

An integrated occupancy and space-use model to predict abundance of imperfectly detected, territorial vertebrates

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Summary

1. It is often highly desirable to know not only where species are likely to occur (i.e. occupancy) but also how many individuals are supported by a given habitat (i.e. density). For many animals, occupancy and density may be determined by distinct ecological processes.

2. Here we develop a novel abundance model as the product of landscape-scale occupancy probability and habitat-scale density given occupancy. One can conceptualize our model as fully packing a landscape with home ranges or territories based on habitat quality, and then subtracting territories based on a probabilistic process that accounts for the fact that species rarely exhibit full occupancy across heterogeneous landscapes. The model is designed to predict abundance at fine spatial scales, using resolutions equal to or smaller than a single home range or territory.

3. We demonstrate this model on the Black-backed Woodpecker (*Picoides arcticus*), a species of management concern linked to post-fire forests. Occupancy is derived from a regional monitoring effort, while density given occupancy comes from a telemetry study of variation in territory size. A Bayesian framework is used to combine independent occupancy and home-range size models and predict abundance of Black-backed Woodpeckers at 4 fires that burned in 2012 or 2013. Predictions are evaluated with independently collected survey data, showing that the model is successful at predicting both absolute abundance at fires as well as relative abundance within and among fires.

4. The conceptual model presents a promising new framework for fine-scale modelling of density and abundance for other territorial yet elusive species. Telemetry and occupancy data are widely collected for many species, but rarely utilized in combination, and the ecological exploration of the factors that determine occurrence versus home-range size may provide useful biological insight. As applied to the Black-backed Woodpecker, the model provides a tool for resource managers to explore trade-offs in retaining burned forest habitat versus managing for other post-fire goals, such as salvage logging or reforestation efforts that require snag removal.

Key-words: Bayesian, Black-backed Woodpecker, density, home range, *Picoides arcticus*, population size, wildlife habitat model

Introduction

Abundance is a critical parameter of interest for management and conservation of wildlife populations, yet it remains an enigmatic quantity that frequently defies estimation. If the target species is stationary and homogeneously distributed, then abundance is a simple scaling of density, but homogeneity is rare and most species show highly skewed abundance profiles within their distributions (Brown, Mehlman & Stevens 1995; Gaston 2003). For total abundance within a closed population, capture–mark–recapture methods provide statistically elegant estimations of population size given fulfilment of data demands and a marked population (Sollmann *et al.* 2013). Prediction of abundance, however, requires understanding of

not just where species occur, but also how they are spatially arranged or aggregated within the areas of occurrence or use (Gaston 2003). Without understanding both processes, accurately predicting abundance surfaces may not be possible. For example, N-mixture models can predict abundance as resulting from a single process related to environmental covariates, but these predictions may only provide relative rather than absolute indices (Royle & Dorazio 2006; Zipkin *et al.* 2014).

Many scientific, management, or conservation goals require accurate and fine-scale predictions of absolute abundance that can be extrapolated to other landscapes. Additionally, many organisms are not distributed in the configurations and concentrations that facilitate abundance modelling by established methods. For example, Poisson-type processes (e.g. N-mixture models) fit better when the number of individuals recorded per sample is >1. For many species, however, abundance data typically are recorded as 1 or 0, and only rarely are abundances >1

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observed (Brown, Mehlman & Stevens 1995). This numerical limitation is the status quo for species that are wide-ranging (i.e. have large home ranges), highly territorial (i.e. exhibit little overlap in territories), or cryptic, including many mammals and birds, particularly those at higher trophic levels and likely to be targets of management or conservation concern (Gopalaswamy *et al.* 2012a,b). Moreover, the concentration of abundance data into counts of 0 or 1 is expected for any non-clumped species when the sampling unit is equal to or smaller than the typical territory or home-range size.

For species with low abundance or low detection rates, occupancy (i.e. the proportion of sampled area occupied or used by a species; MacKenzie *et al.* 2002; MacKenzie 2005) has risen as the preferred metric for evaluating spatial distributions in heterogeneous landscapes (Gopalaswamy *et al.* 2012a). This has been aided by the advent of flexible modelling frameworks that account for detectability (i.e. the probability that not all individuals present are detected) by treating non-detections as a type of zero-inflation that can arise from both state and observation processes (MacKenzie *et al.* 2006). Managers and conservationists, however, are often concerned not only with where a species occurs, but how many individuals occur there. Occupancy is mathematically derived directly from abundance, but the relationship between occupancy and abundance is species-specific, and generally not linear (Gaston 1999). Calibrating occupancy to relative abundance is possible (Royle & Nichols 2003), but has yielded widely variable results, likely due to uncontrollable sampling processes (Gopalaswamy *et al.* 2015). Even at fine spatial resolutions, when occurrence closely approximates abundance, occupancy does not differentiate individuals, and thus should not be summarized across spatial units to approximate abundance. For these reasons, occupancy alone is often a poor surrogate for abundance.

