

Examining the occupancy–density relationship for a low-density carnivore

Daniel W. Linden^{*1} , Angela K. Fuller² , J. Andrew Royle³ and Matthew P. Hare⁴

¹New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources, Cornell University, 211 Fernow Hall, Ithaca, NY 14853, USA; ²U.S. Geological Survey, New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources, Cornell University, 211 Fernow Hall, Ithaca, NY 14853, USA; ³U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD 20708, USA; and ⁴Department of Natural Resources, Cornell University, 205 Fernow Hall, Ithaca, NY 14853, USA

Summary

1. The challenges associated with monitoring low-density carnivores across large landscapes have limited the ability to implement and evaluate conservation and management strategies for such species. Non-invasive sampling techniques and advanced statistical approaches have alleviated some of these challenges and can even allow for spatially explicit estimates of density, one of the most valuable wildlife monitoring tools.

2. For some species, individual identification comes at no cost when unique attributes (e.g. pelage patterns) can be discerned with remote cameras, while other species require viable genetic material and expensive laboratory processing for individual assignment. Prohibitive costs may still force monitoring efforts to use species distribution or occupancy as a surrogate for density, which may not be appropriate under many conditions.

3. Here, we used a large-scale monitoring study of fisher *Pekania pennanti* to evaluate the effectiveness of occupancy as an approximation to density, particularly for informing harvest management decisions. We combined remote cameras with baited hair snares during 2013–2015 to sample across a 70 096-km² region of western New York, USA. We fit occupancy and Royle–Nichols models to species detection–non-detection data collected by cameras, and spatial capture–recapture (SCR) models to individual encounter data obtained by genotyped hair samples. Variation in the state variables within 15-km² grid cells was modelled as a function of landscape attributes known to influence fisher distribution.

4. We found a close relationship between grid cell estimates of fisher state variables from the models using detection–non-detection data and those from the SCR model, likely due to informative spatial covariates across a large landscape extent and a grid cell resolution that worked well with the movement ecology of the species. Fisher occupancy and density were both positively associated with the proportion of coniferous-mixed forest and negatively associated with road density. As a result, spatially explicit management recommendations for fisher were similar across models, though relative variation was dampened for the detection–non-detection data.

5. *Synthesis and applications.* Our work provides empirical evidence that models using detection–non-detection data can make similar inferences regarding relative spatial variation of the focal population to models using more expensive individual encounters when the selected spatial grain approximates or is marginally smaller than home range size. When occupancy alone is chosen as a cost-effective state variable for monitoring, simulation and sensitivity analyses should be used to understand how inferences from detection–non-detection data will be affected by aspects of study design and species ecology.

Key-words: carnivore, density estimation, detection–non-detection data, fisher, hair snares, non-invasive sampling, occupancy, *Pekania pennanti*, remote cameras, spatial capture–recapture

*Correspondence author. Daniel W. Linden, Greater Atlantic Regional Fisheries Office, NOAA National Marine Fisheries Service, Gloucester, MA 01930, USA. E-mail: daniel.linden@noaa.gov

This article has been contributed to by US Government employees and their work is in the public domain in the USA.

Introduction

Species distribution and abundance are fundamental quantities in ecology, and serve as the primary state variables for informing large-scale conservation and management (Jones 2011). The choice of which state variable to use as a monitoring tool depends on the types of population inferences regarding variation over time or space needed to meet objectives (Yoccoz, Nichols & Boulinier 2001). In practice, the choice is also dictated by logistical constraints. Non-invasive survey methods have greatly expanded our capacity to monitor certain wildlife species at large scales (e.g. terrestrial carnivores; Long *et al.* 2008), yet the observations required to estimate abundance as opposed to occurrence can still be more costly and difficult to obtain (Burton *et al.* 2015). Thus, monitoring programmes may use occurrence as a surrogate for abundance or density (MacKenzie *et al.* 2006; Ellis, Ivan & Schwartz 2014), under the assumption that monitoring objectives can still be achieved.

Relationships between occurrence and abundance have been demonstrated within and between species at macro-ecological scales, with biological and statistical mechanisms used to explain variation in the strength of such relationships (Brown 1984; Gaston *et al.* 2000). From a statistical standpoint, a relationship between species occurrence and abundance should result from the fact that both quantities represent areal summaries of the same spatial point pattern of individuals on a landscape (Kéry & Royle 2016, p. 3). The summaries are equivalent when the grain (i.e. size of the spatial unit of observation; Wiens 1989) over which the point pattern gets summarized is small enough such that the maximum number of individuals within a unit is 1. Conversely, a large grain which results in most units being occupied with ≥ 1 individual will produce an occurrence pattern having a weak relationship with variation in abundance. Regardless of grain, the intensity and spatial variation in the point pattern will also determine how well any summaries of occurrence and abundance match. In wildlife studies, the true point pattern of individuals is almost never known and must be sampled, accounting for both spatial variation and detectability (Pollock *et al.* 2002). Thus, the choice of grain will be constrained by study objectives, species ecology, and possible sampling and analytical frameworks (Wiens 1989). In continuous landscapes without naturally defined spatial units, this decision can be especially complicated and have consequences for the inferences derived from sampling. For example, the sampling unit definition in an occupancy model (*sensu* MacKenzie *et al.* 2002) will dictate the necessary data collection, affect model assumptions and interpretation, and potentially alter the relationship between estimated occurrence and true population density (Efford & Dawson 2012).

