

Estimating invasive rodent abundance using removal data and hierarchical models

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Introduction

Invasive species are a significant global issue, with wide-ranging impacts on ecosystems, economies, and public health (Pyšek et al. 2020, Roy et al. 2024). Among these, the financial, epidemiological, social, and ecological costs associated with invasive rodents are substantial, as they damage infrastructures, degrade agricultural systems, and act as reservoirs for zoonotic diseases (Diagne et al. 2023).

Effective management of invasive species requires the estimation of population abundance for guiding control efforts and evaluating the success of eradication or regulation programs (Williams et al. 2002, Thompson et al. 2021). However, the challenge in estimating animal abundance is that individuals are not always observed even when present due to imperfect detection (Borchers et al. 2002, Seber and Schofield 2023). Ignoring imperfect detection leads to biased estimates of population abundance (Kéry and Schmidt 2008). To account for imperfect detection, capture-recapture methods are usually used to correct observed counts (McCrea and Morgan 2015). Yet, for invasive species, capture-recapture is often impractical, as ethical and management concerns typically prevent the release of captured animals.

An alternative approach involves the use of removal methods (Rodriguez de Rivera and McCrea 2021) in which individuals are captured and permanently removed from the study area during successive sampling occasions. This process leads to a decrease in the expected number of captures by a consistent proportion over time (rather than by a fixed amount decline), which informs on the total abundance as the initial population determines how quickly the number of individuals available for capture diminishes.

While standard removal methods are well-established (Moran 1951, Zippin 1956, 1958, Rodriguez de Rivera and McCrea 2021), recent advances in population ecology remain underutilized in the context of invasive species. Hierarchical models, in particular, have gained traction (Royle and Dorazio 2008, Kéry and Royle 2015) due to their ability to: (i) explicitly

separate biological processes of interest (e.g., population dynamics) from observation processes (e.g., imperfect detection), thus enabling more accurate modeling; (ii) incorporate environmental, spatial, or temporal covariates at multiple levels, allowing exploration of how various factors influence ecological processes; and (iii) share information across groups by modeling parameters hierarchically with random effects, which improves estimates for groups with fewer data.

In this paper, I showcase the application of a hierarchical formulation of removal models, the multinomial N-mixture model ([Dorazio et al. 2005](#)), to estimate the abundance of rodents in Europe. In this study, I focus on the coypu (*Myocastor coypus*) in France and the muskrat (*Ondatra zibethicus*) in the Netherlands. Both species are semi-aquatic rodents introduced to Europe in the early 20th century following escapes or releases from fur farms. The coypu, native to South America, has formed widespread invasive populations in France ([Bonnet et al. 2023](#)), where it causes significant damage to infrastructure and crops. Additionally, it serves as a healthy carrier of leptospirosis, a zoonotic disease with potentially serious consequences. Similarly, the muskrat, native to North America, has established extensive populations in the Netherlands. By burrowing into riverbanks, dykes, and dams, muskrats compromise the integrity of these structures, posing a threat to public safety ([Loon et al. 2017](#)).

Using removal data, I demonstrate the application of the multinomial N-mixture model to estimate the abundance of rodent populations. First, I conduct a simulation study to evaluate the model's performance under varying numbers of sampling sites and sampling occasions. Second, I present a case study on a coypu population in France to illustrate the hierarchical structure of the multinomial N-mixture model, demonstrating how covariates can be incorporated to account for variations in abundance and capture probabilities. Third, I use a case study on muskrats in the Netherlands to demonstrate the integration of random effects within the model. To facilitate reproducibility, I provide the accompanying code and data,

aiming to promote the broader adoption of removal models in the study of biological invasions.

Methods

Multinomial N-mixture model

Think of a dice with six sides. The dice has a 1 in 6 chance of landing on face 1, the same for face 2, and so on. If I roll the dice 30 times, I expect to get face 1 five times, face 2 five times, and so on, on average. In this experiment, y_1 , the vector made of the number of 1s, y_2 , the number of 2s, \dots , and y_6 , the number of 6s, follows a multinomial distribution with parameters the number of rolls (30) and probabilities $(1/6, 1/6, \dots, 1/6)$.

