

1 Estimating invasive rodent abundance using removal data
2 and hierarchical models

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4 2025-04-19

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7 Invasive rodents pose significant ecological, economic, and public health challenges. Robust
8 methods are needed for estimating population abundance to guide effective management.
9 Traditional methods such as capture-recapture are often impractical for invasive species due
10 to ethical, legal and logistical constraints. Here, I showcase the application of hierarchical
11 multinomial N-mixture models for estimating the abundance of invasive rodents using removal
12 data. First, I perform a simulation study which demonstrates minimal bias, as well as good
13 precision and reliable coverage of confidence intervals across a range of sampling scenarios.
14 I also illustrate the consequences of violating the population closure assumption, showing
15 how between-occasion dynamics can bias inference. Second, I analyze removal data for two
16 invasive rodent species, namely coypus (*Myocastor coypus*) in France and muskrats (*Ondatra*
17 *zibethicus*) in the Netherlands. Using hierarchical multinomial N-mixture models, I examine
18 the effects of temperature on abundance while accounting for imperfect and time-varying
19 capture probabilities. I also show how to accommodate spatial variability using random effects,
20 quantify uncertainty in parameter estimates, and account for violations of closure by fitting an
21 open-population model to multi-year data. Overall, I hope to demonstrate the flexibility and
22 utility of hierarchical models in invasive species management.

²³ *Keywords:* Invasive species, Multinomial N-mixture, Population size, Statistical ecology

²⁴ Introduction

²⁵ Invasive species are a significant global issue, with wide-ranging impacts on ecosystems,
²⁶ economies, and public health ([Pyšek et al. 2020](#), [Roy et al. 2024](#)). Among these, the financial,
²⁷ epidemiological, social, and ecological costs associated with invasive rodents are substantial, as
²⁸ they damage infrastructures, degrade agricultural systems, and act as reservoirs for zoonotic
²⁹ diseases ([Diagne et al. 2023](#)).

³⁰ Effective management of invasive species requires the estimation of population abundance
³¹ for guiding control efforts and evaluating the success of eradication or regulation programs
³² ([Williams et al. 2002](#), [Thompson et al. 2021](#)). However, the challenge in estimating animal
³³ abundance is that, because of imperfect detection, individuals are not always observed even
³⁴ when present ([Borchers et al. 2002](#), [Seber and Schofield 2023](#)). Ignoring imperfect detection
³⁵ leads to biased estimates of population abundance ([Kéry and Schmidt 2008](#)). To account for
³⁶ imperfect detection, capture-recapture methods are usually used to correct observed counts
³⁷ ([McCrea and Morgan 2015](#)). Yet, for invasive species, capture-recapture is often impractical, as
³⁸ ethical and management concerns typically prevent the release of captured animals.

³⁹ An alternative approach involves the use of removal methods ([Rodriguez de Rivera and McCrea](#)
⁴⁰ [2021](#)) in which individuals are captured and permanently removed from the study area during
⁴¹ successive sampling occasions. This process leads to a decrease in the expected number of
⁴² captures by a consistent proportion over time (rather than by a fixed amount decline), which
⁴³ informs on the total abundance as the initial population determines how quickly the number of
⁴⁴ individuals available for capture diminishes.

⁴⁵ While standard removal methods are well-established ([Moran 1951](#), [Zippin 1956, 1958](#), [Ro-](#)
⁴⁶ [driguez de Rivera and McCrea 2021](#)), recent advances in population ecology remain underuti-
⁴⁷ lized in the context of invasive species. Hierarchical models, in particular, have gained traction
⁴⁸ ([Royle and Dorazio 2008](#), [Kéry and Royle 2015](#)) due to their ability to: (i) explicitly separate

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

55 In this paper, I showcase the application of a hierarchical formulation of removal models, the
56 multinomial N-mixture model ([Dorazio et al. 2005](#)), to estimate the abundance of rodents in
57 Europe. In this study, I focus on the coypu (*Myocastor coypus*) in France and the muskrat (*Ondatra*
58 *zibethicus*) in the Netherlands. Both species are semi-aquatic rodents introduced to Europe in
59 the early 20th century following escapes or releases from fur farms. The coypu, native to South
60 America, has formed widespread invasive populations in France ([Bonnet et al. 2023](#)), where
61 it causes significant damage to infrastructure and crops. Additionally, it serves as a healthy
62 carrier of leptospirosis, a zoonotic disease with potentially serious consequences. Similarly, the
63 muskrat, native to North America, has established extensive populations in the Netherlands.
64 By burrowing into riverbanks, dykes, and dams, muskrats compromise the integrity of these
65 structures, posing a threat to public safety ([Loon et al. 2017](#)). Both species are also widespread
66 in other European countries; updated distribution maps are available via the European Alien
67 Species Information Network (EASIN) platform ([https://easin.jrc.ec.europa.eu/spexplorer/
68 search/](https://easin.jrc.ec.europa.eu/spexplorer/search/)).

69 Using removal data, I demonstrate the application of the multinomial N-mixture model to
70 estimate the abundance of rodent populations. First, I conduct a simulation study to evaluate the
71 model's performance under varying numbers of sampling sites and sampling occasions. Second,
72 I present a case study on a coypu population in France to illustrate the hierarchical structure
73 of the multinomial N-mixture model, demonstrating how covariates can be incorporated to

74 account for variations in abundance and capture probabilities. Third, I use a case study on
75 muskrats in the Netherlands to illustrate the integration of random effects within the model
76 and demonstrate how to relax the closure assumption. To facilitate reproducibility, I provide
77 the accompanying code and data, aiming to promote the broader adoption of removal models
78 in the study of biological invasions.

