

Occupancy patterns of an apex avian predator across a forest landscape

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Abstract Apex predators are integral parts of every ecosystem, having top-down roles in food web maintenance. Understanding the environmental and habitat characteristics associated with predator occurrence is paramount to conservation efforts. However, detecting top order predators can be difficult due to small population sizes and cryptic behaviour. The endangered Tasmanian masked owl (*Tyto novaehollandiae castanops*) is a nocturnal predator with a distribution understood to be associated with high mature forest cover at broad scales. With the aim to gather monitoring data to inform future conservation effort, we trialled an occupancy survey design to model masked owl occurrence across ~800 km² in the Tasmanian Southern Forests. We conducted 662 visits to assess masked owl occupancy at 160 sites during July–September 2018. Masked owl site occupancy was 12%, and estimated detectability was 0.26 (± 0.06 SE). Cumulative detection probability of masked owls over four visits was 0.7. Occupancy modelling suggested owls were more likely to be detected when mean prey count was higher. However, low detection rates hindered the development of confident occupancy predictions. To inform effective conservation of the endangered Tasmanian masked owl, there is a need to develop novel survey techniques that better account for the ecology of this rare, wide-ranging and cryptic predator. We discuss the potential to combine novel census approaches that exploit different aspects of masked owl ecology to obtain more robust and detailed data.

Key words: detectability, forest, occupancy, owl, spatial autocorrelation.

INTRODUCTION

Predators are critical components of healthy ecosystems. Predator presence/absence can be important in shaping lower trophic levels (Ritchie & Johnson 2009); however, predators are globally threatened, and their decline is a disproportionate threat to biodiversity (Sergio *et al.* 2006). Understanding the ecological needs of predators is fundamental to improving conservation management (Geary *et al.* 2018) but studying predators can be challenging due to their often small, wide-ranging and cryptic populations (Ellis *et al.* 2014; Ramsey *et al.* 2015). Recent methodological advances in modelling species occurrence while accounting for imperfect detection (i.e. false absences), such as occupancy models that utilise detection/non-detection data (MacKenzie *et al.* 2017), may be a practical way to estimate occurrence of cryptic predators across large areas of potential habitat.

Forest owls are top order carnivores that are globally threatened by deforestation (McClure *et al.*

2018). Forest owls may be nocturnal, mobile and have low population densities, making it difficult to study fundamental aspects of their ecology (Wintle *et al.* 2005). Surveys for forest owls can generate many false absences (Wintle *et al.* 2005); thus, overcoming low detection probability is critical to designing robust ecological studies for these species (Mackenzie & Royle 2005). Forest owl surveys have typically relied on nocturnal spotlight surveys coupled with call broadcasts (Zuberogoitia *et al.* 2011). Studies may aim to improve precision at the individual survey level with loud call broadcasts and by increasing search time at each site to overcome cryptic behaviours. However, this approach limits the spatial coverage achievable over large study areas because individual surveys are time intensive. These approaches also result in large effective sampling units, which may only be proportionally occupied (MacKenzie *et al.* 2017). Resulting data may exhibit strong site level heterogeneity for covariates affecting occupancy or detection at smaller scales (Efford & Dawson 2012). For widespread species, trading-off survey-level precision for increased spatial replication over large study areas can yield important information about species ecology and habitat

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utilisation (Piorecky & Prescott 2006; Crates *et al.* 2017).

Spatial autocorrelation is another expected feature in species occurrence data (Hawkins 2012). It arises from spatially correlated environmental variables (Lichstein *et al.* 2002), or similar occupancy probabilities in neighbouring sample units (Webb & Merrill 2012), and its effect on the predictions of species occurrence models is varied (Lichstein *et al.* 2002; Hawkins 2012). Where spatial effects are present, employing analytical methods that explicitly account for spatial autocorrelation can improve occupancy estimates (Piorecky & Prescott 2006; Webb *et al.* 2014).

