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Strong inference from transect sign surveys: combining spatial autocorrelation and misclassification occupancy models to quantify the detectability of a recovering carnivore

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Monitoring of species using surveys of ambiguous signs and assuming 100% detectability produces potentially biased occupancy estimates. Novel analytical tools have been developed that correct for bias arising from imperfect detectability, species misidentification and spatial autocorrelation between detection survey replicates that can affect transect surveys. To date they have been applied individually, but their combined value is unclear.

The recovery of carnivores such as the European pine marten *Martes martes* potentially has far reaching, but largely unknown, implications for ecosystem restoration. Analysis of the species' distribution has as yet been crude and hence unsuited for informing management. We aimed to assess the validity of standard scat surveys to provide recommendations to increase inference from future surveys.

We employed spatially replicated scat surveys along forest paths in NE Scotland, genetic verification of scat provenance and occupancy modelling techniques to quantify pine marten detectability and variation therein. Detectability for 1 km and 1.5 km transects, comparable to standard protocols, was estimated to be 0.35 and 0.58 respectively, highlighting the importance of accounting for imperfect detectability. Detection probabilities decreased with vegetation cover and increased with path width. Models accounting for spatial autocorrelation between adjacent transect segments suggested that segments of ≥ 400 m could be analysed as spatial replicates with negligible bias. As is the norm, not all scats yielded DNA to genetically verify they were produced by pine marten. This was accounted for through the use of 'miss-classification occupancy models' which allowed the use of unverified scats, increasing detection probabilities while accounting for the probability of unverified scats being false positive detections.

This study exemplifies that robust inference on species occupancy is achievable through careful consideration of sampling design and the application of readily available analytical techniques. Adopting best-practice need not increase monitoring costs and can even increase cost-efficiency.

The pine marten *Martes martes* is an arboreal mustelid listed on the EU Habitats and Species Directive, Annex V. Like many other carnivores, is recovering from historical persecution by game shooting interests in Britain and Ireland (Croose et al. 2013). In Scotland, the species' recent range expansion has raised concern about its possible impacts on ground nesting game birds including the endangered capercaillie *Tetrao urogallus* persisting in fragmented woodlands (Summers et al. 2009), as well as suggestion it will constrict the distribution of invasive non-native grey squirrels *Sciurus carolinensis* in Britain and Ireland (Sheehy and Lawton 2014). For these reasons, significant resources are invested in monitoring pine marten distribution, employing large scale

scat surveys and genetic methods to verify the identification of pine marten scats (Croose et al. 2013). To date however, surveys have been restricted to presence-absence without explicitly accounting for detectability and the probability of obtaining false-negative results; the failure of detecting the focal species when it is present. Thus management is based on so-called 'naïve' estimates of occupancy.

Yet, it is now widely accepted that the probability of detecting individuals or their signs during a survey is often less than 1 and may vary with environmental and ecological conditions. Effective monitoring is a crucial prerequisite to the diagnosis and management of any wildlife conflict but imperfect and variable detectability creates bias in estimates of species distribution and occupancy, and confounds trends therein (MacKenzie et al. 2002), potentially leading to misguided management. Considering detectability is particularly important for cryptic species that occur at low densities such as carnivores (Karanth et al. 2011).

Current monitoring of pine marten populations in Britain and Ireland is based upon establishing its presence in hectad (100 km²) sampling units based on the detection of scats along typically a single transect (Balharry et al. 1996, O'Mahony et al. 2012, Croose et al. 2013). Determining the species of origin of carnivore scats found during surveys can be inaccurate in the field, for this reason genetic techniques are often used to confirm species identity where misidentification rates are deemed to be non-trivial (Sarre et al. 2013). It has been established that at least 18% of 'pine marten' scats identified by experts in the field are actually produced by red foxes *Vulpes vulpes* (Davison et al. 2002), necessitating the systematic genetic verification of scats collected in pine marten surveys to reduce false positive detections (O'Mahony et al. 2012, Croose et al. 2013).