Much of the divergence of abundance from occupancy can be attributed to behaviour, and the complex ways with which species form spatial aggregations in response to resources (including food), conspecifics, other competitors and predators (Gaston 2003; Yackulic *et al.* 2014). Although an ideal abundance model would account mechanistically for all such factors, a generalized model of such complexity is intractable. For many species, however, the various behavioural responses that integrate to create abundance patterns can be indirectly assessed through variation in home-range or territory size (van Beest *et al.* 2011). In a fully occupied landscape, home-range size and home-range overlap are key determinants of the abundance–occupancy relationship (McLoughlin, Ferguson & Messier 2000).

Here we describe a new theoretical model that integrates the probability of occupancy with home-range size variation to predict absolute abundance across a spatially heterogeneous landscape (Fig. 1). Through the integration of complementary information from different data sources, we build upon the theoretical framework recently developed for spatial capture–recapture models which has sought to better describe home-range shapes in the context of abundance estimation (Sollmann *et al.* 2013; Popescu, De Valpine & Sweitzer 2014). Our model is explicitly developed for fine-resolution spatial

modelling of abundance, where spatial sampling units are equal to or smaller than average home-range sizes, such that occurrence approximates abundance.

We illustrate this model through a case study predicting the abundance of Black-backed Woodpeckers (*Picoides arcticus*) in recently burned forests of California, USA. The stochastic and unpredictable nature of wildfire and the rapid post-fire decline in the economic value of timber necessitates prompt assessment of post-fire forest resources and wildlife populations to make timely decisions about post-fire forest management. Our aim in applying our theoretical model to Black-backed Woodpeckers was to develop a tool to allow land managers to make decisions about burned forest management that account for both spatial variation in abundance and total absolute abundance of Black-backed Woodpeckers on the local landscape. We parameterize our abundance model using occupancy data on Black-backed Woodpeckers collected at 94 fires that burned in California between 2009 and 2013, and with home-range estimates of 22 individual birds tracked at three fires between 2011 and 2013. We then apply the model to make spatially explicit predictions of woodpecker abundance at four fires that burned in 2012 or 2013, and evaluate our predictions using independent survey data collected across those fires one year after they burned.

Conceptual framework

Our abundance model (Fig. 1) integrates the factors that determine where a species is likely to occur (occupancy) with the factors that determine how many individuals inhabit an occupied area (home-range or territory size variation). Such a model accounts for broad-scale environmental gradients that determine distributions (e.g. climate and elevation) as well as fine-scale habitat variables that determine aggregation. A discretized outcome of our model can be imagined as fully packing a landscape with home ranges, and then subtracting home ranges based on a probabilistic model that accounts for the fact that heterogeneous landscapes are rarely occupied at maximum density (Fig. 1). The continuous parameterization of our model as implemented calculates the expected density within any given spatial unit and then calibrates this density by the probability that the spatial unit is used by the target species.

In building a spatial model at the subhome-range scale, we interpret occupancy as the proportion of time that a focal species uses a spatial unit during a defined time period (MacKenzie 2005), which is consistent with and statistically identical to most contemporary uses (Bailey, MacKenzie & Nichols 2014). We also adopt here the terminology of Burt (1943), describing a home range as the area used by an individual over some period of time (e.g. a breeding season). As proposed, our model assumes that home ranges are distinct and do not overlap (typically a characteristic of ‘territories’), although the abundance model could be easily modified to allow for overlapping home ranges (see Discussion).

While occupancy modelling has been widely applied to conservation and management objectives, intra-species variation in home-range size is less frequently evaluated (van Beest *et al.*

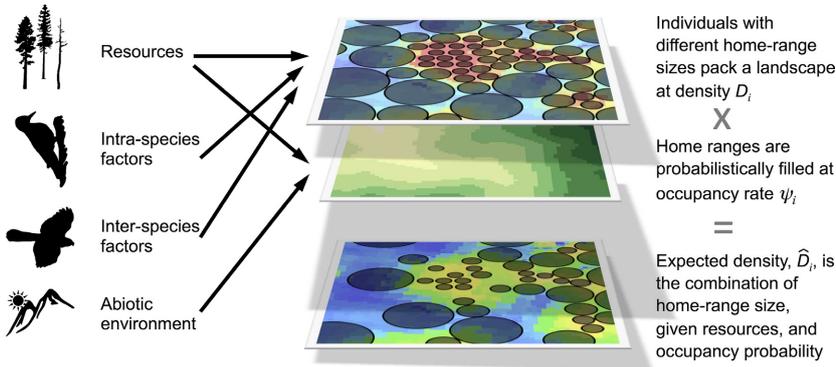


Fig. 1. Conceptual model integrating home-range size variation and occupancy probability to estimate density of individuals in a heterogeneous environment.

2011). A fundamental feature of home-range size variation in many species is that a home range is only as big as necessary to provide adequate resources (Odum & Kuenzler 1955; McLoughlin & Ferguson 2000; Adams 2001). Larger home ranges of territorial species require greater patrolling efforts (Pyke 1979; Hixon, Carpenter & Paton 1983; Eason 1992), giving less time for foraging or parental care (Pyke 1979; Schoener 1983; Sillett, Rodenhouse & Holmes 2008) and incurring greater energetic costs (Myers, Connors & Pitelka 1979; Carpenter, Paton & Hixon 1983; Eason 1992), either of which could reduce individual fitness (Both & Visser 2000; Sillett, Rodenhouse & Holmes 2008). Convergent pressures constrain home-range size to optimize boundaries around the smallest areas that provide the resources necessary for reproduction and survival (Adams 2001).

