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Ravens exploit wildlife roadkill and agricultural landscapes but do not affect songbird assemblages

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ABSTRACT

Future land-use change could supplement populations of opportunistic predatory birds, such as corvids, resulting in amplified predation pressure and negative effects on populations of other avian species. We investigated whether Forest Ravens (*Corvus tasmanicus*) were more likely to be observed in modified landscapes and in areas of higher roadkill density in south-eastern Tasmania. Following this, we examined the effect of Forest Raven density on the abundance of other birds. We surveyed birds along roadsides to investigate the effects of land-use and raven population density on the presence of smaller birds/songbirds. We used species distribution models and generalised linear models to assess the habitat and population dynamics of Forest Ravens. Roadkill presence increased the probability of observing ravens more than six-fold. Forest Raven presence was also higher in agricultural areas than in forested and urban areas. There was no effect of Forest Raven abundance on species richness or abundance of smaller songbirds. This null result may be due to seasonal effects or because ravens moderate the presence or abundance of other avian predators. However, the interactions of meso-predators with other species are complex, and further work is required to assess the long-term effects of anthropogenic supplementation of ravens on the ecosystem.

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Corvus tasmanicus; Forest Raven; land-use change; passerine; species distribution models

Introduction

Land-use change is a major threat to biodiversity (Hepinstall *et al.* 2008). As human populations grow, urban environments and agricultural land expand, resulting in changes to vegetation structure and species composition in the impacted areas (Chamberlain *et al.* 2009; Jokimäki *et al.* 2017). Many animal species have experienced population declines in response to novel threats, such as habitat fragmentation, altered vegetative complexity and increased predation (Marzluff *et al.* 2001; Baltensperger *et al.* 2013). Land-use change is anticipated to lead to reduced biodiversity, species homogeneity and increased settlement of non-native species (Marzluff *et al.* 2001; McKinney 2006). Habitat modification is facilitated by road networks, which, as a crucial component of modern society, are forecast to increase exponentially (Benitez-Lopez *et al.* 2010; Laurance *et al.* 2014). Roads have a number of detrimental impacts on biodiversity (Hobday and Minstrell 2008), both direct (e.g., increased vehicle collisions (Forman and Alexander 1998; Fahrig and Rytwinski 2009)), and indirect (e.g., fragmentation, dispersal barriers, facilitation of invasive species spread and human harvesting (Benitez-Lopez *et al.* 2010)).

Some species adapt readily to human conditions and increase in abundance and range in response to habitat modification (Marzluff and Neatherlin 2006; Santos *et al.* 2011). Species that benefit from humans and anthropogenic environments are known as synanthropes (Wood *et al.* 2014). For example, many scavengers benefit from increases in the abundance of roadside carrion (Lambertucci *et al.* 2009; Planillo *et al.* 2015). As animal remains can be sporadic and difficult to locate in natural environments, the presence, and reliability, of roadkill may favour feeding conditions of opportunistic scavengers and potentially elevate their abundance near roads (Forman and Alexander 1998; Rees *et al.* 2015).

Corvidae, a globally widespread family of large Passerines (perching birds) is an exemplar synanthrope, often having greater population densities within modified environments than in their indigenous habitat (Antonov and Atanasova 2003). Although corvids are often considered a ubiquitous but fairly harmless feature of human-dominated landscapes (Marzluff *et al.* 2001), at high densities they can be detrimental to human activities, which has led to the application of culling strategies (Brook *et al.* 2003). Increased corvid abundance may also affect the viability of other species, exacerbating the

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Supplemental data for this article can be accessed here.

negative impacts of habitat modification on avian diversity (Read and Wilson 2004; Madden *et al.* 2015). Many corvids are opportunistic meso-predators and, given the chance or need, will prey on the nestlings and eggs of other passerines (Rees *et al.* 2015; Ekanayake *et al.* 2016).

The Forest Raven (*Corvus tasmanicus*) is a sedentary and territorial corvid that is widespread throughout Tasmania and southeast mainland Australia (Ratkowsky and Ratkowsky 1977; Lawrence 2009). The species is omnivorous and in winter carrion becomes increasingly important (Rowley and Vestjens 1973; Lawrence 2009). Range expansion of Forest Ravens has been observed in Victoria and New South Wales, which has been attributed to heightened vehicular traffic and consequent increases in roadkill density (Higgins *et al.* 2006). As the species also preys on the eggs and young of woodland birds, seabirds and shorebirds (Debus and Rose 2006; Higgins *et al.* 2006; Talmage 2011), further increases in Forest Raven populations might have negative impacts on the reproductive viability of other birds, particularly small passerine species.

A thorough understanding of the effect of land use change on Forest Raven populations and their subsequent impact on small woodland songbirds is a conservation priority. In this context, we aimed to: (i) investigate how Forest Raven populations respond to the impacts of land-use change, such as habitat modification and roadkill presence, plus any seasonal variation in this response; and (ii) examine the impact of Forest-Raven density on the species richness and abundance of small passerine bird species across a range of habitats, in their role as a facultative avian meso-predator with a potentially increasing impact due to anthropogenic change.

