Received: 13 April 2022 | Accepted: 22 April 2022

DOI: 10.1002/ecs2.4165

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Methods, Tools, and Technologies

A comparison of density estimation methods for monitoring marked and unmarked animal populations

Joshua P. Twining[1] | **Claire McFarlane**[2] | **Denise O'Meara**[3] | **Catherine O'Reilly**[3] | **Marina Reyne**[2] | **W. Ian Montgomery**[2] | **Sarah Helyar**[2] | **David G. Tosh**[4] | **Ben C. Augustine**[1]

[1]Department of Natural Resources, Cornell University, Ithaca, New York, USA

[2]School of Biological Sciences, Queen's University of Belfast, Belfast, UK

[3]Molecular Ecology Research Group, Eco-innovation Research Centre, School of Science and Computing, South East Technological University, Waterford, UK

[4]Raithlin LIFE Project, The Royal Society for Protection of Birds, Belvoir Park Forest, Belfast, UK

Correspondence
Joshua P. Twining
Email: jpt93@cornell.edu

Handling Editor: Debra P. C. Peters

Abstract

Effective monitoring of wildlife populations forms the foundation of modern-day conservation biology. Without reliable estimates of population size, it is not possible to determine population trends, a key requirement in determining species status under international legislation. Carnivores are one of the more difficult taxonomic groups to monitor due to low population densities and elusive behavior. Here, we compare conventional live trapping and two more modern, noninvasive field methods of population estimation: genetic fingerprinting from hair tube sampling and camera trapping for the pine marten (*Martes martes*). We apply marked spatial capture–recapture (SCR) models to the genetic and live-trapping data where individuals were identifiable, and unmarked SCR (uSCR), camera-trap distance sampling (CT-DS), and random encounter models (REMs) to the camera-trap data where individual ID was not possible. All five approaches produced plausible and relatively consistent point estimates (0.49–1.20 individuals/km^2) despite differences in precision, cost, and effort being apparent. Genetic fingerprinting produced the most precise estimate out of the two approaches for marked animal populations and had the key benefit of being noninvasive but was the most expensive of all the methods. Live trapping produced the highest point estimate while being cheapest, but the most labor intensive and least precise. The camera-trapping methods for unmarked animal populations were the most time efficient and precise except uSCR with a moderately informative prior (uSCRm), which produced the second least precise density estimate of all the methods compared. The CT-DS produced the most precise estimate of all the methods, followed by REM and then uSCR with a strongly informative prior (uSCRs). While choice of method of density estimation depends on objectives and funding constraints, as well as the species of interest, we demonstrate the importance of using *a priori* knowledge of target species and consideration of planned statistical analysis to produce appropriate experimental designs with critical

consideration required regarding trap spacing and spatial extent. Such considerations broaden the comparability and applicability of these methods and will serve to provide key reference estimates for researchers, wildlife managers, and non-governmental organizations involved in monitoring wildlife populations.

KEYWORDS
camera trapping, carnivores, density estimation, genetic methods, live trapping, population assessment, population monitoring, species enumeration

INTRODUCTION

Estimating the abundance or density of a population is essential for its management and ultimately the conservation of species and biodiversity. In the case of threatened species, such metrics are typically combined with data on the species' taxonomy, distribution, ecology, and threats to assess its conservation status (e.g., EU Habitats Directive, IUCN Red Lists). Understanding how a species' population changes over time is key to this process, and a plethora of invasive and noninvasive methods are available to inform species management.

Historically, live trapping has been the primary means of assessing densities where unique identifying markers on individuals (e.g., claw clipping, painting, or microchipping) has enabled the application of capture–recapture methods, which have more recently been developed into spatial capture–recapture (SCR) methods to estimate population densities (Efford, 2004). However, live trapping often requires licensing, has ethical considerations, and requires considerable expertise and time to sustain the necessary trapping effort to generate robust datasets (Stanley & Royle, 2005). For carnivores, which are typically wide ranging and occur at low densities, recapture rates are generally low, requiring sustained efforts to produce usable data and reducing the accuracy and precision of density estimates (Gese, 2001; Wilson & Delahay, 2001). Consequently, much effort has been expended in developing noninvasive methods to overcome the issues that live trapping presents.

The application of genetic noninvasive sampling (gNIS) to monitor populations has also increased over the last two decades (Schwartz et al., 2007). DNA is extracted from hairs or scats, and individuals are typically identified from a genetic fingerprint derived from variation across multiple microsatellite loci. This approach assigns unique genotypes to individuals, thus enabling noninvasive estimation of species population size and density using the SCR framework (Lukacs & Burnham, 2005; Schwartz et al., 2007). Although not without its own challenges (Gray et al., 2014; Williams et al., 2009), gNIS overcomes many of the issues associated with live trapping (e.g., De Bondi et al., 2010), offering a viable and attractive alternative to estimate population density from marked individuals (Brazeal et al., 2017).

Since their introduction, camera traps have been used increasingly to enumerate populations (Caravaggi et al., 2017). Camera trapping can be a quantitative, noninvasive approach with minimal environmental disturbance (Silveira et al., 2003). Compared to live trapping, camera trapping has low labor costs and can be used in environments where live trapping is not feasible due to difficult terrain and topology (Wearn et al., 2013). Where individuals can be identified, normal SCR models can be applied to camera-trap data to circumvent issues associated with the use of photographic rates as a proxy for abundance (Jenelle et al., 2002). However, this approach is limited to species where natural, unique markings allow identification of individuals, for example, felids (Karanth & Nichols, 1998; Trolle & Kéry, 2003). To overcome this limitation, there is a growing number of density estimation methods that can be used when individuals are unidentifiable. Unmarked SCR (uSCR) is part of the SCR family of models. However, unlike traditional forms of SCR that require marked animals, uSCR treats individuals' identities as latent variables (Chandler & Royle, 2013). uSCR is recognized to provide imprecise density estimates (Augustine et al., 2019); it is computationally expensive and restricted to Bayesian frameworks (Gilbert et al., 2021). These factors likely underpin the current lack of cross-validation of this method against others. An alternate method and without a doubt the most widely applied to generate density estimates from unmarked animals is the random encounter model (REM; Gilbert et al., 2021; Rowcliffe et al., 2008). Studies applying REM to a range of species have demonstrated the potential of the approach to inform species management (Cusack et al., 2015; Rowcliffe et al., 2008). However, cross-validation alongside other established methods has produced mixed results (Anile et al., 2014; Balestrieri et al., 2016; Palencia et al., 2021). Recently, the well-developed theory of distance sampling, a corner stone of wildlife monitoring, has been adapted and applied to camera-trap distance sampling (CT-DS) data (Howe et al., 2017). While it has been suggested to be suitable for

low-density species, testing and validation of this derivation of distance sampling remain limited (but see Capelle et al., 2019; Palencia et al., 2021).

The wide variety of invasive and noninvasive methods that have been developed to determine abundance and density of species over time generates its own issues, as information on the comparability of existing methods is lacking (but see Doran-Myers et al., 2021; Palencia et al., 2021). As an example, live trapping (Breitenmoser-Wursten et al., 2007), snow track counts (Andrén et al., 2002), camera trapping (Blanc et al., 2013), detection dogs, and genetic techniques (Hollerbach et al., 2018) have all been used to determine population densities of European Lynx (*Lynx lynx*). As the variety of techniques used on lynx demonstrates, researchers' use of methods to determine the density of a species are highly inconsistent, as are resulting estimates (Doran-Myers et al., 2021). User experience, time of year, habitat, budget, and life history of the target species can influence what technique is applied (Gese, 2001; Wilson & Delahay, 2001). Whatever approach is taken, there is a need for rapid, cost efficient, and precise methods to estimate density. The existing diversity of approaches used to estimate population density warrants examination to determine the comparability between methods, and an assessment of their suitability to practitioners in different scenarios with varying goals, expertise, and financial and infrastructural support.

This study aims to compare five approaches widely used to determine population density in carnivores. These comprise normal SCR applied to two field methods with individual identification: live trapping and gNIS using hair samples, and three statistical methods for unmarked populations, uSCR, REM, and CT-DS, applied to camera-trapping data. The five methods were used simultaneously to determine the density of a wide-ranging carnivore, the European pine marten (*Martes martes*). This small (1–2 kg), semiarboreal carnivore is recovering from severe population decline in Britain and Ireland (Sainsbury et al., 2019; Twining, Montgomery, & Tosh, 2020). Despite its ongoing recovery, it is largely restricted to forested habitats (Twining, Montgomery, & Tosh, 2020) and remains elusive, making density estimation difficult. Consequently, the pine marten is an ideal model species to evaluate different methods of population monitoring for elusive carnivores. We consider the merits, drawbacks, and context-dependent suitability of all five methods.

METHODS

Study site

The Ring of Gullion is located in County Armagh in Northern Ireland (NI) (Figure 1a). Designated as an Area of Outstanding Natural Beauty in 1991, it covers an area of 15,353 ha (153.53 km^2). Agricultural grassland dominates (66.8%) while forest cover is low at 7.7%. The sampled area of Slieve Gullion is homogenous across its geographical extent, being formed of fragmented, immature, non-native conifer plantations planted on upland heath. Thus, density of the pine marten population was not expected to vary significantly across the study area.