Empirical evaluations of home-range size can yield species-specific equations that describe the scaling relationship of home ranges to resources. Mathematically, home-range size, H , can be modelled as a linear combination of resources, X , and fit through an appropriate link function (e.g. logarithmic). When such a model is applied to a spatially explicit resource map with grid size smaller than a home range, the resulting value for cell i is interpreted as the expected home-range size of an individual if its habitat were homogeneously filled with resources at the density of cell i . It is thus easier to transform this quantity:

$$D_i = c/H_i = c/f(X_i), \quad (\text{eqn 1})$$

where $f(X_i)$ is the home-range variation function, and c is a constant that rescales from the unit area of home-range size (e.g. km^2) to the area of grid cell i . The transformed quantity, D_i , represents the maximum density of the species expected per unit area given the resources available in area i . The scale at which the model can be implemented is variable, but the incorporation of spatial heterogeneity into both occupancy and home-range size components facilitates model implementation at fine spatial scales (i.e. smaller than a single home range). Where resource heterogeneity exists within home ranges, small predictive grid sizes will be optimal and predicted values of D will be <1 or $\ll 1$.

The maximum density given resources, D_i , implies that all home ranges are occupied and individuals are continuously packed across a landscape. Occupancy is often <1

and thus D_i overestimates true abundance. We must thus separately model the environmental factors, E_i , that describe the probability that cell i is used. This probability of occupancy, ψ_i , can be modelled as a linear combination of cell-specific covariates E_i through a logit link function, and given adequate survey data, this model can estimate parameters while accounting for false absences in the underlying data (e.g. MacKenzie *et al.* 2002). While any specific actualization of home-range filling across a landscape would be conceptualized as a Bernoulli process through which individual home ranges are either occupied or not occupied given underlying environmental conditions, the average outcome can be estimated simply by the equation

$$\hat{D}_i = \psi_i \cdot D_i. \quad (\text{eqn 2})$$

The quantity \hat{D}_i represents the expected density of individuals in area i , accounting for incomplete habitat usage. The total abundance of individuals, N_I , within area I , composed of $i = 1, \dots, m$ cells – each with an expected density – is the sum of those cells:

$$N_I = \sum_{i=1}^m \hat{D}_i. \quad (\text{eqn 3})$$

Simply put, through the multiplicative combination of two component models of space use and space filling, ψ_i and D_i , a spatial summation of absolute abundance, N_I , can be estimated.

Field implementation of model

Our case study implements the previously described conceptual model within a Bayesian framework to predict abundance of Black-backed Woodpeckers in recently burned forests of the Sierra Nevada, southern Cascades and Modoc Plateau of California. The abundance prediction is a derived combination of two component models, one for Black-backed Woodpecker occupancy (Saracco, Siegel & Wilkerson 2011) giving ψ_i and one for home-range size (Tingley *et al.* 2014) giving D_i . For more information on data sources and individual model testing and evaluation, please refer to Saracco, Siegel & Wilkerson (2011) or Tingley *et al.* (2014). For a more thorough

description of our methods than is provided below, particularly parameterizations of ψ_i and D_i as used in this case study, please see Appendix S1 in Supporting Information.

OCCUPANCY MODEL FOR ψ_i

Occupancy models estimate a location's probability of usage by a species, unbiased by false absences (Bailey, MacKenzie & Nichols 2014). Survey data inherently contain an unknown quantity of false absences (i.e. non-detections when the species was truly present), and accounting for them prior to interpretation of data is critical. The model used here to predict ψ_i , parameterized following Saracco, Siegel & Wilkerson (2011), follows a 'single-season' occupancy modelling structure (MacKenzie *et al.* 2002), although a generalized implementation of our abundance model could arguably use any of numerous available methods to model the true probability of a site's usage by a species.

Data to parameterize the occupancy model come from Black-backed Woodpecker surveys we conducted as part of the USDA Forest Service's regional Management Indicator Species (MIS) monitoring programme across ten National Forests in California. Between 2009 and 2013 we visited approximately 50 fires annually that had burned in the 10 years prior to each sampling year (roughly, the time period in which Black-backed Woodpeckers are likely to use burned stands), and surveyed at up to 20 point-count stations per fire. Black-backed Woodpecker surveys were conducted during a single visit to each point, with each point visit divided into five passive and three broadcast survey intervals. Although many fires were surveyed repeatedly in successive years as part of our monitoring, we used data from only the first year in which each fire was surveyed in order to avoid pseudoreplication at the point level. Our occupancy model used data from 1707 unique point counts surveyed across 94 fires between 2009 and 2013.

Different covariates were used for modelling occupancy and detectability, following Saracco, Siegel & Wilkerson (2011). Detectability was modelled as a function of survey interval duration (3-minute versus 2-minute), survey type (passive versus broadcast) and day of year. Occupancy at survey points was modelled with multiple covariates: latitude, elevation (orthogonal to latitude by using elevation~latitude residuals) including a quadratic effect, pre-fire canopy cover, fire severity (% change in canopy cover), the presence of large trees (California Wildlife Habitat Relationships [WHR] size class >3) and WHR forest class (included as a random effect). Although Saracco, Siegel & Wilkerson (2011) also included snag density as a covariate, it was not informative for predicting occurrence, and so we excluded it from our occupancy model.