As with many other species, making rigorous inference based on monitoring requires consideration of the influence of false negative detections, an issue long acknowledged to affect pine marten surveys (Birks et al. 2005, O'Mahony et al. 2012, Croose et al. 2013) and readily dealt with by standard occupancy modelling techniques (MacKenzie et al. 2006). A second issue which arises in cases such as this is that the status of detections is unknown and must be validated genetically or by other means to avoid false positive errors. Viable DNA is not successfully extracted from all collected scats, leaving a fraction with unknown provenance which are typically discarded from analysis and not used to gain inference on occupancy. Here, an analytical solution lies in a recent generalisation of occupancy modelling techniques that allows 'certain' and 'uncertain' detections, which are used to account for the probability that some uncertain detections are in fact false positive where the site is in truth unoccupied (Miller et al. 2011). Thus even though the requirement for genetic verification of species identity has increased the financial costs of pine marten surveys, reliable estimates of occupancy could be obtained by genetically verifying only a subset of collected scats. To date this has not been attempted.

Standard occupancy models require replicated, independent, detection opportunities which are typically replicated temporally (MacKenzie et al. 2006). Alternatively, spatial replication can be used, given that occupancy is interpreted appropriately as being confounded by availability for detection within each spatial replicate, and survey locations are selected randomly with replacement within sites (Kendall and White 2009). Meeting these conditions can however be logistically unfeasible for large scale sign surveys and when they are not met parameter estimates from standard occupancy models can be biased as a result, particularly when the availability of signs is spatially structured, e.g. when scats are deposited in a non-random manner (over-dispersed or aggregated) to mark territory features (Hines et al. 2010). Here too methodological developments exist, the Hines et al. (2010) spatial autocorrelation occupancy model explicitly accounts for dependence in availability for detection between adjacent observations, allowing transect surveys to be split into segments which are then used as replicated surveys. The minimal transect segment length with negligible spatial dependence can be determined by comparing the fit of standard and spatial autocorrelation occupancy models to detection data constructed using the same transect segment

length for a range of transect segment lengths (Thorn et al. 2011). This allows analysis of covariate effects to be carried out using simple models at the smallest scale with negligible autocorrelation, maximising sample size while reducing model complexity.

This study aimed to evaluate and increase the rigour of inference from occupancy sign surveys while promoting the uptake of best practise by providing an example of how recent analytical developments in occupancy modelling can be used to account for imperfect detection and the influence of environmental covariates on detectability. We also sought to make use of scats genetically confirmed to be from pine marten and those of uncertain provenance by including these as unconfirmed detections. We find that the potential limitations inherent to sign surveys, of this and potentially other species can readily be addressed using existing methodological techniques.

Material and methods

Study design

The detectability, deterioration and deposition rates of pine marten scats, along with the likelihood of successful genetic verification, may be influenced by a range of environmental and ecological conditions. Adverse weather conditions during and prior to surveying may reduce the detectability of pine martens by reducing scat deposition rates and increasing scat deterioration. The availability and detectability of scats is also likely to be reduced on more uneven pathtypes and paths with increased vegetation as this may reduce the visibility of scats, alter their deposition rates and provide a microclimate favouring scat and DNA deterioration through the action of microbes and scat-predating invertebrates. Pine martens may be more likely to mark wider forest paths, as marking more prominent features may provide more effective olfactory communication with conspecifics. However, it is also possible that wider paths may be avoided by pine martens in response to perceived predation risk or that the greater area to be searched during surveys reduces detection probability. The red fox is a predator of pine marten (Lindström et al. 1995) and may affect detectability by suppressing pine marten density or increasing predator avoidance behaviour.

Surveying methodology was designed to emulate previous large scale pine marten surveys (Croose et al. 2013) so that results could be used to provide reliable recommendations for improvement. A potential study area of 10 × 11 of the 100 km² hectads was defined in northeast Scotland (Supplementary material Appendix 1), within the pine marten's range reported by Croose et al. (2013), including hectads recently colonised by pine martens. Twenty-nine hectads that contained insufficient pine marten habitat (woodland) in which to complete a ≥ 2 km transect along paths were excluded. Within each hectad, the most extensive woodlot was identified as a potential survey site. Given the relatively small area surveyed within each 100 km² hectad (≈ 3 km transect), it should be noted that it is minimum occupancy that is being estimated for each hectad.

The hypothesis that predation pressure from red fox might influence detection probability was investigated by stratifying site selection based on the occurrence of fox control by land managers (game keepers) as a proxy for fox density. To ensure good representation of sites subjected to fox control, four sites on game-keepered private sporting estate sites were selected a priori. A further 27 sites were selected by randomly sampling without replacement hectads within the study area. The presence or absence of fox control in these sites was determined by communication with land managers.

