey, 1995) suggesting that they can exist in a more diverse range of environments than previously thought (Cooke, 2000). In urban environments,

powerful owls exploit the abundant arboreal marsupial prey base (Cooke et al., 2006), and reside in areas that provide habitat for roosting and in some cases nesting (Cooke et al., 2002b). Few studies, however, have been able to examine powerful owl spatial ecology directly due to their elusive (nocturnal) behaviour, low population densities, high mobility and low detectability (Wintle et al., 2005). They are extremely difficult to capture, which has resulted in a paucity of spatial-use data in this species. The few studies that have been successful in capturing and tracking powerful owls are representative of forest/woodland environments, with no data available for urban owls (Kavanagh, 1997; Soderquist and Gibbons, 2007; Bilney, 2013).

Using powerful owls as a case study this research aims to investigate the accuracy of SDMs derived from substantial citizen science datasets in predicting the fine-scale spatial-use of powerful owls across an urban landscape. This paper provides a rare case study in the spatial ecology of an urban predator, and also demonstrates how GPS tracking data can be used to externally validate SDMs as well as investigate the adequacy of reserve systems for protecting predators.

2. Methods

2.1. Study area

Melbourne is the second largest Australian city (4.5 million people) and has the fastest growing population (2.1% annual growth) (Australian Bureau of Statistics, 2016). It therefore offers an ideal landscape to examine the impact of urbanization on a predator species of conservation priority. Our modelling study site covered 372,136 ha of Melbourne, Australia (Fig. 1). It covered the urban gradient, extending from the urban core (consisting of high levels of disturbance, impervious surfaces, and human population density), through the urban fringe (containing moderate to low disturbance, higher tree cover and a lower population density) to forested environments (lowest disturbance, lowest population densities and highest tree cover).

2.2. Development of SDMs based on atlas records

2.2.1. Powerful owl presence records

We collated powerful owl records from the BirdLife International Atlas, Department of Environment, Land, Water and Planning's Victorian Biodiversity Atlas, and from the Atlas of Living Australia. Additional records were sourced from BirdLife Australia's citizen science "Melbourne Powerful Owl Project". New records were combined with presences from Isaac et al. (2013) in ArcGIS version 10.2.2 (ESRI, 2014). Presence records collected prior to 1997 were removed to limit historical environmental change and any duplicate presences (i.e. multiple records for the same location) were also removed to establish a presence layer with a single presence point per 20 × 20 m grid cell. The resulting presence layer was used in SDM development.

2.2.2. Ecological geographical variables and validation

Environmental layers originally collated by Isaac et al. (2013) were selected based on a priori understanding of powerful owl ecology. Ecogeographical variables used for modelling included lineal density of ephemeral and permanent rivers, Euclidean distance to riparian areas, riparian vegetation, slope position classification, Normalised Difference Vegetation Index (NDVI), land cover and density of tree cover (Table 1).

2.2.3. Species distribution model building

The maximum entropy modelling approach predicts habitat suitability based on the relationship between presence data and eco-geographical variables. We chose MaxEnt (Version 3.3.3k, Phillips et al., 2004), to establish habitat suitability for the powerful owl because it has consistently outperformed other models in terms of predictive performance, particularly for species foraging and presence only datasets (Elith et al., 2011; Yackulic et al., 2013; Fonderflick et al., 2015;

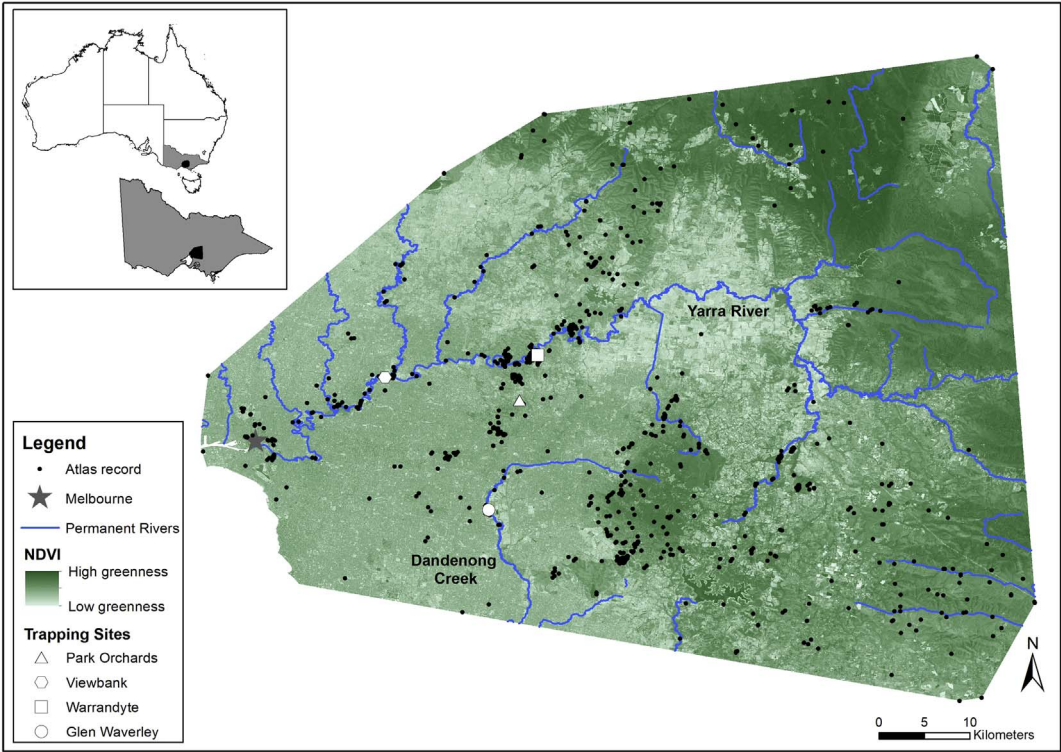


Fig. 1. The area over which this research was conducted in Melbourne, Australia. The background indicates variation in NDVI and thus greenness of the vegetation. The map also includes the atlas record locations the SDM was derived from as well as the 4 locations we were successful in capturing powerful owls.

Guillera-Arroita et al., 2015).