HOME-RANGE SCALING MODEL FOR D_i

To parameterize the model of home-range scaling, we used data from an independent study exploring variation in home-range size of Black-backed Woodpeckers nesting in

montane burned forests of northern California (Tingley *et al.* 2014). For that study, we radio-tracked Black-backed Woodpeckers nesting in three forested areas of California that burned between 2 and 5 years before the initiation of tracking. Results reported by Tingley *et al.* (2014) include data from 15 individual home ranges tracked in 2011 and 2012, and here, we supplement this with seven additional birds tracked in 2013.

To calculate home-range size, we used Brownian bridge kernel estimation, which accounts for the temporal autocorrelation present in most tracking data (Horne *et al.* 2007; Tingley *et al.* 2014). Home-range sizes evaluated at the 95th percentile ranged in size from 24 to 304 ha. Tingley *et al.* (2014) evaluated several factors that could explain this variation and used a multi-model framework to find best support for a loglinear relationship of snag basal area to home-range size. As snag basal area increased, home-range size decreased. We used the 22 home ranges to fit a Bayesian model of home-range size using the same model structure as the final model employed by Tingley *et al.* (2014).

PREDICTING ABUNDANCE

Posterior predictive surfaces of ψ_i and D_i were derived at the four evaluation fires using gridded (raster) spatial data for the various input variables and the respective Bayesian parameter estimates for ψ_i and D_i . Implementing eqn (2), the posterior surfaces of ψ_i and D_i were combined to give a posterior prediction for \hat{D}_i . After deriving \hat{D}_i , any spatial group of pixels can be summed via eqn (3) to produce N_i . The clear advantage of an integrated Bayesian framework for model prediction is that uncertainty in component models of occupancy and home-range variation are propagated through the calculations and into \hat{D}_i , thus providing critical information on spatial uncertainty in abundance, as well as uncertainty in values of management interest, such as N_i .

A limitation in predictively applying the home-range model of Tingley *et al.* (2014) in this context is that snag basal area is not generally an available data layer for recently burned forests. To apply the home-range model in a predictive framework, we had to first model snag basal area as a function of available, remotely sensed habitat variables. We used 3237 sample points of snag basal area within recently burned forests occupied by Black-backed Woodpeckers (Tingley *et al.* 2014) to create a loglinear model predicting snag basal area as a function of three variables: pre-fire canopy cover, burn severity (1st and 2nd order polynomials) and dominant tree size class (ordinal), as well as interactions between burn severity and pre-fire canopy cover (data sources as described previously). Identical to the other component models, we fit this snag basal area model in a Bayesian framework and used the full posterior to propagate uncertainty through to final estimates of \hat{D}_i and N_i .

For the fitting of all Bayesian models used in the case study, we implemented Markov chain Monte Carlo (MCMC) methods in the software package JAGS (Plummer 2003) using the R package 'R2jags' (R Core Team 2014; Su & Yajima 2014). We

used vague prior distributions for all model parameters. For covariate effects in each model we used normal priors with a mean of 0 and a precision of 0.001. For the intercepts of the detection and ψ models, we defined priors for inverse-logit transformed parameters using a uniform prior bounded by 0 and 1. After a burn-in of 25 000, the posterior was sampled from three chains yielding 7500 posterior draws. In all cases, convergence was assumed when the Gelman-Rubin statistic of all monitored parameters calculated across three chains was <1.1 (Gelman *et al.* 2004).

WOODPECKER SURVEYS FOR MODEL EVALUATION

We evaluated our abundance model for Black-backed Woodpeckers by comparing predicted density surfaces for four fires that burned in 2012 or 2013 with thorough grid-based surveys for woodpeckers 1-year post-fire, before post-fire logging occurred. We conducted the evaluation in new fires that had not been previously used for either occupancy or telemetry work, in order to provide an independent predictive test.

Grid-based evaluation surveys were conducted at the Barry Point, Chips and Reading fires in 2013, and the Rim fire in 2014. All sites had burned in the year before surveys, and fires ranged in size from 11 424 ha (Reading) to 102 925 ha (Rim). Surveys were conducted at the vertices of a 500-m grid throughout large subsets of USDA Forest Service land that had been forested pre-fire and could be safely accessed (generally with slope $<35^\circ$). Using 6-min broadcast surveys, we surveyed for Black-backed Woodpeckers at 171, 284, 165 and 488 points within the Barry Point, Chips, Reading and Rim fires, respectively (Fig. 2).

MODEL EVALUATION CALCULATIONS

For each fire, predictive models for ψ_i , snag basal area, D_i and \hat{D}_i were applied on a pixel-by-pixel basis using rasters of remotely sensed environmental and habitat variables. For every pixel, parameter values for component models were randomly drawn 7500 times (an arbitrarily large number) from each posterior distribution and used to derive 7500 posterior predictions of ψ_i , snag basal area, D_i and \hat{D}_i . Posterior prediction distributions were summarized by mode, standard deviation and 95% Bayesian credible interval (BCI) for each pixel. In some sections of each fire, snag basal area was predicted to be far greater or far lower than had been used as training data for the home-range size variation model (H). Because of the log link, such snag values predicted impossibly large or small home-range sizes. Consequently, we truncated home-range size predictions to a minimum of 20 ha and a maximum of 825 ha, which are the limits of observed 95th-or-greater percentile home range sizes of Black-backed Woodpeckers across published studies (Rota *et al.* 2014; Tingley *et al.* 2014).