One strategy for selecting the grain in an occupancy study for highly mobile species has been to use previous

estimates of home range size as a minimum bound to avoid violating the ‘closure’ assumption (Karanth *et al.* 2011; O’Connell & Bailey 2011). Closure in this case relates to changes in the occupancy state between surveys at a given site due to animal movement within the home range, which alters the interpretation of occupancy to mean ‘use’ (MacKenzie & Royle 2005) and differentiates instantaneous from asymptotic occupancy (Efford & Dawson 2012). Selecting a relatively large grain to accommodate wide-ranging, mobile species where movement between surveys is most problematic makes it nearly impossible to truly survey the entire sampling unit (Efford & Dawson 2012). Common non-invasive survey techniques, such as remote cameras, can have very small sampling ‘footprints’ compared to the movements of target species (Clare, Anderson & Macfarland 2015). Even for baited detectors which result in higher observation rates due to larger effective trapping areas at each site (du Preez, Loveridge & Macdonald 2014), the actual trapping area for a given site is still mostly unknown. Finally, selecting the grain to accommodate species ecology becomes complex when movement behaviour and territoriality is differentiated by sex (Sollmann *et al.* 2011), causing some model assumptions to be violated by individuals of one or the other sex. Without understanding how these sampling trade-offs result in modified observation processes, the interpretation of what occupancy estimates represent may be far removed from the truth, reducing the value of occupancy modelling as a proxy for abundance (Efford & Dawson 2012).

Validation and calibration are important steps in determining the utility of a proxy as a tool for natural resource management (Stephens *et al.* 2015). Previous studies have demonstrated the statistical relationships between species occupancy and density by simulating individual point patterns and hypothetical detection surveys (Efford & Dawson 2012; Ellis, Ivan & Schwartz 2014), providing guidance for the sampling design of large-scale monitoring studies. These types of simulations and power analyses require previous information on species ecology that may not always exist, particularly for widespread species with regional variation. Clare, Anderson & Macfarland (2015) empirically estimated the point pattern of individuals using spatial capture–recapture (SCR) modelling (Borchers & Efford 2008; Royle & Young 2008), and demonstrated a strong relationship between estimates of bobcat *Lynx rufus* occupancy and density using species detections and individual encounters, respectively, collected from remote camera traps. Given the typical capture–recapture requirement of encounter data from identified individuals (but see Chandler & Royle 2013), non-invasive sampling applications of SCR have been limited to species with unique features that can be photographed or to surveys that can collect genetic samples for genotyping (Royle *et al.* 2014). For species without identifiable features or monitoring programmes that cannot afford long-term investment in expensive genetic sample processing, a

calibration of the occupancy–density relationship could serve to guide monitoring design.

Here, we used a large-scale monitoring study of fisher *Pekania pennanti* to evaluate the effectiveness of occupancy as an approximation to density, particularly for informing harvest management decisions. A medium-sized mesocarnivore traditionally valued for its fur, fisher had been extirpated from much of eastern North America by the early 20th century due to unregulated trapping and habitat loss; recent population expansions have coincided with furbearer protection measures and conversion of farmland to forest in the region (Lancaster, Bowman & Pond 2008). An increased interest in expanding harvest opportunities prompted the New York State Department of Environmental Conservation (NYSDEC) to implement a monitoring programme for fisher to identify the wildlife management units (WMUs) that could sustain regulated trapping (Fuller, Linden & Royle 2016). We sampled a large landscape across western New York, USA using baited camera and hair snare traps and fit occupancy models to species detection–non-detection data and SCR models to individual encounter data obtained by genotyped hair samples. We also used the species detection–non-detection data to estimate abundance (density) with the Royle–Nichols (RN) model (Royle & Nichols 2003), assuming that species detections were often generated by multiple individuals given the sampling design. All sets of models incorporated similar covariates for the observational and ecological processes, with spatial variation defined on the same raster landscape. We evaluate the use of occupancy as a proxy for density and discuss design-based approaches that can improve the approximation for large-scale monitoring programmes.

Materials and methods

STUDY AREA AND SAMPLING

Our study area spanned all of western New York, USA, encompassing a 70 096-km² region comprised mostly of forest and agriculture (Fuller, Linden & Royle 2016). As with other temperate forests of eastern North America, this region was historically occupied by fisher until extirpation in the early 1900s (Powell & Zielinski 1994; Lewis, Powell & Zielinski 2012). The region was delineated by 13 WMU aggregates, eight of which (totalling 73% of the study area) have been closed to fisher harvest since 1949, while the remaining five WMUs, located near remnant and reintroduced fisher populations in the Adirondack and Catskill Mountains, have had regulated trapping seasons for >20 years (Fig. S1.1 in Appendix S1, Supporting Information; Fuller, Linden & Royle 2016).

Our study design required a discrete representation of the landscape to define sampling units that could be surveyed for fisher and to quantify landscape attributes that might be associated with variation in fisher occurrence and density. Additional details are described in Fuller, Linden & Royle (2016). We divided the study area into a grid having 4400 cells with a resolution of 15 km², chosen to match the territory size of a female fisher (Arthur, Krohn &

Gilbert 1989; Powell & Zielinski 1994). This design was intended to theoretically restrict: (i) the number of individuals within a grid cell and (ii) the number of grid cells overlapped by any given individual. The true maximum for each were unknown and would have depended on differences in movement between sexes, the amount of inter- and intrasexual overlap of territories (fisher are intrasexually territorial), and the configuration of sampled grid cells. We selected a subset of available grid cells using a stratified random approach with clustering (≥ 3 neighbouring cells) to accommodate field logistics. The initial sampling year in 2013 was restricted to grid cells with >60% forest cover, while sampling in 2014 and 2015 included grid cells across a broader range of forest cover values selected in proportion to landscape availability. The number of grid cells sampled in each year was 300 in 2013 and 608 in both 2014 and 2015 (Figs S1.2–S1.4 in Appendix S1). Across all years, 826 unique grid cells were sampled, with replicated sampling across 2 and 3 years for 423 and 129 grid cells respectively.