Now think of a removal campaign conducted over 3 months. We record the number of rodents y_1 captured in month 1, y_2 in month 2, y_3 in month 3, and let y_4 represent the number of rodents never captured. Let p be the probability of capturing a rodent in a given month. The probability of capturing a rodent in the first month is $\pi_1 = p$. The probability of capturing a rodent in the second month is $\pi_2 = (1 - p)p$ the probability of not capturing it in the first month $(1 - p)$ multiplied by the probability of capturing it in the second month p . The probability of capturing a rodent in the third month is $\pi_3 = (1 - p)(1 - p)p$, the probability of not capturing it in the first and second months, $(1 - p)(1 - p)$, multiplied by the probability of capturing it in the third month, p . Finally, the probability of never being captured is $\pi_4 = 1 - (p + (1 - p)p + (1 - p)(1 - p)p)$ the complement of the probability of being captured in the first, second, or third month. If we assume that N represents the abundance, then we have that the vector of counts (y_1, y_2, y_3, y_4) follows a multinomial distribution with parameters N and probabilities $(\pi_1, \pi_2, \pi_3, \pi_4)$. In general, we assume that N follows a Poisson distribution with parameter the expected number of rodents denoted λ . And there you have it, the multinomial N-mixture model for a removal experiment, which is similar to throwing a

dice N times and the π 's give the probabilities that I get a given face of that dice. In general, we monitor rodents on several sites $i = 1, \dots, S$ and we need to estimate local population size N_i for site i . AJOUTER L'INTERET D'AVOIR PLUSIEURS SITES (cf ABSTRACT PAPIER DORAZIO) AND POLISH TEXT.

Parameters N , p , and λ are unknown and need to be estimated. In a frequentist framework, marginalization is performed by summing over all possible values of N (Dorazio et al. 2005). In a Bayesian framework, all these parameters are estimated directly, which simplifies the process (Royle and Dorazio 2006). Both parameters, λ and p , can be modeled as functions of explanatory spatial and temporal variables, in the spirit of generalized linear models, and Poisson or logistic regressions for example. I warmly recommend chapter 7 in Kéry and Royle (2015) for a detailed description of the multinomial mixture model.

MODEL HYPOTHESES. Ici ou en discussion.

Simulations

I conducted a simulation study to evaluate the model's performance by examining parameter bias under varying numbers of sampling sites and sampling occasions. I simulated removal data over 1, 5, 10 and 50 sites using a Poisson distribution with expected number of animals λ between 10 and 100 (20 values) for the ecological process. I simulated the observation process with a capture probability p varying between 0.3 and 0.9 (20 values) across 3, 5 and 10 occasions per site. In total, I considered 4800 scenarios. I fitted the multinomial N-mixture model to the simulated data within the frequentist framework using function `multinomPois()` in the R package `unmarked` (Kellner et al. 2023), and I repeated this procedure 500 times. Eventually, I calculated the relative bias for each parameter.

Case studies

EXPLAIN THE AIM OF EACH CASE STUDY. BIBLIO SUR EFFECT TEMPERATURE.

Coypus in France

Removal data on coypus were collected from annual control operations conducted since 2015 in several cities within the Hérault department, located in the Occitanie region of southern France. These operations are carried out year-round, with the exception of July and August. Coypus are trapped using cages by a network of volunteers coordinated by the Syndicat Mixte du Bassin de l'Or and the Fédération Départementale des Chasseurs de l'Hérault. For this study, I focus on data from 2022, specifically from sampling occasions in February, March, and April. The data, covering $S = 6$ cities, are summarized in Table 1. I fitted a model where the expected number of coypus was modeled as a function of temperature, while the capture probability was allowed to vary by month.

City	Removed in February	Removed in March	Removed in April	Averaged temperature
Candillargues	18	12	38	9.5
Lansargues	15	17	75	8.8
Mauguio	20	9	6	9.2
Saint-Nazaire-de-Pézan	169	41	15	9.3
Saint-Just	85	61	77	9.2
Valergues	0	1	3	9.4

Table 1: Number of invasive coypus removed monthly, and averaged 3-month temperature in several cities of the Hérault department for the year 2022.