Tasmanian masked owls, *Tyto novaehollandiae castanops*, are endangered but widespread, with a preference for mature forest cover (Todd *et al.* 2019). Accurate population estimates and information on fine scale habitat preferences is limited (Bell *et al.* 1997; Mooney 1997), but because the species is threatened, addressing these knowledge gaps is critical to informing conservation action. Here we examine whether habitat characteristics and prey availability predict presence/absence of Tasmanian masked owls across a forest landscape and evaluate the efficacy of rapid surveys using call broadcast over large scales. We applied an occupancy modelling framework to survey habitat in an area subject to widespread and intensive logging. We minimised time spent at individual site visits in order to increase spatial replication of small sample units across the study area (Crates *et al.* 2017; Webb *et al.* 2017) to better understand masked owl habitat occupancy (i.e. use) at the landscape scale. We assess the degree of spatial autocorrelation in our data and employ a second analytical step to account for its possible effects on occupancy estimation. We aim to advance knowledge of the occurrence of masked owls because deforestation may be threatening habitat before the conservation requirements of Tasmanian masked owls can be identified.

METHODS

Study area

We surveyed ~800 km² across the southern forests of Tasmania, including forest patches in adjacent agricultural landscapes. The study area ranged from sea level to ~700 m and was dominated by wet *Eucalyptus* forest, with temperate rainforest and other mesic vegetation in the understorey. These forests have been severely fragmented by industrial logging (Webb *et al.* 2018) that created a patchwork of cleared land, regenerating and old-growth native forest and plantation (Hickey 1994). Mean minimum and maximum temperatures in the region ranged from 0.7 to 12.8°C from July through September 2018 and average monthly rainfall from 40 to 177 mm (BOM 2018).

Study design

Sites

A pilot study indicated that the masked owl call broadcast was weakly audible to humans at <250 m distance from the site centroid using an Ultimate Ears Megaboom. To ensure observer ability to detect owl calls, we defined sites as a 200 m radius around the centroid. We selected 160 survey sites across the study area (Fig. 1) with the aim of maximising site replication within mature habitat and on the basis that they contained large mature eucalypts, ensuring the presence of potential masked owl habitat. Selection was made with the aid of the aerial forest inventories that quantify the extent of mature, cavity bearing forest (FPA 2011) and field assessments. Site selection was limited by road conditions, safety, locked gates and private property lines. Sites ranged from 500 to 2000 m between nearest neighbours with a mean distance to nearest neighbour of ~750 m. 87 of these sites had previously been surveyed for sugar gliders *Petaurus breviceps* (Allen *et al.* 2018) which are an important prey species of masked owls, and predator of swift parrots (Stojanovic *et al.* 2014).

Habitat characteristics

We used QGIS to derive altitude and proportion of mature forest cover within 250, 500, 1000, 1500 and 2000 m radii from the site centroid. We estimated mature forest cover following (Stojanovic *et al.* 2012) using the aerial forest inventories that quantify the extent of mature, cavity bearing forest (FPA 2011). At each site, we used 25 × 20 m quadrats to quantify fine scale habitat characteristics. Within quadrats we recorded the following: (i) the number of trees in seven diameter at breast height (DBH) categories (10–20, 21–50, 51–100, 101–150, 151–200, 201–300 and >300 cm), (ii) height of the tallest tree, (iii) the number of mature tree crowns, (iv) percentage cover of the emergent tree cover, (v) canopy cover, (vi) understorey cover, (vii) combined total cover, (viii) ground cover.

We estimated cover as the mean of the proportion of field of view occupied in a 50 cm square at two points within the quadrat.