Sampling stations were located as close to the grid cell centre as possible and consisted of a baited trap with hair snares to capture genetic samples and a remote camera for photographing species encounters. Stations were baited with beaver *Castor canadensis* meat attached to a tree and surrounded by nine gun brushes, positioned 1–2 m above the ground, with an infrared camera pointed at the bait tree from a location <5 m away. Sampling occurred between January and March of each year, during which active stations were visited approximately weekly (visit interval: ~7 days) to collect hair samples and replace bait as needed; four visits were made to each active station after initial setup in 2013, and three visits in 2014 and 2015.

Genetic samples were defined as a cluster of ≥ 5 hair follicles at a single gun brush. To reduce costs, we processed a subset of the samples for genetic data, ensuring that every site-visit combination that yielded fisher hair was included. Each processed sample had DNA extracted for species identification, molecular sexing, and microsatellite genotyping using fluorescent fragment analysis and DNA sequencers at the Cornell University Institute of Biotechnology (Ithaca, NY, USA). Genetic methods are detailed in Appendix S2.

OCCUPANCY MODEL

We fit a single-season site occupancy model (MacKenzie *et al.* 2002) to estimate the probability of fisher occurrence in grid cells using species detections from the camera data. The model used here was described in Fuller, Linden & Royle (2016) and derived from the model selection process they used to identify important sources of variation in probabilities of detection and occupancy. As the focus was on spatial variation in occurrence, each grid cell \times year combination was considered a distinct site. Fisher detection, y_{jk} , at site j during survey k was considered a Bernoulli random variable:

$$y_{jk} \sim \text{Bernoulli}(z_j \times p_{jk})$$

where z_j is the site-specific latent occurrence state indicating whether a site is occupied ($z_j = 1$) or not ($z_j = 0$), and p_{jk} is the site- and survey-specific detection probability, $\Pr(y_{jk} = 1 | z_j = 1)$. We considered each latent occurrence state a Bernoulli random variable:

$$z_j \sim \text{Bernoulli}(\psi_j)$$

where ψ_j is the site-specific probability of occurrence, $\Pr(z_j = 1)$. We used logit-link functions for each probability to examine

covariates that varied by site or survey. Following the top-ranked model structure from Fuller, Linden & Royle (2016), our detection probability model was a year-specific quadratic function of ordinal date (mean of the survey week) with an effect to account for increased detection after the first survey occasion (i.e. $k = 1$ vs. $k > 1$). The model for detection probability was therefore:

$$\text{logit}(p_{jk}) = \alpha_0 + \alpha_{2014} + \alpha_{2015} + \alpha_{\text{date},\text{yr}} \text{date}_{jk} + \alpha_{\text{date}2,\text{yr}} \text{date}_{jk}^2 + \alpha_{k > 1}$$

where α_{2014} and α_{2015} are additive year effects depending on when site j was surveyed; $\alpha_{\text{date},\text{yr}}$ and $\alpha_{\text{date}2,\text{yr}}$ are the year-specific relationships with survey ordinal date; and $\alpha_{k > 1}$ is the effect of when survey $k > 1$. Our logit-linear model for occupancy included year and the two landscape covariates identified by model selection to be important predictors, proportion of coniferous-mixed forest and road density (Fuller, Linden & Royle 2016):

$$\text{logit}(\psi_j) = \beta_0 + \beta_{2014} + \beta_{2015} + \beta_{\text{conif}} \text{conif}_j + \beta_{\text{roads}} \text{roads}_j$$

Similar to the detection probability model, β_{2014} and β_{2015} depend on the year for site j . The landscape covariates were calculated for each site using freely available GIS data, including the 30-m resolution National Land Cover Database (Fuller, Linden & Royle 2016). We used square-root and natural-log transformations for conif_j and roads_j , respectively, before scaling each to have zero mean and unit variances.

ROYLE-NICHOLS MODEL

We fit a RN model (Royle & Nichols 2003) to the species detection-non-detection data to examine whether unmodelled heterogeneity in detection could be attributed to variation in site abundance. Our sampling design had used prior knowledge of female fisher movement to define sites, yet overlapping male and female territories, non-territorial juveniles, or variation in individual movement could lead to sites being used by multiple individuals (or individuals using multiple sites). Additionally, the RN model generates estimates of abundance or density using the same type of data collected for occupancy estimation, potentially providing another tool for species monitoring that does not require individual identification.

We used the same data structure described earlier for the occupancy model, with sites defined as grid cell \times year combinations. Fisher detections, y_{jk} , were modelled as Bernoulli random variables such that:

$$y_{jk} | N_j \sim \text{Bernoulli}(p_{jk})$$

where N_j is the latent site abundance and p_{jk} is the species detection probability. Importantly, species detection probability was a function of N_j :

$$p_{jk} = 1 - (1 - r_{jk})^{N_j}$$

Here, r_{jk} is the per-individual detection probability. The state process model assumed that site abundance was a Poisson-distributed random variable with mean λ_j :

$$N_j \sim \text{Poisson}(\lambda_j)$$

We used the same linear models to describe variation in both the observation and state process models using appropriate link functions on the relevant parameters:

$$\begin{aligned} \text{logit}(r_{jk}) &= \alpha_0 + \alpha_{2014} + \alpha_{2015} + \alpha_{\text{date},\text{yr}} \text{date}_{jk} + \alpha_{\text{date}2,\text{yr}} \text{date}_{jk}^2 + \alpha_{k > 1} \\ \text{log}(\lambda_j) &= \beta_0 + \beta_{2014} + \beta_{2015} + \beta_{\text{conif}} \text{conif}_j + \beta_{\text{roads}} \text{roads}_j \end{aligned}$$

SPATIAL CAPTURE-RECAPTURE MODEL

We used SCR (Borchers & Efford 2008; Royle & Young 2008) to model the individual encounter data generated by the genotyped hair samples and predict fisher density within the grid cells in our landscape. A standard SCR model uses the spatial distributions of individual encounters at trap locations to jointly estimate the number and location of latent activity centres (representing population size and individual distribution) and trap- and individual-specific encounter probabilities. We assumed that the encounter process for individuals exhibited similar temporal variation to that identified in the occupancy model, and that fisher density potentially varied according to the same landscape attributes influencing occurrence.