We established SDMs by randomly partitioning the powerful owl presence data with 75% used to train the model and 25% used for testing. The parameters that we varied were the regularization beta-multipliers at 0.5, 1, 2, 3, 4 and 5, and the features, using combinations of linear, quadratic, product, threshold and hinge. We did not include a bias file, as it was demonstrated to have very little influence on the overall fit of the data for the powerful owl in previous modelling (Isaac et al., 2013). Each model was run in raw format with 20 replicates at 5000 iterations. Models were evaluated within MaxEnt, based on the area under the receiver operator curve (AUC) (Jiménez-Valverde, 2012), then externally using Akaike information criterion corrected (AICc) values established in ENMtools (Warren, 2016). The model with the highest raw AUC and lowest AICc value was selected as the most parsimonious SDM and was rerun in logistic format. Although thresholds have their limitations (e.g. Merow et al., 2013) we applied the 10% threshold to create a binary map of potential and no potential habitat to conduct further analysis. In the instance where a threshold is required, the 10th percentile threshold is favoured due to its conservative nature

and the production of more ecologically meaningful results (Razgour et al., 2011; Isaac et al., 2014b).

2.3. Locating, catching and GPS telemetry of powerful owls

Site occupancy of powerful owls across Melbourne was established through targeted playback surveys within urban and urban fringe reserves. Playback sites were selected based on known powerful owl territories from previous research by Cooke (2000) and Isaac et al. (2013) as well as from atlas records. Establishing site occupancy for powerful owls allowed us to focus our trapping efforts in locations with confirmed powerful owl occupancy. To capture owls we used the suspended net catching technique described by Kavanagh (1997). When captured in the suspended nets, the owls were immediately lowered to the ground, extracted and processed. Processing entailed weighing the owl, GPS and RF telemetry attachment and feather removal for DNA analysis.

A 35 g telemetry package that included a modified i-GotU GT-120 GPS logger (Mobile Action Technology Inc., Taiwan) and a radio

Table 1
Eco-geographical variables used for the development of the powerful owl SDM.

Eco-geographical variable	Categories	Data source
Tree cover density	Dense, moderate, scattered, none	Tree Cover Density (percent cover) - VICMAP (TREEDEN25)
Land cover	Grass/agriculture, impervious surfaces, tree cover, rivers and water bodies	SPOT 10 Imagery - SPOT10 (Syst.m Pour l'Observation de la Terre)
Riparian vegetation	Present, absent	Ecological Vegetation Classes - (EVC)NV2005_EVCBCS Department of Environment, Land, Water and Planning.
Slope position classification	Ridge, upper, middle, flat, lower slope, valley	Digital Terrain Model (DTM) 20 m - VICMAP
Lineal density of ephemeral rivers	Continuous	Rivers - VICMAP (HYDRO25)
Lineal density of permanent rivers	Continuous	Rivers - VICMAP (HYDRO25)
Normalised Difference Vegetation Index (NDVI)	Continuous	SPOT 10 Imagery - SPOT10 (Syst.m Pour l'Observation de la Terre)
Euclidean distance to riparian areas	Continuous	Ecological Vegetation Classes - (EVC)NV2005_EVCBCS Department of Environment, Land, Water and Planning.

frequency (RF) transmitter (SirTrack, New Zealand, packaged by FaunaTech, Victoria) (Allan et al., 2013) were mounted to the two central tail feathers of captured owls. The GPS logger and RF transmitters ran on separate batteries, with the GPS likely to last for 40 nights, and the RF approximately 4 months. The i-GotU GPS logger was programmed to record a spatial location every 20 min from dusk to dawn. This timing allowed us to capture the daytime roost location of the owls (dawn and dusk) and their nightly foraging movements. Owls were recaptured and the telemetry device removed using the same capture method.

To assign an accurate sex to each tracked bird, two chest feathers were collected from each powerful owl for DNA sexing. DNA was isolated using the QIAGEN DNeasy blood and tissue kit (QIAGEN Inc., Valencia, California). Sex was inferred by amplifying the CHD-1 gene using the primer pair P2/P8 (Griffiths et al., 1998). PCR products were separated on an AB3730 capillary sequencer and analysed using GENEMAPPER v 3.7 software (Applied Biosystems) by Australian Genome Research Facility (AGRF). Sex was determined by scoring the alleles based on size (base pairs) where a male is homozygous 365/365 (ZZ) and the female is heterozygous 365/377 (ZW).

2.3.1. Analysis of powerful owl GPS locations

GPS locations were downloaded from the GPS logger via @trip PC (Mobile Action Technology Inc., Taiwan). We validated position accuracy and converted from Greenwich Mean Time to local time. Positions were imported into ArcGIS and multiple roost locations (i.e. on the same day) were deleted, to minimise the potential impact that roost locations would have on home-range estimates. Home-range size and core-use area estimates were developed in Geospatial Modelling Environment (GME) (Beyer, 2012). Minimum convex polygons (MCP) provided a comparison with other studies, while kernel density estimators (KDE) of 50%, 75% and 95% fixed-kernel isopleths predicted the home-range size and core-use area (Weaving et al., 2014). We used the Plug-in smoothing parameter/bandwidth to provide more accurate home-range estimates for large datasets from satellite or GPS telemetry (Gitzen et al., 2006).

2.3.2. Using a GPS dataset to verify the powerful owl SDM model

The accuracy of the SDM in predicting the fine scale movements of powerful owls was determined by comparing the percentage of GPS telemetry points that were within areas categorised as predicted habitat versus those categorised as non-habitat by our model. Home-range outlines were also plotted against the SDM to allow us to establish the percentage of the home-range that comprised of predicted habitat. An open space layer containing public and private reserves (Department of Environment, Land, Water & Planning, 2013) was also used to determine the number of powerful owl GPS points and the area of home-range estimates covered by the reserve system.

3. Results

3.1. Species distribution models

We collated 749 presence records from the atlas databases and 683

presences from Isaac et al. (2013). After accounting for bias and duplicate records, 851 independent presence locations were used to develop the SDM for powerful owls. A total of 61 powerful owl models were developed with raw AUC test values ranging from 0.75 to 0.80. The best or most parsimonious raw model used the threshold feature, a beta-multiplier of one and had a very good fit with an $AUC_{test} = 0.80$; $AUC_{train} = 0.82$ and the lowest AICc value. When run in logistic format the AUC_{test} and AUC_{train} were 0.79 and 0.81, respectively.