Muskrats in the Netherlands

Removal data on muskrats in the Netherlands were collected by professional trappers. The data were registered in atlas blocks (5×5 km) per periods of four weeks. For this study, I focus on data from 2014, specifically from sampling occasions in January, February, and March. The data were made available through the LIFE MICA project (Cartuyvels et al. 2024) and can be freely

downloaded from <https://www.gbif.org/dataset/7d75109d-a6cb-4e90-89d0-79d08577c580>. I fitted the same model as for the coypus data, except that I added a site random effect on abundance to accommodate the spatial variation that was not explained by temperature.

Implementation

For all analyses, I used the statistical language R (R Core Team 2024). I used the tidyverse (Wickham et al. 2019) suite of packages for data manipulation and visualization, sf (Pebesma and Bivand 2023) for dealing with spatial data and krigR (Kusch and Davy 2022) to get temperature data. For the two case studies, I fitted models within a Bayesian framework using Markov chain Monte Carlo (MCMC) algorithms. I used both the NIMBLE (de Valpine et al. 2017) and the ubms (Kellner et al. 2021) packages. The former offers high flexibility, enabling users to define custom likelihoods, though it requires manual coding, while the latter features simpler syntax with pre-built multinomial N-mixture models, albeit limited to a Poisson distribution for abundance. I specified weakly informative priors for all parameters, specifically normal distributions with mean 0 and standard deviation 1.5 for regression parameters, and a uniform distribution for the standard deviation of the random effects. I ran two chains for a total of 15,000 iterations with a burn-in of 5,000 iterations. I summarized posterior distributions with posterior mean and 95% credible intervals. I assessed model convergence using R-hat values (< 1.1), effective sample size (> 100), and visual inspection of the trace plots.

Results and discussion

The results of the simulation are presented in Figure 2. Overall, the analysis revealed minimal bias, with the exception of one site that showed a notable deviation. Increasing the number of sites to 10 significantly reduced this bias, and no bias was observed with 50 sites, supporting the recommendation by (Dorazio et al. 2005) to analyze data jointly rather than separately.

These findings align with previous simulation studies, which also reported minimal bias in removal models (e.g., [Womack-Bulliner et al. 2019](#)). To enhance reproducibility, I provide the code for the simulation study in the Supplementary Material. This resource can be adapted for various purposes, such as conducting custom simulation studies or designing removal protocols and conducting power analyses.

In the coypus case study, temperature was found to have a negative effect on abundance, with a slope estimate of -0.14 (-0.22, -0.07). Capture probabilities were estimated at 0.43 (0.29, 0.49) in February, 0.35 (0.19, 0.44) in March and 0.84 (0.35, 1.00) in April. The posterior distributions of abundance across the different sites are presented in Figure 3. A key assumption of the multinomial N-mixture model is that abundance follows a Poisson distribution, which assumes the mean and variance are equal. However, this assumption does not appear valid based on the estimated abundance. Fortunately, this limitation can be addressed by relaxing the Poisson assumption. A straightforward approach is to use a negative binomial distribution to account for overdispersion. This adjustment can be implemented in both NIMBLE and unmarked but is not currently supported by ubms. I demonstrate how to fit such a model to the coypus data in the Supplementary Material. Interestingly, under the negative binomial model, the effect of temperature on abundance was no longer significant, with a slope estimate of -0.27 (-1.29, 0.60).

In the muskrats case study, temperature was found to have a negative effect on abundance, with a slope estimate of -0.48 (-0.70, -0.26). The standard deviation of the site random effect was estimated at 1.62 (1.46, 1.79). Capture probabilities were estimated at 0.12 (0.05, 0.25) in January, 0.25 (0.15, 0.35) in February and 0.60 (0.53, 0.75) in March. Estimated abundance across sites is presented in Figure 4. An important feature of multinomial N-mixture models is their ability to quantify uncertainty, which is often overlooked in spatial analyses. Here, I provide the coefficient of variation to represent the uncertainty surrounding abundance estimates. This metric can help identify specific areas where increased sampling effort might be beneficial to

improve estimate precision.