We modelled the encounter histories, y_{ijk} , for individual i at trap j on survey k as Bernoulli random variables that depended on the location of the individuals latent activity centre $\mathbf{s}_i = (s_{i1}, s_{i2})$, such that $\Pr(y_{ijk} = 1 | \mathbf{s}_i) = p_{ijk}$. Importantly, encounter probability was a decreasing function of the Euclidean distance, d_{ij} , between activity centre, \mathbf{s}_i , and the location for trap j :

$$p_{ijk} = p_{0,ijk} \exp(-d_{ij}^2 / 2\sigma_i^2)$$

Here, $p_{0,ijk}$ is the encounter probability when $d_{ij} = 0$ while σ_i is the scale parameter of the half-normal distance function. Both parameters were made functions of covariates:

$$\begin{aligned} \text{logit}(p_{0,ijk}) &= \alpha_0 - \alpha_{2014} + \alpha_{2015} + \alpha_{\text{date},\text{yr}} \text{date}_{jk} \\ &\quad + \alpha_{\text{date}2,\text{yr}} \text{date}_{jk}^2 + \alpha_{\text{behav}} C_{ijk} + \alpha_{\text{male}} \text{sex}_i \\ \text{log}(\sigma_i) &= \delta_0 + \delta_{2014} + \delta_{2015} + \delta_{\text{male}} \text{sex}_i \end{aligned}$$

The effects for year (α_{2014} , α_{2015}) and ordinal date ($\alpha_{\text{date},\text{yr}}$, $\alpha_{\text{date}2,\text{yr}}$) were similar to those for species detection probability; the survey occasion effect was replaced by a trap-specific behavioural response (α_{behav}), where $C_{ijk} = 1$ for all k after the initial encounter of individual i at trap j , and 0 otherwise. The model for σ_i also included year effects, and both models incorporated an effect for the difference between males ($\text{sex}_i = 1$) and females ($\text{sex}_i = 0$). We treated sex as a random variable and estimated $\phi_{\text{male}} = \Pr(\text{sex}_i = 1)$ using the likelihood formulation in Royle *et al.* (2015). This allowed us to estimate the sex of both unencountered individuals and encountered individuals that could not be assigned a sex due to uncertainty in the genetic marker.

To model variation in fisher density, we used an inhomogeneous point process to describe the distribution of activity centres within our study area (Borchers & Efford 2008). We defined a discrete state space representing the possible locations of the realized point process to coincide with the 4400 cell raster used for the occupancy model. To accommodate scales of movement (σ) that were smaller than the grid cell size and improve parameter estimation for σ , we reduced the resolution of the grid from 3.873 km \times 3.873 km (15 km²) to 0.968 km \times 0.968 km (0.938 km²), increasing the total number of grid cells, G , to 70 400. Landscape covariates were recalculated at the new resolution, though a moving-window approach was used to reflect a similar scale (15 km²) for the features as that assessed by the occupancy model. We modelled the expected density in a given grid cell g as the intensity of a point process conditional on a linear model of spatially varying covariates, such that $E(D_g) = \mu(g, \beta)$, where β are regression coefficients for the linear model (Royle *et al.* 2014). Following the model structure for occupancy,

expected density was a linear function of year and the two landscape covariates, here on the log scale:

$$\log(E(D_g)) = \beta_0 + \beta_{2014} + \beta_{2015} + \beta_{\text{conif}}\text{conif}_g + \beta_{\text{roads}}\text{roads}_g$$

The final component of the SCR model involved defining the distribution of activity centres. Note that given the discrete state space, activity centres are now referenced by s_i , a vector with the grid cell ID (g) for each individual, instead of the two-dimensional coordinates. For a basic SCR model having constant density, such that activity centres are distributed uniformly throughout the state space, the probability of an activity centre being located in any given grid cell would be $1/G$. As we were modelling variation in density, the probability was a ratio of the intensity function at a given grid cell, conditional on the coefficients of the linear model and the spatial covariate values, and the summed intensity function across all grid cells:

$$\Pr(s_i = g | \beta) = \frac{\mu(g, \beta)}{\sum_g \mu(g, \beta)}$$

We used a Poisson-integrated likelihood approach (Borchers & Efford 2008; Royle *et al.* 2014) to evaluate the likelihood of the SCR model parameters over all possible grid cells for the activity centres.

MODEL FITTING AND SPATIAL PREDICTIONS

All models were fit using maximum likelihood methods. For the occupancy and RN models, we used the ‘occu’ and ‘occuRN’ functions, respectively, of the unmarked package (Fiske & Chandler 2011) in R (R Core Team 2015) to compute the likelihoods and obtain maximum likelihood estimates (MLEs). For the SCR model, we used the oSCR package (Sutherland, Royle & Linden 2016) in R for computing the likelihood and obtaining MLEs.