When combined, the four eco-geographical variables of land cover, lineal density of ephemeral rivers, the Normalised Difference Vegetation Index (NDVI) and tree cover explained 77.1% of the model's performance. Land cover was the most important contributing variable when used in isolation at 25.4%, while lineal density of ephemeral rivers at 22.8% contributed the most unique information to the model. The contribution of land cover to the model suggests powerful owls are less likely to occur in areas with agriculture, grass and impervious surfaces, but more likely to occur in areas with rivers and tree cover (Supplementary Fig. 1a). Although rivers were highlighted as important for the occurrence of the powerful owl by the land cover layer, their density and nature (ephemeral or permanent) influence the potential occurrence of the powerful owl. Potential powerful owl occurrence was greater in the presence of lower densities of ephemeral rivers but declined as the lineal density of ephemeral rivers increased (Supplementary Fig. 1b). Lineal density of permanent rivers, overall contributed less to the model at 10.9%, but intermediate densities of permanent rivers resulted in the highest probability of occurrence for this species (Supplementary Fig. 1c).

Vegetated environments were also important for the occurrence of the powerful owl, as indicated by the land cover, NDVI, tree density and Euclidean distance to riparian vegetation layers. Tree cover density contributed 13.2% to the model and suggested that habitats with dense tree cover promote a greater potential occurrence of this species (Supplementary Fig. 1d), which is also confirmed by the NDVI (greenness index) (Supplementary Fig. 1e) that contributed 15.7% to the model. Although the presence or absence of riparian vegetation did not greatly influence the occurrence of this species, the distance from riparian vegetation was important with a 10.9% contribution to the model. Potential occurrence declined as the distance from riparian vegetation increased, with a marked decline in potential occurrence of this species at 4.5 km away from riparian vegetation (Supplementary Fig. 1f).

3.1.1. Generating powerful owl spatial data from GPS tracking

We were successful at capturing powerful owls at four trapping sites in the urban landscape after confirming site occupancy of powerful owls. These sites were located in Glen Waverley, Park Orchards, Warrandyte and Viewbank (Fig. 1). In total, 29 nights of catching effort were undertaken to capture urban powerful owls. We trapped five powerful owls during this study comprising of two females (F1 and F2), one male (M3), and one pair (F4 and M4) (Table 2). All birds were sexed based on weight and behaviour, and then validated by subsequent DNA analysis of feathers. Five complete powerful owl nightly foraging datasets totalling 5149 individual GPS points were obtained. The five birds had functional GPS loggers recording data for a total of

Table 2

Powerful owls trapped in this study including breeding pair, location, weight (g), number of nights tracked, total GPS fixes and breeding information.

Breeding pair/ID	Location	Owl weight (g)	Duration tracked (nights)	Total fixes*	Successfully nested for 2016	Successfully fledged chicks
F1	Glen Waverley	1420	48	1720	Y	1
F2	Warrandyte	1317	36	1422	Y	2
M3	Viewbank	1716	29	1034	Y	1
F4	Park Orchards	1430	14	483	Y	2
M4		1616	14	490		

*Total fixes before validation and removal of duplicate diurnal positions.

Table 3

Minimum convex polygon and Kernel density estimates for powerful owl home-range (ha) collected during this study and compared to other studies.

Source	ID	MCP	95% KDE	75% KDE	50% KDE
This study ¹	F1	446	137	48	19
	F2	388	157	57	20
	M3	1805	1162	446	170
	F4	546	401	162	71
	M4	863	605	237	93
This study averages	F	460	232	89	37
	M	1334	884	342	170
Bilney (2013) ²	F	1589	871	228	88
	F	4774	2721	–	–
Soderquist and Gibbons (2007) ³	F	1382	1019	–	–
	M	1770	1431	–	–
	M	2896	2159	–	–
	F	808	715	–	–
Kavanagh (1997) ⁴	F	311	352	–	–
	F	1773	1136	228	88
Other study averages	F	1773	1136	228	88
	M	2333	1795	–	–

Locations: ¹ = Urban Melbourne; ² = Forests of East Gippsland, Victoria; ³ = Box-Ironbark woodland of central Victoria; ⁴ = Forests of south-eastern New South Wales.

141 nights (Table 2). We continued to follow the owls throughout the breeding season to establish whether they successfully bred. All five owls were from previously known breeding pairs and all successfully bred and raised nestlings to the point of fledging for the 2016 season, suggesting that the capture and tracking of these owls had no impact on their breeding success.

The home-range size estimates varied substantially between individual owls and by the sex of the owl, with male powerful owls maintaining larger ranges compared to females (Table 3). These differences in home-range size between sexes is also clearly illustrated with the pair that we captured, the male (M4) having a 33.7% larger 95% KDE home-range compared to the female (F4). The urban powerful owls in our study had comparatively small home-range estimates when compared to forest and woodland birds within the only other reported powerful owl tracking studies (Table 3). One owl in particular (F1) had a 95% home-range estimate that is the smallest home-range ever documented for powerful owls, and is under half of the smallest documented MCP range estimate by McNabb (1996) at 300 ha. The powerful owl we documented with the largest range (M3) however, is more similar to previously recorded estimates of owls in forested landscapes.

3.2. Validation of presence only SDM against GPS tracking datasets

We tested the validity of the SDM using the powerful owl GPS positions and home-range estimates. The SDM predicted very well, with 95.9% (± 5.95 SD) of total powerful owl GPS points (actual locations) situated within predicted habitat (Table 4). The model predicts diurnal roost locations very well at 99.3% (± 3.31 SD), with only one roost location recorded in an area deemed as being non-habitat for powerful owls. Foraging movements were also predicted well at 95.8% (± 6.16

Table 4

Percentage of powerful owl GPS positions in areas predicted as habitat by the SDM (figures in brackets represent the total number of positions) and the percentage of different owl home-range estimates within predicted habitat.

ID	% GPS points			% Home-range estimates			
	Roost	Forage	Total*	MCP	95% KDE	75% KDE	50% KDE
F1	100% (47)	98.0% (1628)	98.0% (1675)	81.0%	95.2%	97.6%	96.7%
F2	100% (36)	96.0% (1352)	96.0% (1388)	85.9%	88.4%	96.0%	96.4%
M3	100% (28)	98.0% (978)	98.0% (1006)	77.7%	87.7%	94.1%	97.0%
F4	92.6% (14)	92.3% (456)	92.3% (470)	64.8%	72.2%	83.0%	88.0%
M4	100% (14)	87.0% (463)	87.4% (477)	65.2%	64.8%	70.0%	78.8%
Total mean	99.3% (139)	95.8% (4877)	95.9% (5016)	74.9%	81.7%	90.1%	91.4%

SD) being higher than we expected given fewer nocturnal atlas records are reported in the atlas data. The foraging movements in predicted habitat for the powerful owl pair (F4 and M4) are slightly less than for the other three owls as their range is embedded in a more urbanized matrix.