Sampling

Live trapping

Twelve Tomahawk 205 live cage traps were deployed along two perpendicular transects spaced approximately 400 m apart (Figure 1b). Trapping was conducted from August to October 2019 with daily trap checks. Traps were covered with tarpaulin to provide shelter, and hay and locally collected mosses and substrates were used to camouflage the trap and provide insulation. Traps were baited with a 2:1 mixture of peanuts and raisins covered in strawberry jam. The traps also contained a whole hen egg, and grapes to provide sustenance and hydration for captives. Traps were checked daily, just after dawn. Trapped animals were anesthetized with an intramuscular injection of ketamine (25 mg/kg) and midazolam (0.2 mg/kg) and scanned for a microchip. Any animal caught for the first time was fitted with a microchip (Friendchip Mini, Avid Identification Systems, Inc.) injected subcutaneously between the shoulder blades. Animals were released once conscious and responsive. Live trapping and anesthesia were conducted under license (Home Office, UK; Northern Ireland Environment Agency License 2228). The number and spatial extent of live traps was set by the maximum number of traps, which could be checked before dawn, ensuring the highest level of ethical care was maintained by minimizing time animals spent in traps and resultant stress.

Camera traps

Thirty Bushnell HD Trophy Cam 8 MP camera traps (model number: 119577) with 8-gigabyte SD cards were deployed during June and July 2019. Camera traps were deployed randomly at 30 locations across the study area (Figure 1d). All cameras were attached to trees at a height of approximately 30 cm. As per the REM and CT-DS methods, cameras were not baited (Howe et al., 2017; Rowcliffe et al., 2008). Camera traps were set to capture three photographs when triggered with a 1-s interval between triggers. Camera density was predetermined by calculating the ratio between number of

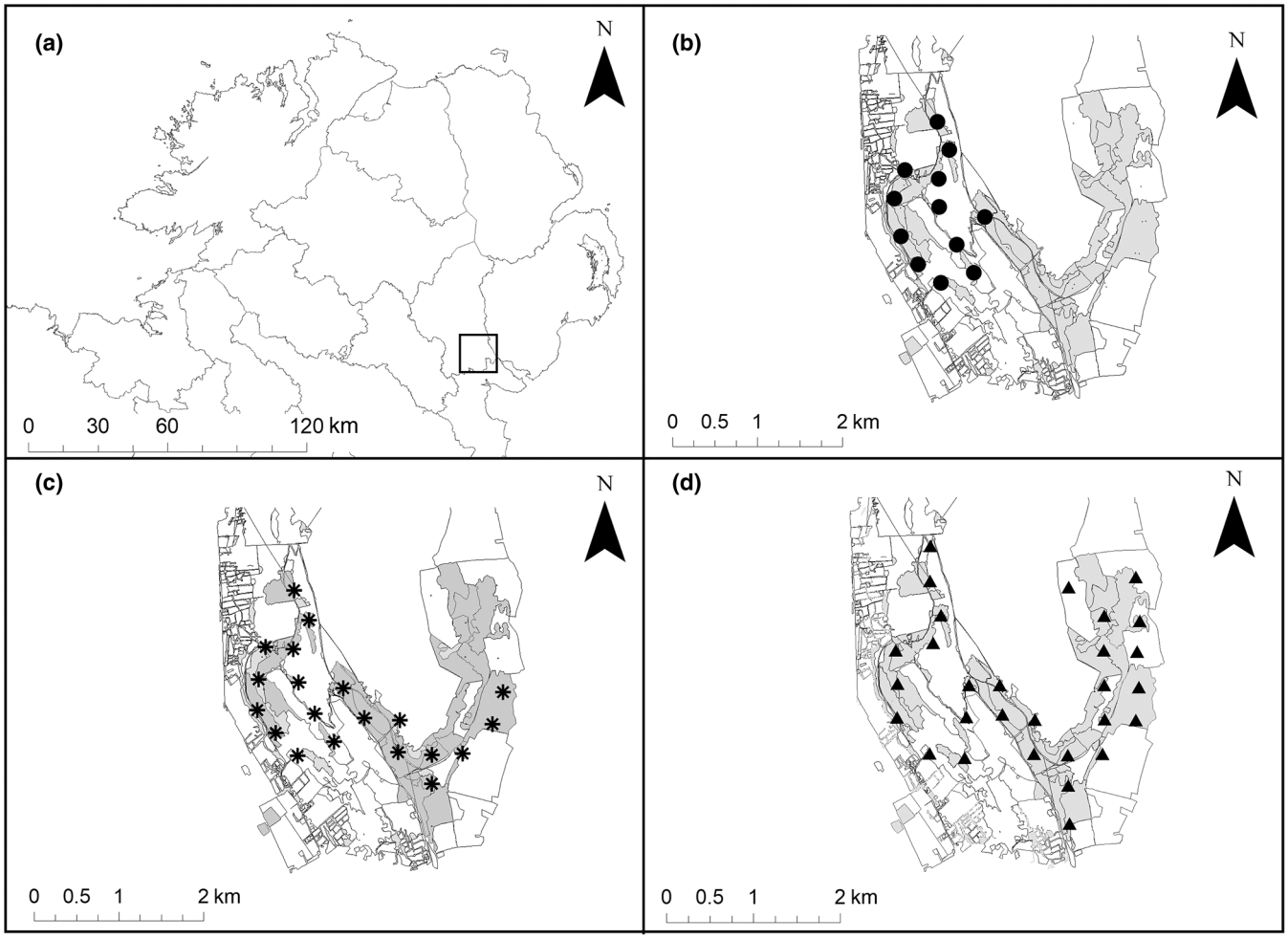

FIGURE 1 (a) Map showing Slieve Gullion in the context of Northern Ireland. (b) Map showing deployment location of live traps (circles) on Slieve Gullion. (c) Map showing hair tubes (asterisks) on Slieve Gullion. (d) Map showing deployment of camera traps (triangles) on Slieve Gullion. Gray represents forested habitat, and white represents nonforested habitat.

camera traps available (30) and study area size (6 km^2), and the inverse square root of this was used to calculate approximate distance between camera placements (0.4 km; Balestrieri et al., 2016). Trapping sites were plotted on a grid with 400-m spacing across the study area using ArcGIS (Figure 1b).

At the end of the survey period, camera traps were checked, and for each detection (the first image in a trigger sequence of an individual pine marten), distance to animal (in meters) and angle of detection (in degrees) were measured in situ. A 10-min interval was originally used to define an independent capture event, but, in practice, the shortest time between two consecutive detections was 28 min.

Genetic noninvasive sampling

Twenty hair tubes based on those developed by Mullins et al. (2010) were deployed across the study site between June and July 2019 with weekly checks (Figure 1c). Hair tubes were fixed vertically to trees approximately 1.5 m above ground level at approximately 400-m intervals along the same transects used for live traps. Hair tubes were baited with raw chicken tied to the top end with metal wire, with peanut butter smeared on the inside of the lid. A strong, adhesive, rat trap glue (The Big Cheese, STV International Ltd, UK) was affixed inside the entrance of the hair tube to collect a hair sample as the pine marten entered. Hair tubes were checked weekly, and sticky patches and bait were replaced on each visit. Hair samples were frozen at −20°C prior to DNA extraction.

DNA analysis

Genomic DNA was extracted from hair samples using the *Quick*-DNA Miniprep Plus Kit (Zymo Research) according to the manufacturer's protocol for hair samples.

Real-time quantitative polymerase chain reaction (qPCR) assays for species and sex determination were

carried out in replicate as described in Mullins et al. (2010). Females were identified through the amplification of ZFX only, while a signal from both ZFX and ZFY probes indicated when male DNA was amplified. The ZFX allele therefore acted as an internal amplification control for the assay.

Microsatellite analysis to identify individual pine marten was carried out using up to 11 microsatellite markers (Appendix S1: Table S1). The PCR amplifications were performed in a total volume of 10 μl with 3 μl DNA extract, 5 μl GoTaq Hot Start Green Master Mix (Promega), and primer concentrations as shown in Appendix S1: Table S1. The PCR conditions were as follows: initial denaturation at 95°C for 5 min, followed by 40 cycles of 95°C for 30 s, 57°C for 30 s, and 72°C for 30 s with a final extension at 60°C for 30 min. Samples were rapidly cooled to 4°C. Samples were diluted 1:4 in molecular grade water, and 1 μl of each diluted sample was denatured in 15 μl Hi-Di formamide (Applied Biosystems) with 0.15 μl GS500LIZ size standard (Applied Biosystems) for 5 min at 95°C, followed by rapid cooling to 4°C. The samples were run on an ABI3500 genetic analyzer (Applied Biosystems). The genotypes were scored using GeneMapper V5 (Applied Biosystems). Each sample was analyzed in duplicate, and only samples giving identical results in the replicates were scored. Genotype data were analyzed for probability of identity (PI and PI_{sibs}), observed (H_o) and expected (H_e) heterozygosity, and allele frequencies using GENALEX V6.

Precision

We provide an estimate of the precision of estimates through calculating the coefficient of variation of the mean. This is calculated using the following equation:

$$CV_{mean} = \left(\frac{SE}{\overline{\gamma}}\right) \times 100,$$

where SE is the standard error (or posterior standard deviation for the Bayesian uSCR and REM estimates) and $\overline{\gamma}$ is the point estimate.

Efficacy

To provide an estimate of time effectiveness, the number of hours required to undertake each stage of the density assessment technique was recorded. The whole process for each technique was divided into four stages: (1) setup, the time taken to deploy traps in the field; (2) maintenance, the time taken for checks, collection of samples, replenishing of bait, and handling of animals; (3) exit, the time required to retrieve all traps from the field; and (4) analysis, the time taken after the completion of fieldwork to produce density estimates including laboratory work if required and statistical analysis.