Survey

We undertook repeated 10-min site visits (3–5 visits per site) from July to early September of 2018. We chose winter, to maximise call responses (Todd *et al.* 2018), potentially arising from increased territoriality prior to breeding (Mooney 1997). Surveys involved the following: (i) 2 min of listening and scanning the forest with a thermal imaging telescope (Pulsar Quantum Thermal HD XQ), (ii) 6 min of intermittent masked owl call broadcast from a portable speaker and (iii) 2 min of listening and scanning with the thermal imaging telescope. We recorded masked owl detections (by sight or sound) throughout the survey period. We observed potential prey species using a thermal imaging scope and confirmed species (where possible) using binoculars and spotlight during the 2 min preceding and following the call broadcast. We conducted surveys from dusk until

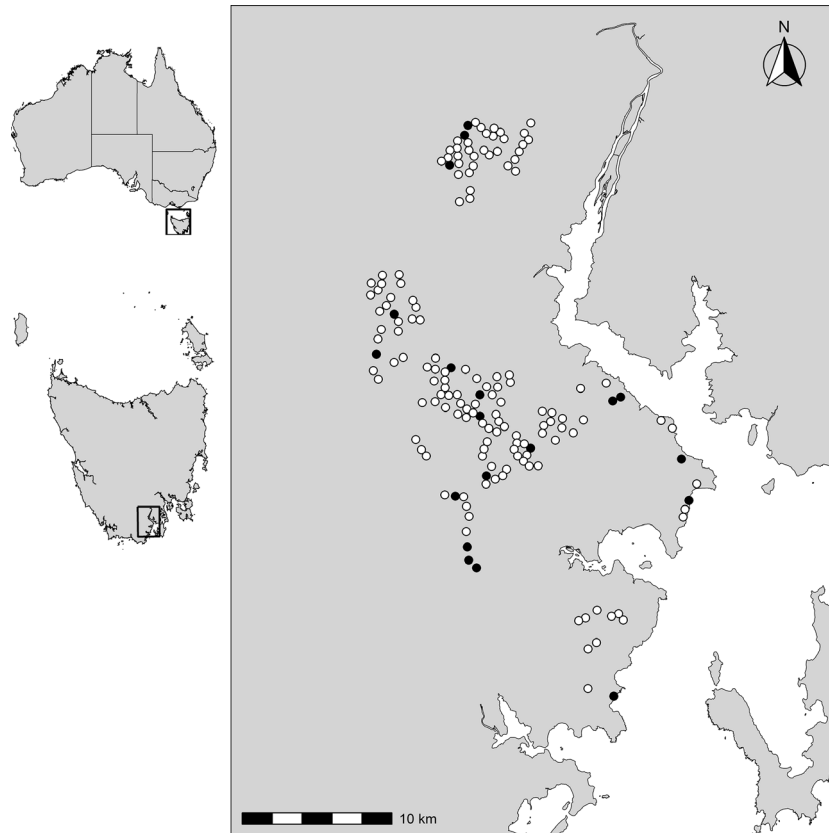


Fig. 1. The study region was across 800 km² in the Tasmanian Southern Forests. Open circles indicate sites where Tasmanian masked owl were not detected and closed circles indicate sites where Tasmanian masked owl were detected.

dawn. To reduce the potential effects of weather on detection likelihood, we only conducted surveys in fine conditions with $<10 \text{ km h}^{-1}$ wind and no rain (Takats & Holroyd 2006; Todd *et al.* 2019). We recorded the following: (i) detection/non-detection of Tasmanian masked owl, (ii) counts of prey (sugar glider, ringtail possum *Pseudocheirus peregrinus*, brushtail possum *Trichosurus vulpecula* and other small ground and scansorial mammals (we did not attempt to identify non-arboreal mammals to species); (iii) temperature (0–5, 6–10 and $>10^\circ\text{C}$); (iv) moon phase. To estimate prey abundance at sites, we calculated mean prey abundance at each site as \sum (per visit prey count)/number of visits. To estimate prey diversity at sites, we pooled prey into five groups: (i) sugar glider, (ii) ringtail, (iii) brushtail, (iv) small ground and (v) unknown arboreal. Per visit prey diversity was the total number of prey groups observed divided by five. Mean site prey diversity was \sum (per visit diversity)/number of visits (i.e. detecting every prey group at every visit would yield a mean diversity of 1).