All five powerful owl core home-range estimates (i.e. 50% kernel density isopleths) aligned well with the SDM, with an average of 91.4% of the core home-range areas predicted as habitat (Fig. 2). As the home-range estimates were expanded (i.e. 75% and 95% KDEs), more area classified as non-habitat was incorporated. This is the case in particular for the powerful owl pair (F4 and M4), where their range is within a residential landscape with fragmented patches of quality habitat (Fig. 2). The KDE's are extrapolated from powerful owl GPS data and incorporate tracts of non-habitat, however we know based on their GPS positions that they mostly avoid these areas. The KDEs of 95% suggest F4 and M4 only use 72.2% and 64.8% predicted habitat, while their GPS data is much higher at 92.3% and 87.4% within predicted habitat respectively (Table 4).

3.3. How well do reserves protect powerful owl home-ranges?

We also compared the SDM to an open space layer containing managed public and private reserves to the powerful owl GPS positions and home-range estimates (Figs. 2 and 3). For powerful owls (F1, F2 and M3) that contain extensive continuous tracts of suitable habitat within their home-range (Table 4), they also have the majority of their range protected by managed reserves (Table 5). We observed three different tiers of powerful owls utilizing reserves: 1. Owls that roost and forage almost exclusively within reserves, not in the surrounding residential landscape; 2. Owls that almost exclusively roost within reserves, but utilize some of the surrounding land-use to forage; and 3. Owls that spend approximately two-thirds of their time outside of reserves, but still in areas predicted as habitat by the SDM.

4. Discussion

We have successfully demonstrated the utility of a large citizen science data set of predator records in developing accurate models of habitat availability across an entire urban landscape. The models were externally validated against real fine-scale spatial use data, an aspect we encourage other researchers to consider, but is rarely conducted in the validation of species distribution models. Using the SDM and real spatial use data we have shown that much of the habitat for powerful owls across this urban landscape is not in the current reserve system with powerful owls readily utilizing habitat outside of reserves to survive. Continued occupancy of powerful owls in urban landscapes will require careful urban planning to maintain enough habitat outside of the current reserve system. The SDM developed during this research however, allows urban planners to identify the critical tracts of powerful owl habitat in urban environments and adjust planning approaches towards protecting this habitat.

In this research we focussed on the powerful owl as a case study

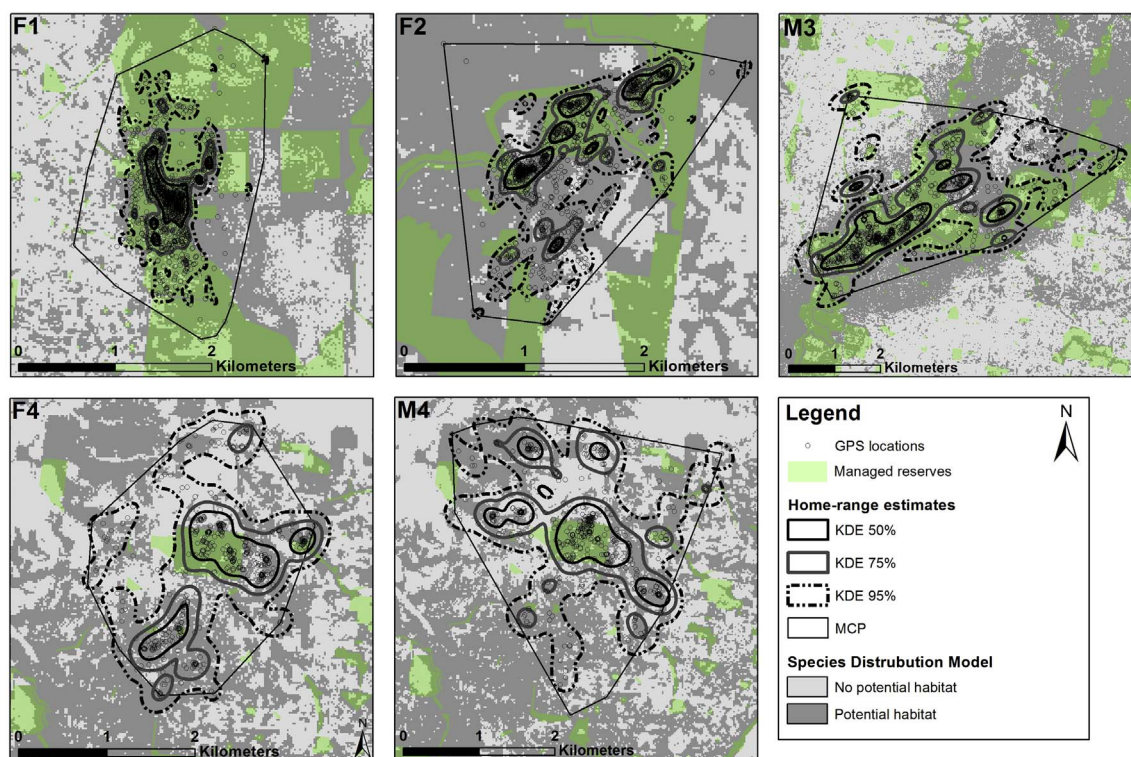


Fig. 2. Home range maps of the five tracked powerful owls. The background represents the habitat predictions from the SDM as well as the current reserve network (in green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

predator in an urbanizing landscape. This is a species of interest to citizen scientists, and as such many records exist for the species across Melbourne's urban landscape. Citizen science and atlas survey data is a crucial resource for biodiversity monitoring around the world (Weston et al., 2006) and encourages public participation in the process of science (Bonney et al., 2009), but there are limitations to using atlas data.

