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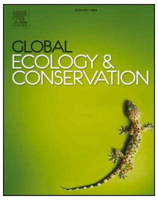

Original research article

Optimizing sampling interval length in species abundance comparison using the Royle-Nichols occupancy model

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ABSTRACT

The Royle-Nichols occupancy model is commonly used for comparison of wildlife abundance between sites or years with biomonitoring data, such as camera-trap or bioacoustics records. The method requires that records of species are subdivided into sampling intervals with detection or non-detection. Here, we evaluated how the choice of interval length - which is commonly chosen arbitrarily - affects the outcomes of such comparisons. Using simulations and field data, we find that interval length can affect model results substantially. In some cases, different interval lengths can yield opposite differences in abundance between locations. Our results indicate that the interval length should be carefully selected based on properties of the data rather than arbitrarily chosen. Careful selection increases the accuracy of species' abundance comparisons, and makes population comparisons more effective. We provide guidelines for optimizing the choice of interval length.

1. Introduction

Accurate estimation of species abundance is crucial for assessing the effectiveness of conservation actions and informing management strategies. Understanding population dynamics enables conservationists to evaluate the impact of interventions, prioritize resources, and implement adaptive management practices. In recent years, the use of continuous recorders has gained traction for broad-scale occurrence monitoring, providing a valuable tool for collecting extensive data on species presence across diverse habitats. This large amount of occurrence data enables the use of advanced methods like the Royle-Nichols model (Royle and Nichols, 2003), which is a commonly used method for abundance analysis with wildlife monitoring data, such as bioacoustics or camera-trapping data. Using the model, one can estimate the relative abundances of a species in given areas while accounting for uncertainty in detection, which is common in ecological surveys. The model typically employs a hierarchical Bayesian framework, which allows for the incorporation of various levels of uncertainty in the data. This is particularly useful in ecological studies, where data can be sparse or variable. In particular, the model allows for the inclusion of environmental variables that may influence species abundance and detection. This enables researchers to assess how factors like habitat type, climate, and human activities such as hunting affect species populations (Van Kuijk et al., 2022). Because of its competence to estimate relative abundances, it is often used in studies aimed at conservation and management of wildlife populations. By providing accurate estimates of relative abundance and understanding the

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factors that influence it, conservationists can make informed decisions.

A central component of the Royle-Nichols model is the estimation of detection probability. This is the likelihood that a species is observed, given that it is present. The model uses basic recordings of captures and non-captures to estimate the probability that an individual that is present is actually detected (i.e. the detection probability; MacKenzie et al., 2002; Mackenzie and Royle, 2005; O'Connel et al., 2011; Steenweg et al., 2018). It requires multiple repeated surveys or sampling occasions over a period of assumed population closure, and yields a series of detection and non-detection points (Royle and Nichols, 2003). The model then relates the number of observations to the detection probability. Specifically, it can account for the heterogeneity in detection probabilities between locations that characterizes biomonitoring data (Tobler et al., 2015). The model then derives a probability of detecting occupancy, which corresponds to the probability that at least one individual is available for detection at a sampling point (Welsh et al., 2013). By modelling this probability of detecting occupancy as a function of the per-individual detection rate and estimated local abundance, relative abundance estimates can be calculated (Royle and Nichols, 2003). These can be used to, for example, compare species populations between areas, years, or treatments, a commonly used approach to assess impacts of wildlife conservation and management on biodiversity (O'Connel et al., 2011; Steenweg et al., 2017; Oliver et al., 2023).

To use the model, the continuous data produced by camera traps, bioacoustics devices, and other sensors are transformed into a detection/non-detection matrix by splitting the data into repeated sampling intervals, which requires balancing the number and length of the sampling intervals or repeated surveys. The number of repeated surveys is known to affect model outcomes (MacKenzie et al., 2002; Tyre et al., 2003; Field et al., 2005; Mackenzie and Royle, 2005). Overall, increasing the number of repeated surveys enhances both the precision and accuracy of an occupancy estimation (MacKenzie et al., 2002). When only two repeated surveys are utilized, accuracy is generally low (unless detection probabilities are high); hence, a minimum of three repeats is recommended (Mackenzie and Royle, 2005). When detection probability is low, the number of required repeats increases (Field et al., 2005).