79 **Methods**

80 **Multinomial N-mixture model**

81 Think of a dice with six sides. The dice has a 1 in 6 chance of landing on face 1, the same for
82 face 2, and so on. If I roll the dice 30 times, I would expect, on average over many repetitions
83 of this experiment, to get face 1 five times, face 2 five times, and so on. You can test this in
84 R by running the command `rmultinom(n = 1, size = 30, prob = c(1/6, 1/6, 1/6, 1/6,`
85 `1/6, 1/6))` repeatedly. In this experiment, y_1 , the number of 1s, y_2 , the number of 2s, ..., and
86 y_6 , the number of 6s, follows a multinomial distribution with parameters the number of rolls
87 (30) and probabilities $(1/6, 1/6, \dots, 1/6)$.

88 Now think of a removal campaign conducted over 3 months. We record the number of rodents
89 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
90 never captured. Let p be the probability of capturing a rodent in a given month. The probability
91 of capturing a rodent in the first month is $\pi_1 = p$. The probability of capturing a rodent in the
92 second month is $\pi_2 = (1 - p)p$ the probability of not capturing it in the first month $(1 - p)$
93 multiplied by the probability of capturing it in the second month p . The probability of capturing
94 a rodent in the third month is $\pi_3 = (1 - p)(1 - p)p$, the probability of not capturing it in the
95 first and second months, $(1 - p)(1 - p)$, multiplied by the probability of capturing it in the
96 third month, p . Finally, the probability of never being captured is $\pi_4 = 1 - (\pi_1 + \pi_2 + \pi_3)$

97 the complement of the probability of being captured in the first, second, or third month. If we
98 assume that N represents the abundance, then we have that the vector of counts (y_1, y_2, y_3, y_4)
99 follows a multinomial distribution with parameters N and probabilities $(\pi_1, \pi_2, \pi_3, \pi_4)$. This
100 is the observation process. In general, we assume that N follows a Poisson distribution with
101 parameter the expected number of rodents denoted λ . This is the state or ecological process.
102 And there you have it, the multinomial N-mixture model for a removal experiment, which
103 is similar to throwing a dice N times and the π 's give the probabilities that I get a given face
104 of that dice. Unlike a fair die, however, the probabilities in a removal experiment are not
105 equal; they reflect varying detection probabilities over time, which depend on factors like effort,
106 animal behavior, or environmental conditions. Also, in general, we monitor rodents in several
107 populations $i = 1, \dots, S$ and we need to estimate local abundance N_i . To do so, Dorazio et al.
108 (2005) extended multinomial N-mixture models to account for spatial variation in abundance
109 and/or capture, and showed that abundance estimates had similar or better precision than
110 those obtained from analyzing removal data for each population separately.

111 Parameters N , p , and λ are unknown and need to be estimated. In a frequentist framework,
112 marginalization is performed by summing over all possible values of N (Dorazio et al. 2005). In
113 a Bayesian framework, all these parameters are estimated directly, which simplifies the process
114 (Royle and Dorazio 2006). Both parameters, λ and p , can be modeled as functions of explanatory
115 spatial and temporal variables, in the spirit of generalized linear models, and Poisson (with a
116 log link function) or logistic regressions (with a logit link function) for example.

117 To evaluate model adequacy, I used standard goodness-of-fit procedures adapted to both
118 frequentist and Bayesian frameworks. In the frequentist framework, we apply a parametric
119 bootstrap approach: we generate a large number of replicate datasets from the maximum likeli-
120 hood estimates, refit the model to each replicate, and compute diagnostic statistics such as the
121 Freeman–Tukey statistic. If the resulting bootstrap p-values fall within a non-extreme range, this

122 indicates no evidence of lack of fit. In the Bayesian framework, I assessed model adequacy using
123 posterior predictive checks based on Bayesian p-values. At each MCMC iteration, a replicate
124 dataset is drawn from the joint posterior distribution, and the Freeman–Tukey discrepancy is
125 computed for both the observed and replicate data. Given the conditional multinomial structure
126 of the model, which separates the observation process from the abundance process, I calculated
127 two discrepancy measures: one for the detection histories and another for the total counts
128 observed. Bayesian p-values near 0.5 (and away from 0 or 1) indicate no evidence of systematic
129 lack of fit.

130 For a detailed description of the multinomial mixture model, I warmly recommend chapter 7 in
131 Kéry and Royle (2015).

132 **Simulation study**

133 I conducted a simulation study to evaluate the model's performance by examining parameter
134 bias under varying numbers of sampling sites and sampling occasions. I simulated removal
135 data over 1, 5, 10 and 50 sites using a Poisson distribution with expected number of animals λ
136 between 10 and 100 (20 values) for the ecological process. I simulated the observation process
137 with a capture probability p varying between 0.3 and 0.9 (20 values) across 3, 5 and 10 occasions
138 per site. In total, I considered 4800 scenarios. I fitted the multinomial N-mixture model to
139 the simulated data within the frequentist framework using function `multinomPois()` in the R
140 package `unmarked` (Kellner et al. 2023), and I repeated this procedure 100 times. Eventually, I
141 calculated the relative bias, root mean square error (RMSE), and coverage of the 95% confidence
142 interval for each parameter.