Methods

Study area

Study sites were located in south-eastern Tasmania (Figure 1). For repeat surveys of roadkill, eight transects were selected within the Huon Valley and Tasman Peninsula areas based on the following criteria: 15 km in length, a speed limit of 80 km/h or above, avoided urban areas, had two lanes and evidence of both live animal and roadkill presence (Hobday and Minstrell 2008). We surveyed for Forest Ravens on the roadkill

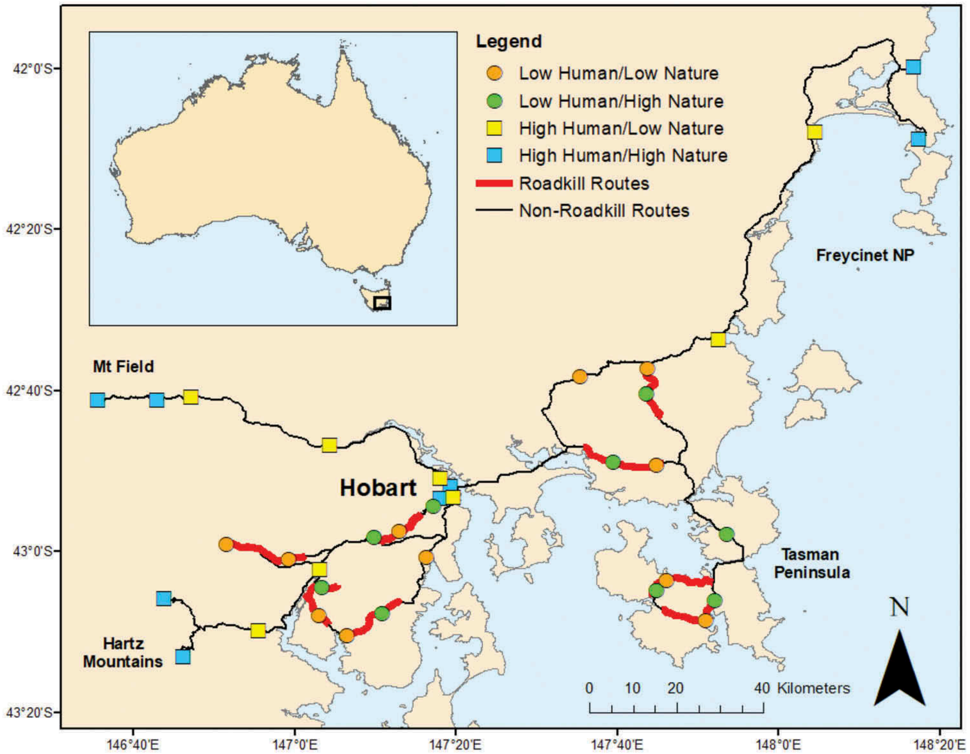

Figure 1. Roads surveyed for Forest Raven occurrence in Tasmania, Australia for the period September 2016 to July 2017. The black and red lines indicate the route that was travelled with the red lines denoting where roadkill surveys were done. Community survey site locations are denoted by the coloured circles and squares. There were 10 sites in areas of low human/low nature density (red circles; e.g. agricultural areas), 10 sites in areas of low human/high nature density (green circles; e.g. roadside forests), eight sites in areas of high human/high nature density (yellow squares; e.g. national parks), and eight sites in areas of high human/high nature density (blue squares; e.g. urban parks).

roads and stretches between the designated roadkill routes to examine the effect of land-use (Figure 1).

To assess the diversity of bird communities, sites were selected within south-eastern Tasmania (Figure 1). These sites were located on or adjacent to the road transects (between 0 and 100 metres from the road). We chose 20 sites in low-human-density areas within the Huon Valley and the Tasman Peninsula regions. Of these sites, 10 were situated in low-nature areas (e.g., agricultural areas) and ten in high-nature areas (e.g., roadside forests). We surveyed 16 further sites in high-human density areas, with eight sites selected in high-nature areas (e.g., national parks) and eight sites in low-nature areas (e.g., urban parks).

Data collection

For the road surveys of roadkill and Forest Ravens, data were collected between September 2016 and July 2017. Within each season, we repeat surveyed each route once a week for four weeks. Surveys began within an hour of dawn and continued until approximately 3 h before dusk. The order of the survey routes was alternated each week to minimise any temporal bias. We collected roadkill and Forest Raven location data by driving at 40–50 km/hr and geolocating (Garmin eTrex 30) all roadkill and Forest Raven observations. All Forest Ravens observed on the road or within the visible roadside habitat (surveyed with binoculars) were documented. This process was also completed for other 'focal species' that are known to prey on small songbirds: Laughing Kookaburra (*Dacelo novaeguineae*), Black Currawong (*Strepera fuliginosa*), Grey Currawong *(Strepera versicolor*), Grey Butcherbird (*Cracticus torquatus*) and Australian Magpie (*Gymnorhina tibicen hypoleuca*).

We completed bird community surveys from late-July 2017 to September 2017. Surveys were completed within a two–hectare circular area over a 20–minute period, documenting each individual bird that was seen or heard (distinguished by call) (Loyn 1986). To ensure any calls that could not be identified in the field were not misidentified, an audio recording device (Philips 2510 Voice Tracer) was used during surveys for later verification. Species other than the 'focal species' were grouped based on taxonomy and ecological relatability (Table S1, supplementary material). At each site, we completed four surveys, at different times to minimise temporal bias, over a two-week period. During each survey, we also recorded the weather and counted the number of pedestrians and traffic.