Atlas records can have strong spatial biases towards easily accessible areas such as towns, roads or walking tracks (Barrett et al., 2003; Bonney et al., 2009; Phillips et al., 2009; Elith et al., 2011). There is also bias towards more easily detected species, with rare and cryptic taxa detected less frequently (Bonney et al., 2009; Robertson et al., 2010; Geldmann et al., 2016). Some species, such as apex predators,

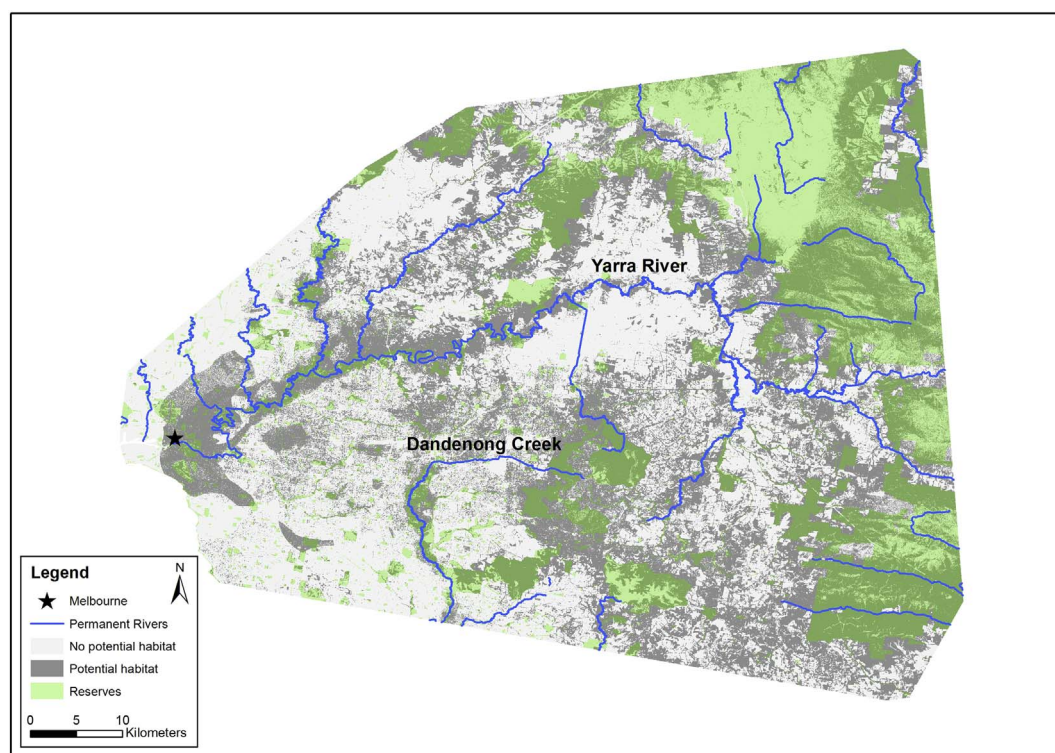


Fig. 3. Habitat availability for powerful owls as predicted by our SDM aligned with the current reserve network.

Table 5

Percentage of powerful owl GPS positions within a reserve system (figures in brackets represent the total number of positions) and the percentage of owl home-range within a reserve system.

ID	% GPS points			% Home-range estimates			
	Roost	Forage	Total*	MCP	95% KDE	75% KDE	50% KDE
F1	100% (47)	93.1% (1628)	94.8% (1675)	66.8%	86.9%	93.8%	94.7%
F2	97.2% (36)	53.9% (1352)	55.0% (1388)	28.9%	38.9%	61.4%	65.0%
M3	96.4% (28)	71.5% (978)	72.2% (1006)	47.3%	58.3%	74.2%	82.9%
F4	35.7% (14)	29.2% (456)	29.4% (470)	9.9%	11.7%	23.5%	38%
M4	35.7% (14)	29.8% (463)	30.0% (477)	8.0%	9.1%	19%	35.5%
Total mean	85.6% (139)	65.9% (4877)	66.6% (5016)	34.2%	39.0%	52.0%	62.2%

*Total fixes after validation and removal of duplicate diurnal positions.

undergo taxonomic reporting bias, and are more likely to be reported by citizen scientists as they are species of public interest (Bonney et al., 2009; Robertson et al., 2010; Geldmann et al., 2016). In the case of this research, we have benefitted from these biases by focussing on a predator species of high public interest in an urban landscape where the density of citizen scientists is high. This resulted in a very large database of independent presence records ($n = 851$) across Greater Melbourne which we were able to use in the development of a SDM.

Although prey is an important driver in the occurrence and home-range size of powerful owls (Soderquist and Gibbons, 2007), if an abundant prey base in urban environments was the only determinate of powerful owl distribution, we would expect the citizen science presence records to be evenly distributed across urban Melbourne. This is because the main prey species the common ringtail possum (*Pseudocheirus peregrinus*) and common brushtail possum (*Trichosurus vulpecula*) are distributed widely across the more urban components of the landscape (Isaac et al., 2014c). Presence records, however, were concentrated in hotspots throughout the landscape (Fig. 1) indicating that factors other than prey are driving the distribution of powerful owls in urbanized landscapes.

During the species distribution model development land cover, river type and distance to riparian habitat were the most influential variables in predicting habitat for powerful owls across the urban landscape. More specifically, powerful owl occurrence is driven by dense vegetation, containing intermediate densities of permanent rivers and lower densities of ephemeral rivers. The importance of riparian habitat was also highlighted, with occurrence declining with distance from riparian areas. Riparian areas are ecologically significant in the conservation of biodiversity because they provide refuges and important dispersal corridors for aquatic and terrestrial species (Palmer and Bennett, 2006; Palmer et al., 2008). Although the distribution of this species is associated with water sources, the dependence on these areas within urban environments may be an artefact of protection from past vegetation removal practices.

Prior to this study VHF tracking had been employed ad-hoc and on small scales to attempt to gauge home-ranges for powerful owls. Significant advances in GPS telemetry allowed us to collect regular and precise locations (majority of positions < 10 m Estimated Horizontal Position Error) for this species, which is a benefit in the urban landscape where private property is predominant, and access is extremely limited. Using GPS loggers significantly reduced the amount of disturbance to the owls as it eliminated the need to follow each individual with VHF radio-tracking every night. Lastly, these devices were very cost effective (approximately AUD\$ 500 each) allowing us to deploy multiple trackers, compared to one traditional satellite tracker costing several thousand dollars (Allan et al., 2013).

Through observation and atlas data alone we have evidence of powerful owls residing in and around the urban component of our study landscape, which suggests, at a minimum, some urban areas are providing resources suitable for powerful owls to persist. Surprisingly, during this research we were able to document the smallest ever home-

range estimates for powerful owls, with four of the five urban powerful owls having much smaller home-ranges when compared to research on powerful owls in forest environments. The question then arises as to why powerful owl home-range estimates are smaller than those in other studies? It is likely that prey is an important driver in establishing the size of the powerful owls home-range, as has been recorded in previous research for raptors (Chace and Walsh, 2006; Donazar et al., 2016).