143 To assess the effect of violating the closure assumption, I implemented an additional set of
144 simulations in which the population could change between sampling occasions. Specifically,
145 individuals staying in the population with probability 0.8, and new individuals arrive according

¹⁴⁶ to a Poisson process with mean 1. Apart from these between-occasion dynamics, all other
¹⁴⁷ aspects of the simulation setup remained the same. This setup breaks the closure assumption
¹⁴⁸ in two ways. Some individuals leave the population between sampling occasions, violating
¹⁴⁹ the assumption that declines in abundance are due to removal alone; this can bias detection
¹⁵⁰ probability and abundance estimates. New individuals enter between sampling occasions,
¹⁵¹ inflating the pool of animals available for detection and leading to overestimation of abundance.
¹⁵² Since I deliberately fit a closed model to data from an open process, any resulting bias directly
¹⁵³ reflects the impact of violating closure. While this simulation focuses on geographic closure, the
¹⁵⁴ same logic applies to demographic closure, where the stay and arrivals parameters correspond
¹⁵⁵ to survival and recruitment processes.

¹⁵⁶ Note that I used a frequentist implementation for the simulation study to reduce computation
¹⁵⁷ time given the large number of scenarios. The model structure remains hierarchical, as in the
¹⁵⁸ Bayesian case studies, and both inferential approaches would yield similar results. The aim
¹⁵⁹ was to assess model performance across ecological and sampling conditions, not to compare
¹⁶⁰ statistical paradigms.

¹⁶¹ Case studies

¹⁶² In this section, I analyzed removal data from two rodent species: coypus in France and muskrats
¹⁶³ in the Netherlands. With these case studies, I aimed at illustrating specific features of hierarchical
¹⁶⁴ multinomial N-mixture models. For both species, I explored the potential effect of temperature
¹⁶⁵ on abundance (e.g., [Gosling 1981](#), [Simpson and Boutin 1993](#)). A comprehensive analysis of the
¹⁶⁶ ecological factors influencing population dynamics was beyond the scope of this work and will
¹⁶⁷ be addressed in future studies.

168 **Coypus in France**

169 Removal data on coypus were collected from annual control operations conducted since 2015 in
170 several cities within the Hérault department, located in the Occitanie region of southern France.
171 These operations are carried out year-round, with the exception of July and August. Coypus are
172 trapped using cages by a network of volunteers coordinated by the Syndicat Mixte du Bassin
173 de l'Or and the Fédération Départementale des Chasseurs de l'Hérault ([https://etang-de-l-](https://etang-de-l-or.com/lutte-ragondins/)
174 [or.com/lutte-ragondins/](https://etang-de-l-or.com/lutte-ragondins/)). For this study, I focus on data from 2022, specifically from sampling
175 occasions in February, March, and April. The data, covering $S = 6$ cities, are summarized in
176 Table 1. I fitted a model where the expected number of coypus was modeled as a function of
177 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 the average 3-month temperature across several cities in the Hérault department, France, in 2022.

178 A key assumption of the multinomial N-mixture model is that abundance follows a Poisson
179 distribution, which implies equal mean and variance. When this assumption is violated - i.e., in
180 the presence of overdispersion - a common and effective solution is to replace the Poisson with
181 a negative binomial distribution. I illustrate how to fit such an overdispersed model using the
182 coypu dataset. Note that a site random effect was not included here, as the spatial scale of the
183 coypu dataset was limited. However, such effects may be important to consider in broader-scale
184 programs where unobserved spatial heterogeneity is likely to be more pronounced, as in the
185 muskrat case study.

¹⁸⁶ **Muskrats in the Netherlands**

¹⁸⁷ Removal data on muskrats in the Netherlands were collected by professional trappers. The data
¹⁸⁸ were registered in atlas blocks (5×5 km) per periods of four weeks. For this study, I focus on
¹⁸⁹ data from 2014, specifically from sampling occasions in January, February, and March. The data
¹⁹⁰ were made available through the LIFE MICA project (Cartuyvels et al. 2024) and can be freely
¹⁹¹ downloaded from <https://www.gbif.org/dataset/7d75109d-a6cb-4e90-89d0-79d08577c580>
¹⁹² (Moerkens et al. 2021). The data, covering $S = 215$ cities (out of the 342 cities in the Netherlands),
¹⁹³ are presented in Figure 1. I fitted the same model as for the coypus data, except that I added a
¹⁹⁴ site random effect on abundance to accommodate the spatial variation that was not explained
¹⁹⁵ by temperature.