Another key assumption underlying the proper use of multinomial N-mixture models is that of population closure, which assumes no births, deaths, immigration, or emigration occur during the trapping period. A straightforward approach to relax this assumption is to fit multiple years of data (i.e., stacking the data) into a standard multinomial N-mixture model. In this approach, year-site combinations are treated as separate sites, and year is included as a site covariate or random effect in the model. In the muskrats example, this method can be used to evaluate a temporal effect on the relationship between temperature and abundance. Assuming an increase in temperature over time, one might hypothesize a decoupling or weakening of the relationship between abundance and temperature. To test this hypothesis, I conducted an additional analysis of the muskrat dataset spanning the 1987–2014 period, modeling the slope of the temperature-abundance relationship as a linear function of time. The results revealed a negative trend in the slope, estimated at -0.040 (-0.042, -0.039), providing evidence to support the hypothesis of a temporal weakening of this relationship.

Several perspectives arise from this work. From a methodological standpoint, this study highlights the suitability of hierarchical models for capturing dependencies in space and time, which are common in ecological systems and removal experiments in particular. Two areas stand out as particularly worth exploring.

I see at least two areas worth investigating. First, in this paper I considered only static models for which populations were assumed to be closed (see however the previous paragraph). First, this study focused exclusively on static models under the assumption of population closure (see the previous section for a discussion of relaxing this assumption). When the mechanisms underlying population dynamics—such as survival, recruitment, or dispersal—are of interest, multinomial N-mixture models can be extended to open populations ([Matechou et al. 2016](#), [Link et al. 2018](#), [Zhou et al. 2019](#)). These extended models can be implemented using unmarked

or NIMBLE, though they are not yet available in ubms.

Another area of investigation concerns the spatial dimension of multinomial N-mixture models that relates to the assumption of independence among removal sites, in other words les prélèvements sur un site n'affectent pas ceux faits sur un autre site. A possible solution is to consider site random effects as in the muskrat case study. To better account for spatial autocorrelation, restricted spatial regression (RSR) can also be considered ([Johnson et al. 2013](#), [Broms et al. 2014](#)) - ici peux-tu expliquer les intrinsic conditional autoregressive models en une phrase? - In RSR models, the random effect is built so that it is uncorrelated with the fixed covariates (otherwise causing problems), and it can be significantly less computationally intensive. Easy to fit avec ubms, possible aussi avec NIMBLE ([Cook et al. 2022](#)), Pas possible avec unmarked. A possible extension would be to consider stream networks particularly relevant for semi-aquatic rodents ([Gimenez 2024](#), [Lu et al. 2024](#)).

A second area of investigation concerns the spatial dimension of multinomial N-mixture models, particularly the assumption of independence among removal sites (i.e., that removals at one site do not influence those at another). One possible solution is to include site random effects, as demonstrated in the muskrat case study. To better address spatial autocorrelation, restricted spatial regression (RSR) can also be employed ([Johnson et al. 2013](#), [Broms et al. 2014](#)) to impose a structure where spatially adjacent sites are modeled to have correlated random effects, effectively accounting for spatial autocorrelation. RSR models are advantageous because their random effects are constructed to be uncorrelated with fixed covariates, avoiding potential confounding issues, and they are computationally efficient. These models are easy to fit using ubms, also possible with NIMBLE ([Cook et al. 2022](#)), but not currently supported by unmarked. A promising extension would involve adapting these models to account for stream networks, which is particularly relevant for semi-aquatic rodents ([Gimenez 2024](#), [Lu et al. 2024](#)). This direction could help refine models to better reflect ecological processes in connected

aquatic habitats.

From an ecological perspective, the main contribution of this paper is to demonstrate the estimation of abundance for rodent populations in Europe. The European Union Regulation No. 1143/2014 was established to mitigate the negative impacts of invasive alien species on biodiversity. This regulation mandates measures to prevent the introduction of invasive alien species and manage their established populations. In this study, I focused on two species listed as species of Union Concern under the regulation, which requires member states to implement appropriate management actions.

In this context, I argue that estimates of abundance alone are of limited utility, or even meaningless, if considered in isolation. While it is straightforward to calculate the number of coypus or muskrats remaining after removal campaigns (including associated uncertainty), these estimates achieve their full potential only when integrated into a decision-making framework. Such a framework enables the evaluation of the efficiency of eradication or control operations, facilitates the optimal allocation of limited resources, and incorporates uncertainty into the management of invasive species (Shea et al. 2002, Yackel Adams et al. 2024). This perspective highlights the critical role of abundance estimates in supporting evidence-based decision-making and enhancing the effectiveness of management strategies.