Cost

In addition to time, we compared costs of each technique used. We separated this out into two phases: setup and consumables. Due to difficulties producing a cost estimate for the infrastructural requirements of a molecular laboratory, we produced costs for noninvasive genetic sampling on the proviso of contracting the work out to a commercial laboratory (while ours were conducted by a partner institution). Access to a laptop and necessary open access software (e.g., R) is assumed and not included in estimates. Labor hours are excluded as costs (as these can be observed and approximated from the efficacy estimates).

Statistical analysis

Live traps and gNIS

Spatial capture–recapture (SCR) models were used to estimate density for both live trapping and gNIS (Efford & Boulanger, 2019). The SCR framework is increasingly used as it incorporates spatial information on an individual's capture location and home range activity center, overcoming issues associated with nonspatial estimation techniques (Borchers & Fewster, 2016; Efford, 2004). A standardized, four times root pooled square variance of movement was used as a buffer to trapping locations in each density estimation. Adequacy of buffer width was checked after model fitting using the effective sampling area plots (Appendix S1: Figure S1; Borchers & Efford, 2008). Maximum-likelihood models with a half-normal detection function containing two key parameters: g_0 (baseline detection rate is the probability of detection of an individual at the center of an animal's activity center per occasion) and σ (the spatial scale parameter [in meters] of the half-normal detection function that describes animal movement) were used for all models (Efford, 2004). Occasion lengths for live trapping were 1 day, while for gNIS were 1 week. For live trapping, we specified a single-use detector type, while for gNIS we specified a proximity-based detector type. These detector types are currently indistinguishable, as there is strictly no SCR model for the single-detector type. While this remains an open question, simulations have demonstrated that while estimates of the detection parameter g_0 may be biased, density estimates are essentially unbiased (Efford et al., 2009).

In addition to the above, we considered three variables and their potential impact on density estimates for both live trapping and gNIS: sex-based differences in movement and home range; learned responses of individuals to traps (trapping changing behavior leading to trap

happy or trap shy individuals); and time (detection rate changing over time due to factors other than trapping history, e.g., changes in local weather conditions). We fitted 15 a priori models with varying effects on the detection parameters, g_0 and σ, for both methods (Tables 1 and 2). We account for potential heterogeneous capture probabilities between males and females by modeling sex as a two-part finite mixture model on g_0 and σ. To account for animals becoming trap happy or trap shy, we included a trap-specific behavioral response (bk) on g_0. Additionally, as animals may adjust their behavior over time to traps regardless of their previous capture history, we include a time response (t) on g_0. Akaike information criterion (AIC) was used to identify the most parsimonious model (Burnham & Anderson, 2002). The highest ranked model (i.e., lowest AIC value) for both live trapping and gNIS was used to estimate density, population size, and both detection parameters g_0 and σ.

To explore sex-based heterogeneity in detection, for example, where one sex is more detectable than the other, we examined sex ratios of detections for live trapping and gNIS. To ensure any observed differences were explained by method-based differences in detectability as opposed to differing spatial extents, we only compare results from the 10 live traps with the 10 hair tubes over the same area. Two proportion z tests were used to compare proportions of males and females detected by live trapping and genetic sampling. We report 95% confidence interval (CI) of the density estimates. Analyses were performed using R 3.6.3 (R Core Team, 2020) using the secr package (Efford, 2020).

Camera traps

Density was calculated from camera traps using REM (Rowcliffe et al., 2008), CT-DS (Howe et al., 2017), and uSCR (Chandler & Royle, 2013). Estimates from REM were calculated using MCMC in nimble (de Valpine et al. 2021). The typical REM density estimator uses the following equation:

$$D = \frac{y}{t} \times \frac{\pi}{vr(2+\theta)},$$

where D is density, y is number of detections, t is survey effort in days, v is daily distance moved by species, r is maximum detection distance from camera, and θ is detection arc. Estimation uncertainty is characterized via bootstrapping the site-level detections, y_j, that sum to the total number of detections, y. Sensor detection zone (r and θ) were measured individually in the field for each photograph taken using topography and land features for scale.

In our Bayesian implementation, we assume the number of detections at site j on occasion k are negative binomial random variables with mean parameter λ and dispersion (size) parameter φ, where the mean parameter is a function of the density and detection area:

$$\lambda = \left(\frac{(2+\theta)}{\pi}\right) vrD$$

Then, we assume $y_{j,k} \sim \mathrm{NB}(p, \varphi)$, where

$$p = \frac{\varphi}{(\varphi+\lambda)}$$

Sensor detection zone (r and θ), were modelled as fixed values, taking the maximum detection distance and detection arc observed. The max detection distance was 8.54 m, and the max detection arc was 1.92 radians. The requirement of an independent estimate of v is a long-recognized constraint of REM (Rowcliffe et al., 2008). To test the sensitivity of density estimates to v parameterization, we conducted sensitivity analyses using a variety of parameter estimates (Appendix S1: Figure S3; Twining, unpublished). As the requirement of costly local biologging data nullifies the main advantages of REM, we used a range of relevant values adapted from the literature for the main analysis. The distribution of values used for distance traveled per day (v) for pine martens was derived from radio-tracked animals in Białowieża Forest, Poland (Zalewski et al., 2004), in spring and summer. To incorporate the uncertainty in v into the D estimate, we treated v as a random variable informed entirely by a prior distribution summarizing the estimates in the literature. We specified the v prior as a uniform distribution between the minimum reported daily distance traveled (3.8 km) and the maximum daily distance traveled (12.7 km; Zalewski et al., 2004). Outside of breeding season (March–August), the pine marten are thought to be solitary (Birks, 2017); therefore, group size was taken as 1. Finally, we specified both the D and the φ priors as uniform distributions between 0 and 100. For this model we ran three chains for 1,000,000 iterations with a thinning rate of 10. We removed a burn-in of 95,000 from the thinned chains yielding a total burn-in of 995,000 iterations per chain. Estimates were only considered if visual inspections of posterior distributions displayed good mixing of chains for all parameters and upper CIs of $\hat{r}$ of each parameter were <1.01 (Gelman & Rubin, 1992).

We estimated density from the camera-trap data using CT-DS, and we adapted methods from Howe et al. (2017), using the equation:

$$\widehat{D} = \frac{\sum_{k=1}^{K} n_k}{\pi w^2 \sum_{k=1}^{K} e_k \widehat{p}_k},$$

where D is the density and e_k is the sampling effort at point k, calculated as:

$$e_k = \frac{\theta T_k}{2\pi t},$$

where θ is the angle of view of the camera, taken as the widest angle of detection recorded, here 0.95 radians, and w is the truncation distance beyond which recorded distances are discarded. Data were right truncated when the detection probability was <0.1 (6 m) to ensure detection was monotonically decreasing. n_k is the number of observations of animals at point k, and $\widehat{p}_k$ is the estimated probability of detecting an animal that is within the angle of view (AOV, θ), T_k is the time-period that cameras were set to record images, and t is the discrete unit of time between snapshot moments (interval set to 1 s). Following Howe et al. (2017), we assumed that animals were available only during apparent times of peak activity discerned from the camera-trap images and calculated temporal effort and took a subset of distance observations accordingly. Martens were rarely photographed between 12:00 and 8:00 PM (see Appendix S1: Figure S2), and, thus, 8:00 PM to 11:59 AM was used as the peak activity times for calculating effort and density. We considered models with a half-normal key detection function with 0, 1, or 2 cosine or Hermite polynomial adjustment terms, a hazard rate key function with 0, 1, or 2 cosine adjustment terms, and a uniform key function with 0 or 1 cosine adjustments. Where required, adjustment terms were constrained to ensure detection functions were monotonically decreasing. The top detection function was selected for by comparing AIC values. We report 95% CI of the density estimate. All analyses were performed using Distance 7.2 (Thomas et al., 2010).

We estimated density from the camera-trap data using uSCR (Chandler & Royle, 2013). The key difference between uSCR and SCR is that uSCR models use spatial correlations in observed counts to infer the number and locations of activity centers of unidentified individuals (Chandler & Royle, 2013). A typical encounter history as used in normal SCR is replaced by a vector of counts of unmarked individuals at each detector. The counts are modeled as a Poisson random variable:

$$n_j \sim \text{Poisson}(\Lambda_j),$$

where

$$\Lambda_j = K_j \lambda_0 \sum_{i=1}^{M} g(d_{ij}),$$

λ_0 is the baseline encounter rate at $d = 0$, M is an assumed number of individuals using data augmentation, d_{ij} is the trap locations, $g(d)$ is a positive-valued, monotonically decreasing function of distance, and K_j is the number of occasions detector j was in operation. As per Chandler and Royle (2013), we use a half-normal detection function (Buckland et al., 2001), where

$$g(d) = \exp\left(\frac{-d^2}{2\sigma^2}\right).$$

This Bayesian approach to modeling density requires data augmentation, that is, setting the population to a certain augmented size (M) by adding potential unobserved individuals with all zero-encounter histories. The number of animals in the state space (N) is derived as a product of M and Ψ. Density, D, can then be calculated by dividing N by the state space (S), which is an area encompassing all detectors as well as surrounding area large enough to contain all individuals that could possibly be detected during the survey.