Fuller, Linden & Royle (2016) present additional information regarding model selection, relative variable importance, and goodness-of-fit in an expanded occupancy analysis of these fisher detection data from the camera trapping. For the purposes of our comparisons here, we conditioned our inferences on a single model structure for each of the model types. Following MacKenzie & Bailey (2004), we used parametric bootstrapping to assess goodness-of-fit for the occupancy and RN models and calculated an overdispersion parameter (\hat{c}) to compare the model types (Appendix S3). We avoided a fit assessment for the SCR model given the general lack of guidance on best practices, particularly when using maximum likelihood approaches, though we were generally less concerned with model fit given the flexibility and robustness of SCR to deviations from model assumptions (Royle *et al.* 2014). We also considered the SCR model to represent a better approximation to the actual state variable of interest (i.e. individual fisher distribution) than either model using detection–non-detection data.

We generated spatial predictions from each model for the 4400 grid cells in the landscape of interest. For the occupancy and RN models, landscape covariates for all grid cells were transformed and then scaled using the values calculated across the surveyed grid cells. For the RN model, we generated spatial predictions of expected fisher density ($\#/\text{km}^2$) using $E(\lambda_i)/15$, the expected abundance divided by area for a grid cell. For the SCR model, expected density ($\#/\text{grid cell}$) was predicted across the high-resolution state space ($G = 70\,400$) using the MLEs for β , then an aggregate mean density ($\#/\text{km}^2$) was calculated for each of the

4400 cells from the original grid. Following Fuller, Linden & Royle (2016), we calculated mean values for the grid cells within each of the 13 WMUs to compare how management decisions may differ between the models; standard errors described spatial variation in predicted values and did not include model estimation uncertainty. Finally, we used least-squares regression to examine relationships between predictions from the models using detection–non-detection data (occupancy and RN) to predictions from the SCR model. Values were transformed to the appropriate scale (logit or log) before fitting the regressions. Hereafter, we refer to each regression according to the relationship that was modelled, where ‘SCR = occupancy’ was $\log(\text{SCR density}) \sim \text{logit}(\text{occupancy})$ and ‘SCR = RN’ was $\log(\text{SCR density}) \sim \log(\text{RN density})$. We report the slope coefficient for the SCR = RN regression given that a 1 : 1 relationship was possible.

Results

Data collection results can be found in Appendix S1. Model estimates for the observation processes of the three model types indicated similar patterns within and between years (Table 1), including a decrease in average detection and encounter probabilities from 2013 to 2015. The regression coefficients for observation covariates were nearly identical for the occupancy and RN models, which was expected given that they used the same detection–non-detection data. The directions of most effects in the SCR model matched those for the other models; the only coefficient that differed ($\alpha_{\text{date2},2014}$) was estimated near zero for each model. Across years, mean detection probability during survey 1 for the species ranged 0.16–0.47, while that for individuals ranged 0.10–0.28; for surveys >1 , the ranges of mean detection probabilities increased to

Table 1. Parameter estimates from the observation process components of the occupancy, Royle–Nichols (RN) and spatial capture–recapture (SCR) models. The parameters describe the logit-linear model (α) of trap-specific encounter probability for individuals (RN, SCR) or species (occupancy), and the loglinear model (δ) of the half-normal distance function in SCR

Parameter	Occupancy		Royle–Nichols		Spatial capture–recapture	
	Mean	SE	Mean	SE	Mean	SE
α_0	−0.122	0.132	−0.946	0.169	−4.475	0.457
α_{2014}	−0.531	0.165	−0.489	0.226	−0.383	0.416
α_{2015}	−1.573	0.192	−1.284	0.258	−1.196	0.518
$\alpha_{\text{date},2013}$	0.151	0.030	0.142	0.030	0.644	0.150
$\alpha_{\text{date},2014}$	0.109	0.023	0.110	0.022	0.166	0.081
$\alpha_{\text{date},2015}$	−0.023	0.022	−0.024	0.022	−0.107	0.087
$\alpha_{\text{date2},2013}$	−0.032	0.008	−0.029	0.008	−0.317	0.101
$\alpha_{\text{date2},2014}$	0.002	0.007	0.004	0.007	−0.027	0.068
$\alpha_{\text{date2},2015}$	0.049	0.007	0.045	0.007	0.264	0.083
$\alpha_{k>1}$	0.621	0.090	0.580	0.083	—	—
α_{behav}	—	—	—	—	3.842	0.366
α_{male}	—	—	—	—	−0.425	0.420
δ_0	—	—	—	—	1.267	0.242
δ_{2014}	—	—	—	—	0.456	0.313
δ_{2015}	—	—	—	—	0.811	0.358
δ_{male}	—	—	—	—	0.298	0.341

0.25–0.62 and 0.16–0.41 for species and individuals, respectively. The SCR model indicated a strong local behavioural response [$\alpha_{\text{behav}} = 3.842$ (SE: 0.366)], suggesting individuals were much more likely to return to a trap after an initial visit. The loglinear coefficients for σ_i indicated that the movement scale was larger in the later years [$\delta_{2014} = 0.456$ (SE: 0.313); $\delta_{2015} = 0.811$ (SE: 0.358)] and for males [$\delta_{\text{male}} = 0.298$ (SE: 0.341)]. This resulted in mean σ_i estimates that ranged 3.55–7.98 km for females and 4.78–10.76 km for males, across the years. The goodness-of-fit statistics indicated some overdispersion for the models using detection–non-detection data (Appendix S3), more so for the occupancy model ($\hat{c} = 2.78$) than for the RN model ($\hat{c} = 1.59$).

The relationships between the landscape covariates and the ecological processes for each model type were largely consistent (Table 2), with effects of coniferous-mixed forest proportion being strongly positive and those of road density being strongly negative. There was little support for differences in occupancy and abundance across the years. According to back-transformed model intercepts, mean fisher occupancy per 15-km² grid cell was relatively high [0.69 (95% CI: 0.61–0.75)], while mean fisher density (#/km²) was relatively low for both the RN model [0.088 (95% CI: 0.071–0.109)] and the SCR model [0.045 (95% CI: 0.020–0.101)]. The probability of being male was estimated as 0.47 (95% CI: 0.23–0.73) in the SCR model, suggesting a nearly even sex ratio.