Bioclimate Envelope model

We created a climate-only species distribution model (SDM) for the Forest Raven in Tasmania. The purpose of the SDM within this study was to ensure that all field-based survey sites, despite varying in vegetation type and altitude, were a climatically appropriate habitat for the Forest Raven. SDMs are computational algorithms that seek to predict the distribution of species by statistically combining spatial environmental data with georeferenced observations of species occurrence and abundance (Elith and Leathwick 2009). A gridded map of Tasmania, with a cell resolution size of ~1 km^2, was used to fit the SDMs for the Forest Raven. We obtained climatic data at a 0.01 degree resolution for the period 1976–2005 from the Biodiversity & Climate Change Virtual Laboratory (BCCVL; bccvl.org.au). We tested the data for collinearity and removed variables with inter-correlation above 0.7. Six climatic layers were used for the SDM: isothermality, temperature seasonality, mean temperature of wettest quarter, mean temperature of driest quarter, precipitation seasonality, and precipitation of warmest quarter. Variables were produced by aggregating the monthly data from Australian Water Availability Project (AWAP; csiro.au/awap) to Bioclim variables in accordance with the methodology of WorldClim (worldclim.org/methods) (VanDerWal *et al.* 2013).

We gathered species occurrence data for the Forest Raven in Tasmania from the Atlas of Living Australia (ALA; ala.org.au), refining the data to only BirdLife Australia and eBird databases recorded from 1990 to the present. Duplicates and spatially suspect records were removed, leaving 23,765 Forest Raven occurrences. We set the resolution for the subsequent analysis at 2 × 2 km, as it reflected the average territory size (2 km^2) of a breeding pair of Forest Ravens (Higgins *et al.* 2006). For each occupied cell of the map grid, a single record was retained, resulting in a final tally of 2,058 presence points.

Since no true absences were available (this requires quantification of detection error via repeated surveys), we used apparent absences to generate pseudo-absences. To achieve this, we gathered species occurrence data for all avian species recorded in Tasmania from the Atlas of Living Australia, confined to BirdLife Australia and eBird databases that were recorded from 1990 to the present. Firstly, duplicates and spatially suspect records were removed. We then excluded all records in which a Forest Raven was present, before filtering records to ensure they were spaced at least 2 km from any presence point or other pseudo-absence points. This resulted in 558 observations of bird species in which a Forest Raven was not observed, which we used as our pseudoabsences.

The SDMs were fitted in R using the package SDM (Naimi and Araújo 2016). We selected six methods for the final ensemble: generalised additive model (GAM); multivariate adaptive regression spline (MARS); boosted regression tree (BRT); random forests (RF); mixture discriminant analysis (MDA); and flexible discriminant analysis (FDA). To minimise bias in parameter estimation, a k-fold cross validation resampling approach was used (in this case, $k = 5$) (Peterson *et al.* 2011). To create the final ensemble prediction, we weighted individual models according to the threshold-dependent true-skill statistic (TSS) (Allouche *et al.* 2006). This final ensemble SDM was used to create a climate suitability index (CSI) map for the Forest Raven in Tasmania.

Statistical analysis

Statistical analyses were done in Program R v3.3.1 (R Core Team 2016). We used a chi-squared test and Fisher's exact binomial test to investigate whether individual Forest Raven occurrences were randomly distributed across the four survey seasons. We used the package MuMIn (Barton 2013) in R for the GLM model selection. We used multi-model inference and the Akaike Information Criterion, corrected for small-sample bias (AIC_c) (Burnham and Anderson 2002) to examine the predictive power of models, and selected the most parsimonious one(s) according to the ΔAIC_c (difference between the AIC_c of a given model and the best model) (Grueber *et al.* 2011). All analyses included the null (intercept-only) model in the model selection process. We tested a suite of ecologically appropriate models (Table S2, supplementary material) that were determined *a priori*, to ensure that the best model was informative and ecologically interpretable. After selecting the best model set for each predictor, we calculated the Akaike weight (w_i), which can be interpreted as the probability that the *i*th model is best given the data and model set, for each model (Burnham and Anderson 2002). We determined the absolute model fit of the top models by calculating the AUC (area under the curve) and predictive R^2. The weighted ensemble (model-averaged) predictions for each top-model set was used to investigate the effects of the predictor variables (Grueber *et al.* 2011). We calculated the estimate, unconditional standard error, confidence interval and standardised regression coefficient (based on z-values) for each predictor after model averaging. The effect size (ES) was calculated for any variables that were supported (95% confidence limit did not overlap with zero) by comparing the model-averaged predicted probability when that categorical variable was applied, against the probability of the intercept when the effect was absent.