We ran all models using the nimble package in R (de Valpine et al., 2021). We conducted MCMC sampling with a marginal observation model as the MCMC sampler that updated the latent IDs of individuals sequentially did not converge due to a failure to produce an irreducible Markov chain (e.g., Schofield & Bonner, 2015). In all model runs, we set M to 200, well above the expected population size. We ran one model with uninformative priors, another with a moderately informative prior (uSCRm) on σ and a final version with a strongly informative prior (uSCRs) on σ. For the uninformative model, we specified the σ prior with a uniform distribution between 0 and 100. For both moderately and strongly informative prior, we considered pine marten home range sizes from the study locality (2.07 km^2, 95% CI 1.46–2.69; Twining, unpublished). For the strongly informative prior, we used a gamma distribution where $\alpha = 200$ and $\beta = 0.0016$, and for the moderately informative prior, we used a gamma distribution where $\alpha = 24$ and $\beta = 0.015$. For all three models, the λ_0 prior was specified as a uniform distribution between 0 and 10, and the Ψ prior was a uniform distribution between 0 and 1. For all the models, we ran three chains for 100,000 iterations with a thinning rate of 25. We removed a burn-in of 100 iterations from the thinned chains yielding a total burn-in of 2500 iterations per chain. For all models, an occasion length of 1 day was used, and we applied a buffer of 1.5 km (>3 times the calculated σ for a home range of 2.07 km^2) around the detectors resulting in a state space of 36.02 km^2. Estimates were only considered if visual inspections of posterior distributions displayed good mixing of chains for all parameters and upper CIs of $\widehat{r}$ of each parameter were <1.1 (Gelman & Rubin, 1992).

RESULTS

Density estimates

Live trapping: Normal SCR

Six individuals were trapped 35 times at nine of 10 trapping sites over 546 trap nights. Five animals were male and one female. Four were adults (three males and one female), and two yearlings (both males). All effects on g_0 and σ showed redundancy, being <2 AIC points different from models without the additional parameters (Arnold, 2010). Thus, the most parsimonious model was the base model (Table 1; $g_0 \sim 1$, $\sigma \sim 1$), which produced a density estimate of 0.96 individuals/km^2 (95% CI 0.39–2.37; Figure 2).

Noninvasive genetic sampling: Normal SCR

In total, 86 pine marten hair samples were collected from the 20 hair tubes (100%) over the survey period. DNA was extracted from all samples, and 62 were successfully sexed (72%) of which 27 were female (43.5%) and 35 were male (56.5%). Fifty-one hair samples were successfully genotyped using at least six microsatellite loci (59.3%). The PI (the probability that two random individuals in a given population have the same genotype using the same set of markers) was between 7.2×10^{-4} and 3.9×10^{-7} depending on the number of loci used. The PI_{sib} (the probability that two related individuals will have the same genotype using the same set of markers) was between 2.1×10^{-2} and 9.5×10^{-4}. Out of the 11 loci, only 1 (Mar58) demonstrated

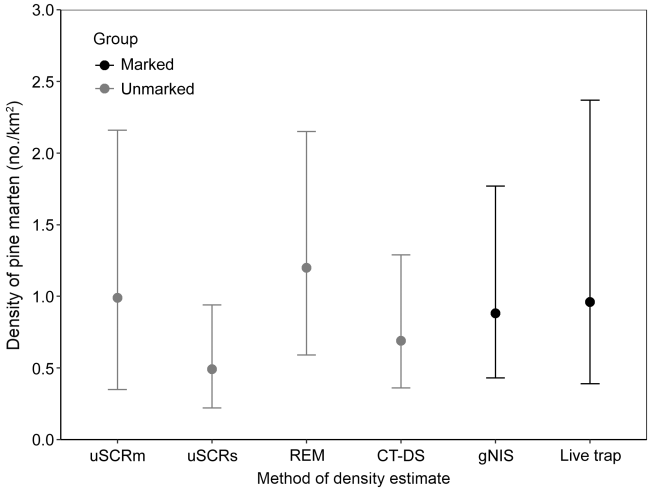

FIGURE 2 Mean density with 95% confidence intervals, of the pine marten population in Slieve Gullion, Northern Ireland, using five different methods; unmarked spatial capture–recapture with moderately informative prior (uSCRm) and with a strongly informative prior (uSCRs) applied to camera-trap data, random encounter models (REM) applied to camera-trap data, distance sampling applied to camera-trap data (CT-DS), normal SCR applied to genetic noninvasive sampling (gNIS), and normal SCR applied to live trapping. Methods for marked animal populations are in black, and methods for unmarked animal populations are in light gray.

TABLE 1 Model selection results for 15 fitted models ranked by Akaike information criterion (AIC) for estimating European pine marten density using live traps.

Model structure	Parameters (*n*)	logLik	AIC	ΔAIC	AIC weight
$g_0 \sim bk + sex, \sigma \sim sex$	7	−163.81	341.63	0.00	0.17
$g_0 \sim bk, \sigma \sim sex$	6	−164.90	341.81	0.18	0.15
$g_0 \sim T, \sigma \sim 1$	4	−167.20	342.40	0.77	0.11
$g_0 \sim 1, \sigma \sim 1$	3	−168.30	342.59	0.96	0.10
$g_0 \sim bk, \sigma \sim 1$	4	−167.58	343.15	1.52	0.08
$g_0 \sim bk + time + sex, \sigma \sim sex$	8	−163.70	343.40	1.77	0.07
$g_0 \sim bk + time, \sigma \sim sex$	7	−164.79	343.58	1.95	0.06
$g_0 \sim time + sex, \sigma \sim sex$	7	−164.85	343.70	2.08	0.06
$g_0 \sim 1, \sigma \sim sex$	5	−166.86	343.72	2.09	0.06
$g_0 \sim sex, \sigma \sim sex$	6	−166.00	343.99	2.36	0.05
$g_0 \sim bk + time, \sigma \sim 1$	5	−167.06	344.11	2.48	0.05
$g_0 \sim time + sex, \sigma \sim 1$	6	−167.20	346.40	4.77	0.02
$g_0 \sim sex, \sigma \sim 1$	5	−168.30	346.59	4.96	0.01
$g_0 \sim bk + sex, \sigma \sim 1$	6	−167.58	347.15	5.52	0.01
$g_0 \sim bk + sex + time, \sigma \sim 1$	7	−167.06	348.11	6.48	0.01

Note: Bold text indicates the top model after uninformative parameters have been removed.

significant deviation from Hardy–Weinberg equilibrium ($p < 0.05$). However, this was likely due to the small sample size and did not impact on subsequent analyses.

Nine individuals were identified, four males and five females. All effects explored on g_0 and σ showed redundancy (Arnold, 2010), and thus, the base model was the most parsimonious (Table 2; $g_0 \sim 1$, $\sigma \sim 1$), producing a density estimate of 0.88 individuals/km^2 (95% CI 0.43–1.77; Figure 2).

Sex-based differences in detectability using live traps and genetic sampling

The sex ratio of detections for live trapping was male biased (33 males:2 females) compared to the more balanced ratio from genetic sampling from the same areas (27 males:35 females). The frequency of female detections was significantly higher using genetic sampling compared to live traps (z test, $\chi^2 = 22.31$, $p < 0.001$).

Camera traps: Random encounter models, distance sampling, and unmarked SCR

A total of 85 pine marten detections occurred at 16 (53.3%) of the 30 camera traps over 1036 camera-trap days. The average number of detections per camera was 5.3. In 83 (97.6%) detections, pine martens occurred alone but in 2 (2.3%) detections, two animals were photographed together. The REM model resulted in good mixing with acceptable $\hat{r}$ values and effective sample sizes ($\hat{r} < 1.1$; see Appendix S1: Table S2, Figure S4). REM produced density estimates of 1.20 individuals/km^2 (95% CI 0.59–2.15; Figure 2). For CT-DS, all models were fitted successfully to the peak activity dataset. The hazard rate model with no adjustments minimized AIC and was used to estimate density. CT-DS produced a density estimate of 0.69 individuals/km^2 (95% CI 0.36–1.29). For uSCR, the uninformative model run resulted in poor mixing and thus was not usable. However, both the models with a moderately and strongly informative prior on σ resulted in good mixing with acceptable $\hat{r}$ values and effective sample sizes ($\hat{r} < 1.1$; see Appendix S1: Tables S3 and S4, Figures S5 and S6). The uSCR model with a strongly informative prior (uSCRs) produced a density estimate of 0.49 (95% CI 0.22–0.94), while the uSCR model with a moderately informative prior (uSCRm) produced a density estimate of 0.99 (95% CI 0.35–2.16).

Precision

The methods applied to marked animal populations generally produced less precise estimates than those applied to unmarked animal populations. Between the two methods for marked animal populations, noninvasive genetic sampling was more precise than live trapping (Table 3). For the methods applied to unmarked animal populations, CT-DS was the most precise, followed by REM, with the two uSCR methods providing the least precise estimates (Table 3).

TABLE 2 Model selection results for 15 fitted models ranked by Akaike information criterion for estimating European pine marten density using noninvasive genetic sampling.