Statistical analysis

Given that owl surveys are expected to produce many false absences (Wintle *et al.* 2005), we first used an occupancy modelling approach (MacKenzie *et al.* 2002) to fit single season occupancy models in R (R-Core-Team 2018) using

the package *unmarked* (Fiske & Chandler 2011). This package fits zero-inflated binomial models to detection/non-detection data and allow for site specific and survey specific covariates to be fit with occupancy and detection probability estimates, respectively (Fiske & Chandler 2011). Site-level covariates that could influence masked owl occupancy of a site were fitted in the occupancy component of models, including the forest cover radii, altitude, habitat characteristics derived from quadrats, mean site prey abundance and the mean site prey diversity. Observation level covariates (that could affect detection likelihood) were fitted in the detection component of models and included temperature and moon phase. Wind and precipitation were not included as we controlled for these in the study design. Due to a sparse dataset (see Results), we chose not to over-parameterise and to assess models with only a single term in detection and occupancy. We selected the best model using the Akaike information criterion (AIC) where the best models were $\Delta \text{AIC} < 2$. Model fit was tested with a Mackenzie and Bailey goodness of fit test, which tests whether a bootstrapped χ^2 (chi-squared) statistic simulated from the observed data is within the distribution of expected χ^2 (Mazerolle & Mazerolle 2017).

Given the likelihood of spatially correlated detections from our study design, we assessed spatial autocorrelation (SAC) in our data using spatial correlograms based on global Moran's I (Tiefelsdorf 2006) in the R package *pgirmess*

(Giraudoux *et al.* 2018). We used spatial simultaneous autoregressive (SAR) models to account for the effects of SAC at multiple spatial scales. SARs include a spatially weighted matrix based on neighbourhoods by distance that accounts for effects of neighbouring location values on the response variable at each location (Kissling & Carl 2008). We justify a simple spatial modelling process that does not account for imperfect detection (Crates *et al.* 2017) because, although our detection probability was low, our survey effort was substantial and therefore our cumulative detection probability is sufficiently high at most sites (Garrard *et al.* 2008). We started with an elimination process based on AIC scores in a generalised linear model (GLM binomial) framework, for parameter reduction from a saturated model. We then defined spatial simultaneous autoregressive models (SARs) for the best model, including weighted matrices generated for multiple neighbourhoods by distance bands ranging from 0.5 to 33 km radii, as a spatial covariate. SARs were implemented in the *spdep* package (Bivand *et al.* 2011) in R. We ranked the SARs based on AIC scores.

RESULTS

We undertook 662 surveys over 160 sites, (median of four surveys per site). We detected masked owls in 29 surveys at 19 sites. Table 1 summarises the key habitat variables at each site.

Naïve masked owl occupancy was 0.12, approximately 2/3 the modelled occupancy estimate

Table 2. Model selection results for single season occupancy models

Model	nPars	Δ AIC [†]	logLik
ϕ (mean prey abundance). ρ (.)	3	0	-97.57
ϕ (mean prey abundance). ρ (temperature)	4	0.93	-97.04
ϕ (mean prey abundance). ρ (moon phase)	4	1.2	-97.17
ϕ (mean prey diversity). ρ (.)	3	3.63	-99.39
ϕ (mean prey diversity). ρ (temperature)	4	4.3	-98.72
ϕ (mean prey diversity). ρ (moon phase)	4	4.68	-98.91
ϕ (.). ρ (.)	2	13.48	-105.32

nPar, number of parameters.

[†]AIC of the top model was 201.15.