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Data availability statement

Data and code are available at <https://github.com/oliviergimenez/counting-rodents>.

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Conflict of interest disclosure

The author has no conflicts of interest to declare.

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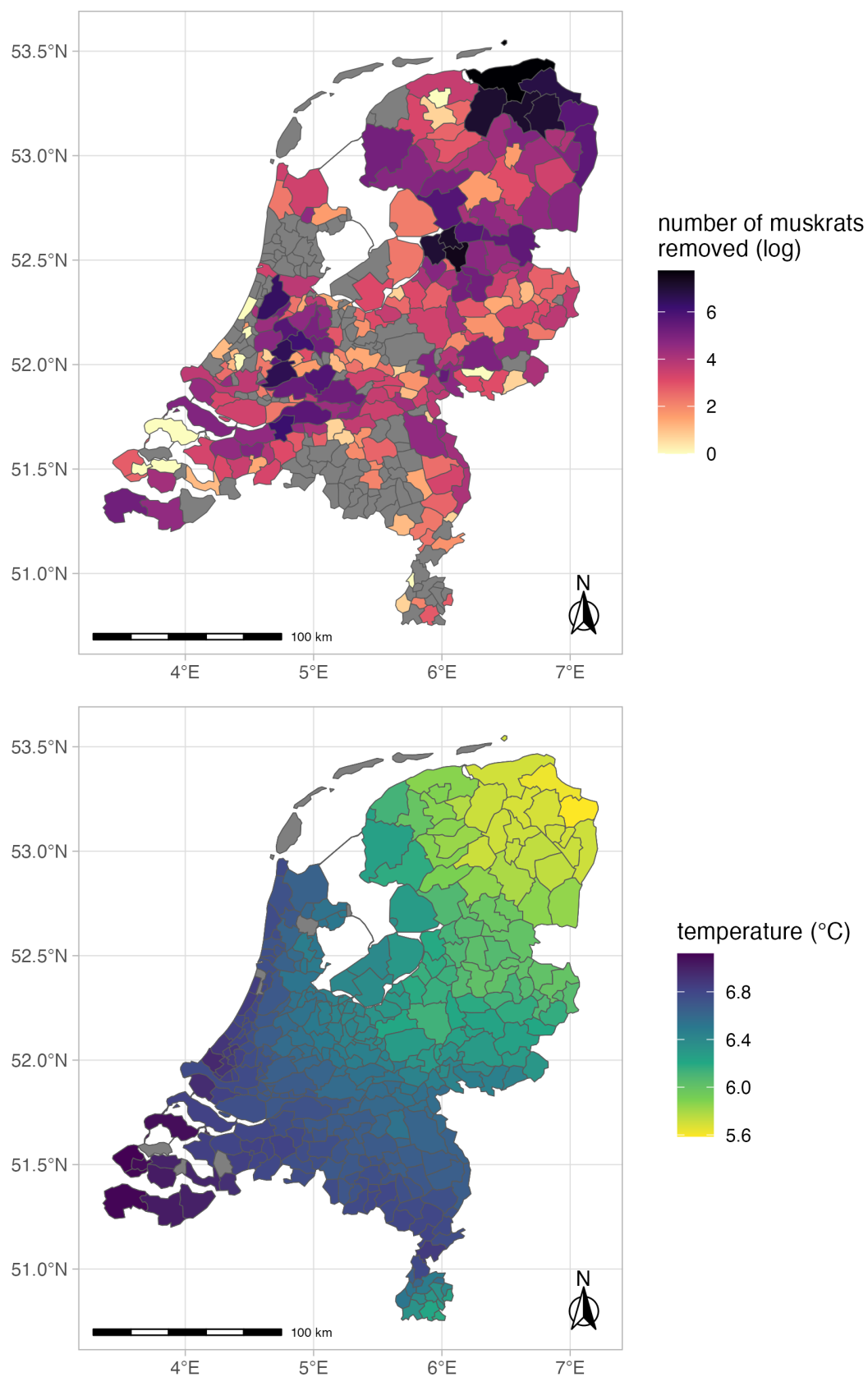


Figure 1: Data. Top removal data. Bottom temperature. DIFFICILE DE FAIRE LA DIFFERENCE AVEC LES DONNEES NON?