The spatial predictions indicated similar patterns of variation (Fig. 1), which were expected given the consistency in estimated relationships with the landscape covariates. The SCR = occupancy and SCR = RN regressions both had R^2 values >0.94 (Fig. S1), though the slope coefficient for the SCR = RN regression was 2.670 (SE: 0.010). This slope >1 was consistent with the smaller estimates for β_{conif} and β_{roads} in the RN model than in the SCR model (Table 2). The spatial distribution of residuals further illustrated how the SCR = occupancy and

SCR = RN regressions generally overpredicted in areas of low density, and underpredicted in areas of high density (Fig. 1b,c). Mean values across WMUs exhibited a strong correlation between predictions from the SCR model and those from the occupancy and RN models (Fig. 2), indicating mostly similar inferences regarding variation in fisher distribution and density at the management-unit level. Differences in mean predictions between WMUs currently open vs. closed to fisher harvest were relatively larger for density (#/km²) estimates from the SCR model [0.070 (SE: 0.020) vs. 0.045 (SE: 0.008)] compared to those for the RN model [0.077 (SE: 0.007) vs. 0.069 (SE: 0.005)]; these same differences were relatively small for the occupancy model [0.59 (SE: 0.05) vs. 0.52 (SE: 0.03)].

Discussion

An understanding of the statistical and ecological relationships between species occupancy and density can improve the design of monitoring programmes that aim to make inferences on wildlife populations at large scales. Complete knowledge on the distribution of individuals would provide the necessary information for management and conservation, but such data almost never exist, particularly for wide-ranging terrestrial species such as carnivores. Therefore, the distribution of individuals must be sampled and statistically summarized, with limitations for each step being determined by the selected study design and the ecology of the focal species. Sampling a collection of sites for species occurrence is typically easier and less cost prohibitive at large scales than sampling and identifying individuals, yet the resulting data summary may not provide an adequate approximation to the information of interest. We presented empirical evidence that models of occupancy and density can generate similar predictions and management recommendations when species movement ecology is considered in the sampling design, even when some modelling assumptions are violated.

Table 2. Parameter estimates from the ecological process components of the occupancy, Royle–Nichols (RN) and spatial capture–recapture (SCR) models. The parameters describe the linear model (β) of species occurrence probability on the logit scale (occupancy) or abundance on the log scale (RN, SCR). The intercept represents the mean for a 15-km² grid cell (occupancy, RN) or a 0.938-km² grid cell (SCR). The SCR model includes the logit scale probability of being male (ϕ_{male})

Parameter	Occupancy		Royle–Nichols		Spatial capture–recapture	
	Mean	SE	Mean	SE	Mean	SE
β_0	0.785	0.172	0.279	0.109	−3.159	0.407
β_{2014}	−0.385	0.209	−0.147	0.147	−0.250	0.511
β_{2015}	−0.169	0.267	−0.194	0.176	−1.004	0.562
β_{conif}	0.434	0.081	0.223	0.037	0.583	0.088
β_{roads}	−0.301	0.094	−0.105	0.043	−1.174	0.282
ϕ_{male}	—	—	—	—	−0.120	0.556

FISHER OCCUPANCY VS. DENSITY

Our study currently represents one of the largest applications of SCR modelling in terms of both landscape extent and coverage. Obbard, Howe & Kyle (2010) have the only comparable extent (across Ontario, Canada) for an SCR study, but their sampling was of distinct populations and did not involve contiguous landscape predictions. A benefit to our comprehensive effort was that spatially explicit density estimates could be used to evaluate the ability of occupancy models to guide wildlife management decisions at regional scales (Clare, Anderson & Macfarland 2015; Fuller, Linden & Royle 2016). Our evaluation suggests that detection–non-detection data can be a useful tool for indexing density and addressing large-scale monitoring needs under certain conditions. The estimates of average fisher occupancy and density were highly correlated at the

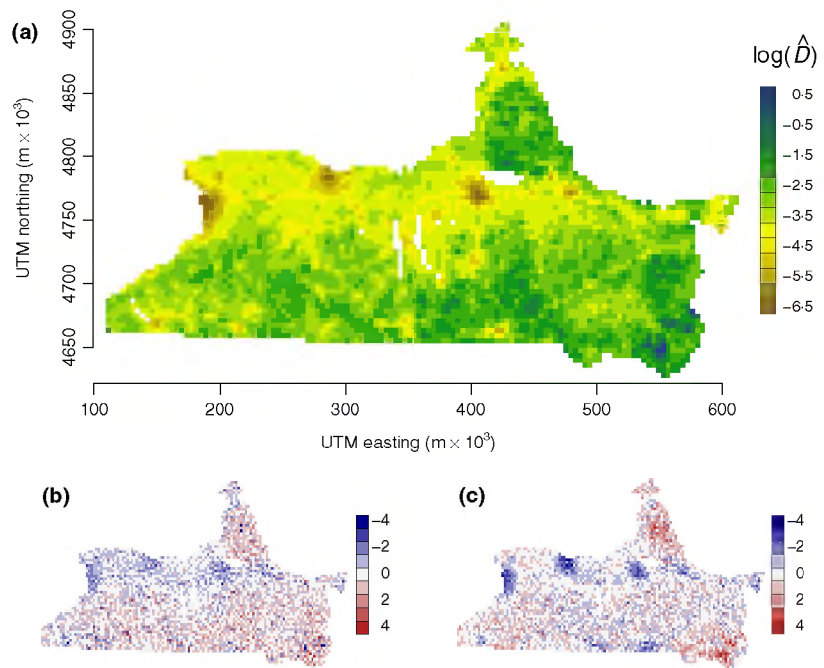


Fig. 1. Spatial predictions from the models of fisher occupancy and abundance in western New York, including: (a) expected fisher density ($\#/\text{km}^2$) on the log scale as predicted by the spatial capture-recapture (SCR) model; (b) standardized residuals from the SCR = occupancy regression; and (c) standardized residuals from the SCR = RN regression. Blue values in (b, c) represent grid cells where the detection–non-detection data overpredicted density, while red values represent underpredictions.