(0.18 ± 0.05 SE) assuming constant occupancy and detection. Based on AIC scores (Table 2), the top ranked model included a significant positive effect of the mean prey abundance on the likelihood of masked owl occupancy (model estimate: 1.79 ± 0.773 , z : 2.32, P : 0.02, Fig. 2) and assumed constant detection (model estimate: -1.08 ± 0.31 , z : -3.49, P : 0.0005). The other 2 top models based on Δ AIC < 2 (Table 2) included a significant positive effect of mean prey abundance on occupancy and a positive, though not significant, effect of temperature

Table 1. Summary of habitat variables within site quadrats where masked owls were detected and were not detected. (a) DBH 10–20 cm. (b) Other variables

Stem count	0–25	26–50	51–75	76–100	>100
(a)					
Proportion of sites					
Masked owl detected	0.37	0.16	0.26	0.11	0.11
Masked owl not detected	0.21	0.17	0.30	0.11	0.21
Mean (standard deviation; standard error)					
Habitat variable	Masked owl detected		Masked owl not detected		
(b)					
DBH 21–50 cm	8.9 (7.7) (1.8)		8.9 (7.2) (0.6)		
DBH 51–100	4.2 (4.7) (1.1)		3.1 (4.0) (0.3)		
DBH 101–150	0.5 (1.1) (0.2)		0.6 (1.2) (0.1)		
DBH >151	1.3 (1.5) (0.3)		1.0 (1.5) (0.1)		
Mature crowns (count)	15.3 (8.5) (2.0)		13.9 (8.6) (0.7)		
Tallest tree (m)	45.3 (15.0) (3.4)		42.9 (13.0) (1.1)		
Emergent tree cover (%)	25.2 (20.0) (4.6)		16.4 (17.9) (1.5)		
Canopy cover (%)	32.1 (28.6) (6.6)		37.7 (24.6) (2.1)		
Understory (%)	34.7 (25.2) (5.8)		42.3 (26.4) (2.2)		
Combined total cover (%)	64.0 (22.4) (5.1)		70.0 (18.2) (1.5)		
Ground cover (%)	71.6 (21.9) (5.0)		66.5 (24.5) (2.1)		

[†]Stems greater than DBH 200 cm were rare and pooled with all stems >150 cm.

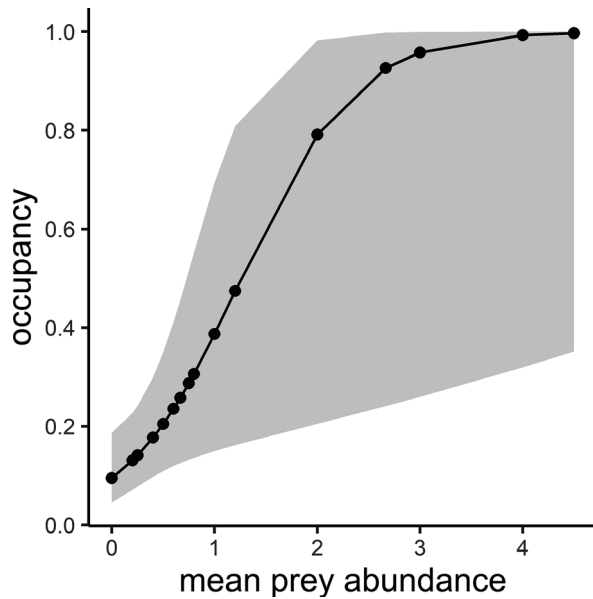


Fig. 2. The probability of masked owl occupancy with increasing mean prey abundance at a site, predicted from a single season occupancy framework, implemented in *unmarked*. 160 sites in the Tasmanian Southern Forest region were surveyed 3–5 times each for the Tasmanian masked owl (using call broadcasts) and prey (using thermal imaging). Shaded area is the 95% confidence interval for predictions.