Transects were ≥ 2 km long (3 km where possible) and were separated by ≥ 3 km from transects in neighbouring hectads to ensure independence of sampling between different sites. Transect start points used by Croose et al. (2013) were re-used where available ($n = 19$). Otherwise transect started upon entering the selected forest block from the access point (i.e. car park/public road). At path intersections, direction was determined randomly with directions that could not lead to a completed 3 km transect being excluded, unless 3 km of path was unavailable in which case the direction leading to the longest possible transect was selected. Transects were mapped onto 1: 25 000 Ordnance Survey maps using ArcMap10.

Scat survey

Selected transects were surveyed in June 2013. Transects were searched and all possible pine marten scats were collected by the lead author. To assess the potential of using observer identification certainty as a surrogate for genetic verification, each scat was scored on a subjective 1–10 scale of certainty of correct identification based on morphology and characteristic ‘fruity’ smell relied upon by studies prior to the development of effective genetic verification techniques (Balharry et al. 1996). Scats were lifted into separate plastic sealable sample bags using disposable wooden spatulas to prevent DNA contamination, given a unique identification number and frozen at -20°C . The locations of collected scats were recorded using GPS (minimum precision ± 15 m).

Recent weather and survey weather were included as site specific covariates, recorded as binary variables based on the occurrence of rain in the 48 h previous to surveying and during surveying respectively. Transect-specific covariates relating to path characteristics were assessed and recorded approximately every 50 m, with additional records taken at path intersections where changes in path characteristics typically occurred, and marked using GPS. Mean percentage vegetation cover over the width of the path was estimated by

eye to the nearest 10%. Mean path width and mean vegetation height at a resolution of 10 m were estimated by eye, or using a measuring tape when unsure, precise to the nearest 0.5 m and 0.05 m respectively. The paths on which surveys were conducted were typically uniform in their characteristics, with changes typically occurring at path intersections and being more extreme than the degrees of precision considered here. For this reason the relatively crude estimation of path covariates was deemed appropriate. All covariates recorded are described in Table 1.

DNA analysis

To account for the common confusion between red fox and pine marten scats collected in the field, species of origin was determined using quantitative PCR techniques described by O’Reilly et al. (2008). As is often the case, funding limitations constrained the number of scats for which provenance could be verified using DNA analysis. Of the 120 scats collected, 109 subjectively deemed most likely to yield viable DNA (based on degradation, age etc.) were selected for genetic analysis. The remaining 11 were categorised as ‘unconfirmed pine marten scats’ for the purposes of analysis. Scats selected were analysed for the presence of pine marten DNA using methods described by O’Reilly et al. (2008) at the Waterford Institute for Technology, Ireland. Scats that tested positive for pine marten DNA were classed as ‘certain pine marten scat’. Those negative for pine marten DNA were assessed for the presence of fox DNA, and those positive were classed as ‘certain fox scat’. Analysed scats for which no DNA was extracted were also categorised as ‘unconfirmed pine marten scats’.

Analyses

Standard single-season occupancy models were applied to data collected in the field to provide estimates of detectability under different site and transect conditions. Spatial autocorrelation models were used to determine the smallest segment length at which spatial-autocorrelation could be considered negligible. Misclassification models were used to assess the potential utility of including unconfirmed pine marten scats in analysis.

The distance of each scat detection and covariate record from the start of each transect was calculated using ArcMap10. Scat detection histories were then constructed for each site by splitting transects into adjacent segments of equal length and using these segments as replicate observations, with positive detections occurring when a scat was

Table 1. Description of covariates used to model probability of detecting pine martens, p , during scat surveys.

Abbreviation	Description	Type
PW	proportion of hectad containing woodland	site specific, proportion
VC	proportion of path covered by vegetation	survey specific, proportion
VH	mean height of vegetation on transect	survey specific, continuous
W	mean width of transect	survey specific, continuous
PT	path type: forest road, 4x4 vehicle track, foot path	survey specific, categorical
FC	presence of fox control	site specific, categorical
RW	recent weather: occurrence of rain in last two days	site specific, categorical
SW	survey weather: occurrence of rain during survey	site specific, categorical