We used GLMs with a binomial distribution to investigate the predictors (presence of roadkill, vegetation cover, habitat type and season) of the presence or absence and occurrence of groups of Forest Ravens along the road transects. For use in the GLMS, pseudo-absences were randomly generated along the roads at a ratio of 5:1, being chosen randomly at least 80 m from a presence or other pseudo-absence point. We used the presence/pseudo-absence data collected on the eight roadkill routes to test whether Forest Ravens were more or less likely to be observed when roadkill was present, with any raven <10 m from roadkill categorised as 'on roadkill'. We also used these data to test whether Forest Ravens were more likely to be observed in areas with certain densities of vegetation cover. Vegetation covers on each side of the road was calculated at 50 m intervals using satellite imagery and field validation; areas were classified as either forest/forest (F/F), forest/open (F/O) or open/open (O/O). All the data were used to test the predictive value of land type (forest, urban or agriculture) on the presence of single and groups of Forest Ravens. These data were also used to test the effect of season on the presence/absence of Forest Raven groups. Layers from TASVEG (data.gov.au/dataset/tasveg-3–0) were used to calculate the distance of each Forest Raven to the nearest habitat type. To avoid skewed distances in the data, we categorised each Forest Raven presence as belonging to a habitat type if it was within 100 m of that environment.

We used GLMs to assess the predictors (habitat type, Forest Raven abundance, introduced species abundance, traffic density and human density) of passerine group richness and total number of passerines. To fit the GLMs, we assumed the data followed a Gaussian distribution with a log link function (Limpert *et al.* 2001). For each site, results were averaged across the four surveys to mitigate the effects of temporal-bias. As some sites had skewed values (e.g., city parks with high volumes of traffic), we grouped traffic and human density into low, medium and high categories (traffic: low ≤10, medium 11–79, high ≥80; human density: low ≤1, medium 2–19, high ≥20). At two sites (Mt Hartz and Lake Dobson) we observed almost no birds because of snow presence. These were therefore omitted from the final analysis. Wind severity was recorded at each survey, and this was used as a control variable within the GLMs.

Results

Bioclimate Envelope model

The results of fitting the six species distribution models based on out-of-sample predictive skill are summarised in Table S3 (supplementary material). We used the statistics of each model to create a weighted ensemble species distribution model for the Forest Raven based on relative climate suitability index (CSI) (Figure 2). As illustrated in Figure 2, the survey regions were of high suitability for Forest Ravens, with all routes having on average >0.7 CSI.

Road surveys

In total, we recorded 783 Forest Ravens over the four seasons of the road surveys (Table S4, supplementary material). Counts of Forest Raven occurrences varied significantly across seasons ($\chi^2 = 38.01$, df = 3, $p < 0.001$; Table S4). There was no difference between spring and summer (Fisher's exact binomial test: odds ratio (OR) = 1.033, 95% CI = 0.76–1.41, overlaps with the null expectation of 1) or winter and autumn (OR = 0.90, 95% CI = 0.69–1.19). Winter had the highest number of Forest Raven occurrences (winter/spring OR = 1.60, 95% CI = 1.20–2.14; winter/summer OR = 1.65, 95% CI = 1.24–2.22) and autumn had the second highest number of Forest Ravens observed (autumn/spring OR = 1.45, 95% CI = 1.08–1.94; autumn/summer OR = 1.50, 95% CI = 1.11–2.01).

We used the Forest Raven observations from the eight roadkill routes to assess the effect of roadkill and vegetation cover on raven occurrence. We found that the roadkill-only model was the best model to explain Forest Raven presence (ES = 6.39; Table 1; Figure 3(a)). When analysing the presence of a Forest Raven group on the eight routes, vegetation cover (open versus forest) was the best model, with O/O and F/O environments having higher probabilities of observing Forest Raven groups in comparison to F/F areas (ES: O/O = 4.73, F/O = 3.72; Figure 4(a)).

To analyse the effect of land-use type on the occurrence of Forest Ravens and the effect of season and land-use type on the occurrence of Forest Raven groups we used all data from the road surveys (Table 1). For the presence of at least a single Forest Raven, the model-averaged 'farm' parameter had a positive effect (ES = 1.29; Figure 3(b)), while the 'urban' parameter had a negative effect on raven presence (ES = −2.50; Figure 3(c)). The farm and summer parameters were supported when evaluated against the presence of Forest Raven groups, with a higher probability of raven groups being observed in farm habitats in contrast to non-farmland (ES = 1.96; Figure 4(b)) and a higher probability of being observed in summer compared to spring (ES = 2.23; Figure 4(c)).

Community surveys

We observed 4,391 birds over 144 surveys at 36 sites (Table S5, supplementary material). In total, we counted 818 Forest Ravens and other 'focal species', with the majority of these being Forest Ravens (*n* = 613). Passerine species made up 2,426 of the total count, with