Arboreal marsupials, the predominant prey of powerful owls, are also affected by urbanization. Along the forest to urban gradient, the diversity of arboreal marsupials declines, but urban regions maintain a highly elevated density of the two generalist prey items (common brushtail possums and common ringtail possums), providing a high density and consistent prey base for the powerful owl (Cooke et al., 2006; Isaac et al., 2014c). The powerful owl is able to capitalise on this prey resource, with these two prey items shown to dominate the diet of owls from more urbanized areas (Cooke et al., 2006), whereas forests owls maintain a broader range of prey items in their diet (Cooke et al., 2006; Bilney et al., 2011; Bilney, 2013). This plentiful prey resource means that urban owls do not need to travel as far as their forest counterparts to source enough food to support their day to day energy and seasonal breeding requirements. The reverse of this is indicated by prior work by Soderquist and Gibbons (2007) who reported much larger home-range estimates within regions where arboreal marsupial prey was scarce resulting in prey substitution with a greater percentage of birds represented within their diet.

A key aspect of this research was to use real spatial use data of powerful owls to assess the predictive performance of SDMs. While SDM approaches are beneficial in efficiently assessing potential habitat for species over large landscapes their utility in providing an accurate representation of biological systems has been questioned (Phillips et al., 2009; Guisan et al., 2013; Ochoa-Ochoa et al., 2016). These queries are prompted by various factors including, but not limited to: biased data leading to false positives and false negatives when assigning habitat suitability (Phillips et al., 2009; Elith et al., 2011), default model parameter use by proxy (Merow et al., 2013; Radosavljevic and Anderson, 2014) and insufficient validation of models (Lobo et al., 2008; Warren and Seifert, 2011; Radosavljevic and Anderson, 2014). The majority of these issues can be controlled for by varying model parameters and employing multi-level validation. Despite recent technological advancements (e.g. Fonderflick et al., 2015; Pinto et al., 2016) the use of independent datasets collected by rigorous field surveys or telemetry for validation is still a rare practice. We utilized a novel approach to model validation, likely the first for an apex predator, by using independently collected spatial movement data to establish the predictive capabilities of our SDM. We were interested in the accuracy and potential bias that atlas records may introduce in predicting the fine scale habitat use of a cryptic species.

Powerful owls, being nocturnal, extremely cryptic and often unresponsive during playback surveys (Wintle et al., 2005) are most often sighted within diurnal roosts. We predicted that the atlas records may lack nightly foraging data, and would skew habitat predictions towards

habitat suitable for roosting, which can be very different to foraging habitat, particularly in modified environments. Surprisingly, over 95% of our GPS locations occurred within areas predicted as habitat by our SDMs. Home-range estimates derived from GPS locations were also compared to the SDM habitat predictions. Home-range estimates are known to contain habitat and areas of non-habitat due to their extrapolation from telemetry data. We found all owls were refining their movements within their home-range to use the predicted habitat component of their home-range, demonstrating they can quickly cross areas considered as non-habitat to connect suitable patches and reserves.

The use of real spatial use data in this study has allowed us to demonstrate the extent of unprotected, privately owned land powerful owls utilize in urban environments. Not all reserves contain enough habitat to support a powerful owl, therefore, owls are required to travel outside of reserves and spend a large amount of time on private land to forage. Areas of habitat for the powerful owl not protected by a reserve are likely to be most at risk of development with expanding and intensifying urbanization. Our results align with previous research suggesting the adaptability of the powerful owl to minor changes in urban environments (Webster et al., 1999; Cooke et al., 2002b; Cooke and Wallis, 2004; Isaac et al., 2013). Ongoing urban expansion to accommodate human populations will continue to lead to an increase in impervious surfaces, fragmentation and modification of remnant vegetation degrading it to a point where it is no longer habitat (Beissinger and Osborne, 1982). How then do we retain enough powerful owl habitat in expanding urban environments? Conserving and expanding large reserves is usually the main strategy to protect biodiversity (Palmer et al., 2008) however this may not be possible in urban landscapes. We have however shown that native vegetation on private land holds significant conservation value. We suggest for the persistence of powerful owls in urban landscapes it will be critical to focus conservation efforts on identifying and minimizing actions responsible for degrading habitat for this species on private land (Williams et al., 2014; Angelieri et al., 2016). The SDM produced in this research could provide a useful tool for comprehensive urban planning in Melbourne to maintain key habitat for refuges and corridors, not only for the powerful owl but also for biodiversity conservation as a whole (Williams et al., 2014; Ochoa-Ochoa et al., 2016).

5. Conclusion

The conservation management of predators in urbanizing landscapes is critical yet challenging due to the paucity of data and research on predators in urbanized environments. We demonstrate the potential importance of high quality citizen science datasets in developing accurate SDMs of a predator in response to urbanization. Utilizing modern tracking approaches on a predator species in an urban environment, while challenging and rarely conducted, has yielded significant information on how they utilize urban landscapes and more importantly providing a rare external validation approach to assessing SDMs. Finally, the spatial data has revealed the importance of habitat outside the traditional conservation reserve system in maintaining large predators. The challenge in the future will be developing urban planning strategies that can maintain non-reserve predator habitat as urbanization intensifies.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.06.039>.

Acknowledgments

A special thank you to the Goldschlager family, for your interest and financial support in this research. We are extremely grateful for being awarded the Goldschlager Award for Environmental Science in *Manningham* because without this funding this research would not have been possible. Thanks also to our land management contacts for your

continued support and information. In particular we would like to thank Cathy Willis, Warren Murphy, Vanessa Bluett, Brendan Sullivan, Alan Webster and Lochie Egan. Fiona Hogan is thanked for undertaking the genetic analysis. This project involved the use of wild animals and the project was conducted in accordance with the regulations of the Deakin University Animal Ethics Committee under Ethics No. B20-2015 and in accordance with Department of Environment, Land, Water and Planning Wildlife and National Parks Act research Permit No. 10007728.