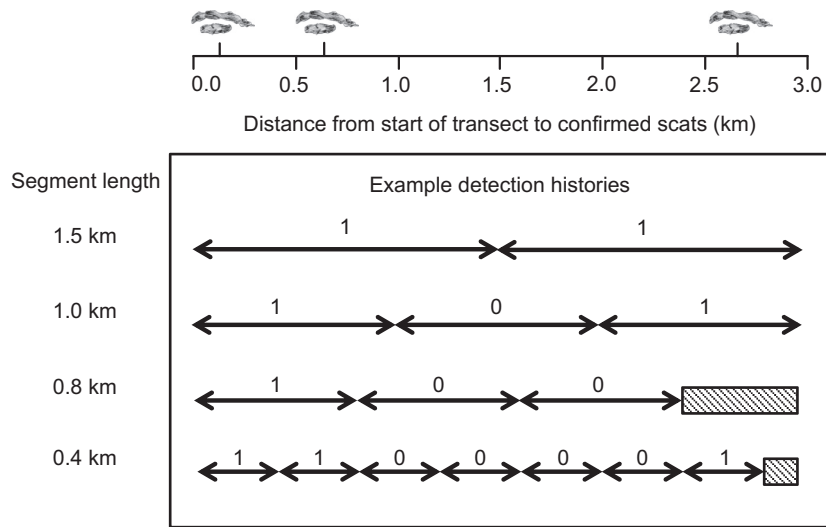


Figure 1. Schematic to illustrate the methodology for the construction of standard detection histories using the positions of genetically confirmed pine marten scats (🐾) collected along survey transects. Transects are split into adjacent segments (↔) of equal length and detections/non-detections within each segment are used to construct detection histories. Segments ranged in length from 0.1 to 1.5 km, where complete transect length is not divisible by the segment length the final incomplete segment (▨) is ignored.

detected within that segment (Fig. 1 for schematic representation). Detection histories take the form of binary series denoting a detection or lack of detection for each replicated observation at a site (e.g. 1001 denotes four observations of an occupied site with positive detections on the first and fourth observations but not the second or third). Standard detection histories (using confirmed pine marten scats) (MacKenzie et al. 2006), misclassification detection histories (using confirmed and unconfirmed pine marten detections) (Miller et al. 2011) and sampling covariate histories (covariate values for each replicated observation) were constructed. Where individual segments contained varying covariate records (e.g. vegetation cover), the mode over length was used for categorical covariates and mean over length for continuous covariates.

To allow estimation of detection probabilities for transect segments of differing length a suite of 15 sets of detection (standard and misclassification) histories were constructed from the sampling data, with each set using a different segment length (0.1–1.5 km). Detection histories were imported into PRESENCE ver. 10.2 (Hines 2006) for analysis of occupancy models. Null single-season occupancy models assuming constant occupancy, $\psi(\cdot)$, and detection probability, $p(\cdot)$, (MacKenzie et al. 2002) were generated for each set of detection histories to determine the effect of segment length on the probability of detecting pine martens using conventional survey methodology (used by Croose et al. 2013).

Parameters estimated from standard occupancy models using adjacent spatial sampling units may be biased by autocorrelation in availability for detection between replicated observations. The Hines et al. (2010) spatial autocorrelation occupancy model explicitly accounts for between-segment non-independence by estimating the probability of availability given availability in the previous segment, θ' , and the probability of availability given no availability in the previous segment, θ . Bias due to autocorrelation between adjacent observations can be considered negligible when model

selection by AIC (at the level of $\Delta AIC > 2$) favours the null model over the spatial autocorrelation model and $\theta' \approx \theta$ (Thorn et al. 2011). We applied this model to the sets of standard detection histories for each segment length to test for between-segment spatial dependence. Following recommendations by Hines et al. (2010), only detection histories of three or more observations (segment lengths between 0.1 km and 1 km) were considered.

Spatial auto-correlation occupancy models require the estimation of four parameters (ψ , p , θ and θ') prior to the inclusion of covariates. With this in mind and considering the sample size, there was a concern of overparameterisation if covariate effects and spatial dependence were considered in the same model. For this reason, we utilised an approach employed by Thorn et al. (2011) whereby the minimal segment length with negligible spatial autocorrelation (where $\theta \approx \theta'$) was identified prior to the inclusion of covariates. This was achieved by comparing the AIC scores of the spatial auto-correlation occupancy model; $\psi(\cdot)$, $p(\cdot)$, $\theta(\cdot)$, $\theta'(\cdot)$, with the null occupancy model; $\psi(\cdot)$, $p(\cdot)$ for each of the standard detection histories constructed (representing each segment length) separately. Detection histories for the smallest segment length with no evidence of spatial autocorrelation were used in further analysis to assess the influence of covariates on detection probabilities. Candidate models capturing different hypotheses were constructed where occupancy was assumed to be constant, $\psi(\cdot)$, or varying with proportion woodland, $\psi(PW)$, and detection probability, p , was influenced by sampling covariates (e.g. vegetation cover: $p(VC)$). Top ranked models were selected based on the threshold of $\Delta AIC > 2$.