Model structure	Parameters (n)	logLik	AIC	ΔAIC	AIC weight
$g_0 \sim 1, \sigma \sim$ sex	5	−74.78	159.57	0.00	0.49
$g_0 \sim 1, \sigma \sim 1$	3	−77.57	161.07	1.51	0.23
$g_0 \sim$ sex, $\sigma \sim$ sex	6	−74.77	161.54	1.97	0.18
$g_0 \sim$ sex, $\sigma \sim 1$	5	−76.33	162.65	3.09	0.10
$g_0 \sim$ bk + time, $\sigma \sim 1$	5	−116.11	246.22	86.66	0
$g_0 \sim$ bk + time, $\sigma \sim$ sex	7	−116.72	247.44	87.88	0
$g_0 \sim$ sex+ time, $\sigma \sim$ sex	7	−115.80	247.59	88.03	0
$g_0 \sim$ time + bk + sex, $\sigma \sim$ sex	8	−119.86	249.72	90.15	0
$g_0 \sim$ time, $\sigma \sim 1$	4	−121.08	250.17	90.60	0
$g_0 \sim$ time + bk + sex, $\sigma \sim 1$	7	−118.22	250.43	90.86	0
$g_0 \sim$ time + sex, $\sigma \sim 1$	6	−119.64	251.27	91.71	0
$g_0 \sim$ bk, $\sigma \sim$ sex	6	−124.27	260.53	100.96	0
$g_0 \sim$ bk + sex, $\sigma \sim$ sex	7	−127.06	262.12	102.56	0
$g_0 \sim$ bk + sex, $\sigma \sim 1$	6	−124.18	262.36	102.80	0
$g_0 \sim$ bk, $\sigma \sim 1$	4	−125.61	263.22	103.66	0

Note: Bold text indicates the top model after uninformative parameters have been removed.

Efficacy

Overall, the camera-trapping methods were the most time efficient followed by gNIS and then live trapping (Figure 3a). Although camera-trap setup and exit time were greater than the other methods, no maintenance was required once deployed and statistical analysis was rapid for REM and CT-DS, albeit more time-consuming for uSCR. gNIS setup and exit were the shortest, while maintenance was second shortest, and the time in the laboratory for analysis of hair samples was substantial. Finally, live trapping was the most labor intensive overall but exit and analysis were short.

Cost

Live trapping was the cheapest, followed by camera trapping, while genetic sampling was the most expensive approach (Figure 3b). In terms of setup, camera trapping was the most expensive, but once the initial purchase of cameras is made, consumable costs are low (i.e., just batteries for each deployment). By contrast, the setup costs of noninvasive genetic sampling are relatively low; however, consumables costs are very high (i.e., DNA extraction and genotyping of each sample).

TABLE 3 Coefficient of variation of the mean (CV_{mean}) results for each of the density estimates using five different methods; unmarked spatial capture–recapture (SCR) with moderately informative prior (uSCRm) and with a strongly informative prior (uSCRs) applied to camera-trap data, random encounter models (REM) applied to camera-trap data, distance sampling applied to camera-trap data (CT-DS), normal SCR applied to genetic noninvasive sampling (gNIS), and normal SCR applied to live trapping.

Method	CV_{mean} (%)
CT-DS	34.38
REM	36.67
uSCRs	37.48
gNIS	38.84
uSCRm	47.87
Live trapping	52.61

DISCUSSION

This study sheds light on the precision, efficacy, and cost of increasingly used noninvasive methods for monitoring animal populations and conventional live trapping. Using methods applied to both marked and unmarked animal populations, we produce density estimates within reported ranges for the target species in Europe (0.01–1.75

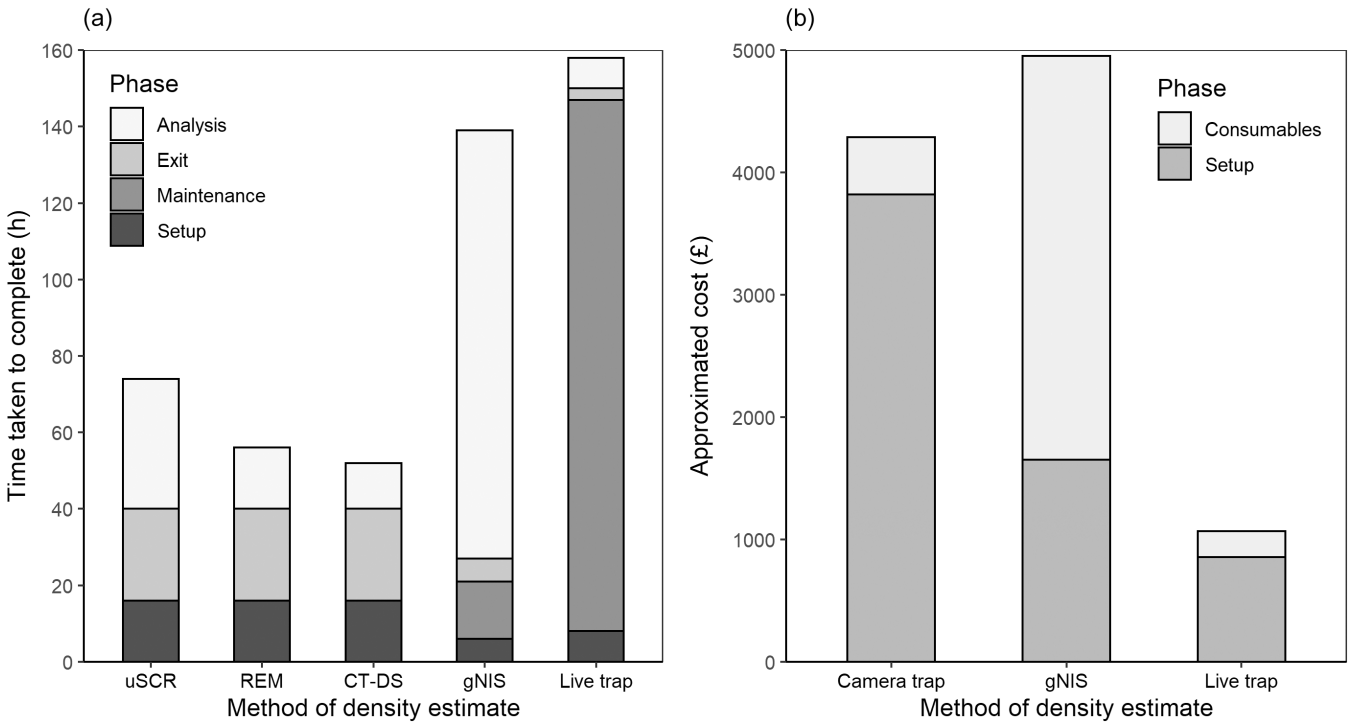

FIGURE 3 A bar plot showing (a) time taken to complete each of the five methods used to estimate pine marten density: unmarked spatial capture–recapture (uSCR), random encounter modeling (REM), camera-trap distance sampling (CT-DS), genetic noninvasive sampling (gNIS), and live trapping split up into the main phases of each project. (b) Approximated total costs in GBP () to complete each of the five methods of estimating density: uSCR, REM, and CT-DS have been grouped together as camera trapping, alongside gNIS and live trapping.

individuals/km^2; Zalewski & Jedrzejewski, 2006) and Ireland where densities are highest for the species (0.12–4.42 individuals/km^2; Mullins et al., 2010; Sheehy et al., 2013; O'Mahony et al., 2017; Twining, Montgomery, Reid, et al., 2020). Despite similar point estimates from all five methods sitting within each other's CIs, differences in the precision, cost, and effort of each method were apparent. The estimates from the three camera-trapping methods for unmarked animals required the least effort, and all bar uSCRm were more precise than those from the methods for individually identifiable animals. While it was the most expensive approach, gNIS provided the more precise density estimate of the two methods for marked populations and identified the most individuals. Live trapping was the cheapest but required the most time and produced the least precise density estimate of all methods. The results add to an emerging body of work seeking to assess the comparability of density estimates for wildlife populations (Burgar et al., 2018; Doran-Myers et al., 2021; Morin et al., 2022; Palencia et al., 2021). Combined, these efforts will increase the amount of data available to conservationists and land managers and lead to more informed assessments.

To our knowledge, we are the first to apply the CT-DS or uSCR methods to a small carnivore (Chandler & Royle, 2013; Howe et al., 2017). We see that while both methods produce feasible density estimates, in consensus with initial testing, CT-DS underestimates density when compared to other methods such as REM and normal SCR (Corlatti et al., 2020; Palencia et al., 2021). However, CT-DS provided the most precise estimate of the methods compared. Previous comparative work on European wildcats (*Felis felis*) and pine marten has resulted in the suggestion that REM may be more suitable for low-density species than gNIS (Anile et al., 2014; Bartolommei et al., 2012). While the underestimation of pine marten density via REM was not observed here as it has been in the past (Balestrieri et al., 2016), our gNIS results contrast markedly to other European studies where the approach has been deemed ineffective (Bartolommei et al., 2012; Kubasiewicz et al., 2017). The lack of consensus across investigations suggests that no single approach is infallible and that local conditions, animal behavior, and surveyor experience may come into play. While some studies have observed gNIS using hair tubes to underestimate density of pine martens comparative to other methods (Croose et al., 2019), we argue that disparities in cross study comparisons likely stem from a failure to appropriately consider their target species movement patterns in order to inform experimental design, specifically trap spacing and spatial extent (Sun et al., 2014). For example, Croose et al. (2019) deployed only 1 detector/1 km^2, less than a quarter of the density that we opted for in our survey design, and five times the σ value estimated for female martens. Traps spaced too widely apart relative to home ranges of the target species can lead to fewer recaptures, or individuals not being detected at all due to holes in trapping arrays (Dillon & Kelly, 2007). This can lead to biased estimates of σ and thus density in SCR and issues in traditional capture–recapture due to difficulties in determining the effective sampling area. If traps are too far apart, only the very largest of movements are registered. This results in overestimating mean maximum movement distance, thus overestimating the effective sampling area, and underestimating density. Consequently, we suggest that previous studies using hair tube sampling for gNIS and observing it to underestimate density, or to be ineffective, have likely trapped at an insufficient density (trap spacing is optimized for precision in normal SCR at $2 \times \sigma$ spatial scale parameter; Sollmann et al., 2012). Here, we see the importance of considering a target species' home range size and typical movement behaviors when deciding on sampling protocols and experimental design.