We compared location and frequency of Black-backed Woodpeckers at the 4 fires to posterior predictions of \hat{D}_i . We wished to test whether \hat{D}_i provided both a strong relative index of abundance (i.e. through comparisons across space) and an accurate absolute estimate of abundance. Although evaluation data were not the true abundances (i.e. the evaluation data were also biased by imperfect detection), the high overall probability of detection of our survey methods (~ 0.70 ; Saracco, Siegel & Wilkerson 2011) justifies the use of these data for evaluation purposes. To compare relative abundance we used two metrics to assess predictive performance. Since the conceptual model was developed for fine-scale predictions at the

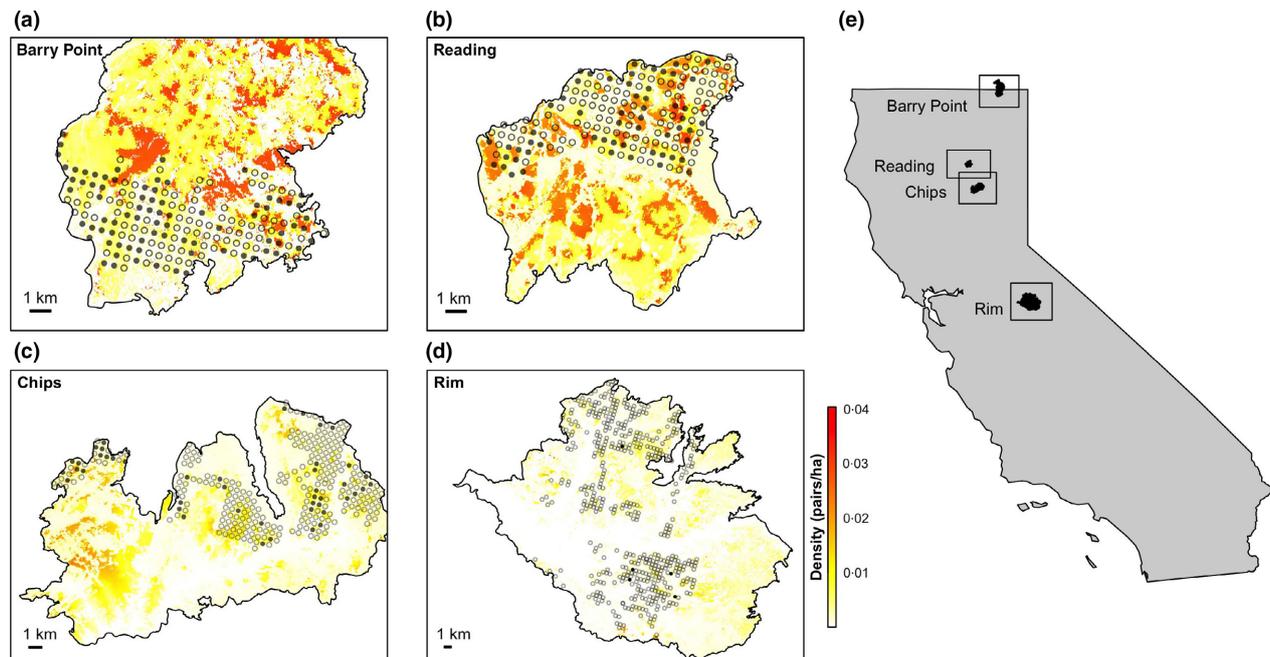


Fig. 2. Predicted density of Black-backed Woodpeckers (pairs/ha) at four fires, (a) Barry Point, (b) Reading, (c) Chips and (d) Rim, within (e) California. Independent evaluation points were surveyed for woodpeckers across 500-m grids within accessible USDA Forest Service land at each fire. Points with detections (solid circles) generally overlap with areas of higher predicted density (redder colours).

subhome-range scale where abundance approximates occurrence, observed abundance data were predominantly binary and were treated as strictly binary. Consequently, evaluation metrics were chosen for their ability to evaluate discrimination of dichotomous variables (i.e. presence of a woodpecker at a survey site versus its assumed absence) by a continuous predictor (\hat{D}_i). Chosen metrics were: (i) the area under the receiving operator curve (AUC); and (ii) the point biserial correlation (r_{pb}), which is equivalent to a Pearson correlation (Elith & Graham 2009). AUC evaluates discrimination based on relative ranks, while r_{pb} takes into account how far the prediction is from the observation (Elith & Graham 2009). AUC scores vary from 0 to 1, with a score of 0.5 indicating discrimination no better than random. Biserial correlation, like the familiar Pearson correlation, varies from -1 to 1 , and follows a t distribution. To assess absolute abundance, we took the total number of grid points with detections as our best estimate of the true number of Black-backed Woodpeckers occupying the surveyed portion of each fire. To calculate an equivalent prediction of N_I , we summed all values of \hat{D}_i within 250 m of each point (assumed maximum detection radius) to estimate a point-level abundance, \hat{D}_{pt} , and then excluded points with an average \hat{D}_i that represented home ranges >825 ha (i.e. too low density to support individuals). The remaining \hat{D}_{pt} were summed and doubled, to translate from pairs (i.e. what the model predicts) to individuals (i.e. what the surveys measure).