In practice, interval length varies widely among camera-trap studies (Burton et al., 2015), from as short as one day (Ahumada et al., 2011; Beaudrot et al., 2016) to as long as 30 days (e.g., Sunarto et al., 2015). Also, it is common practice to choose a single time-interval length for all species in a study, regardless of their abundance (Bowler et al., 2017; Van Kuijk et al., 2022). The choice of interval length is rarely justified explicitly, but most studies seem to aim for many short intervals (1 – 5 days) to retain more detections.

It is likely that interval length affects the Royle-Nichols model's outcomes, because interval length affects the estimation of detection rates. When interval length increases and the corresponding number of intervals thus decreases, detectability increases. Selecting too large intervals will remove any differences in detections between sites, as non-detections become absent. Non-detections at sampling points with detections are needed to estimate the detection probability, providing insight in the probability that individuals have been present but have not been recorded at sampling points with non-detections only. On the other hand, selecting too short intervals (i.e. 1 day) may lead to zero inflation (which causes problems with model fitting and statistical power; Denes et al., 2015) and very low detection probabilities, which can be difficult to estimate.

Here, we assess how the choice of interval length affects the relative differences in abundance between sites estimated by the Royle-Nichols model. First, we tested whether and how results change when using different interval lengths, using camera-trapping data from

Table 1

Per species, we estimated the optimal interval length for the comparison between FSC and non-certified sites. From left to right, the corresponding average sampling effort per location-pair (i.e. total number of survey days), difference in detection rates (Δr) between the areas, difference in the proportion of sampling points with detections (Δp), the interval length (dT, in days) that minimizes the estimated difference in relative abundance, the estimated difference in relative abundance associated with this interval length, and the estimated difference in relative abundance when a 1-day interval length is used are shown.

Common species name	**Latin species name**	N_{SE}	Δr	Δp	dT	**Δ rel. abund.**	
						dT	**1 day**
African brush-tailed porcupine	*Atherurus africanus*	5213	0.03	0.07	8	0.023	0.026
Marsh mongoose	*Atilax paludinosus*	5439	0.00	0.12	2	0.040	0.049
Black footed mongoose	*Bdeogale nigripes*	4529	0.07	0.34	26	0.023	0.032
Peter's duiker	*Cephalophus callipygus*	4860	0.19	0.32	27	0.019	0.042
Bay duiker	*Cephalophus dorsalis*	4860	0.01	0.00	27	0.023	0.049
White-bellied duiker	*Cephalophus leucogaster*	4832	0.03	0.19	16	0.042	0.049
Ogilby's duiker	*Cephalophus ogilbyi*	4860	0.01	0.00	27	0.023	0.040
Yellow-backed duiker	*Cephalophus silvicultor*	4832	0.07	0.33	16	0.023	0.026
Emin's pouched rat	*Cricetomys emini*	6375	0.09	0.36	28	0.023	0.047
Lady Burton's rope squirrel	*Funisciurus isabella*	5299	0.01	0.02	6	0.023	0.026
Servaline genet	*Genetta servalina*	5321	0.01	0.07	5	0.026	0.040
Western gorilla	*Gorilla gorilla*	4860	0.05	0.21	27	0.042	0.049
Water chevrotain	*Hyemoschus aquaticus*	5471	0.00	0.05	1	0.026	0.026
African forest elephant	*Loxodonta cyclotis*	4529	0.09	0.42	26	0.022	0.024
Mandrill	*Mandrillus sphinx*	5471	0.00	0.00	1	0.023	0.023
African palm civet	*Nandinia binotata*	4221	0.01	0.07	22	0.031	0.040
Chimpanzee	*Pan troglodytes*	6448	0.09	0.23	29	0.029	0.049
Blue duiker	*Philantomba monticola*	4529	0.02	0.02	26	0.023	0.026
Red river hog	*Potamochoerus porcus*	4894	0.03	0.23	14	0.031	0.032
Forest giant squirrel	*Protoxerus stangeri*	6448	0.03	0.05	29	0.023	0.040
Long-nosed mongoose	*Xenogale naso*	5439	0.00	0.02	2	0.023	0.026