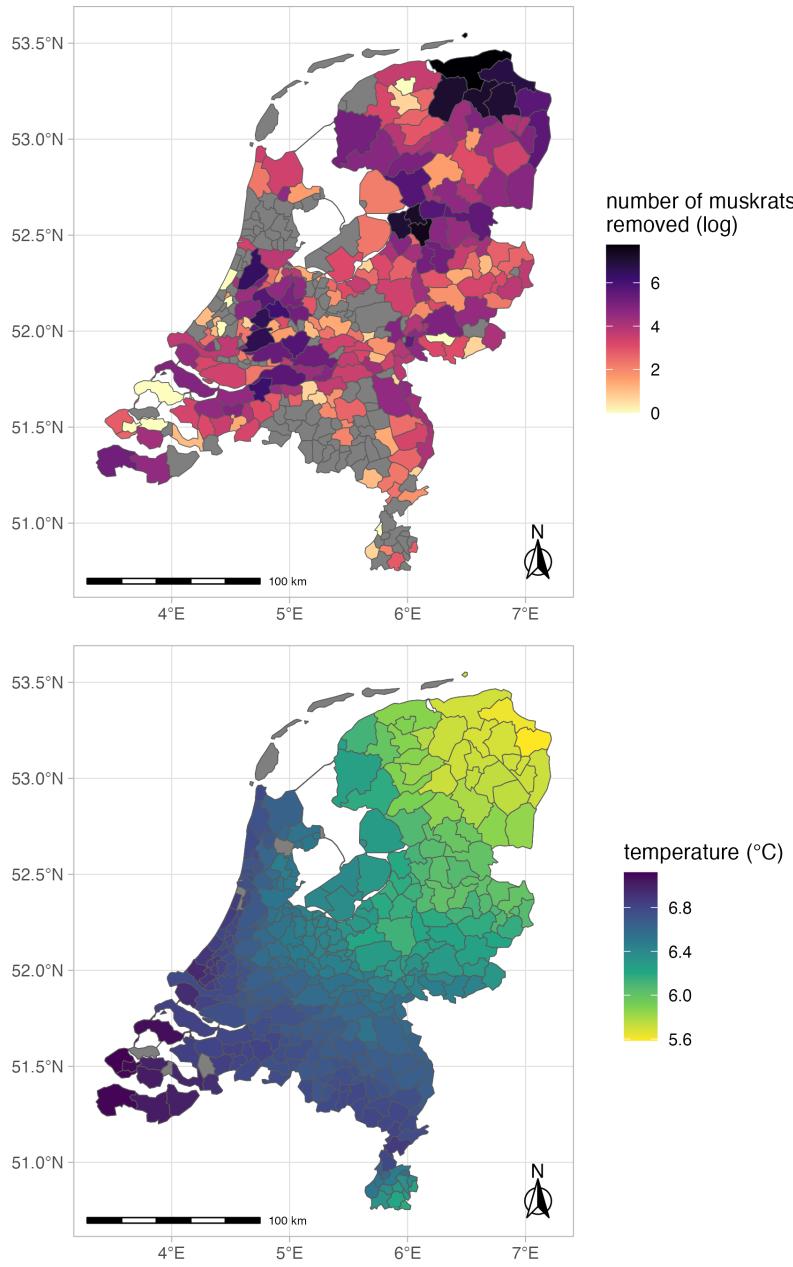


Figure 1: Total number of invasive muskrats removed over the period January–February–March (top panel), and the average 3-month temperature (bottom panel) across the Netherlands in 2014.

¹⁹⁶ A key assumption underlying the proper use of multinomial N-mixture models is that of
¹⁹⁷ population closure, which assumes no births, deaths, immigration, or emigration occur during

198 the trapping period. A straightforward approach to relax this assumption is to fit multiple
199 years of data (a.k.a. stacking the data) into a standard multinomial N-mixture model. In this
200 approach, year-site combinations are treated as separate sites, and year is included as a site
201 covariate or random effect in the model. I used this method to evaluate a temporal effect on the
202 relationship between temperature and abundance. Assuming an increase in temperature over
203 time, one might predict a decoupling or weakening of the relationship between abundance and
204 temperature. To test this, I conducted an additional analysis spanning the 1987–2014 period,
205 modeling the slope of the temperature-abundance relationship as a linear function of time.

206 Implementation

207 For all analyses, I used the statistical language R ([R Core Team 2024](#)). I used the tidyverse ([Wick-](#)
208 [ham et al. 2019](#)) suite of packages for data manipulation and visualization, sf ([Pebesma and](#)
209 [Bivand 2023](#)) for dealing with spatial data and krigR ([Kusch and Davy 2022](#)) to get temperature
210 data. For the simulations, I used the R package unmarked ([Kellner et al. 2023](#)), see the Simulation
211 study section. For the two case studies, I fitted models within a Bayesian framework using
212 Markov chain Monte Carlo (MCMC) algorithms. I used both the NIMBLE ([de Valpine et al. 2017](#))
213 and the ubms ([Kellner et al. 2021](#)) packages. The former offers high flexibility, enabling users to
214 define custom likelihoods, though it requires manual coding, while the latter features simpler
215 syntax with pre-built multinomial N-mixture models, albeit limited to a Poisson distribution
216 for abundance. I specified weakly informative priors for all parameters, specifically normal
217 distributions with mean 0 and standard deviation 1.5 for regression parameters, and a uniform
218 distribution for the standard deviation of the random effects. I ran two chains for a total of
219 200,000 iterations with a burn-in of 20,000 iterations. I summarized posterior distributions with
220 posterior mean and 95% credible intervals. I assessed convergence using standard Bayesian
221 diagnostics: the R-hat statistic (values close to 1 indicate convergence), effective sample size
222 (which reflects the amount of independent information in the posterior sample, should be >

²²³ 100), and visual inspection of trace plots (which should show good mixing and stationarity of
²²⁴ the chains).

²²⁵ **Results and discussion**

²²⁶ The results of the simulation study are presented in Figures 2 and 3. Overall, the analysis
²²⁷ revealed minimal bias, with the exception of one site (first row) that showed a notable deviation
²²⁸ (Figure 2).