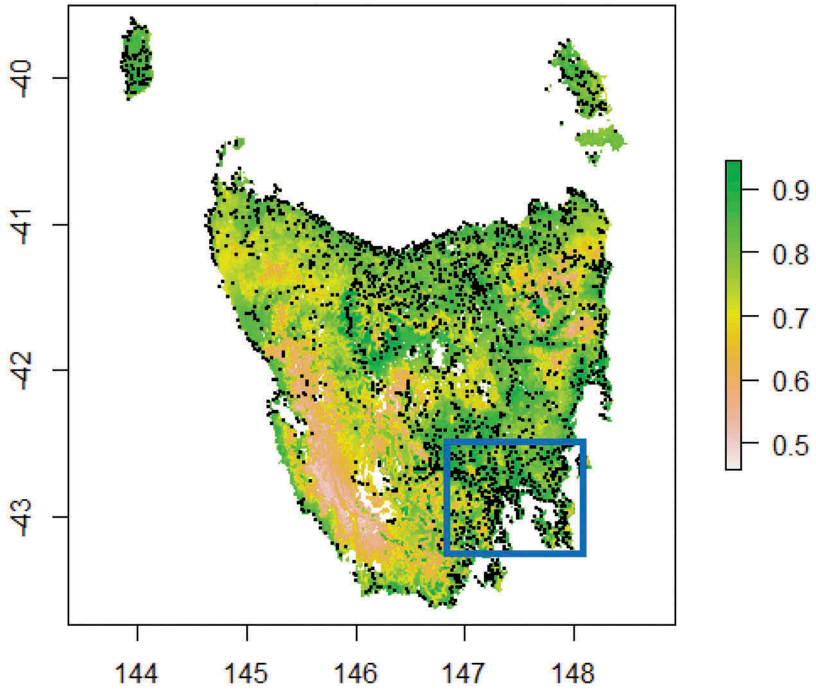

Figure 2. Climate suitability index map for the Forest Raven (*Corvus tasmanicus*) generated from climate-based species distribution models. The black dots indicate historical presence data for the species. Green areas represent grid cells that the ensemble model forecasts as climatically highly suitable and white areas indicate low climate suitability. The approximate location of the road survey regions are indicated by the rectangular inset box.

Table 1. Model rankings for Forest Raven presence along roads in south-east Tasmania. 'On route' models used raven presences found on the eight roadkill data routes and 'all data' models used all raven presences. AIC_c = Akaike's Information Criterion, corrected for small sample size (w_i = AIC_c weight; k = number of parameters). The top three models or all models with $\Delta\text{AIC}_c < 2$ are listed for each analysis. All analyses included a null model in model comparison. The AUC (area under the curve) was calculated for the top models to indicate absolute model fit. Right-hand side of the table shows the model-averaged effects of each parameter on the relevant response variable (SE = standard error; 95% CI = 95% confidence interval; Std. coef = standardised regression coefficient). For the vegetation parameter, F = Forest, O = Open and F/F was the reference factor. For the season parameter, spring was the reference factor.

	Models + variables	AIC_c	ΔAIC_c	w_i	k	AUC	Model-avg parameter	Estimate	SE	95% CI	Std. coef	Effect size
On route	Single raven											
	Roadkill	2258.9	0	0.56	2	0.634	Roadkill	3.33	0.26	(2.82, 3.85)	0.89	6.39
	Roadkill + vegetation	2259.6	0.75	0.38	4	0.634	F/O	0.10	0.15	(−0.19, 0.38)	0.05	-
	Roadkill * vegetation	2263.4	4.49	0.06	6	0.634	O/O	0.11	0.16	(−0.20, 0.42)	0.05	-
							F/O: roadkill	−0.01	0.17	(−0.36, 0.33)	0.005	-
							O/O: roadkill	−0.02	0.18	(−0.37, 0.33)	0.005	-
	Group											
	Vegetation	409.4	0	0.52	3	0.588	Roadkill	0.57	1.01	(−1.42, 2.55)	0.09	-
	Roadkill * vegetation	410.8	1.35	0.27	6	0.588	F/O	1.45	0.66	(0.15, 2.74)	0.34	3.72
	Roadkill + vegetation	411.3	1.82	0.21	4	0.588	O/O	1.74	0.66	(0.44, 3.04)	0.41	4.73
							F/O: roadkill	−0.49	0.98	(−2.42, 1.44)	0.08	-
							O/O: roadkill	−0.59	1.12	(−2.78, 1.60)	0.08	-
All data	Single raven											
	Urban + farm	4135.5	0	0.87	3	0.597	Farm	0.31	0.15	(0.02, 0.59)	0.20	1.29
	Urban + forest	4139.3	3.81	0.13	3	0.596	Urban	−1.02	0.13	(−1.27, −0.77)	0.77	−2.50
	Urban	4147.9	12.40	0.00	2	0.596	Forest	0.04	0.10	(−0.17, 0.24)	0.03	-
	Group											
	Farm + forest + season	595.7	0	0.44	6	0.763	Farm	0.74	0.33	(0.08, 1.39)	0.30	1.96
	Farm + season	596.3	0.58	0.32	5	0.763	Urban	−0.12	0.31	(−0.72, 0.47)	0.05	-
	Farm + urban + season	596.9	1.17	0.24	6	0.744	Forest	−0.17	0.25	(−0.66, 0.32)	0.09	-
							Autumn	0.10	0.36	(−0.60, 0.80)	0.04	-
							Summer	0.88	0.35	(0.20, 1.57)	0.34	2.23
							Winter	0.44	0.34	(−0.22, 1.10)	0.18	-

a large proportion being native passerine species (n = 1,608) and the remainder being introduced (n = 818). Several of the analyses (diversity of native passerines, total number of native passerines) had multiple models with an $\Delta\text{AIC}_c< 2$, but the model-averaged predictors were not supported statistically (Table 2). The total number of passerines had the only supported parameter, the presence of forest habitat, with a slight negative effect (ES = −1.02) on the abundance of passerine birds.