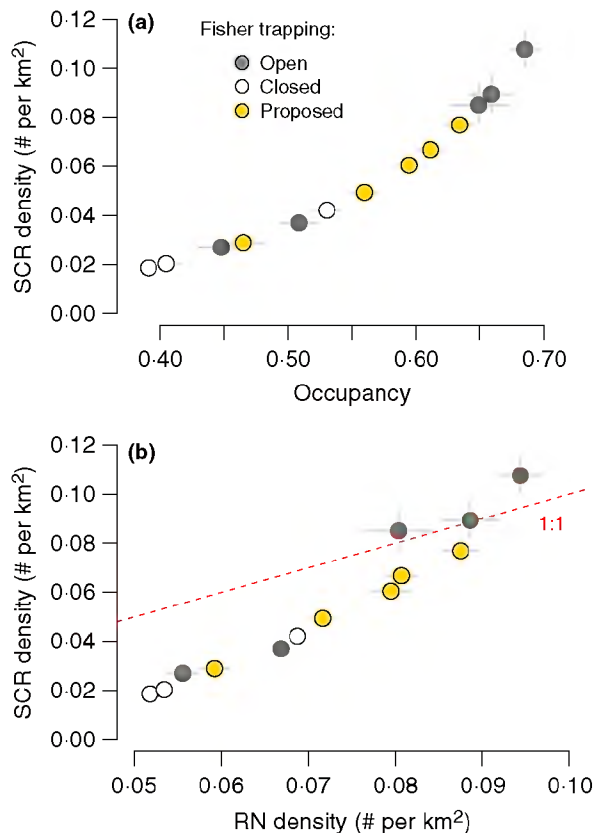


Fig. 2. Mean (± 2 SE) predicted occupancy and density for wildlife management unit (WMU) aggregates in western New York, 2013–2015, comparing estimates from the spatial capture-recapture (SCR) model to those from the occupancy model (a) and the RN model (b). The trapping status for each WMU indicates whether fisher harvest is open (grey), closed (white), or being proposed for opening (yellow). Red line in (b) indicates 1 : 1 relationship. [Colour figure can be viewed at wileyonlinelibrary.com]

WMU scale (Fig. 2) and would likely lead to similar management decisions regarding expanded harvest opportunities (Fuller, Linden & Royle 2016).

The correspondence among model types was largely due to the strong associations between the estimated state variables and the two landscape attributes that exhibited wide variation across the region. The positive effect of coniferous-mixed forest and negative effect of road density are consistent with previous knowledge on fisher ecology (Powell 1993; Powell & Zielinski 1994). Interestingly, the models using detection–non-detection data had relatively smaller effect sizes for each covariate, though this result could have been expected. The occupancy model involves a logistic regression of latent occurrence, a binary random variable, yet the number of individual fisher occurring within or using a grid cell could be >1 . Therefore, the coefficients in the logit-linear model should underestimate the effects of covariates if variation exists among grid cells with ≥ 1 individual. Estimates from the SCR model indicated larger scales of individual movement for each sex than suggested by the literature (Arthur, Krohn & Gilbert 1989; Powell & Zielinski 1994), more than enough for individuals to encompass multiple 15-km² grid cells regardless of sex. Combined with intersexual territory overlap (Powell 1993), this would have resulted in many sampled grid cells having >1 individual in areas of relatively high density. The RN model was specifically designed to deal with abundance-induced heterogeneity in detection probability (Royle & Nichols 2003) and had a lower estimate of overdispersion than the occupancy model, suggesting a potentially superior fit. But both models of detection–non-detection data struggled to explain the number of observed detection histories that were all 1s or all 0s (Appendix S3), suggesting

additional unmodelled heterogeneity and/or overdispersion. While we might have improved the RN model fit using a different latent abundance distribution (e.g. negative binomial), doing so would have eliminated the point process interpretation (Diggle & Milne 1983) and convenient equivalence to the activity centre distribution of the SCR model. Given sex-specific differences in movement and individual differences in the location of activity centres, several other assumptions of the detection–non-detection models were violated (e.g. equal per-individual detection probability for the RN model). Despite these limitations, each model of detection–non-detection data adequately approximated density, as estimated by SCR.

Additional model complexity may have improved our use of the detection–non-detection data, for example, by incorporating a spatial dependence structure (Johnson *et al.* 2013). The size of our grid cells in comparison to the observed animal movement and the clustered pattern of sampled cells may have warranted some type of autoregressive function. Johnson *et al.* (2013) present an approach that is computationally efficient for large landscapes and, importantly, addresses concerns with possible confounding between latent spatial effects and landscape or habitat covariates (Hodges & Reich 2010). For many species, this approach may be particularly useful when ecological or observational processes exhibit spatial correlation and have the potential to affect inferences. In our application of occupancy modelling, the latent spatial process that likely caused overdispersion problems was related to individual distribution – the very state variable that is estimated by SCR. Depending on the scale and extent of the study, SCR represents a more comprehensive approach for making inferences about species distribution in continuous landscapes than that which can be estimated by detection–non-detection data (Efford & Dawson 2012).