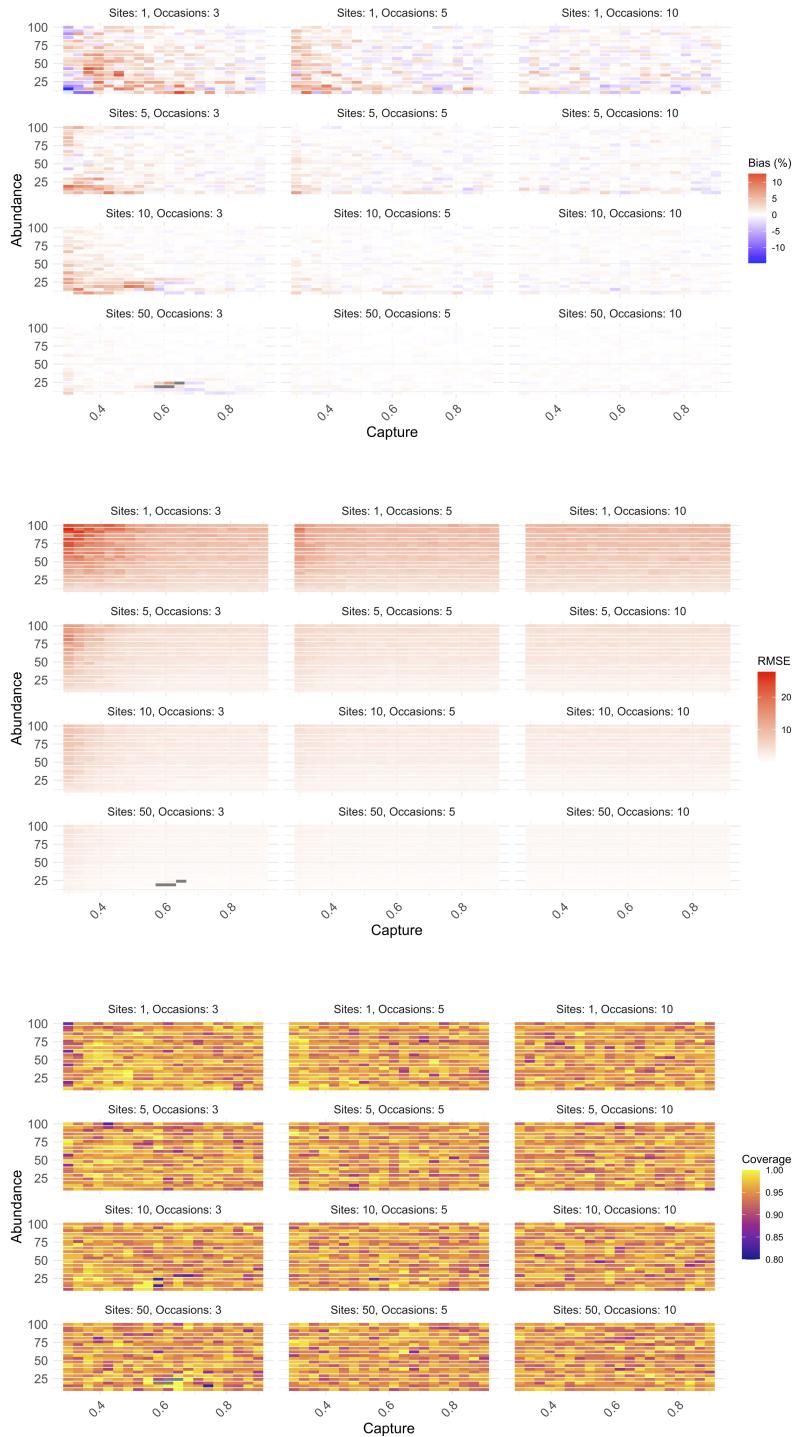


Figure 2: Relative bias (top panel), root mean square error (RMSE; middle panel) and coverage of the 95% confidence interval (bottom panel) for abundance estimates from a multinomial N-mixture model with constant parameters. Capture probabilities (X-axis) range from 0.3 to 0.9, while abundance (Y-axis) varies between 10 and 100 individuals. Scenarios consider 3, 5, and 10 capture occasions (columns) and 1, 5, 10, and 50 sites (rows). Results are based on 100 simulations.

²²⁹ Increasing the number of sites to 10 significantly reduced this bias, and no bias was observed
²³⁰ with 50 sites, supporting the recommendation by ([Dorazio et al. 2005](#)) to analyze data jointly
²³¹ rather than separately.

²³² When the closure assumption was not met, the analysis revealed that both bias and precision
²³³ metrics were highly sensitive to the introduction of between-occasion population dynamics
²³⁴ (Figure 3). Specifically, relative bias increased and coverage dropped in many scenarios, partic-
²³⁵ ularly when detection probability was low or the number of sites and occasions was limited.
²³⁶ These results highlight how violations of closure can substantially compromise the reliability of
²³⁷ abundance estimates derived from closed-population models.

²³⁸ Overall, these findings align with previous simulation studies on binomial N-mixture models
²³⁹ (e.g., [Womack-Bulliner et al. 2019](#), [Fogarty and Fleishman 2021](#)).

²⁴⁰ To enhance reproducibility, I provide the code for the simulation study in the Supplementary
²⁴¹ Material. This resource can be adapted for various purposes, such as conducting custom
²⁴² simulation studies or designing removal protocols and conducting power analyses.