The potential utility of including scat identification error rates modelled using subjective scoring as a surrogate for DNA species verification was assessed using a binomial GLM. A binary response variable was constructed using the scats which yielded viable DNA (1 for certain pine marten 0 for certain fox) and the respective subjective pine marten certainty scores were used as an explanatory variable.

Occupancy models accounting for the possibility of misclassifying a site as occupied (Miller et al. 2011) were used to investigate the potential value of including unconfirmed pine marten scats in analysis. Misclassification models estimate the probabilities of: site occupancy (ψ); obtaining a detection during a survey of an occupied site (p_{11}); obtaining a detection during a survey of an unoccupied site (p_{10}); and obtaining a 'certain' detection during a survey, given the site is occupied and a detection occurred (b).

Results

Approximately one hundred kilometres of scat transects were walked at 31 sites in June 2013 and used to create detection histories based on 1005 spatially replicated observations using 100 m transect segments. One hundred and twenty possible pine marten scats were collected, of which 109 underwent DNA analysis to verify species identity. Of these, 47 were 'confirmed pine marten scat' (43%), 15 (12%) were 'confirmed fox scat' and 47 (43%) were 'unconfirmed pine marten scats'. 'Confirmed pine marten scats' were detected in 39 100 m segments (potential spatial replicates) in 21 of the 31 sites, yielding a naive occupancy estimate of 0.68. 'Unconfirmed pine marten scats' were detected in a further 50 100 m segments in a further five sites, yielding a higher naive occupancy estimate of 0.81 if field identification of scats had been used alone.

The probabilities of detecting confirmed pine marten scats using transect segment lengths comparable to transects used in previous surveys (O'Mahony et al. 2012, Croose et al. 2013) were $0.35 (\pm 0.05 \text{ SE})$ for 1 km and $0.58 (\pm 0.10 \text{ SE})$ for 1.5 km transects. Detection probabilities estimated using standard single season occupancy models, $\psi(\cdot)$, $p(\cdot)$, increased from 0.04 to 0.58 for segment lengths ranging from 0.1 km to 1.5 km with an approximately linear relationship (Fig. 2).

Spatial autocorrelation analyses produced no evidence that the availability of pine marten scats was dependent on availability in adjacent segments ≥ 400 m long. Estimated 95% confidence intervals for spatial dependence parameters θ and θ' overlapped for all segment lengths considered

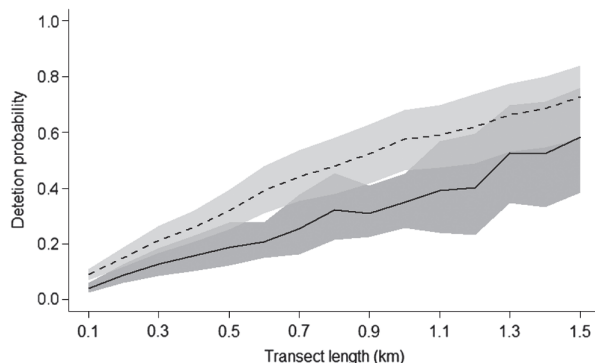


Figure 2. Mean probability of detecting pine marten scats at occupied sites during survey transects of different lengths ($n = 15$) using only DNA confirmed scats (solid line) and both confirmed and uncertain scats (dashed line). Grey polygons represent 95% confidence intervals.

(Table 2). Accounting for spatial autocorrelation reduced model parsimony for all segment lengths except 300 m, for which no difference was detected relative to the null model ($\Delta\text{AIC} = 1.59$; Table 2). Given this lack of support for between-segment dependence, models accounting for spatial auto-correlation were not considered further. As a precaution to minimise the risk of bias, detection histories using segments of 400 m were used in analysis of covariate effects.