The contribution of component models to overall uncertainty in N_I predictions at each fire was evaluated by calculating three additional posterior N_I distributions. For each of these N_I posteriors, component model parameters were held fixed at mean posterior values for two models, while parameters for the third model were drawn from the full posterior. Thus, each calculation of N_I illustrates the relative contribution of uncertainty in overall N_I predictions per fire from component models.

Results

After implementing the combined occupancy-telemetry abundance model, predicted abundance of Black-backed Woodpeckers at four fires showed strong agreement with both relative and absolute abundance as measured through grid-based surveys 1-year after fire. Woodpecker abundance and

density varied widely across the four fires, with detections at 47% of survey points at Barry Point, 35% of points at Reading, 16% of points at Chips and 1% of points at Rim, which translate to observed densities of 9.4, 6.9, 3.2 and 0.2 ($\times 10^{-3}$ pairs/hectare), respectively (Table 1; Fig. 2). These results correlated strongly ($\rho = 0.98$, $P = 0.02$) with modal predicted average densities of woodpeckers in the surveyed portions of these 4 fires, which varied from 6.8, to 6.1, to 2.1, to 1.3 ($\times 10^{-3}$ pairs/hectare) for Barry Point, Reading, Chips and Rim, respectively (Table 1).

While the comparison of average predicted densities across fires indicated that the abundance model was spatially transferrable, it is advantageous for management purposes for \hat{D}_i predictions to be relative within fires. In other words, we tested whether areas with high predicted densities within individual fires were also more likely to have detections. Points with detections had a significantly higher mean predicted density than points without detections ($r_{pb} = 0.402$, $t = 14.6$, $P < 0.001$; Fig. 3). Overall discrimination ability was high, with an AUC value of 0.806.

Estimates of the total number of Black-backed Woodpeckers in surveyed areas of the four fires demonstrated the model was moderately successful at predicting absolute abundance (Table 1). Observed totals overlapped 95% BCI of N_I for Reading and Chips and were just below and just above 95% BCI for Rim and Barry Point, respectively. Relative contribution of component models to overall uncertainty in N_I predictions varied from fire to fire based on the underlying environmental conditions, but generally the occupancy and home-range size models contributed equally to overall uncertainty, while the snag basal area model contributed less (Fig. 4).

Discussion

CASE STUDY AS EVALUATION OF CONCEPTUAL MODEL

Abundance is a notoriously difficult ecological phenomenon to predict as it is affected by myriad factors that can change in importance at different spatial scales (Gaston 2003; He & Gaston 2003). Here, we have outlined a new conceptual model for predicting abundance that can be used at smaller spatial scales, and which centres on independently modelling the

Table 1. Results of model-based abundance predictions and grid-based Black-backed Woodpecker surveys for four fires in California serving as evaluation tests

Fire	Predictions*		Observations	
	Mean \hat{D}_i (pairs per ha)	N_I (total individuals)	Density (pairs per ha) [†]	N_I (total individuals)
Barry point	0.0068 (0.0044–0.0113)	45.9 (29.3–75.8)	0.0094	80
Chips	0.0021 (0.0013–0.0043)	24.6 (10.3–47.2)	0.0032	45
Reading	0.0061 (0.0038–0.0102)	39.8 (23.4–66.0)	0.0069	57
Rim	0.0013 (0.0008–0.0024)	19.2 (7.6–41.8)	0.0002	6

*Model estimates given as: posterior mode (95% BCI).

[†]Observed density estimate assumes that males and females within pairs can be detected separately.

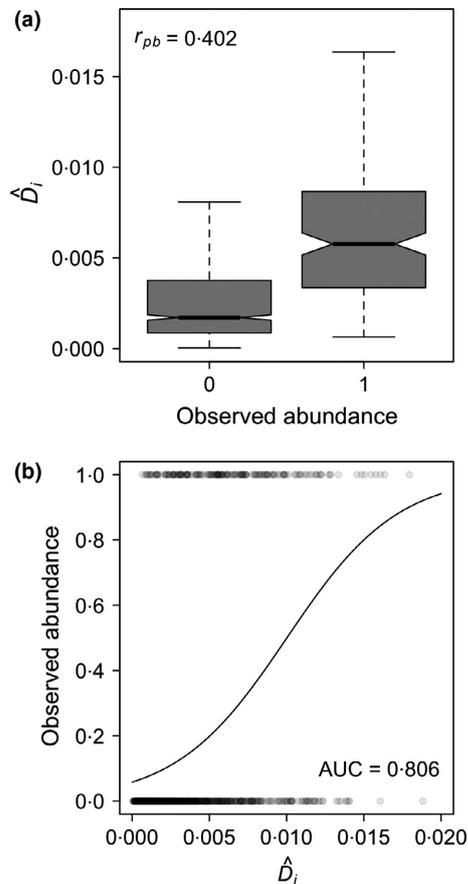


Fig. 3. Predictive ability of abundance model evaluated by independent survey points combined across four fires. Boxplot (a) and logistic regression model (b) of observed abundance versus the average predicted point-level density (pairs per ha). The ability of the model prediction to discriminate points with woodpeckers versus points without woodpeckers is supported by both r_{pb} and AUC.

relationships between the factors that determine home-range size and the factors that determine landscape usage. Our case study, which applies this model to Black-backed Woodpeckers in burned forests of California, indicates that the method can ably predict relative abundance across space, as well as absolute abundance within defined areas.