a study in Western Equatorial Africa (Republic of Congo and Gabon; Zwerts et al., 2024). Second, using individual-based simulations, we explored how the difference between actual relative abundance and that estimated with the Royle-Nichols model depends on interval length, species density, study duration, and number of sampling points. Third, we created a simple tool to select the optimal interval length. As an example, we applied this tool to the data from Zwerts et al. (2024).

2. Methods

2.1. Does interval length affect population comparisons?

We evaluated how the choice of interval length affected the relative differences in abundance between sites, using camera-trapping data of mammals in tropical forests across the Republic of Congo and Gabon from Zwerts et al. (2024). The study deployed a total of 474 camera traps (Bushnell Trophy Cam HD and Browning 2018 Spec Ops Advantage) across 7 paired logging concessions (seven non-certified seven FSC-certified—timber logged according to principles of the Forest Stewardship Council) in Gabon and the Republic of Congo, during 2018 – 2021. Cameras were installed in 1 km × 1 km grids with a random starting point, resulting in roughly 28–36 cameras per concession while minimizing spatial autocorrelation. Each camera was mounted 30 cm above the ground on the nearest suitable tree offering at least 4 m of visibility. The habitats encompassed mixed lowland rainforest stands within relatively intact forest matrices; at each camera point, microhabitat features such as visibility, slope, presence of fruiting trees, nearby watercourses, and signs of hunting were recorded. Cameras were deployed simultaneously within each paired set of concessions for approximately 2–3 months, ensuring comparable temporal coverage and limiting seasonal bias. Each paired set of logging concession was sampled once; hence there were no repeat samplings across years. With the collected data, Zwerts et al. (2024) estimated encounter rates, which they then used to examine whether FSC-certification benefits animals in logged forests.

The dataset includes 21 mammalian species with each > 150 detections (Table 1). For each of these species, we stored daily detections per camera in an *i* by *j* presence/absence matrix, where *i* was the number of cameras and *j* was the number of recording days for a camera. Column length depended on the survey effort (in days) of the camera with the highest number of camera trapping days. Row length depended on the number of cameras used in the study. Each cell (*i,j*) of the matrix contained the values 0, 1, or NA (0 for non-detection of the species by camera *i* on day *j*, 1 for detection of the species by camera *i* on day *j*, and NA in case the camera had already stopped recording at that day). Because of the daily activity cycle that most animals have, the interval length used in the Royle-Nichols model must be a multiple of one full day.

For a range of interval lengths ($1 \leq dT \leq 30$ days), we calculated the relative abundance of each species in FSC-sites versus non-certified sites. We disregarded all cameras with an individual sampling effort shorter than 3 x dT. Incomplete sampling intervals were disregarded. For example, interval lengths of 4 days with a cut-off at 30 days yielded a study duration of 28 days. We analyzed the data using the *occuRN* function (Fiske and Chandler 2011) in R version 4.1.2 (R Core Team 2022). We used the presence/absence matrix created with the selected interval length in the Royle-Nichols model to estimate how much a species' abundance differs between the two forest management types, in terms of estimated relative abundance (Θ_{FSC} / ($\Theta_{FSC} + \Theta_{non\text{-}FSC}$); estimation Θ_{FSC} for actual abundance λ_{FSC} and estimation $\Theta_{non\text{-}FSC}$ for actual abundance $\lambda_{non\text{-}FSC}$). We also recorded the Z-score of the comparison, which indicates the certainty of a difference in relative abundance between the two area types (when $Z = 0$, abundances are estimated to be exactly equal; when $Z > 1.96$, a species' abundance was estimated to be significantly higher in FSC-certified than in non-certified sites ($p < 0.05$); likewise, when $Z <$ -1.96, a species' abundance was estimated to be significantly lower in FSC-certified than in non-certified sites). We assumed that detection probability (r) at each camera was affected by visibility (v; which was visually assessed into 0–10 m, 11–20 m, and > 20 m categories), and abundance (λ_i) was affected by area type (FSC versus non-certified). To avoid pseudo replication, each location-pair was analyzed separately to obtain the pair specific values for Θ_{FSC} and $\Theta_{non\text{-}FSC}$. Subsequently, we performed a Bayesian analysis on these values of all pairs combined, using the glmer-function from the R-package rstanarm (Goodrich et al., 2025).