The influence of site and survey covariates were assessed using 400 m segment detection histories, as this provided the maximum number of replicated surveys while minimising bias due to dependence in availability between adjacent segments. Thirteen plausible candidate occupancy models that relate variation in detection and occupancy probability to different covariates were ranked by AIC (Table 3). Vegetation height and cover were the most influential covariates (AIC weights = 0.315 and 0.272 respectively), detection probability was negatively affected by both vegetation height ($\beta_0 = -1.29 \pm 0.21 \text{ SE}$; $\beta_{\text{VH}} = -8.64 \pm 3.15 \text{ SE}$) and cover ($\beta_0 = -1.21 \pm 0.23 \text{ SE}$; $\beta_{\text{VC}} = -2.35 \pm 0.83 \text{ SE}$). Model selection also suggested that path width had a positive effect on detection probability when considered additively with vegetation height ($\beta_0 = -2.12 \pm 0.77 \text{ SE}$; $\beta_{\text{VH}} = -7.58 \pm 3.25 \text{ SE}$; $\beta_{\text{W}} = 0.25 \pm 0.22$) or cover ($\beta_0 = -1.87 \pm 0.81 \text{ SE}$; $\beta_{\text{VC}} = -2.04 \pm 0.89 \text{ SE}$; $\beta_{\text{W}} = 0.19 \pm 0.22$). The combined weight of the four top ranked models considering only vegetation height, vegetation cover and path width was 0.96. Candidate models accounting for the effect of recent weather, survey weather, fox control, path type and proportion woodland on detection probability and the effect of proportion woodland on occupancy were not supported as they all reduced model parsimony (Table 3).

The subjective scoring of scats based on certainty was not a viable surrogate for genetic verification: certainty scores were unrelated to the verified species that produced the scat ($z = 0.17$, $\text{DF} = 59$, $p = 0.9$) and was not considered in further analysis. The false positive model $\psi(\cdot)$, $p_{11}(\cdot)$, $p_{10}(\cdot)$, $b(\cdot)$ allowed detections of scats for which genetic analysis failed to confirm species identity to be included in analysis by explicitly modelling miss-classification probability. The probability of correctly detecting pine martens where present increased with segment length (Fig. 2). Utilising unconfirmed pine marten scats and accounting for the possibility of mis-identification increased detection probabilities at occupied sites relative to using only scats confirmed by DNA analysis. However, this difference was not statistically significant for all segment lengths, indicated by overlapping 95% CIs (Fig. 2; see Supplementary material Appendix 1 Table A2 for parameter estimates).

Discussion

We evaluated the effectiveness of standard pine marten scat survey techniques and found high occurrence of false-negative observations using standard methods. If not corrected for, imperfect detectability will negatively and substantially bias estimates of distribution and occupancy and may lead to increased noise in sampling results; masking spatial and temporal trends in true species occupancy. Additionally, the influences of vegetation height, cover and

Table 2. Comparison of parameter estimates for spatial autocorrelation occupancy models based on detection histories using different segment lengths. θ is the probability of availability for detection in one segment given no availability in the previous segment and θ' is the probability of availability for detection on a segment given availability in the previous segment. Δ AIC *cf.* $\psi(\cdot), p(\cdot)$ is the increase in AIC of spatial autocorrelation occupancy models relative to simple models assuming no spatial dependence for that transect length.

Segment length (km)	θ	95% CI (θ)	θ'	95% CI (θ')	Δ AIC <i>cf.</i> $\psi(\cdot), p(\cdot)$
1.00	0.733	0.232–0.961	1.000	0.000–1.000	2.76*
0.9	0.329	0.235–0.440	0.222	0.086–0.465	3.18*
0.8	0.366	0.222–0.538	0.269	0.134–0.467	3.38*
0.7	0.598	0.196–0.901	1.000	0.000–1.000	2.43*
0.6	0.211	0.149–0.290	0.185	0.079–0.375	3.91*
0.5	0.653	0.121–0.963	1.000	0.000–1.000	3.45*
0.4	1.000	0.000–1.000	0.743	0.015–0.998	3.86*
0.3	1.000	0.000–1.000	0.401	0.101–0.800	1.59
0.2	0.083	0.054–0.125	0.125	0.053–0.267	3.31*
0.1	0.040	0.026–0.061	0.077	0.025–0.213	2.57*

*Null model, $\psi(\cdot), p(\cdot)$, is favoured at the level of Δ AIC > 2; no evidence for statistically significant spatial autocorrelation in availability for detection between adjacent segments.

path width estimated here can be used to plan future surveys to maximise detection probabilities, these surveys should however account for and re-estimate these effects.