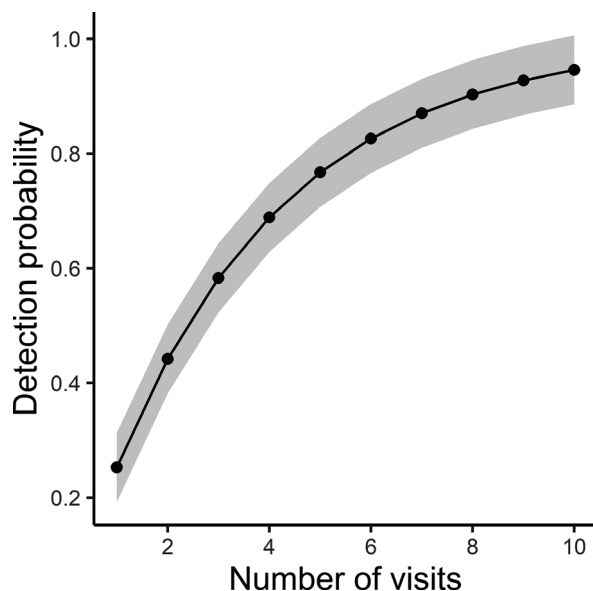


Fig. 3. Cumulative probability of detecting Tasmanian masked owl, in the Tasmanian Southern Forest region using a call broadcast, based on a constant detection probability of 0.26 determined from single season occupancy model fit in *unmarked*. The black line indicates the cumulative probability of detecting Tasmanian masked owl after multiple site visits. The grey ribbon indicates the standard error.

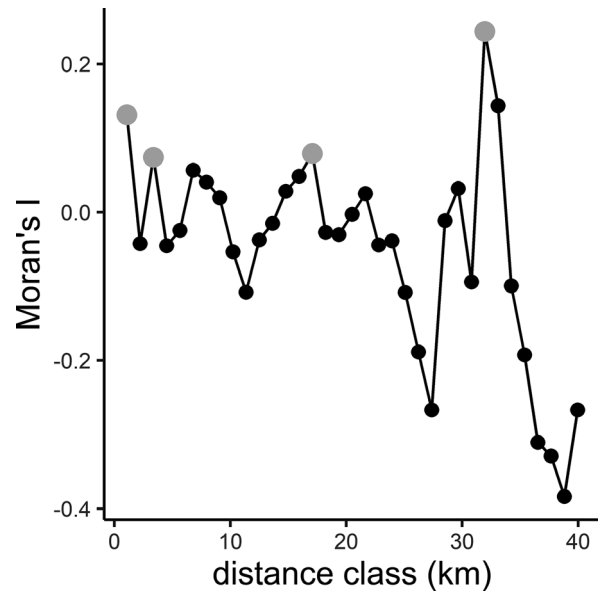


Fig. 4. Spatial autocorrelation (Moran's I) of Tasmanian masked owl detection/ non-detection in a single season occupancy survey of the Tasmanian Southern Forests region in winter of 2018. Grey dots present significant spatial autocorrelation ($P < 0.05$) and black dots non-significant spatial autocorrelation ($P > 0.05$).

(model estimate: 0.353 ± 0.343 , z : 1.03, P : 0.3) or moon phase (model estimate: 0.188 ± 0.211 , z : 0.89, P : 0.4), on detectability. As neither temperature or moon phase contributed significantly to the models ($\Delta \text{AIC} < 2$) or significantly affected detectability, we accepted the simpler model which included only the effect of mean prey abundance and constant detection. That model passed the Mackenzie and Bailey goodness of fit test ($P = 0.683$, where H_0 is no difference between the observed and expected χ^2 statistics). Mean prey abundance ranged from 0 to 4.5 (mean: 0.29 ± 0.05 SE). Given the estimated detection probability of the preferred model was 0.26 (± 0.06 SE), the cumulative probability of detecting masked owls if they were present at a site was 0.7 by the fourth visit (Fig. 3; Garrard *et al.* 2008).

Spatial correlograms demonstrated that masked owl detection data were spatially autocorrelated at distances of 1–3.5 km (Fig. 4). The best fit GLM based on AIC scores included a significant positive effect of mean prey abundance (estimate 1.239 ± 0.436 SE, z : 2.8, $P = 0.004$) and non-significant effects of altitude (estimate -0.003 ± 0.002 SE, z : -1.9 , $P = 0.06$) and mature forest cover at 500 m (estimate 2.378 ± 1.258 SE, z : 1.9, $P = 0.06$). The best SAR model using the GLM formula, and identified by AIC scores (Table 3), included a weighted matrix for a distance radius of 1 km as the spatial covariate. The contribution of altitude and mature forest cover at 500 m in this model was small, indicated by a $\Delta \text{AIC} \ll 2$