2.2. Does interval length affect the accuracy of the Royle-Nichols model?

We assessed the accuracy of the Royle-Nichols model in terms of the difference between the actual simulated relative abundance and that estimated using the Royle-Nichols model. To estimate accuracy per interval length, we used the Royle-Nichols model to compare site data generated with a spatially explicit individual-based model (similar to the approach in Neilson et al., 2018). In our model, we had individuals move randomly within a 5 × 5 km area consisting of 1000 × 1000 patches (i.e., one cell represented a 5 ×5 m area, consistent with the average detection range of a camera trap). Of all the patches, 100 represented camera traps, which we placed in a grid with 500 m spacing between consecutive sampling points (Fig. S1). We let the number of individuals in the area differ between simulation runs to obtain a range of 10 densities (0.32, 0.48, 1.28, 1.60, 3.84, 4.80, 7.68, 9.60, 11.52, and 14.40 individuals km-2). We randomly placed the individuals in the area, and had them move for 90 days using steps of three patches per minute, and turning in a random direction after each step. Directions ($0 < \alpha \leq 2\pi$) were drawn from a van Mises distribution with $\kappa = 1$ (see Fig. S1 for simulations with different values of κ). During nighttime, movement stopped for 11 consecutive hours. If an individual moved outside the simulation area, it re-appeared on the other side (i.e. periodic boundary conditions). For each simulated day, we recorded the number of captures per camera trap. We simulated each density 50 times.

We created datasets for comparison by combining data from two different density simulations into one presence/absence matrix plus a corresponding covariate matrix that included the location information (Loc_1 for the data from simulations with the first density and Loc_2 for the data from simulations with the second density). We subsampled each of the 5000 obtained datasets (100 density combinations x 50 replicates) and created detection histories using 30 different interval lengths ($dT = 1$–30 days). We formatted the data to an input matrix that contains presence/absence (1/0) data per sampling point (= row) and time interval number (= column). We tested our simulations for temporal autocorrelation by following 10 individuals over 7 days. We used the *acf* function in the *tseries* library, with a one day lag in the autocorrelation estimation. We observed that autocorrelation is negligible, even at the smallest interval length of one day (mean = −0.118, median = 0.190, min = −0.857, max = 0.560).

In addition, we generated 6 different study durations by cutting of the simulation data at $T = 7, 14, 21, 30, 60$, and 90. Furthermore, we use subsampling to generate datasets with different numbers of sampling points: 25, 50, 75, and 100 per location.

We did not simulate any differences in detection probabilities (r) between sampling points. Using the Royle-Nichols model, we estimated the two abundances (estimation Θ_1 for actual abundance λ_1 and estimation Θ_2 for actual abundance λ_2) for each of the 1000 density-combinations and calculated the estimated relative abundance as (Θ_1 / ($\Theta_1 + \Theta_2$). Using the estimated and actual relative abundances, we calculated the difference in relative abundance as our measure of accuracy.

2.3. *Choosing the optimal interval length*

We created a simple tool to select the optimal interval length. Using the Royle-Nichols results of the simulation data, accuracy of the Royle-Nichols model per interval length can be estimated for a given dataset. To do so, we calculated average accuracy (A; here denoting the difference between actual relative abundance and relative abundance estimated with the Royle-Nichols model) for 2646 combinations of three variables that can be easily derived from empirical data: (i) the difference in detection rates (r, the average number of presence recordings in the presence/absence matrix) between two simulations (Δr, $0 \leq \Delta r < 1$, in 21 equidistant intervals), (ii) the difference in the proportion of sampling points with detections between two simulations (Δp, $0 \leq \Delta p < 1$, in 21 equidistant intervals), and (iii) the survey effort (i.e. total number of sampling days, N_{SE}, $175 < N_{SE}$, divided in 6 intervals: 175–1500, 1500–2250, 2250–3000, 3000–4500, 4500–6750, > 6750 survey days). We excluded all simulations without any detections.