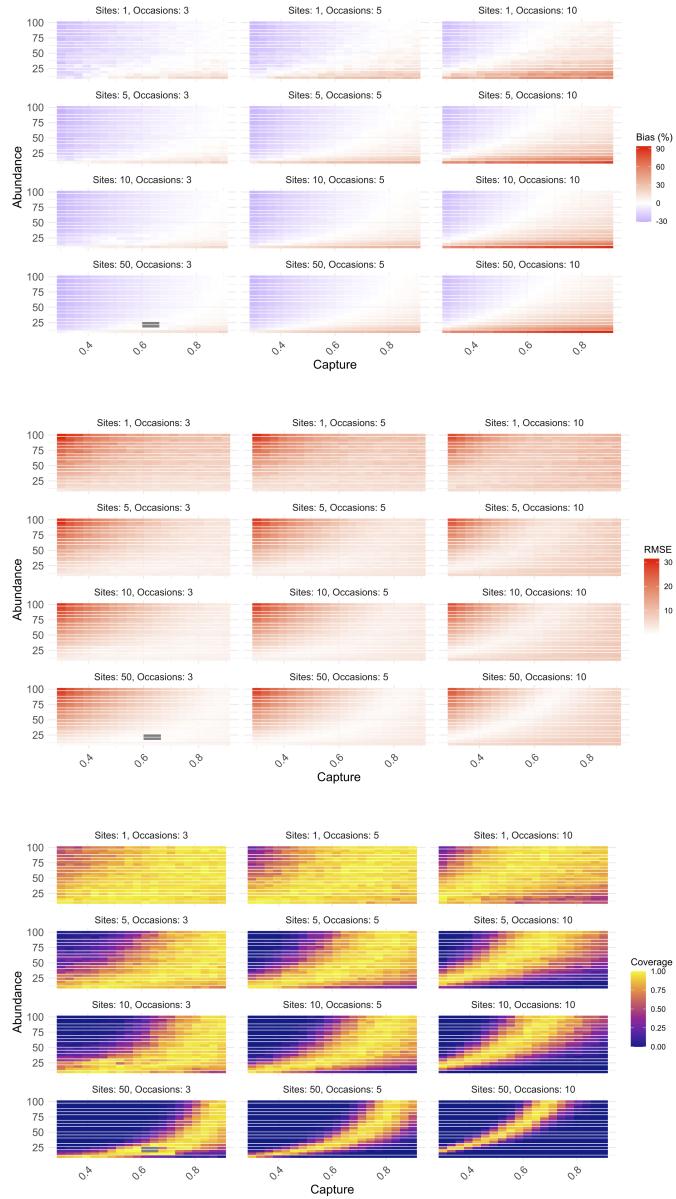


Figure 3: Relative bias (top panel), root mean square error (RMSE; middle panel) and coverage of the 95% confidence interval (bottom panel) for abundance estimates from a multinomial N-mixture model with constant parameters, fitted to data where the closure assumption was deliberately violated. Between capture occasions, individuals remained in the population with probability 0.8, and new individuals arrived according to a Poisson process with mean 1, introducing both emigration and immigration between sampling events. Capture probabilities (X-axis) range from 0.3 to 0.9, while abundance (Y-axis) varies between 10 and 100 individuals. Scenarios consider 3, 5, and 10 capture occasions (columns) and 1, 5, 10, and 50 sites (rows). Results are based on 100 simulations.

243 In the coypus case study, temperature was found to have a negative effect on abundance, with a
 244 slope estimate of -0.14 (-0.22, -0.07). Capture probabilities were estimated at 0.43 (0.29, 0.49) in
 245 February, 0.35 (0.19, 0.44) in March and 0.84 (0.35, 1.00) in April. The posterior distributions of
 246 abundance across the different sites are presented in Figure 4.

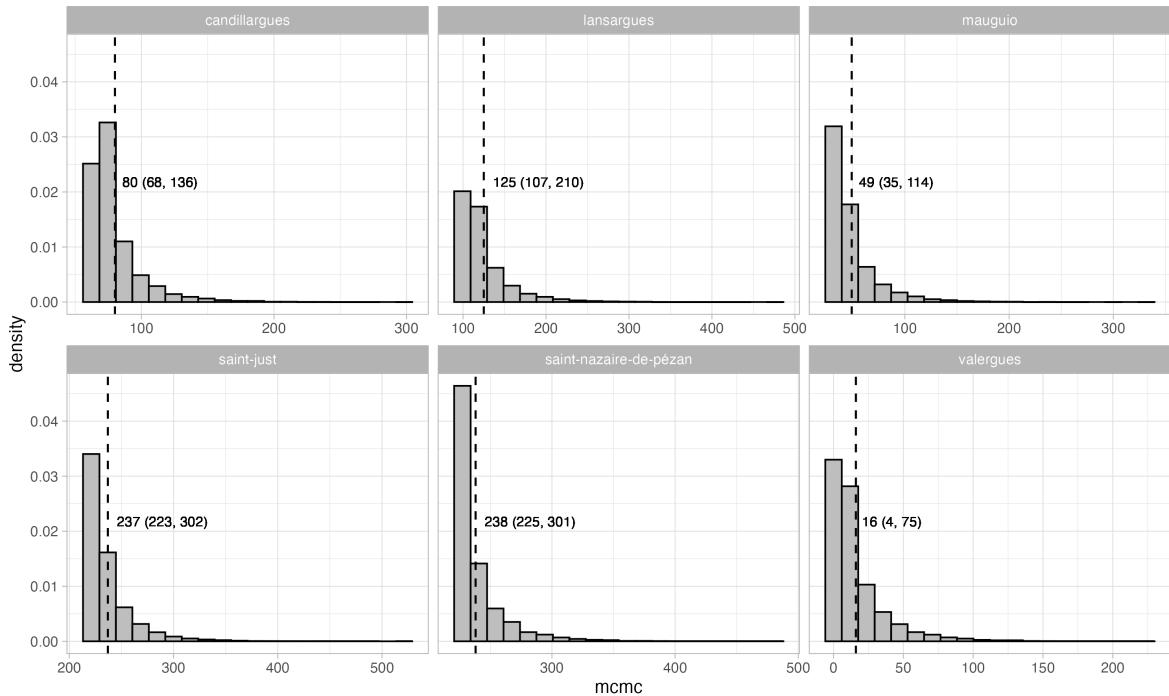


Figure 4: Posterior density plots for coypu abundance across several cities in the Hérault department, France, in 2022. The vertical shaded line indicates the posterior mean abundance, accompanied by its credible interval. See Table 1 for the raw data.