However successfully our model predicted Black-backed Woodpecker abundance, the evaluation identified several aspects that could be improved. Foremost, our model predictions showed low precision in total abundance (N_i), with wide 95% BCIs. While the general accuracy of the predictions should moderate concern over lack of precision, the model would yield lower uncertainty with better data. Foremost, we modelled snag basal area, adding uncertainty to home-range size estimates (Fig. 4) that could have been avoided with direct spatial sampling of snag basal area (e.g. via LiDAR). Uncertainty in estimates is very important to know – even if inconvenient – and the Bayesian implementation of the full model provided a relatively simple way to propagate parameter uncertainty through to final abundance predictions (Fig. 4).

It is also important to consider that the evaluation data are not perfect measures of abundance. Individual Black-backed

Woodpeckers may have gone undetected, resulting in underestimates of abundance. We consider this effect to be minimal, however, as previous work has shown our broadcast surveys to have a relatively high cumulative detection probability (0.705; Saracco, Siegel & Wilkerson 2011). For Rim, in particular, our model overpredicted abundance, perhaps because the fire was so large (3rd largest in recorded California history) that colonizing woodpeckers may have not yet saturated available habitat after only 1 year. Rim was also larger than any of the fires used to parameterize either the occupancy or home-range size model. The size of fires is particularly relevant given that the colonization dynamics by Black-backed Woodpeckers in post-fire landscapes are poorly known (Pierson *et al.* 2010). Within our study region, Black-backed Woodpeckers may inhabit unburned forest in low densities (Fogg, Roberts & Burnett 2014), but colonizers of new fires are believed to often be immigrants from other, older fires. With extremely large fires, such as Rim, there may not have been a large enough colonizing population to saturate available home ranges, leading to the apparent over-prediction unique to that fire.

In the other three fires (Reading, Barry Point and Chips), the abundance model appears to have under-predicted (Table 1). We caution, however, that grid-based surveys may have overestimated true abundance through double-counting. Survey points were placed 500 m apart, yet Black-backed Woodpeckers have home ranges that can encompass over 500 ha (Tingley *et al.* 2014). Efforts were made to limit double-counting (e.g. by conducting survey points consecutively on the same day), but without a fully colour-banded population, it would be impossible to eliminate the possibility.

GENERALIZATION OF THE CONCEPTUAL MODEL

The conceptual model (Fig. 1) holds strong potential for application to other species, particularly those that are territorial, wide-ranging and poorly detected. This includes many mammals, particularly carnivores, as well as many birds, including but not limited to woodpeckers, raptors, pheasants and quail. For many of these species, telemetry data have already been extensively collected (e.g. <https://www.movebank.org/>) and occupancy-style surveys are frequently conducted as part of standard monitoring. While home-range scaling relationships have not been modelled for most species, both theory and empirical tests indicate that the negative relationship between resource availability and home-range size is broadly generalizable (McLoughlin & Ferguson 2000). To suggest just one application, the model could be applied to populations of Spotted Owl (*Strix occidentalis*), as this organism has been tracked widely (Glenn, Hansen & Anthony 2004; Bond *et al.* 2013) and surveyed extensively (Yackulic *et al.* 2014), and its population size is of conservation and management importance.

The conceptual model is flexible, however, and the case study with the Black-backed Woodpecker illustrates several ways in which the model could be expanded, modified, or improved for this or other species. To begin, the case study presented a relatively simple example where home-range size