Twenty four percent of the scats from which DNA was successfully extracted were verified as fox scats. This reinforces the need to use genetic species verification when drawing inference on pine marten (and indeed other species identified through their scats) ecology using scats (Davison et al. 2002). In our study, as in others by more experienced marten specialists, subjective scores of certainty of identification were no surrogate for DNA analyses. It is however important to consider that potential correlation between the species that produced the scat and the probability of successful DNA extraction may confound these results.

Substantial survey effort has been expended in Scotland and Ireland to monitor the distributional dynamics of pine martens but no study to date has explicitly or statistically accounted for imperfect detectability (Balharry et al.

Table 3. Model selection results: role of site and survey specific covariates in determining the probability of detecting confirmed pine marten scats using 0.4 km transect segments. Number of sites = 31. Covariates considered are: proportion of hectad containing woodland (PW), vegetation cover (VC), vegetation height (VH), path width (W), recent weather (RW), survey weather (SW), fox control (FC) and path type (PT). Models are ranked by AIC a measure of parsimony, w_i is model weight a measure of support for the model relative to candidate models, and K is the number of parameters.

Model	AIC	Δ AIC	w_i	K	Model likelihood
$\psi(\cdot), p(\text{VH})$	202.69*	0.00	0.315	3	1.000
$\psi(\cdot), p(\text{VC})$	202.98*	0.29	0.272	3	0.865
$\psi(\cdot), p(\text{VH} + \text{W})$	203.34*	0.65	0.227	4	0.723
$\psi(\cdot), p(\text{VC} + \text{W})$	204.22*	1.53	0.146	4	0.465
$\psi(\cdot), p(\text{W})$	208.52*	5.83	0.017	3	0.054
$\psi(\cdot), p(\text{W} + \text{W}^2)$	210.35	7.66	0.007	4	0.022
$\psi(\cdot), p(\text{RW})$	211.26	8.57	0.004	3	0.014
$\psi(\cdot), p(\cdot)$	211.28	8.59	0.004	2	0.014
$\psi(\cdot), p(\text{PW})$	213.11	10.42	0.002	3	0.006
$\psi(\cdot), p(\text{SW})$	213.17	10.48	0.002	3	0.005
$\psi(\cdot), p(\text{FC})$	213.23	10.54	0.002	3	0.005
$\psi(\text{PW}), p(\cdot)$	213.24	10.55	0.002	3	0.005
$\psi(\cdot), p(\text{PT})$	215.10	12.41	0.001	4	0.002

*Significantly improved fit relative to the null model $\psi(\cdot), p(\cdot)$ at the level of Δ AIC > 2.

1996, O'Mahony et al. 2012, Croose et al. 2013). In order to maximise scope for comparison and illustrate the cost-efficiency of our more rigorous approach we used a field sampling design similar to O'Mahony et al. 2012 and Croose et al. 2013. Our quantification of detection probabilities for commonly used transect lengths of 1 km and 1.5 km (Croose et al. 2013 and O'Mahony et al. 2012 respectively) were substantially below the value of 1 implicitly assumed by naïve estimates, namely 0.35 and 0.58 respectively. These large discrepancies have no doubt led to bias in the past, i.e. the underestimation of the true occupancy of pine marten at a given time, and bias of unknown magnitude and direction in estimates of its rate of spread and predictors thereof. We thus reiterate the evidence that ignoring the issue of less than perfect detectability occupancy is a misuse of resources. Occupancy modelling must be used in future surveys of the distribution of pine marten and many other species to maximise the scope of inference using those surveys (Sarre et al. 2013). The cost of applying appropriate analytical methods is minimal relative to the cost of performing field surveys. While it is natural that methods improve over time, sophisticated methodological developments pioneered with studies of water voles show it is possible to make use of detectability estimates when analysing data collected using 'naïve design' that predate awareness of the importance of detectability without jettisoning valuable historical data (Sutherland et al. 2014). While these methods impart appropriate uncertainty to historical estimates they are no substitute for appropriate contemporary survey designs to maximise power.