247 The Poisson assumption does not appear valid based on the estimated abundance in Figure
 248 4, which shows a skewed posterior distribution of site-level abundances and wide credible
 249 intervals, suggesting greater variability than expected under a Poisson distribution. This is
 250 confirmed by a goodness-of-fit test, which yielded a p-value of 0.04, indicating a lack of fit.
 251 Fortunately, this limitation can be addressed by relaxing the Poisson assumption and use a
 252 negative binomial distribution instead. This adjustment can be implemented in both NIMBLE
 253 and unmarked but is not currently supported by ubms. Interestingly, under the negative binomial
 254 model, the effect of temperature on abundance was no longer significant, with a slope estimate

255 of -0.27 (-1.29, 0.60). Moreover, the goodness-of-fit test for the abundance component of the
256 model no longer indicated a lack of fit, with a p-value of 0.39.

257 In the muskrats case study, temperature was found to have a negative effect on abundance,
258 with a slope estimate of -0.48 (-0.70, -0.26). The standard deviation of the site random effect was
259 estimated at 1.62 (1.46, 1.79). Capture probabilities were estimated at 0.12 (0.05, 0.25) in January,
260 0.25 (0.15, 0.35) in February and 0.60 (0.53, 0.75) in March. Estimated abundance across sites
261 after removal is presented in Figure 5. A goodness-of-fit test for the abundance component of
262 the model yielded a p-value of 0.44, indicating no evidence of lack of fit. However, the test for
263 the observation component revealed a lack of fit (p-value = 0), for reasons that remain to be
264 investigated.

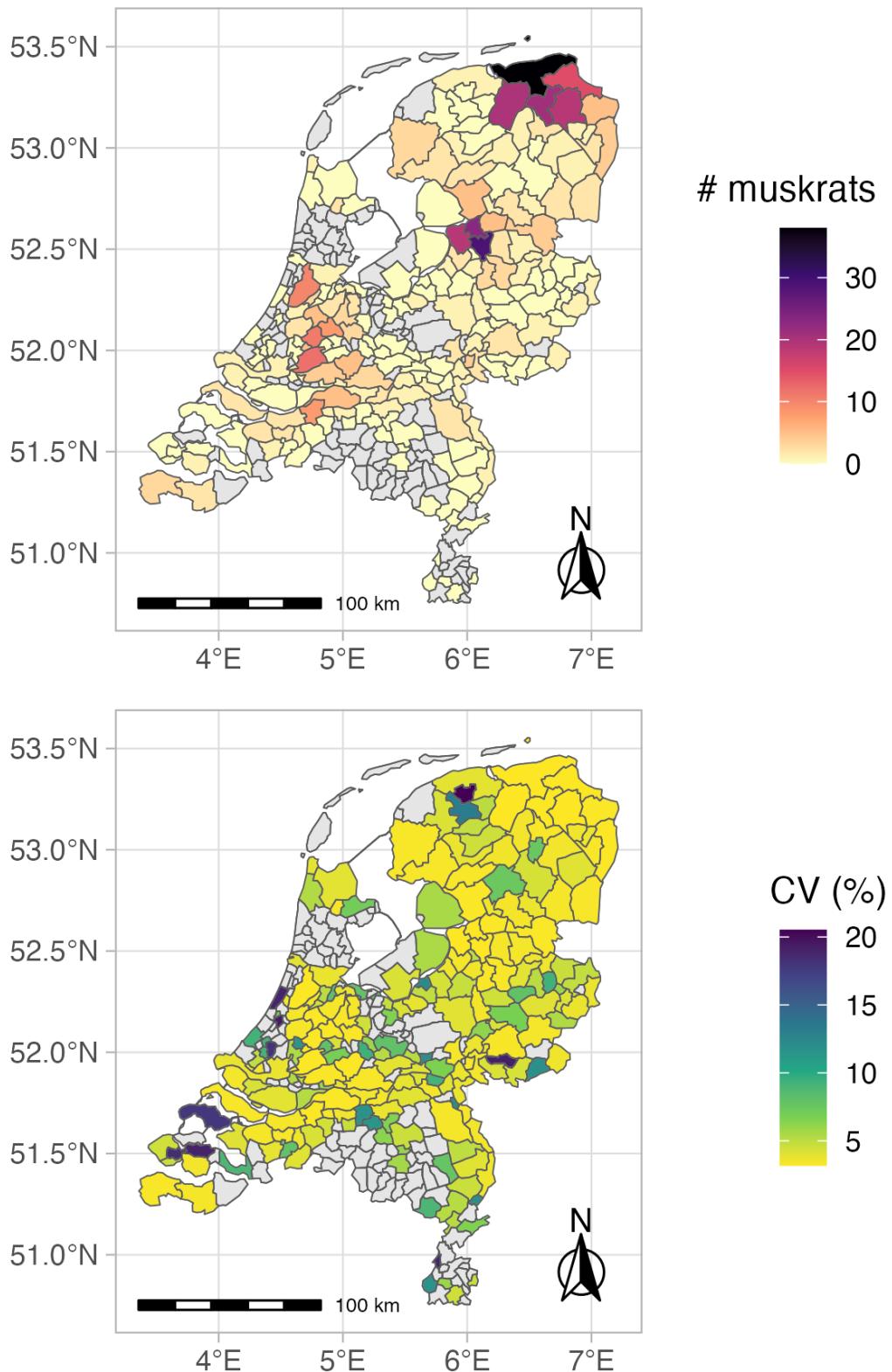


Figure 5: Posterior mean estimates of the number of muskrats remaining after removal in the Netherlands in 2022 (top panel) and the corresponding coefficient of variation (bottom panel). See Figure 1 for the raw data.