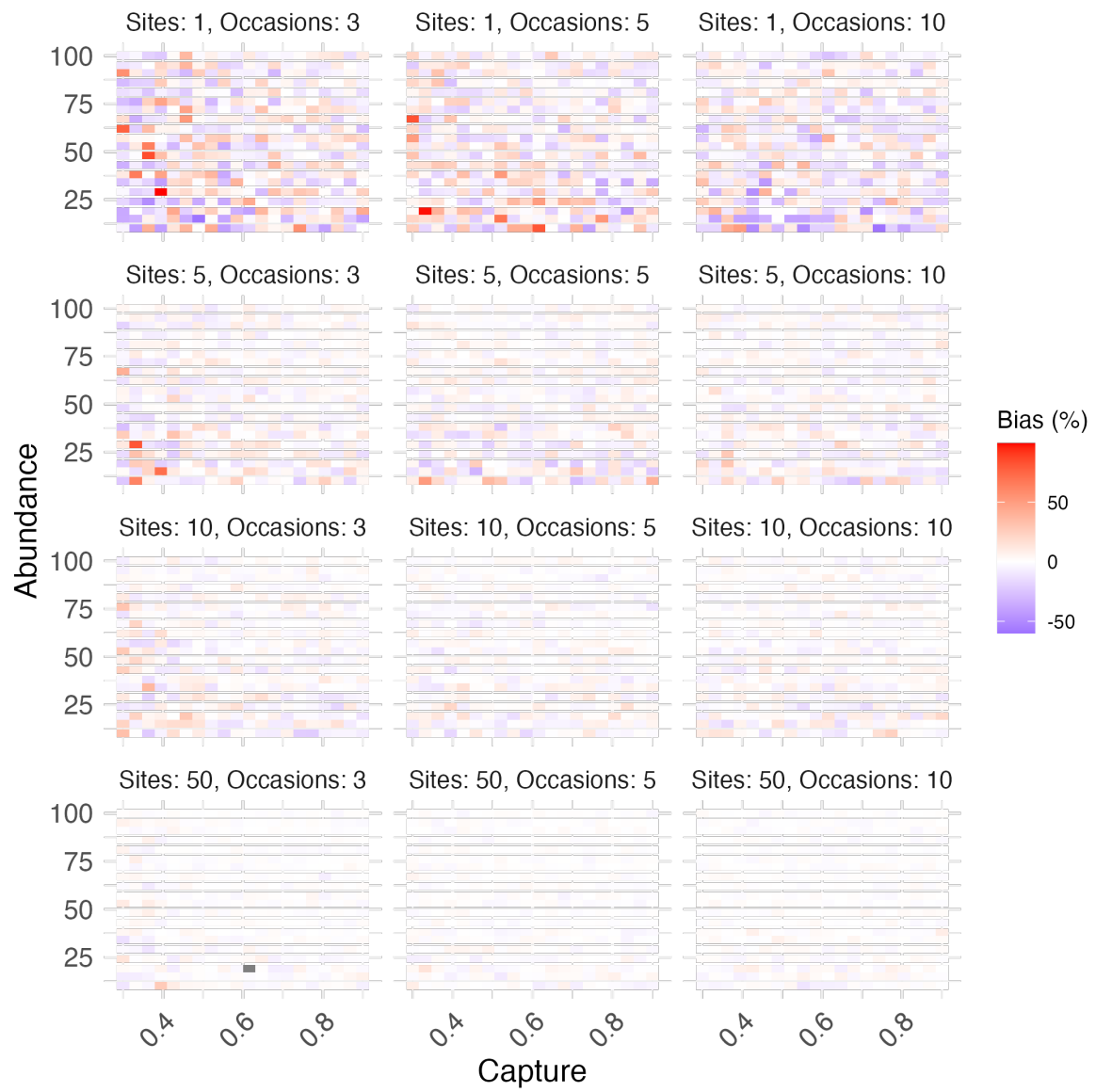


Figure 2: Relative bias.