Table 3. Model selection results for simultaneous autoregressive (SAR) models

Terms [†]	Spatial weights [‡] (m)	Δ AIC [§]	logLik
Altitude + mature forest (500 m) + prey abundance	1000	0	-24.38
Prey abundance	1000	0.2	-26.48
Altitude + mature forest (500 m) + prey abundance	750	4.3	-26.57
Prey abundance	750	5	-28.88

[†]The terms included in the model; altitude at the centroid, proportion of mature forest cover in a 500 m radius around the centroid and the mean site prey abundance (average across all visits).

[‡]Spatial weights matrix created on neighbourhood by the distance indicated in metres.

[§]The AIC of the top model was 62.8.

between it and the next top model, with just mean prey abundance (Table 3). We removed the insignificant terms for a final SAR model ($\rho: 0.43 \pm 0.13$, $z: 3.2$, $P: 0.001$) including only a significant positive effect of mean prey abundance (estimate 0.2 ± 0.03 SE, $z: 5.9$, $P: <<0.0001$). There was no significant residual SAC in this final SAR model (Moran's I: 0.003, $P: 0.45$).

DISCUSSION

The effects of habitat and vegetation characteristics on masked owl site occupancy did not rank highly relative to the prey models. However, only 19 sites were used by masked owls during the survey period, and so we interpret our results with caution. We found a positive effect of mean prey abundance per site on the likelihood of masked owl occupancy (Table 2). A model with prey diversity also ranked highly (Table 2). Prey counts were mostly low, and our confidence in estimating the probability of owl occurrence at high mean prey abundance was low (Fig. 2). Other predators show high occupancy at sites where prey is predicted to be more abundant (Martin *et al.* 2009; Harihar & Pandav 2012) although, in those studies, rates of predator detection are higher. Our data possibly included multiple species, some unidentified and each likely with their own site and survey-level detectability, so we did not attempt to model the occurrence of prey species. Still, our models indicate that prey availability is likely to be an important factor predicting the occurrence of masked owls, and further information about prey populations may yield insight into why some sites are occupied and others are not. The prey species detected in our study were diverse, with equally

diverse habitat preferences (Driessen *et al.* 1996; Lindenmayer *et al.* 2008; Cawthen & Munks 2012; Fancourt *et al.* 2013). For example, the three arboreal species are broadly distributed within mature forested landscapes (Lindenmayer & Cunningham 1997; Allen *et al.* 2018), whereas both the eastern barred bandicoot and eastern quoll are common at the forest edge (Driessen *et al.* 1996; Fancourt *et al.* 2015). In a region of intensive logging and agriculture, prey community assemblages, distributions and abundances will be directly affected by land use (Kavanagh & Stanton 2005; Flynn *et al.* 2011) and changes to land management (Driessen *et al.* 1996). Further research is needed to confirm that masked owl habitat use may reflect shifts in prey availability.

In our study, detection data were spatially autocorrelated, which can inflate occupancy estimates and the effects of explanatory covariates (Lichstein *et al.* 2002; Hawkins 2012). Therefore, we employed analytical methods that separate spatial effects and independent effects (Lichstein *et al.* 2002). In our analyses, the occupancy predictions of spatial models largely agreed with the predictions of occupancy models; therefore, in our case it is likely that spatial autocorrelation was not affecting the model estimates. Given that spatial autocorrelation was present at small distance classes (1–3.5 km), spatial dependency may have resulted from an increased probability of site occupancy due to the presence of multiple occupied neighbouring sites within an owl home range (Efford & Dawson 2012; Bardos *et al.* 2015). Designing a survey where sites are spatially independent for species for which home ranges are large and the characteristics are unknown is problematic (Efford & Dawson 2012). Spatially structured detection data can be exploited to estimate species density and delineate home ranges (Chandler & Royle 2013); however, these models require a higher density of detections (Ramsey *et al.* 2015) than was achieved in our survey. Therefore, we are unable to explicitly attribute spatial structure in our data to masked owl home range characteristics.