Discussion

We examined the effect of roadkill on Forest Raven population density. The probability of observing a Forest Raven was heightened in areas with higher quantities of roadkill. Additionally, the probability of observing Forest Ravens was higher in agricultural areas and lower in urban environments. There was no apparent net effect of the abundance of Forest Ravens on the total number of passerines or species richness of native passerines. However, there was a slight negative effect of forest habitats on the total number of all passerines. As demonstrated in the climate-based SDM, the survey area was within climatically suitable habitat for Forest Ravens. The SDM also indicates that lower elevation coastal areas are more climatically suitable habitat than the high elevation areas of Tasmania.

Nearly a quarter (23.7%) of all Forest Ravens observed on the eight roadkill routes were within 10 m of roadkill (Table S4), with ravens being six times more likely to be observed when roadkill was present than when roadkill was absent (Table 1; Figure 3(a)). Although omnivorous, Forest Ravens consume large quantities of meat and the presence of roadkill could favour their feeding conditions and elevate their activity and abundance (Rowley and Vestjens 1973; Rees *et al.* 2015). The regular source of roadkill along roadsides may be a superior and more predictable source of nourishment than their regular diet (Lambertucci *et al.* 2009; Planillo *et al.* 2015). Corvid species have demonstrated great cognitive capability, including an extensive memory and the ability to plan ahead by caching resources for later use (Kabadayi and Osvath 2017; Müller *et al.* 2017). It could be argued that the utilisation of roads and roadkill is concomitant with this ability to plan, with ravens understanding the resourcefulness of these roads. Therefore, this research aligns with the hypothesis that ravens modify their foraging behaviour to include regular scavenging of roadsides or nesting closer to roads, because of the reliable source of sustenance they provide (Rowley and Vestjens 1973).

Forest Ravens are able to nest in a range of habitats, and this behavioural plasticity may allow them to thrive in environments of increasing vegetation clearance

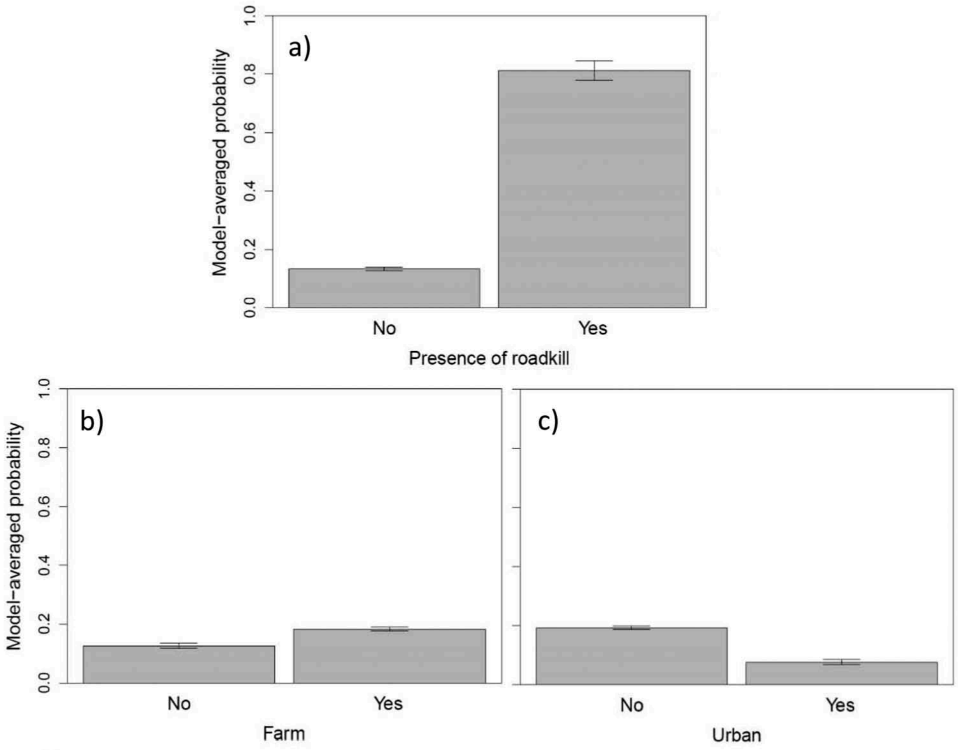

Figure 3. Model-averaged probability of observing a single Forest Raven: (a) given the presence of roadkill, against the absence of roadkill; (b) in a farm habitat in contrast to a non-farm habitat; and (c) in an urban environment in contrast to non-urban habitat. The black vertical lines represent the standard error of the predictions.

(Higgins *et al.* 2006). The results of this study revealed that Forest Ravens were 30% more likely to be observed in farmland environments compared to non-agricultural areas (Table 1; Figure 3(b)). Similarly, groups of ravens were twice as likely to be seen in farmland areas as in areas without agriculture (Figure 4(b)), and more likely in areas with some (3.7×) or all (4.7×) open vegetation, in contrast to areas with closed vegetation (Table 1; Figure 4(a)). One of the largest groups of Forest Ravens (*n* = 32) was observed in a recently ploughed field, suggesting that ravens may benefit from the increased accessibility to invertebrates and seeds associated with the freshly turned soil. Ravens are also found to frequent grazing paddocks, such as those of sheep and cattle, and have been observed in groups of over 500 individuals (Higgins *et al.* 2006; Talmage 2011). We found that urban environments support relatively few Forest Ravens, with the species being 2.5 times more likely to be observed in non-urban areas, in contrast to urban areas (Table 1; Figure 3(c)). This is contrary to the hypothesis and conflicts with the results of past literature, which largely found a positive relationship between corvid populations and urbanisation (Marzluff and Neatherlin 2006; Marzluff *et al.* 2007; Wilson *et al.* 2015). However, the negative effect found within this study could be due to the study design's lack of focus on urban areas or through neglecting certain features of urbanisation, such as refuse centres (Karlsson 2003; Higgins *et al.* 2006).