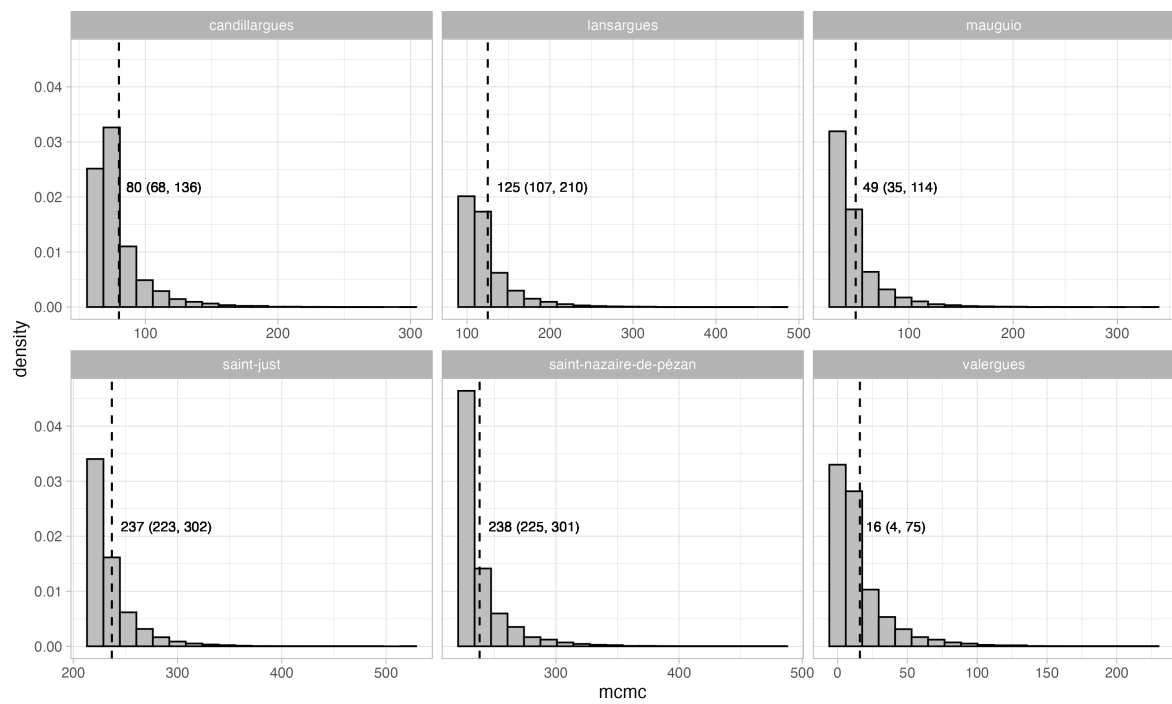


Figure 3: Posterior abundance.