265 An important feature of multinomial N-mixture models is their ability to quantify uncertainty,
266 which is often overlooked in spatial analyses. Here, I provide the coefficient of variation
267 to represent the uncertainty surrounding abundance estimates. This metric can help identify
268 specific areas where increased sampling effort might be beneficial to improve estimate precision.

269 Turning to the open-population analysis, the results revealed a negative trend in the slope,
270 estimated at -0.040 (-0.042, -0.039), providing evidence to support the hypothesis of a temporal
271 weakening of this relationship.

272 Several perspectives arise from this work. From a methodological standpoint, this study
273 highlights the suitability of hierarchical models for capturing dependencies in space and time,
274 which are common in ecological systems and removal experiments in particular. Two areas
275 stand out as particularly worth exploring. First, although much of the paper focuses on static
276 models under the assumption of population closure, I have taken a first step toward relaxing
277 this assumption by fitting an open-population model in the muskrats case study. This extension
278 does not yet incorporate explicit demographic mechanisms, but it illustrates the potential of
279 such models to better account for temporal population dynamics. When the mechanisms
280 underlying population dynamics—such as survival, recruitment, or dispersal—are of interest,
281 multinomial N-mixture models can be extended to open populations ([Matechou et al. 2016](#), [Link et al. 2018](#), [Zhou et al. 2019](#), [Tiberti et al. 2021](#)). These extended models can be implemented
282 using unmarked or NIMBLE, though they are not yet available in ubms.

284 A second area of investigation concerns the spatial dimension of multinomial N-mixture models,
285 particularly the assumption of independence among removal sites (i.e., that removals at one
286 site do not influence those at another). One possible solution is to include site random effects,
287 as demonstrated in the muskrat case study. To better address spatial autocorrelation, restricted
288 spatial regression (RSR) can also be employed ([Johnson et al. 2013](#), [Broms et al. 2014](#)) to
289 impose a structure where spatially adjacent sites are modeled to have correlated random effects,

290 effectively accounting for spatial autocorrelation. RSR models are advantageous because their
291 random effects are constructed to be uncorrelated with fixed covariates, avoiding potential
292 confounding issues, and they are computationally efficient. These models are easy to fit
293 using `ubms` and can also be implemented in NIMBLE ([Cook et al. 2022](#)), although they are
294 not currently supported by `unmarked`. A promising extension would involve adapting the
295 covariance structure in these models to account for stream networks ([Gimenez 2024](#), [Lu et al.](#)
296 [2024](#)), which is particularly relevant for semi-aquatic rodents.

297 Third, in many real-world removal programs, detection probability is strongly influenced by
298 effort-related factors such as trap density, frequency of checks, or personnel availability (e.g.,
299 [Davis et al. 2016](#)). Unfortunately, explicit effort data were not available for the case studies
300 analyzed here. To account for temporal variation in detection probability, likely driven in part
301 by effort and other factors such as weather, seasonal activity, or habitat changes, I modelled
302 detection as a time-varying parameter. While this approach provides a practical solution when
303 effort is missing or inconsistently reported, it does not allow for prospective analyses, such
304 as estimating the level of effort required to achieve a desired level of precision on abundance
305 estimates or statistical power to detect changes or trends in abundance over time. Addressing
306 such questions requires explicitly incorporating effort into the model. I therefore emphasize the
307 importance of properly recording removal effort and caution against interpreting its omission
308 here as a reason to neglect it. On the contrary, I hope this work underscores the value of
309 systematic effort reporting to improve both inference and future survey design.

310 From an ecological perspective, the main contribution of this paper is to demonstrate the
311 estimation of abundance for rodent populations in Europe. The European Union Regulation
312 No. 1143/2014 was established to mitigate the negative impacts of invasive alien species on
313 biodiversity. This regulation mandates measures to prevent the introduction of invasive alien
314 species and manage their established populations. In this study, I focused on two species listed

³¹⁵ as species of Union Concern under the regulation, which requires member states to implement
³¹⁶ appropriate management actions.

³¹⁷ In this context, although it is straightforward to calculate the number of coypus or muskrats
³¹⁸ remaining after removal campaigns (including associated uncertainty; see Figure 5), abundance
³¹⁹ estimates realize their full potential only when integrated into a decision-making framework.
³²⁰ Such a framework allows for evaluating the efficiency of eradication or control efforts, optimiz-
³²¹ ing the allocation of limited resources, and accounting for uncertainty in the management of
³²² invasive species (Shea et al. 2002, Yackel Adams et al. 2024).

³²³ Acknowledgments

³²⁴ I would like to warmly thank Nathalie Vazzoler-Antoine and Tanguy Lebrun for sharing the
³²⁵ coypus data, and the team LIFE MICA for sharing the muskrats data. This work was funded by
³²⁶ a grant from the University of Montpellier through its ExposUM institute.

³²⁷ Data availability statement

³²⁸ Data and code are available at <https://github.com/oliviergimenez/counting-rodents>.

³²⁹ References

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