Financial, time, and welfare considerations interplay to set a maximum number of traps. Consequently, a sampling trade-off occurs between spatial extent and trap spacing (Sun et al., 2014). In this study, we see that hair tubes (low effort) over live traps (high effort), allowed a greater sampling area resulting in the detection of more individuals. Larger spatial extents increase the expected number of unique individuals detected and increase the probability of capturing the full range of movement of individuals (Royle et al., 2013). Although hair tubes detected more individuals, the similar σ values produced from live trapping suggest that the lower spatial extent used for live trapping was sufficient to detect the full range of movement of individual pine martens (Appendix S1: Figure S7). Consequently, our empirical data are in consensus with previous simulation studies that have suggested that in normal SCR, a trap extent equal to that of 1.5 times the average home range size of a female is sufficient to produce unbiased parameter estimates (Sollmann et al., 2012). However, this is not the case for unmarked SCR. Despite being applied to a dataset from a detector array that was >4 times the average home range size of a female, the use of uninformative priors resulted in poor mixing. While this issue was resolved with a moderately informative prior on σ, we suspect the biased σ estimates from the data that resulted in poor mixing could have been avoided with a larger trapping array. This would have facilitated capturing the necessary patterns of spatial correlation in detections to result in unbiased estimates of σ. In needing to test

various priors of different strengths, we revealed evidence that uSCR density estimates are highly sensitive to their σ prior. It is intriguing to note that while a stronger prior increased precision of the resultant estimate, it also lowered the point estimate notably, making it less consistent with the estimates from the other methods. While we urge caution in establishing guidelines from single realizations of empirical datasets, we see here how *a priori* knowledge of both the statistical method and the species ecology is required to appropriately inform decisions on spatial extents of trapping arrays.

Perfect detector array deployment is rarely feasible in the field. While the overlap of our detectors arrays was not ideal, we are confident this had limited effect on our results. The camera-trap array covered the largest area and contained all other detector arrays (live traps and hair tubes). When we measured the area of each trap array, hair tubes for gNIS covered 80.6%, while the live traps surveyed 51.2% of the area of the camera-trap array. Additionally, 83% of the live trapped individuals were detected at the hair tubes. When combined with biologging research on the local population (Twining, Montgomery, Reid, et al., 2020), it is clear we sampled the same population, and mostly the same individuals. Thus, variation among detector arrays is unlikely to explain differences in the parameter estimates produced here.

Clear sex-based differences in detection by the methods for marked animals were observed, with females appearing to avoid live traps, which was not observed in gNIS. On a landscape scale, pine marten occurrence is negatively correlated with human disturbance (Twining, Montgomery, & Tosh, 2020). In this study, we argue the sex-based differences in detection observed between gNIS and live trapping may represent this at a fine spatial scale. The male-biased sex ratio of live trapping compared to gNIS from traps over the same spatial extent suggests females either avoid, or are less willing to interact with, live traps compared to hair tubes. Greater human disturbance associated with live trapping compared to gNIS and the stress of being trapped, anesthetized, and handled likely combine to cause avoidance of live traps (De Bondi et al., 2010). This highlights a key advantage of noninvasive sampling methods for monitoring low density and difficult to detect species.

In terms of person-hours, the camera-trapping approach for unmarked populations was the most efficient. These methods also had the lowest financial cost after initial setup, generally requiring less specialist equipment and knowledge. However, this is not the case for uSCR, where the requirement to work in a Bayesian framework resulted in more person-hours, and the expertise required may inhibit uptake by some practitioners. Despite uSCR and CT-DS underestimating density comparative to the other methods, camera trapping provides an attractive option for cheap long-term monitoring of populations. However, recent power analyses have suggested that camera-trap methods with unmarked individuals rarely achieve the precision required to detect even large declines without a huge number of sampling sites or inclusion of local telemetry data (Morin et al., 2022). Thus, the extra investment in terms of time and cost required by gNIS may be warranted where feasible. All methods used here require initial investment in equipment, but the processing of samples in noninvasive genetic sampling makes the running costs far more expensive than either camera trapping or live trapping. These costs can be significantly reduced if the user has access to an ecology laboratory and associated infrastructure. However, in the absence of this, there are alternative options including: partnering with institutions that have in-house expertise and equipment, outsourcing to commercial companies, or utilizing novel equipment, which drives down setup costs (e.g., Blanco et al., 2020), and the requirement for a conventional laboratory. With any of these approaches, it is important to be mindful of the limitations: commercial companies or partner institutions must have experience in the use of gNIS, ideally with the relevant species and system. Without these, typical difficulties associated with gNIS due to the varying and poor-quality DNA obtained can be compounded (Broquet et al., 2007). Poor-quality genotypes result in an increased risk of genotyping errors, which can subsequently drive under- or overestimation of individuals in a population, directly biasing density estimates.

Despite the time and financial benefits camera trapping provides for unmarked animal populations, density estimates alone are a crude measure of the health and potential sustainability of a species' population. Other population factors, including sex and age, can impact the provision of ecosystem services and sustainability of a population. For example, populations with male-biased sex ratios can increase rates of inter- and intrasexual conflict including infanticide, and territorial disputes, resulting in a decrease in overall fitness of a population (Palombit, 2015; Twining et al., 2017). Consequently, methods for marked animals, which rely on individual identification, have the capacity to provide a more informative approach compared to methods for unmarked animal populations (Morin et al., 2022).

None of the methods used here are without potential bias. In the case of random encounter modeling, two issues are evident. Firstly, the requirement of *a priori* knowledge of a focal species' average movement speed. Observation records and telemetry data (Rowcliffe

et al., 2008, 2016) have been used elsewhere to inform movement parameters but when unavailable, extrapolation of values from the literature is common (e.g., Anile et al., 2014; Balestrieri et al., 2016). Intraspecific home ranges can vary significantly with changes in habitat and environment (Zalewski et al., 2004), and this potentially introduces error when adopting values from the literature. We used sensitivity analysis to examine how estimates of daily distance moved, and resultant density estimates can vary markedly. Notably, the greatest differences were between two methods of movement estimation based on the same locally collected biologging dataset (Appendix S1: Figure S3). While sensitivity to v increases potential for inaccuracy and bias in density estimates from REM, the estimates produced were feasible and within the CIs of all other methods. Generally, researchers using REM have applied a single point estimate for v (e.g., Anile et al., 2014; Bartolommei et al., 2012; Caravaggi et al., 2016; Manzo et al., 2012), likely resulting in an underestimation in the size of CIs. Uncertainty in estimation of v, and its impacts on resultant density estimates, may be more appropriately captured by using an MCMC approach with the prior for v specified as a uniform distribution based on minimum and maximum estimates available for daily distance moved by the species, as we did here. Secondly, there is an additional issue when considering both heterogeneity and uncertainty in the detection zone of cameras. Whilst here we follow the established method of using a single max value for r and θ, this fails to propagate uncertainty in these parameters into the resultant density estimate and thus artificially increases precision. Finally, REM assumes that an individual animal's movement is random, and independent of one another (Rowcliffe et al., 2008). However, carnivores like the pine marten are typically not nomadic, and do not move at random (Powell, 2012), with resources and conspecifics influencing an individual's movement. Thus, carnivores and indeed most animals violate this key underlying model assumption. Nevertheless, the point estimate produced by REM here is consistent with the other four methods used (sitting within the CIs of all), albeit being higher.

Our results highlight the specific information each of the reviewed methods here can collect, and the required time and financial investment. If the time and funding are available to collect sufficient samples to produce precise estimates, or additional information on identities of individuals or demographic structure is required, SCR applied to gNIS is likely the best option. However, the financial costs, expertise, and required infrastructure for gNIS may be prohibitive to this technique's uptake by wildlife managers unless alternatives such as outsourcing can be utilized. If rapid, or large-scale, assessment of populations is the objective, then use of methods for unmarked populations applied to camera trapping may prove suitable due to their higher precision when sampling over short time frames, and their superiority in terms of running costs and effort required. Live trapping remains the least appealing option for use in large-scale, long-term monitoring due to the amount of labor and expertise required, and the overall invasiveness of the approach. The results here further emphasize the importance of a priori knowledge of the study species to inform experimental design, where trap spacing, and spatial extent of trapping should be based on consideration of the statistical method to be employed, and the target species detectability, home range, and movement behavior. Ultimately, the most appropriate method and analysis to use will be dependent on the goals of a study, the ecology of the target species, the relevant expertise of the researcher, and the financial and logistical constraints presented by the strictures of research funding.