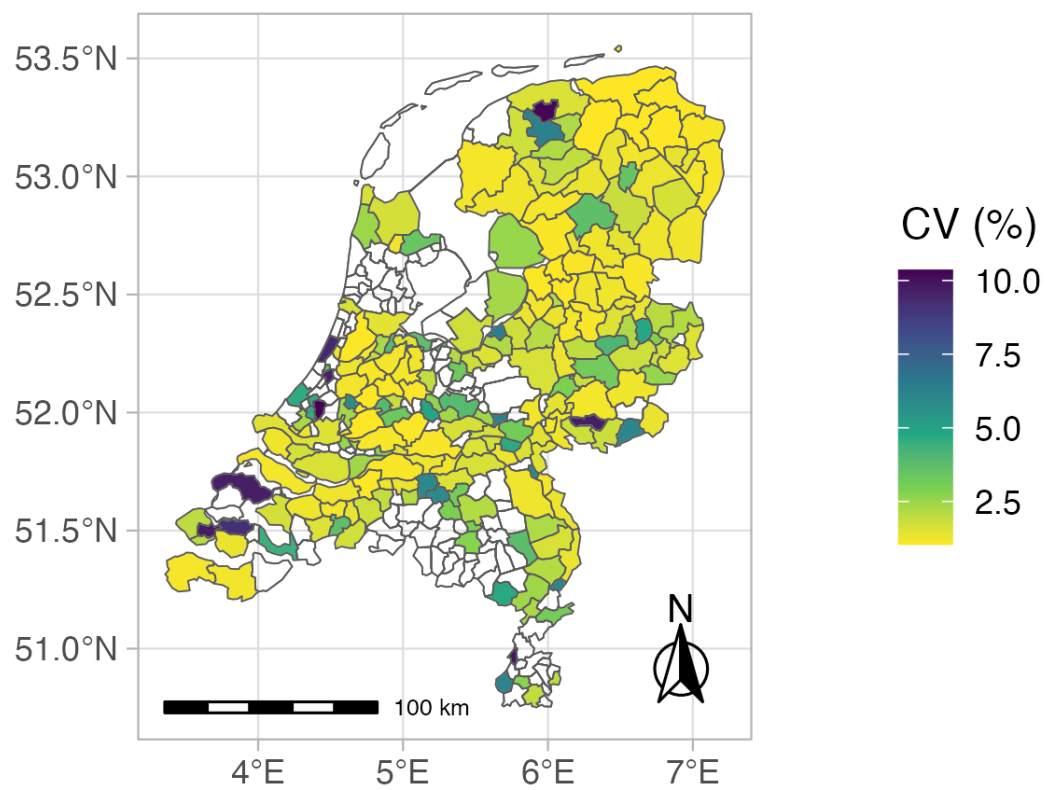
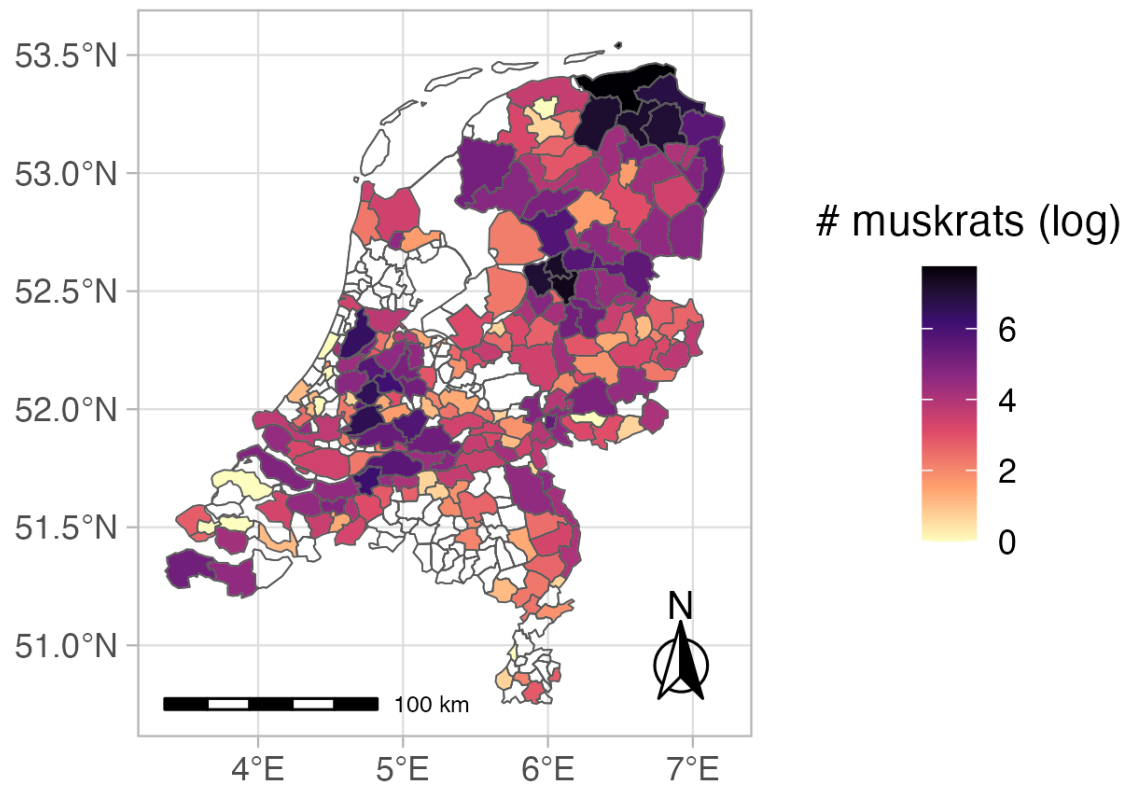


Figure 4: Muskrats.