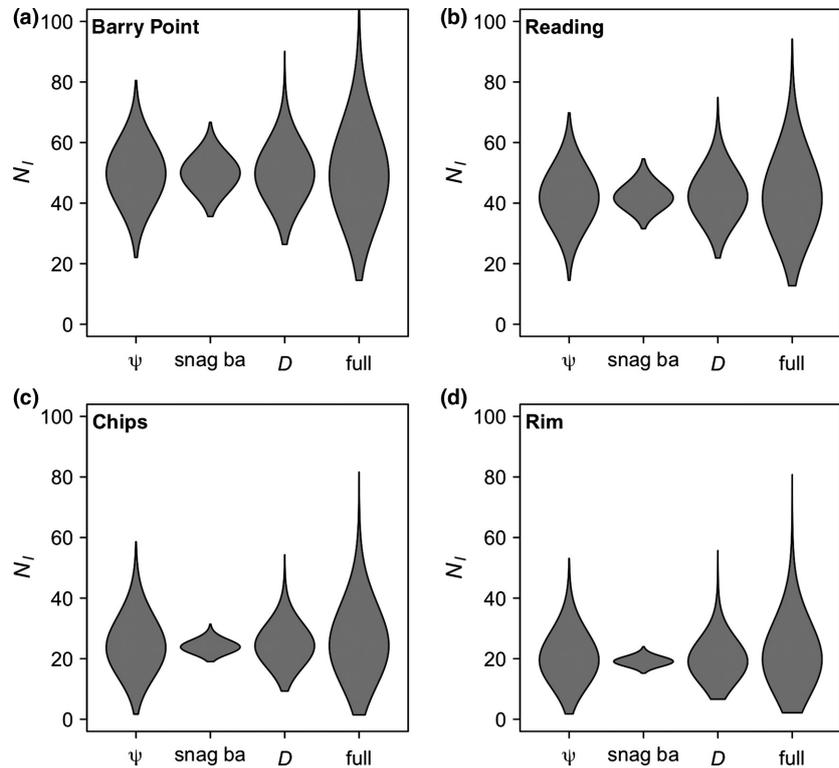


Fig. 4. Violin plots showing density of posterior estimates of Black-backed Woodpecker abundance (N_i) at each modelled fire (a–d) for four different error propagations. In the first three distributions in each plot, uncertainty from only one model (occupancy, snag basal area and home-range density, respectively) is propagated through to N_i . In the final distribution, uncertainty from all component models is propagated.

was determined to be well-predicted by a single resource. Applications to other species may require more complicated home-range size models, such as including multiple resources, or age- and sex-specific relationships. It is generally poorly known if different environmental and habitat factors influence occurrence versus home-range size; jointly modelling these two processes may produce ecological and macroecological insights, in addition to the desired abundance estimates.

It is also possible to incorporate more complicated intraspecific interactions into the abundance model. We previously found that home ranges of Black-backed Woodpeckers closely abutted each other but showed little overlap (Tingley *et al.* 2014). Thus, in this species, home-range size approximates territory size (*sensu* Adams 2001); however, some species may show consistent overlap with neighbours even when home ranges are described with realistic, concave polygons. If overlap occurs by a consistent percentage or absolute amount, then home-range size models (eqn 1) can be scaled to account for this shared area, or territory size can be used instead. If overlap occurs commonly but unpredictably, then the model would underestimate absolute abundance but would likely still predict relative abundance.

It is worth noting that this conceptual model of abundance prediction relies on the focal species holding combined feeding and breeding (i.e. Type-A) territories (Nice 1941) and showing variation in territory size. Non-territorial, flocking or otherwise aggregating species would not be modelled well with this method, even where group size is likely determined by resource availability. Neither would species with spatial patterns that are strongly influenced by other species (e.g. mutualists or parasites), although abundance models of two-species systems could be a valid extension of this model. Alternatively, species

showing no variation in home-range size (e.g. regularly spaced territories) have abundance patterns that would be perfectly correlated with occupancy, and thus require only a scaling factor to convert occupancy predictions to abundance predictions.

Finally, as presented, our abundance model is static with respect to time, yet abundance changes over time, and home ranges can change in size over days, weeks and seasons (van Beest *et al.* 2011). In the case study, we developed an abundance prediction that was time-invariant, in that while our model for ψ assumes that fire-level occurrence declines with years since fire (see Appendix S1), neither the probability of occupancy at points within fires nor home-range size were modelled to vary with years since fire. Tingley *et al.* (2014) found no strong temporal effect of fire age on Black-backed Woodpecker home-range size in landscapes 2–5 years post-fire, although a positive relationship has been suggested by others working in other geographies (Rota *et al.* 2014). Future extensions could include more dynamic temporal components in either occupancy or home-range models to provide time-specific abundance predictions.

APPLICATION TO MANAGEMENT

In addition to illustrating the conceptual model, the case study provides a tool to make post-fire forest management decisions in California while accounting for the potential impacts on Black-backed Woodpeckers. We suggest that managers use the abundance predictions to examine the relative benefits of retaining one patch of forest versus another in the course of exploring different forest management scenarios, as evaluation indicated that abundance estimates held relative value across

landscapes within our 4 evaluation fires. In some cases, other competing land management objectives may preclude retaining some of the best habitat; our model allows managers to make quantitative predictions about the number and proportion of expected Black-backed Woodpecker pairs that are predicted to be conserved or lost under any particular, spatially explicit scenario of post-fire forest management, such as salvage logging.

Further use of our Black-backed Woodpecker abundance model could estimate abundance in different fires, abundance across different forest management regimes or ownerships, and changes in abundance over time. Given enough computational time (likely weeks to months, for one desktop processor), it could be used to estimate total Black-backed Woodpecker population sizes across all recently burned fires in the region. We caution, however, that the model should be applied with care to conditions outside the range of covariates upon which the model was fit. For example, applying the model outside California, applying it to unburned forest, or applying it to forest that burned >10 years previously, are not recommended without additional testing. The models for home-range variation and occupancy can be updated with new information, so the model parameterization could be expanded in the future to include these additional conditions.

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Data accessibility

We provide JAGS model code for the three component models, Bayesian posteriors for each model, and R code to calculate predicted density surfaces and total abundance for an example fire (Reading). Data deposited in the Dryad repository <http://datadryad.org/resource/doi:10.5061/dryad.4ff53>. We have also made data available on Github: https://github.com/mtingley/BBWO_abundance (Tingley *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary methods for component models and data sets.