In comparison to summer and spring, we found there were a greater number of Forest Raven observations in winter and autumn (Table S4). During the winter and autumn months, carrion becomes an increasingly important resource for Forest Ravens as invertebrates and seeds are found at lower densities (Rowley and Vestjens 1973). Therefore, ravens may be observed more often along roads during these seasons because they modify their behaviour to favour roads for foraging, where they find a reliable source of roadside carrion (Higgins *et al.* 2006; Hobday and Minstrell 2008). We found that groups of Forest Ravens were 2.2 times more likely to be observed in summer than in spring (Table 1). During the spring breeding season, Forest Ravens are generally found singly or in breeding pairs, with established pairs maintaining a breeding territory (Lawrence 2009). While adult breeding pairs can occupy a territory throughout the year, ravens are regularly seen in large flocks outside the breeding season with juveniles joining mobile flocks after the breeding season (Rowley 1973; Higgins *et al.* 2006; Lawrence 2009).

There was no effect of Forest Raven abundance on either the total number or the species richness of passerines (Table 2). In fact, in this study, there was a higher

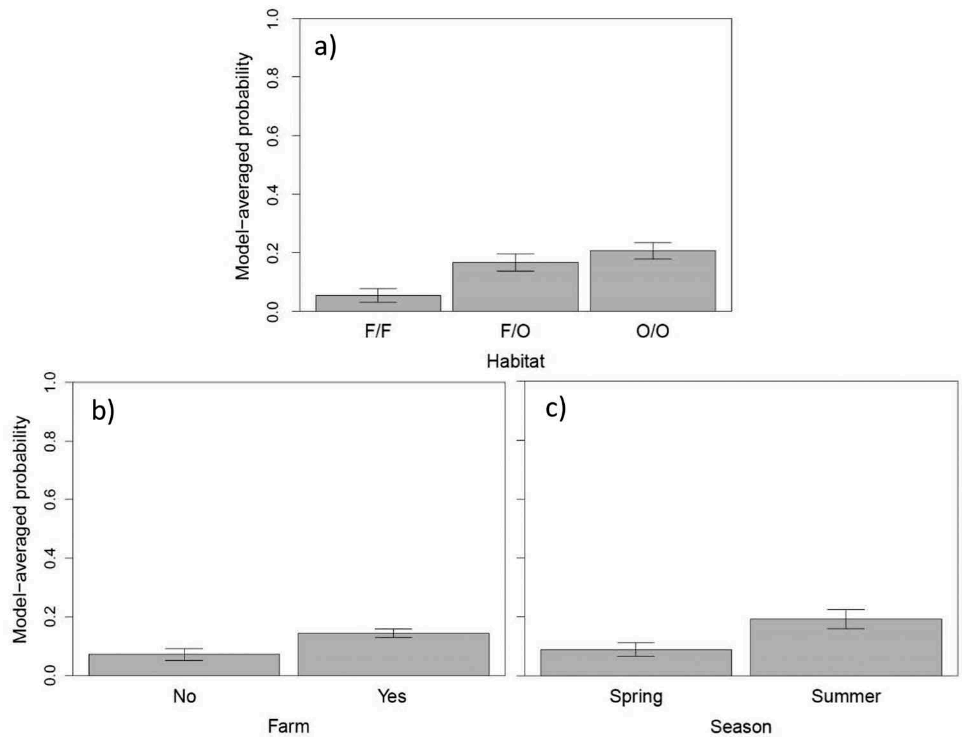

Figure 4. Model-averaged probability of observing a group of Forest Ravens: (a) in areas of open/open (O/O) and forest/open (F/O) vegetation cover in comparison to an area with forest/forest (F/F) vegetation cover; (b) in a farm habitat in contrast to a non-farm habitat; and (c) in the season of summer in contrast to spring. The black vertical lines represent the standard error of the predictions.

Table 2. Model rankings for bird community surveys at sites in south-east Tasmania. AIC_c = Akaike's Information Criterion corrected for small sample size (w_i = AIC_c weight; k = number of parameters). The top three models or all models with $\Delta AIC_c < 2$ are listed for each analysis. All analyses included a null model in model comparison. Predictive R^2 was calculated for the top models to indicate absolute model fit. Right-hand side of the table shows the model-averaged effects of each parameter on the relevant response variable (SE = standard error; 95% CI = 95% confidence interval; Std. coef = standardised regression coefficient). Human = human density; Traffic = traffic density; Raven = abundance of Forest Ravens.