AUTHOR CONTRIBUTIONS

Joshua P. Twining and David G. Tosh conceived and designed the research. Joshua P. Twining and Claire McFarlane conducted the fieldwork. Denise O'Meara, Catherine O'Reilly, Claire McFarlane, and Marina Reyne conducted the laboratory work. Joshua P. Twining and Ben C. Augustine conducted the statistical analysis. Joshua P. Twining wrote first draft of the manuscript. All co-authors contributed critically to revisions of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Twining et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.xwdbrv1g2.

ORCID

Joshua P. Twining https://orcid.org/0000-0002-0881-9665
Denise O'Meara https://orcid.org/0000-0003-1372-5505
W. Ian Montgomery https://orcid.org/0000-0001-9715-4767
Sarah Helyar https://orcid.org/0000-0002-1600-997X
Ben C. Augustine https://orcid.org/0000-0001-6935-6361

REFERENCES

Andrén, H., J. D. C. Linnell, O. Liberg, P. Ahlqvist, R. Andersen, A. Danell, R. Franzén, T. Kvam, J. Odden, and P. Segerström. 2002. "Estimating Total Lynx (*Lynx lynx*) Population Size from Censuses of Family Groups." *Wildlife Biology* 8: 299–306.

Anile, S., B. Ragni, E. Randi, F. Mattucci, and F. Rovero. 2014. "Wildcat Population Density on the Etna Volcano, Italy: A Comparison of Density Estimation Methods." *Journal of Zoology* 293: 252–61.

Arnold, T. W. 2010. "Uninformative Parameters and Model Selection Using Akaike's Information Criterion." *Journal of Wildlife Management* 74(6): 1175–8.

Augustine, B. C., J. A. Royle, S. W. Murphy, R. B. Chandler, J. J. Cox, and M. J. Kelly. 2019. "Spatial Capture–Recapture for Categorically Marked Populations with an Application to Genetic Capture–Recapture." *Ecosphere* 10(4): e02627.

Balestrieri, A., A. Ruiz-Gonzalez, M. Vergara, E. Capelli, P. Tirozzi, S. Alfino, G. Minuti, C. Prigioni, and N. Saino. 2016. "Pine Marten Density in Lowland Riparian Woods: A Test of the Random Encounter Model Based on Genetic Data." *Mammalian Biology* 81: 439–46. https://doi.org/10.1016/j.mambio.2016.05.005.

Bartolommei, P., E. Manzo, and R. Cozzolino. 2012. "Evaluation of Three Indirect Methods for Surveying European Pine Marten in a Forested Area of Central Italy." *Hystrix, the Italian Journal of Mammalogy* 23(2): 90–2.

Birks, J. D. S. 2017. *Pine Martens (the British Natural History Collection)*. Essex: Whittet Books Ltd.

Blanc, L., E. Marboutin, S. Gatti, and O. Gimenez. 2013. "Abundance of Rare and Elusive Species: Empirical Investigation of Closed Versus Spatially Explicit Capture-Recapture Models with Lynx as a Case Study." *The Journal of Wildlife Management* 77: 372–8.

Blanco, M. B., L. K. Greene, F. Rasambainarivo, E. Toomey, R. C. Williams, L. Andrianandrasana, P. A. Larsen, and A. D. Yoder. 2020. "Next-Generation Technologies Applied to Age-Old Challenges in Madagascar." *Conservation Genetics* 21: 785–93.

Borchers, D. L., and M. G. Efford. 2008. "Spatially Explicit Maximum Likelihood Methods for Capture-Recapture Studies." *Biometrics* 64: 377–85.

Borchers, D., and R. Fewster. 2016. "Spatial Capture-Recapture Models." *Statistical Science* 31(2): 219–32.

Brazeal, J. L., T. Weist, and B. N. Sacks. 2017. "Noninvasive Genetic Spatial Capture-Recapture for Estimating Deer Population Abundance." *The Journal of Wildlife Management* 81(4): 629–40.

Breitenmoser-Wursten, C., F. Zimmermann, A. Molinari-Jobin, P. Molinari, S. Capt, J. Vandel, P. Stahl, and U. Breitenmoser. 2007. "Spatial and Social Stability of a Eurasian Lynx *Lynx lynx* Population: An Assessment of 10 Years of Observation in the Jura Mountains." *Wildlife Biology* 13: 365–80.

Broquet, T., N. Menard, and E. Petit. 2007. "Noninvasive Population Genetics: A Review of Sample Source, Diet, Fragment Length and Microsatellite Motif Effects on Amplification Success and Genotyping Error Rates." *Conservation Genetics* 8(1): 249–60.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. S. T. Thomas. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford: Oxford University Press.

Burgar, J. M., F. E. C. Stewart, J. P. Volpe, J. T. Fisher, and A. C. Burton. 2018. "Estimating Density for Species Conservation: Comparing Camera Trap Spatial Count Models to Genetic Spatial Capture-Recapture Models." *Global Ecology and Conservation* 15: e00411.

Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. New York: Springer.

Capelle, N., M.-L. Despres-Einspenner, E. J. Howe, C. Boesch, and H. S. Kühl. 2019. "Validating Cmera Trap Distance Sampling for Chimpanzees." *American Journal of Primatology* 81(3): e22962.

Caravaggi, A., P. B. Banks, C. Burton, C. Finlay, P. Haswell, M. W. Hayward, M. Rowcliffe, and M. D. Wood. 2017. "A Review of Camera Trapping for Conservation Behaviour Research." *Remote Sensing in Ecology and Conservation* 3: 109–22. https://doi.org/10.1002/rse2.48.

Caravaggi, A., M. Zaccaroni, F. Rica, S. C. Schai-Braun, J. T. A. Dick, W. I. Montgomery, and N. Reid. 2016. "An Invasive-Native Mammalian Species Replacement Process Captured by Camera Trap Survey Random Encounter Models." *Remote Sensing in Ecology and Conservation* 2(1): 45–58.

Chandler, R. B., and J. A. Royle. 2013. "Spatially Explicit Models for Inference about Density in Unmarked or Partially Marked Populations." *The Annals of Applied Statistics* 7(2): 936–54.

Corlatti, L., S. Sivieri, B. Sudolska, S. Giacomelli, and L. Pedrotti. 2020. "A Field Test of Unconventional Camera Trap Distance Sampling to Estimate Abundance of Marmot Populations." *Wildlife Biology* 4: 1–11. https://doi.org/10.2981/wlb.00652.

Croose, E., J. D. S. Birks, J. Martin, G. Ventress, J. MacPherson, and C. O'Reilly. 2019. "Comparing the Efficacy and Cost-Effectiveness of Sampling Methods for Estimating Population Abundance and Density of a Recovering Carnivore: The European Pine Marten (*Martes martes*)." *European Journal of Wildlife Research* 65: 37–47.

Cusack, J. J., A. J. Dickman, J. M. Rowcliffe, C. Carbone, D. W. Macdonald, and T. Coulson. 2015. "Random Versus Game Trail-Based Camera Trap Placement Strategy for Monitoring Terrestrial Mammal Communities." *PLoS One* 10(5): e0126373.

De Bondi, N., J. G. White, M. Stevens, and R. Cooke. 2010. "A Comparison of the Effectiveness of Camera Trapping and Live Trapping for Sampling Terrestrial Small-Mammal Communities." *Wildlife Research* 37: 456–65.

Dillon, A., and M. J. Kelly. 2007. "Ocelot Leopardus Pardalis in Belize: The Impact of Trap Spacing and Distance Moved on Density Estimates." *Oryx* 41: 469–77.

Doran-Myers, D., A. J. Kenney, C. J. Krebs, C. T. Lamb, A. K. Menzies, D. Murray, E. K. Studd, J. Whittingdon, and S. Boutin. 2021. "Density Estimates for Canada Lynx Vary among Estimation Methods." *Ecosphere* 12: e03774.

Efford, M. G. 2004. "Density Estimation in Live–Trapping Studies." *Oikos* 106: 598–610.

Efford, M. G. (2020). "secr: Spatially Explicit Capture-Recapture Models. R Package Version 4.3.1." https://CRAN.R-project.org/package=secr.

Efford, M. G., D. L. Borchers, and A. E. Byrom. 2009. "Density Estimation by Spatially Explicit Capture–Recapture: Likelihood-Based Methods." In *Modeling Demographic Processes in Marked Populations*, edited by D. L. Thomson, E. G. Cooch, and M. J. Conroy, 255–69. Boston, MA: Springer.

Efford, M. G., and J. Boulanger. 2019. "Fast Evaluation of Study Designs for Spatially Explicit Capture–Recapture." *Methods in Ecology and Evolution* 10: 1529–35.

Gelman, A., and D. B. Rubin. 1992. "Inference from Iterative Simulation Using Multiple Sequences." *Statistical Science* 7(4): 457–72.

Gese, E. M. 2001. "Monitoring of Terrestrial Carnivore Populations." USDA National Wildlife Research Center—Staff Publications. 576. https://digitalcommons.unl.edu/icwdm_usdanwrc/576.

Gilbert, N. A., J. D. Clare, J. L. Stenglein, and B. Zuckerberg. 2021. "Abundance Estimation of Unmarked Animals Based on Camera-Trap Data." *Conservation Biology* 35(1): 88–100.

Gray, T. N. E., T. N. C. Vidya, S. Potdar, D. K. Bharti, and P. Sovanna. 2014. "Population Size Estimation of an Asian Elephant Population in Eastern Cambodia through Non-invasive Mark-Recapture Sampling." *Conservation Genetics* 15(4): 803–10.