References

- Allan, B., Arnould, J.P.Y., Martin, J.K., Ritchie, E.G., 2013. A cost-effective and informative method of GPS tracking wildlife. *Wildl. Res.* 40, 345–348.
- Angelier, C.C.S., Adams-Hosking, C., Ferraz, K.M.P.MdB, de Souza, M.P., McAlpine, C.A., 2016. Using species distribution models to predict potential landscape restoration effects on puma conservation. *PLoS One* 11, e0145232.
- Australian Bureau of Statistics, 2016. 3218.0 - Regional population growth, Australia, 2014–15. <http://www.abs.gov.au/ausstats/abs@.nsf/mf/3218.0> > (ABS, Canberra).
- Barrett, G., Silcocks, A., Barry, S., Cunningham, R., Poulter, R., 2003. *The New Atlas of Australian Birds*. Royal Australasian Ornithologists Union, Hawthorn East, Victoria.
- Beissinger, S.R., Osborne, D.R., 1982. Effects of urbanization on avian community organization. *Condor* 84, 75–83.
- Beyer, H.L., 2012. Geospatial modelling environment (version 0.7.3.0). (software). URL: <http://www.spatial ecology.com/gme>.
- Bilney, R.J., 2013. Home-range, diet and breeding of a powerful owl *Ninox strenua* in East Gippsland, Victoria. *Australian Field Ornithology* 30, 40–46.
- Bilney, R.J., Cooke, R., White, J.G., 2011. Potential competition between two top-order predators following a dramatic contraction in the diversity of their prey base. *Anim. Biol.* 61, 29–47.
- Bonney, R., Cooper, C.B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K.V., Shirk, J., 2009. Citizen science: a developing tool for expanding science knowledge and scientific literacy. *Bioscience* 59, 977–984.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J., Mace, G.M., 2004. Human population density and extinction risk in the world's carnivores. *PLoS Biol.* 2, e197.
- Chace, J.F., Walsh, J.J., 2006. Urban effects on native avifauna: a review. *Landsc. Urban Plan.* 74, 46–69.
- Cooke, R., 2000. Ecology of Powerful Owls in Contrasting Habitats of the Yarra Valley Corridor, Victoria, Australia. PhD Thesis. Deakin University, Australia.
- Cooke, R., Wallis, R., 2004. Conservation management and diets of powerful owls (*Ninox strenua*) in outer urban Melbourne, Australia. In: Shaw, W., Harris, L., Vandruuff, L. (Eds.), *Proceedings of the 4th International Symposium on Urban Wildlife Conservation*. University of Arizona, Tucson, Arizona, pp. 110–113.
- Cooke, R., Wallis, R., Webster, A., 2002a. Urbanisation and the ecology of powerful owls (*Ninox strenua*) in outer Melbourne, Victoria. In: Newton, I., Kavanagh, R., Olsen, J., Taylor, I. (Eds.), *Ecology and Conservation of Owls*. CSIRO Publishing, Australia, pp. 100–106.
- Cooke, R., Wallis, R., White, J., 2002b. Use of vegetative structure by powerful owls in outer urban Melbourne, Victoria, Australia - implications for management. *J. Raptor Res.* 36, 296–299.
- Cooke, R., Wallis, R., Hogan, F., White, J., Webster, A., 2006. Diet of powerful owls (*Ninox strenua*) and prey availability in a continuum of habitats from disturbed urban fringe to protected forest environments in south-eastern Australia. *Wildl. Res.* 33, 199–206.
- Department of Environment, Land, Water & Planning, 2013. Vicmap data layer: Parks and Conservation Reserves (PARKRES). Department of Environment, Land, Water & Planning, Victoria, Australia. <http://services.land.vic.gov.au/catalogue/metadata?anzlicid=ANZVI0803004883&publicid=guest&extractionProviderId=1>.
- Donazar, J.A., Cortés-Avizanda, A., Fargallo, J.A., Margalida, A., Moleón, M., Morales-Reyes, Z., Moreno-Opo, R., Pérez-García, J.M., Sánchez-Zapata, J.A., Zuberogoitia, I., Serrano, D., 2016. Roles of raptors in a changing world: from flagships to providers of key ecosystem services. *Ardeola* 63, 181–234.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17, 43–57.
- Environmental Systems Research Institute (ESRI), 2014. ArcGIS Desktop, Release 10.2.2. Environmental Systems Research Institute, Redlands, California.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. *Science* 333, 301–306.
- Fonderflick, J., Azam, C., Brochier, C., Cosson, E., Quékenborn, D., 2015. Testing the relevance of using spatial modeling to predict foraging habitat suitability around bat maternity: a case study in Mediterranean landscape. *Biol. Conserv.* 192, 120–129.
- Geldmann, J., Heilmann-Clausen, J., Holm, T.E., Levinsky, I., Markussen, B., Olsen, K., Rahbek, C., Tøttrup, A.P., 2016. What determines spatial bias in citizen science? Exploring four recording schemes with different proficiency requirements. *Divers. Distrib.* 22, 1139–1149.
- Gitzen, R.A., Millsap, J.J., Kernohan, B.J., 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *J. Wildl. Manag.* 70, 1334–1344.
- Griffiths, R., Double, M.C., Orr, K., Dawson, R.J.G., 1998. A DNA test to sex most birds.