Models + variables	AIC_c	ΔAIC_c	w_i	k	Pred. R^2	Model-avg parameter	Estimate	SE	95% CI	Std. coef	Effect size
Diversity of native passerines											
Forest	107.2	0	0.51	4	0.13	Forest	0.24	0.19	(−0.14, 0.61)	0.63	-
Forest + human	108.5	1.34	0.27	5	−0.07	Human	0.04	0.09	(−0.14, 0.23)	0.37	-
Null	108.9	1.66	0.22	3	0.08						
Total number of native passerines											
Raven	220.4	0	0.28	4	−0.02	Raven	0.006	0.01	(−0.01, 0.03)	0.45	-
Null	220.6	0.20	0.25	3	−0.03	Traffic	−0.04	0.1	(−0.25, 0.16)	0.30	-
Traffic	220.8	0.40	0.23	4	−0.01	Urban	−0.05	0.13	(−0.31, 0.22)	0.25	-
Urban	221.9	1.58	0.13	4	−0.05						
Urban + raven	222.2	1.88	0.11	5	−0.06						
Total number of all passerines											
Forest + human	266.2	0	0.33	5	−0.01	Forest	−0.56	0.22	(−1.02, −0.10)	0.59	−1.02
Forest	267.0	0.89	0.21	4	0.01	Human	−0.18	0.24	(−0.68, 0.31)	0.18	-
Forest + urban	267.3	1.16	0.19	5	−0.01	Urban	−0.07	0.19	(−0.45, 0.31)	0.09	-
Forest + human + traffic	267.8	1.65	0.14	6	−0.10	Traffic	−0.02	0.08	(−0.19, 0.14)	0.07	-
Forest + farm	268.0	1.86	0.13	5	0.03	Farm	0.04	0.14	(−0.24, 0.33)	0.07	-

number of passerines and greater passerine species richness in areas with higher densities of Forest Ravens (Table S5), which could be due to several explanations. Firstly, Forest Ravens could be reducing the number of true predators, such as raptors, for small passerine species, as they are commonly seen mutually chasing away larger threatening birds (Higgins *et al.* 2006). Therefore, ravens could be suppressing raptor predation on small birds in areas the ravens frequent, and thus indirectly maintaining higher populations of passerine species by reducing both perceived and realised predation risk. Secondly, both populations could be maintained by large quantities of resources and the overall productivity of the area. As we completed the community surveys in early spring there may have been sufficient resources to support ravens without needing to predate on birds or nests. Over winter, Forest Ravens depend heavily on carrion; however, during early spring there is an increase in insect availability, which reaches a peak in summer (Rowley and Vestjens 1973). Forest Ravens may give preference to insects during this period as it may be less energy consuming to feed on insects than preying on small passerines. Thirdly, prey species could demonstrate varied anti-predator behaviour throughout the year. Outside the breeding season, many prey species utilise ‘safety in numbers’ anti-predator strategies, such as aggregation in flocks (Lima and Dill 1990). It is possible that passerine species may only use predator avoidance techniques, such as hiding and nesting away from predators, during the breeding season when flocking is rare (Lima 2009). Therefore, the effect of Forest Raven density on passerine abundance and species diversity may only be evident during the breeding season. Finally, passerine density could be influencing the presence of Forest Ravens, because they are prey items for the ravens, but this is less likely given that the inferred predation pressure (raven density) did not vary between sites of high and low passerine abundance.

Our results indicated there was a minor negative association between forest habitats and the total number of passerines. During several surveys, large flocks (>30) of Common Starlings (*Sturnus vulgaris*) were observed in agricultural and urban areas but were generally absent from forested areas. As there was no effect of forest habitats on the total number of native passerines and the total number of all passerines included introduced species, it is likely that these large flocks of Common Starlings are producing this negative effect. While our study found no compelling evidence to support the hypothesis that Forest Ravens are currently having an impact on smaller bird species, increases in Forest Raven abundance due to agricultural expansion and increased carrion could result in the amplification of predation pressure on avian prey in future decades (Rees *et al.* 2015). Forest Ravens have been observed to attack and eat birds as large as Little Penguins (*Eudyptula minor*), and raid seabird colonies for eggs and young (Higgins *et al.* 2006; Talmage 2011). It has been suggested that, in most cases, corvids will have an impact on the productivity and abundance of potential prey species (Madden *et al.* 2015).

To understand the effects of forest-raven predation on passerine species, community surveys should be extended over all four seasons to investigate seasonal influences. As we completed surveys in late winter/early spring, Forest Ravens probably had sufficient resources during this period (e.g., invertebrates) and were thus not compelled to prey on passerines (Rowley and Vestjens 1973). Expanding the study over an entire year might reveal impacts that were potentially masked by a seasonal effect. Further study could also focus on areas that are indicated as climatically unsuitable for Forest Ravens. This will allow for a comparative study between areas of high and low Forest Raven density and test the accuracy of the SDM.

Conclusion

This study assessed how Forest Ravens make use of roadkill, the influence of different land-use types on Forest-Raven presences, and the implications that Forest Ravens might exert on the smaller bird fauna. The results show that the probability of observing a Forest Raven is higher in agricultural environments and areas with greater quantities of roadkill. However, there was no evident effect of the abundance of Forest Ravens on the species richness or abundance of passerines. This could be due to a seasonal effect that was not examined within this study, or Forest Ravens could be offsetting this effect by benefiting woodland birds via the reduction of predation from other species, such as raptors. These aspects require further investigation. As fluctuations in the population and range of corvids could have ecological, social and economic consequences, it is vital the group is the subject of continued study, with specific emphasis on how corvids interact with other bird species and humans alike.

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