Hollerbach, L., M. Heurich, T. E. Reiners, and C. Nowak. 2018. "Detection Dogs Allow for Systematic Non-invasive Collection of DNA Samples from Eurasian Lynx." *Mammalian Biology* 90: 42–6.

Howe, E. J., S. T. Buckland, M. L. Despres-Einspenner, and H. S. Kuhl. 2017. "Distance Sampling with Camera Traps." *Methods in Ecology and Evolution* 8(11): 1558–65.

Jenelle, C. S., M. C. Runge, and D. I. MacKenzie. 2002. "The Use of Photographic Rates to Estimate Densities of Tigers and Other Cryptic Mammals: A Comment on Misleading Conclusions." *Animal Conservation* 5: 119–20.

Karanth, K. U., and J. D. Nichols. 1998. "Estimation of Tiger Densities in India Using Photographic Captures and Recaptures." *Ecology* 79: 2852–62.

Kubasiewicz, L., C. P. Quine, R. W. Summers, R. Coope, J. E. Cottrell, S. W. A'Hara, and K. Park. 2017. "Non-invasive Genotyping and Spatial Mark-Recapture Methods to Estimate European Pine Marten Density in Forested Landscapes." *Hystrix* 28(2): 265–71.

Lukacs, P. M., and K. P. Burnham. 2005. "Review of Capture-Recapture Methods Applicable to Noninvasive Genetic Sampling." *Molecular Ecology* 14: 3909–19.

Manzo, E., P. Bartolommei, J. M. Rowcliffe, and R. Cozzolino. 2012. "Estimation of Population Density of European Pine Marten in Central Italy Using Camera Trapping." *Acta Theriologica* 57: 165–72.

Morin, D. J., J. Boulanger, R. Bischof, D. C. Lee, D. Ngoprasert, A. K. Fuller, B. McLellan, et al. 2022. "Comparison of Methods for Estimating Density and Population Trends for Low-Density Asian Bears." *Global Ecology and Conservation* 35: e02058.

Mullins, J., M. J. Statham, T. Roche, P. D. Turner, and C. O'Reilly. 2010. "Remotely Plucked Hair Genotyping: A Reliable and Non-invasive Method for Censusing Pine Marten (*Martes martes*, L. 1758) Populations." *European Journal of Wildlife Research* 56(3): 443–53.

O'Mahony, D. T., C. Powell, J. Power, R. Hanniffy, F. Marnell, P. Turner, and C. O'Reilly. 2017. "Non-invasively Determined Multi-Site Variation in Pine Marten *Martes martes* Density, a Recovering Carnivore in Europe." *European Journal of Wildlife Research* 63: 48.

Palencia, P., J. M. Rowcliffe, J. Vicente, and P. Acevedo. 2021. "Assessing the Camera Trap Methodologies Used to Estimate Density of Unmarked Populations." *Journal of Applied Ecology* 58(8): 1583–92.

Palombit, R. A. 2015. "Infanticide as Sexual Conflict: Coevolution of Male Strategies and Female Counterstrategies." *Cold Spring Harbour Perspectives in Biology* 7(6): a017640. https://doi.org/10.1101/cshperspect.a017640.

Powell, R. A. 2012. "Movements, Home Ranges, Activity, and Dispersal." In *Carnivore Ecology and Conservation: A Handbook of Techniques*, edited by L. Boitani and R. A. Powell, 188–217. New York: Oxford University Press.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008. "Estimating Animal Density Using Camera Traps without the Need for Individual Recognition." *Journal of Applied Ecology* 45: 1228–36.

Rowcliffe, J. M., P. A. Jansen, R. Kays, B. Kranstauber, and C. Carbone. 2016. "Wildlife Speed Cameras: Measuring Animal Travel Speed and Day Range Using Camera Traps." *Remote Sensing in Ecology and Conservation* 2: 84–94.

Royle, J. A., R. B. Chandler, R. Solmann, and B. Gardner. 2013. *Spatial Capture-Recapture*, 617. Cambridge, UK: Academic Press.

Sainsbury, K. A., R. F. Shore, H. Schofield, E. Croose, R. D. Campbell, and R. A. Mcdonald. 2019. "Recent History, Current Status, Conservation and Management of Native Mammalian Carnivore Species in Great Britain." *Mammal Review* 49: 171–88.

Schofield, M., and S. J. Bonner. 2015. "Connecting the Latent Multinomial." *Biometrics* 71(4): 1070–80.

Schwartz, M. K., G. Luikart, and R. S. Waples. 2007. "Genetic Monitoring as a Promising Tool for Conservation and Management." *Trends in Ecology & Evolution* 22: 25–33.

Sheehy, E., D. O'Meara, C. O'Reilly, A. Smart, and C. Lawton. 2013. "A Non-invasive Approach to Determining Pine Marten Abundance and Predation." *European Journal of Wildlife Research* 60: 223–36.

Silveira, L., A. T. A. Jácomo, and J. A. F. Diniz-Filho. 2003. "Camera Trap, Line Transect Census and Track Surveys: A Comparative Evaluation." *Biological Conservation* 114: 351–5.

Sollmann, R., B. Gardner, and J. L. Belant. 2012. "How Does Spatial Study Design Influence Density Estimates from Spatial Capture-Recapture Models?" *PLoS One* 7(4): e34575.

Stanley, T. R., and J. A. Royle. 2005. "Estimating Site Occupancy and Abundance Using Indirect Detection Indices." *The Journal of Wildlife Management* 69: 874–83.

Sun, C. C., A. K. Fuller, and J. A. Royle. 2014. "Trap Configuration and Spacing Influences Parameter Estimates in Spatial Capture-Recapture Models." *PLoS One* 9: e88025.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham. 2010. "Distance Software: Design and Analysis of Distance Sampling Surveys for Estimating Population Size." *Journal of Applied Ecology* 47(1): 5–14.

Trolle, M., and M. Kéry. 2003. "Estimation of Ocelot Density in the Pantanal Using Capture Recapture Analysis of Camera-Trapping Data." *Journal of Mammalogy* 84(2): 607–14.

Twining, J., B. Augustine, D. Tosh, D. O'Meara, C. McFarlane, M. Reyne, S. Helyar, and I. Montgomery. 2022. "A Comparison of Density Estimation Methods for Monitoring Marked and Unmarked Animal Populations." Dryad. Dataset. https://doi.org/10.5061/dryad.xwdbrv1g2.

Twining, J. P., H. Bernard, and R. M. Ewers. 2017. "Increasing Land-Use Intensity Reverses the Relative Occupancy of Two Quadrupedal Scavengers." *PLoS One* 12(5): e0177143. https://doi.org/10.1371/journal.pone.0177143.

Twining, J. P., W. I. Montgomery, N. Reid, N. Marks, D. G. Tosh, and D. M. Scantlebury. 2020. "All Forests Are Not Equal: Population Demographics and Denning Behaviour of a Recovering Small Carnivore in Human Modified Landscapes." *Wildlife Biology* 2020(4): 1–10. https://doi.org/10.2981/wlb.00760.

Twining, J. P., W. I. Montgomery, and D. G. Tosh. 2020. "Declining Invasive Grey Squirrel Populations May Persist in Refugia as

Native Predator Recovery Reverses Squirrel Species Replacement." *Journal of Applied Ecology* 58(2): 248–60. https://doi.org/10.1111/1365-2664.13660.

de Valpine, P., C. Paciorek, D. Turek, N. Michaud, C. Anderson-Bergman, F. Obermeyer, C. Wehrhahn-Cortes, A. Rodrìguez, D. Temple Lang, S. Paganin 2021. NIMBLE: MCMC, Particle Filtering, and Programmable Hierarchical Modeling. R Package Version 0.12.2. https://cran.r-project.org/package=nimble.

Wearn, O. R., J. M. Rowcliffe, C. Carbone, H. Bernard, and R. M. Ewers. 2013. "Assessing the Status of Wild Felids in a Highly-Disturbed Commercial Forest Reserve in Borneo and the Implications for Camera Trap Survey Design." *PLoS One* 8(11): e77598.

Williams, B. W., D. R. Etter, D. W. Linden, K. F. Millenbah, S. R. Winterstein, and K. T. Scribner. 2009. "Non-invasive Hair Sampling and Genetic Tagging of Co-Distributed Fishers and American Martens." *Journal of Wildlife Management* 73(1): 26–34.

Wilson, G. J., and R. J. Delahay. 2001. "A Review of Methods to Estimate the Abundance of Terrestrial Carnivores Using Field Signs and Observation." *Wildlife Research* 28: 151–64.

Zalewski, A., and W. Jedrzejewski. 2006. "Spatial Organisation and Dynamics of the Pine Marten *Martes martes* Population in Białowieza Forest (E Poland) Compared with Other European Woodlands." *Ecography* 29(1): 31–43.

Zalewski, A., W. Jedrzejewski, and B. Jedrzejewska. 2004. "Mobility and Home Range Use by Pine Martens (*Martes martes)* in a Polish Primeval Forest." *Ecoscience* 11(1): 113–22.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Twining, Joshua P., Claire McFarlane, Denise O'Meara, Catherine O'Reilly, Marina Reyne, W. Ian Montgomery, Sarah Helyar, David G. Tosh, and Ben C. Augustine. 2022. "A Comparison of Density Estimation Methods for Monitoring Marked and Unmarked Animal Populations." *Ecosphere* 13(10): e4165. https://doi.org/10.1002/ecs2.4165