FISHER MANAGEMENT IN NY

The spatial predictions of fisher occurrence and density provide wildlife managers with tools for population assessment and can potentially assist with identifying certain harvest management strategies in western NY. Several WMUs appeared to have configurations of high coniferous-mixed forest proportion and low road density conducive to supporting a local fisher population on par with WMUs that have sustained regulated trapping in recent years (Fuller, Linden & Royle 2016). Regional decisions regarding where to allow harvest in the state would be similarly informed by the predictions generated from the detection–non-detection data and those generated by the individual encounter data, as using the minimum predicted value of WMUs currently open to harvest as a threshold identifies the same proposed units regardless of model type (Fig. 2).

More specific fisher management decisions (e.g. spatially explicit harvest quotas) may not be adequately informed by the detection–non-detection data in the

absence of some calibration with information on population size. The models of detection–non-detection data indicated less relative variation in the fisher population between WMUs when compared with the SCR model, including smaller differences between units open and closed to fisher harvest. The relative differences in predictions between open and closed units were ~13% for occupancy and ~12% for RN density, much lower than the ~36% difference in density predictions for SCR. While the RN model provided density estimates that were potentially directly applicable to harvest quotas, the overprediction for low-density WMUs would be problematic. In contrast, multiple assumptions would be required to roughly translate an occupancy prediction into a harvest quota recommendation given that occupancy in a continuous landscape for a mobile species is a complex function of species presence, individual movement, and sampling design (Efford & Dawson 2012). Here, the relationship between predicted fisher occupancy and density on the unit scales (as opposed to model link scales) was nonlinear, such that density increased at an incrementally faster rate than occupancy – mean fisher density within a WMU doubled when estimated occupancy increased from 0.40 to 0.55, and doubled again from 0.55 to 0.70 (Fig. 2). Thus, some type of calibration for models of detection–non-detection data would be necessary to make predictions reliable for setting spatially explicit harvest quotas. In the absence of monitoring that can provide information on fisher density, a conservative approach to harvest quotas would be necessary until an adequate time series of harvest data is collected (Williams, Nichols & Conroy 2002).

CONSIDERATIONS FOR LARGE-SCALE MONITORING

An ideal monitoring programme for wide-ranging, low-density species such as carnivores involves a study design that can collect individual encounters across a large landscape and allow for fitting the data to SCR models. Unfortunately, the associated costs and logistical difficulties will limit the application of such designs in many situations (Efford & Dawson 2012; Ellis, Ivan & Schwartz 2014), particularly when the species cannot be easily identified using distinguishable individual features (Sollmann *et al.* 2011; Clare, Anderson & Macfarland 2015). While non-invasive genetic sampling can solve the identity problem for species without unique markings, a drawback is the often low amplification rates due to poor quality DNA (e.g. from hair follicles), resulting in data with fewer useable individual encounters than the species detections that could be obtained by other means. Integrated approaches allow opportunities to calibrate inferences from detection–non-detection data by periodically including more expensive or intensive sampling to obtain individual encounters (Chandler & Clark 2014), and may represent the best compromise for designing robust monitoring programmes that can make inferences across time and space.

When occupancy alone is chosen as a cost-effective state variable for monitoring, simulation and sensitivity analyses should be used to understand how inferences from detection–non-detection data will be affected by aspects of study design and species ecology (Ellis *et al.* 2015). Here, we illustrated that models using detection–non-detection data can make similar inferences regarding relative spatial variation of the focal population to models using more expensive individual encounters when the selected spatial grain approximates or is marginally smaller than home range size. Technically, our spatial grain or plot size was indeterminate given the baiting scheme (Efford & Dawson 2012), but this did not appear to be problematic for relative comparisons (and is a non-issue for density estimation with SCR). Transitioning from relative to absolute measures for specific management questions related to population density (e.g. allowable harvest) will require calibration to justify the use of occupancy as a proxy. While occupancy may have been useful for making relative spatial comparisons on which WMUs might support fisher harvest, in the absence of information on density, there would be little guidance on the magnitude of allowable harvest within any given unit. Thus, interpretation of occupancy estimates in a management context requires one to carefully consider the limitations of potential inferences. Monitoring objectives that are concentrated on other population attributes (e.g. temporal change) may require separate design considerations to ensure reliable inferences from occupancy.

Authors' contributions

A.K.F. and J.A.R. conceived and designed the study. M.P.H. led the processing of genetic samples and wrote the genetic methods. D.W.L. prepared the data, conceived and performed the analyses and wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank the following NYSDEC staff for coordinating and conducting field surveys: K. Baginski, M. Clark, E. Duffy, L. Durfey, R. Holevinski, A. MacDuff, M. Putnam, A. Rothrock, B. Schara and S. Smith. We thank B. Swift, M. Schiavone and P. Jensen for project support and H. Borchardt-Wier for genotyping. We thank R. Holevinski for assistance in obtaining relevant GIS databases and for helping to coordinate field efforts. This work was supported in part by Federal Aid in Wildlife Restoration Grant W-173-G. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data accessibility

The data used in this study are archived in Dryad Digital Repository <https://doi.org/10.5061/dryad.d3q4q> (Linden *et al.* 2017).

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Received 16 July 2016; accepted 3 February 2017

Handling Editor: Jacqueline Frair

Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Additional information regarding non-invasive sampling of fisher in New York, USA during 2013–2015.

Appendix S2. Technical details of fisher genetic methods.

Appendix S3. Goodness-of-fit for models of fisher detection–non-detection data.

Fig. S1. Grid-cell relationships between predicted values from the models for detection–non-detection data and predicted values from the spatial capture–recapture model.