- Mol. Ecol. 7, 1071–1075.
- Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R., Wintle, B.A., 2015. Is my species distribution model fit for purpose? Matching data and models to applications. *Glob. Ecol. Biogeogr.* 24, 276–292.
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.J., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. *Ecol. Lett.* 16, 1424–1435.
- Isaac, B., White, J., Ierodiaconou, D., Cooke, R., 2013. Response of a cryptic apex predator to a complete urban to forest gradient. *Wildl. Res.* 40, 427–436.
- Isaac, B., Cooke, R., Ierodiaconou, D., White, J., 2014a. Does urbanization have the potential to create an ecological trap for powerful owls (*Ninox strenua*)? *Biol. Conserv.* 176, 1–11.
- Isaac, B., White, J., Ierodiaconou, D., Cooke, R., 2014b. Urban to forest gradients: suitability for hollow bearing trees and implications for obligate hollow nesters. *Austral Ecol.* 39, 963–972.
- Isaac, B., White, J., Ierodiaconou, D., Cooke, R., 2014c. Simplification of arboreal marsupial assemblages in response to increasing urbanization. *PLoS One* 9, e91049.
- Jiménez-Valverde, A., 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Glob. Ecol. Biogeogr.* 21, 498–507.
- Kavanagh, R.P., 1997. Ecology and Management of Large Forest Owls in South-eastern Australia, PhD Thesis. University of Sydney, Australia.
- Kavanagh, R.P., 2004. Conserving owls in Sydney's urban bushland: current status and requirements. In: Lunney, D., Burgin, S. (Eds.), *Urban Wildlife: More Than Meets the Eye*. Royal Zoological Society of New South Wales, Mosman, NSW, pp. 93–108.
- Lambeck, R.J., 1997. A multi-species umbrella for nature conservation. *Conserv. Biol.* 11, 849–856.
- Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. *Glob. Ecol. Biogeogr.* 17, 145–151.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience* 52, 883–890.
- McNabb, E.G., 1996. Observations on the biology of the powerful owl *Ninox streuna* in southern Victoria. In: *Australian Bird Watcher*. 16, pp. 267–295.
- Merow, C., Smith, M.J., Silander Jr., J.A., 2013. A practical guide to MaxEnt for modelling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36, 1058–1069.
- Monterroso, P., Brito, J.C., Ferreras, P., Alves, P.C., 2009. Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. *J. Zool.* 279, 27–35.
- Ochoa-Ochoa, L.M., Flores-Villela, O.A., Bezaury-Creel, J.E., 2016. Using one vs. many, sensitivity and uncertainty analysis of species distribution models with focus on conservation area networks. *Ecol. Model.* 320, 372–382.
- Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.* 14, 483–488.
- Palmer, G.C., Bennett, A.F., 2006. Riparian zones provide for distinct bird assemblages in forest mosaics of south-east Australia. *Biol. Conserv.* 130, 447–457.
- Palmer, G.C., Fitzsimons, J.A., Antos, M.J., White, J.G., 2008. Determinants of native avian richness in suburban remnant vegetation: implications for conservation planning. *Biol. Conserv.* 141, 2329–2341.
- Pavey, C.R., 1995. Food of the powerful owl *Ninox strenua* in suburban Brisbane, Queensland. *Emu* 95, 231–232.
- Phillips, S.J., Dudík, M., Schapire, R., 2004. A maximum entropy approach to species distribution modeling. In: *Proceedings of the Twenty-First International Conference on Machine Learning*. 655–662.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.
- Pinto, C., Thorburn, J.A., Neat, F., Wright, P.J., Wright, S., Scott, B.E., Cornulier, T., Travis, J.M.J., 2016. Using individual tracking data to validate the predictions of species distribution models. *Divers. Distrib.* 22, 682–693.
- Radosavljevic, A., Anderson, R.P., 2014. Making better MaxEnt models of species distributions: complexity, overfitting and evaluation. *J. Biogeogr.* 41, 629–643.
- Razgour, O., Hanmer, J., Jones, G., 2011. Using multi-scale modelling to predict habitat suitability for species of conservation concern: the grey long-eared bat as a case study. *Biol. Conserv.* 144, 2922–2930.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343 (6167), 1–11. <http://dx.doi.org/10.1126/science.1241484>.
- Roberge, J., Angelstam, P., 2004. Usefulness of the umbrella species concept as a conservation tool. *Conserv. Biol.* 18, 76–85.
- Robertson, M.P., Cumming, G.S., Erasmus, B.F.N., 2010. Getting the most out of atlas data. *Divers. Distrib.* 16, 363–375.
- Santos, X., Brito, J.C., Sillero, N., Pleguezuelos, J.M., Llorente, G.A., Fahd, S., Parellada, X., 2006. Inferring habitat-suitability areas with ecological modelling techniques and GIS: a contribution to assess the conservation status of *Vipera latastei*. *Biol. Conserv.* 130, 416–425.
- Sattler, T., Pezzatti, G.B., Nobis, M.P., Obrist, M.K., Roth, T., Moretti, M., 2014. Selection of multiple umbrella species for functional and taxonomic diversity to represent urban biodiversity. *Conserv. Biol.* 28, 414–426.
- Sergio, F., Schmitz, O.J., Krebs, C.J., Holt, R.D., Heithaus, M.R., Wirsing, A.J., Ripple, W.J., Ritchie, E., Ainsley, D., Oro, D., Jhala, Y., Hiraldo, F., Korpimäki, E., 2014. Towards a cohesive, holistic view of top predation: a definition, synthesis and perspective. *Oikos* 123, 1234–1243.
- Soderquist, T., Gibbons, D., 2007. Home-range of the powerful owl (*Ninox strenua*) in dry sclerophyll forest. *Emu* 107, 177–184.
- Sorace, A., Gustin, M., 2009. Distribution of generalist and specialist predators along urban gradients. *Landsc. Urban Plan.* 90, 111–118.
- Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J., Shanas, U., 2015. What is an apex predator? *Oikos* 124, 1453–1461.
- Wang, Y., Allen, M.L., Wilmers, C.C., 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biol. Conserv.* 190, 23–33.
- Warren, D., 2016. Package 'enmtools'. Available online at: <https://github.com/danwarren/ENMTools>.
- Warren, D.L., Seifert, S.N., 2011. Ecological niche modeling in maxent: The importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* 21, 335–342.
- Weaving, M.J., White, J.G., Hower, K., Isaac, B., Cooke, R., 2014. Sex-biased space-use response to urbanization in an endemic urban adapter. *Landsc. Urban Plan.* 130, 73–80.
- Webster, A., Cooke, R., Jameson, G., Wallis, R., 1999. Diet, roosts and breeding of powerful owls *Ninox strenua* in a disturbed, urban environment: a case for cannibalism? Or a case of infanticide? *Emu* 99, 80–83.
- Weston, M.A., Silcocks, A., Tzaros, C., Ingwersen, D., 2006. A survey of contributors to an Australian bird atlasing project: demography, skills and motivation. *Aust. J. Volunteering* 11, 51–58.
- Wilcox, B.A., 1984. In situ conservation of genetic resources: determinants of minimum area requirements. In: McNeely, J., Miller, K. (Eds.), *National Parks, Conservation and Development: The Role of Protected Areas in Sustaining Society*. Smithsonian Institution Press, Washington D.C., pp. 639–647.
- Williams, P.J., Whitmore, S.A., Gutiérrez, R.J., 2014. Use of private lands for foraging by California spotted owls in the Central Sierra Nevada. *Wildl. Soc. Bull.* 38, 705–709.
- Wintle, B.A., Kavanagh, R.P., McCarthy, M.A., Burgman, M.A., 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. *J. Wildl. Manag.* 69, 905–917.
- Yackulic, C.B., Chandler, R., Zipkin, E.F., Royle, A., Nichols, J.D., Campbell Grant, E.H., Veran, S., 2013. Presence-only modelling using MaxEnt: when can we trust the inferences? *Methods Ecol. Evol.* 4, 236–243.