Poor detectability limits the precision of occupancy models (; O'Connell Jr *et al.* 2006; Durso *et al.* 2011). Employing methods that maximise detections can thus improve occupancy estimation (Bailey *et al.* 2007; Dupuis *et al.* 2011; Baumgardt *et al.* 2014; Specht *et al.* 2017). Call broadcasts increase the detectability of owls (Wintle *et al.* 2005); however, the effectiveness of call broadcasts may be affected by many factors, for example, distance, topography and habitat structure affect the passage of sound (Efford & Dawson 2012) or observer error (Takats & Holroyd 2006; Zuberogitia *et al.* 2011). Seasonal or other sources of variation in calling behaviour may also bias responses to broadcasts (Zuberogitia *et al.* 2019), though there is no evidence for this in the Tasmanian masked owl

(Todd *et al.* 2018). Our study design traded off time spent at each site for greater spatial replication, coupled with a softened call broadcast, targeted at masked owls within our small sampling units. Our detection probability is low, but consistent with other call broadcast studies (Todd *et al.* 2019); however, we detected owls at fewer locations. When occupancy is low, a sampling design with a high number of sites is advisable as detectability is estimated from occupied sites (Mackenzie & Royle 2005). Given that both occupancy and detectability were low (0.18 and 0.26, respectively), our survey effort of medium repetition at a high number of sites delivered an acceptable level of precision (see simulations in Appendix S3; Mackenzie & Royle 2005). A low occupancy rate may simply reflect the species use of only a small fraction of their large home ranges at a given time (Kavanagh & Murray 1996; McNabb *et al.* 2003; Wintle *et al.* 2005).

Delivering protection for masked owls will require a broad knowledge of how they interact with forest structure and the ecology of their prey. Masked owls occupy large home ranges and may preferentially use different habitat for foraging, roosting and nesting (Kavanagh & Murray 1996; McNabb *et al.* 2003). It may therefore be difficult to model the effects of habitat characteristics with bird detections made throughout the night. Sampling designs, for example, that target dawn and dusk may have more power to estimate the influence of mature forest characteristics in masked owl occupancy associated with roosting habitat. Detecting sparsely distributed, nocturnal, mobile and cryptic species may be improved by identifying indices of occurrence (Harihar & Pandav 2012; Wolff *et al.* 2015), rather than trying to detect individual animals. Scats, hair, feathers and footprints are all indicators that a species occurs at a site (Levy 1999; Johnson *et al.* 2013). Novel techniques such as the use of detection dogs, trained to find owl pellets (Wasser *et al.* 2012), could improve detection of owls, irrespective of whether they are present at a given site at the time of a survey. Presence of regurgitated pellets may be associated with roosting and nesting sites (Kavanagh 2002), which are important habitats that may go undetected during call broadcast surveys. Future study designs that incorporate multiple methods of detection might increase detection of the species across broader scales and contexts (Nichols *et al.* 2008). The development of new methods of detection and survey designs is likely to advance habitat models for the species.

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AUTHOR CONTRIBUTIONS

Adam Cisterne: Conceptualization (equal); data curation (lead); formal analysis (equal); methodology (equal); writing-original draft (lead); writing-review & editing (equal). **Ross Crates:** Formal analysis (equal); methodology (supporting); writing-original draft (supporting). **Phil Bell:** Supervision (supporting); writing-original draft (supporting); writing-review & editing (supporting). **Robert Heinsohn:** Project administration (lead); supervision (supporting); writing-original draft (supporting); writing-review & editing (supporting). **Dejan Stojanovic:** Conceptualization (equal); methodology (equal); supervision (lead); writing-original draft (equal); writing-review & editing (equal).

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. rscript. Rcode for occupancy models
Appendix S1. result. Complete results for occupancy models

Appendix S2. rscript. Rcode for spatial models
Appendix S2. result. Complete results of spatial models

Appendix S3. Occupancy predictions under varying study designs.