Our expectation that pine martens scats would have a spatial structure in their distribution, based on their role in territory marking (Caryl et al. 2012), a potential source of bias in occupancy estimates when using spatial replicates, was not supported by evidence. Spatial-autocorrelation occupancy models identified transect segment lengths of 400 m as the minimal segment length where bias due to spatial non-independence in detection histories could be considered negligible. Thus it is possible to use standard single-season occupancy models without increasing the length of transect and so the cost of conducting surveys. In this case relatively small adjacent transect segments could be considered as spatially replicated observations without

significant spatial dependence, however the generality of this may be limited and spatial autocorrelation models should always be considered in similar analyses. The evidence here does however suggest that spatial autocorrelation in pine marten detections operates at a small scale and that data from earlier surveys can therefore be reanalysed using occupancy modelling techniques, provided locations of transects and detected scats were recorded and that scats were selected for genetic analysis independently. Croose et al. (2013) selected the scats perceived to be most likely to yield extractable DNA and to be pine marten at the site level where multiple possible pine marten scats were detected, while O'Mahon et al. (2012) sequentially tested scats deemed most likely to originate from pine marten collected within each hectad until a certain pine marten scat was verified. Directly applying occupancy models to data from these previous pine marten surveys (O'Mahony et al. 2012, Croose et al. 2013) may negatively bias detection probabilities by systematically reducing the number of confirmed detections in sites with a relatively high number of possible detections. Thus we recommend a standard design be adopted for selecting scats for DNA verification, analysing all collected scats when possible (Sarre et al. 2013). Resources may be conserved by analysing all scats detected within a single replicate survey segment together, choosing the finest scale for replicate surveys allowed by resource limitations.

Of the covariates considered, vegetation height and cover had the greatest influence on the probability of pine marten detection. Vegetation may decrease detectability directly and decrease scat deposition rates. Additionally, increased vegetation may increase scat deterioration rates by providing relatively favourable conditions for microbe and invertebrate activity. Detection probabilities were positively related to transect width, when considered additively with the influence of vegetation cover or height. The availability of pine marten scats may increase for wider paths, possibly due to increased deposition rates of these more prominent territory features. The occurrence of rain in the two days prior to and during surveys did not affect estimations of detectability. However, weather during fieldwork was generally dry which may have reduced the statistical power to detect an effect. Additionally, the occurrence of rain could have an effect over a longer, prolonged, period. There was no evidence of any influence of fox control on detectability, suggesting that fox control on private estates was ineffective at reducing densities to a level sufficient to affect pine marten scat deposition behaviour. Indeed there is evidence to suggest that culling of foxes is generally ineffective at reducing population density (Baker and Harris 2006). Proportion woodland did not affect occupancy probability suggesting that, over the range of sites in this study, pine marten are not limited by habitat availability. Proportion woodland also had no effect on detectability indicating that, independent of transect length, the proportion of available habitat surveyed has no effect on detection rates. Model selection by AIC was considered an appropriate method to identify the covariates influencing pine marten detection probabilities, however were effect determining effect sizes is of prime interest future studies may wish to consider a model averaging approach to account for the impact of uncertainty in model selection.

False positive occupancy models provided an effective method for including scats from which no viable DNA was

extracted by explicitly modelling the probability of unconfirmed detections being misidentified. As estimated occupancy of sites was relatively high, it was difficult to assess the benefit of models accounting for false positive detections in terms of improved precision. However the results from these false-positive models demonstrate how unconfirmed sign detections can be effectively used to improve estimates of species occupancy from transect surveys. Use of false positive models will improve the value of future surveys, particularly on the expanding front of the species' range where the availability of scats with extractable DNA is likely to be lower as a result of low population density.

This study has demonstrated that, thanks to the analytical advancements being developed in the field of wildlife monitoring, existing methodological solutions were available for many of the practical and logistical constraints encountered during surveying. Most notably, this study has shown how the adoption of best practice need not cost more and indeed may reduce the costs of acquiring information of greater value on wildlife populations, leading to more effective and efficient monitoring and management. It is striking however that these techniques and the free software to implement them predates publications that made sub-optimal use of hard won data. With this in mind, low practitioner uptake of methods currently available to maximise inference from wildlife surveys represents an important barrier to effective wildlife management that needs to be overcome through improved training and collaboration.

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Supplementary material (available online as Appendix wlb-00146 at <www.wildlifebiology.org/appendix/wlb-00146>). Appendix 1.