Given a presence/absence matrix, the three variables Δr, Δp, and N_{SE} can be calculated per interval length (dT). For each of these combinations of Δr, Δp, and N_{SE}, we select the corresponding accuracy from the simulation data. We can then evaluate which interval length will result in the most reliable predictions.

We tested our tool on the simulation data. For each combination of density-pair, number of sampling points, and study duration, we

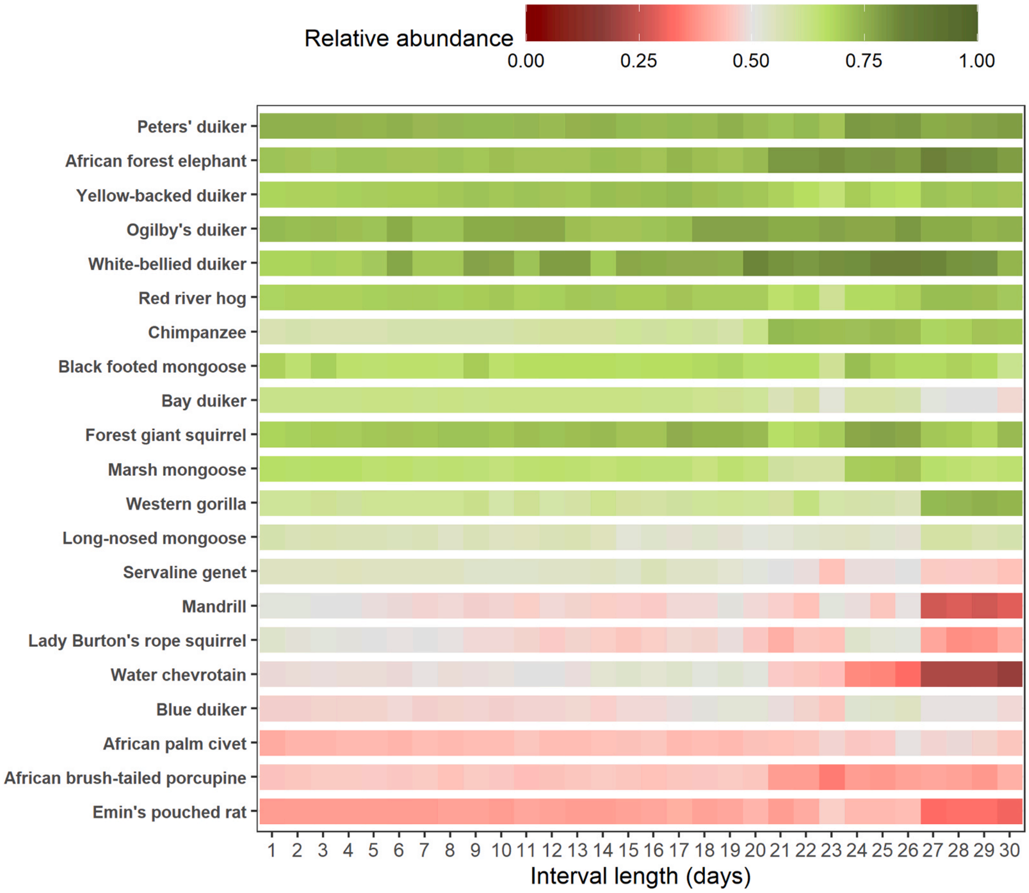

Fig. 1. Relative abundances per species and interval length in FSC compared to non-certified timber logging concessions. (red: higher abundances in non-certified than in FSC sites; green: higher abundances in FSC than in non-certified sites). Latin species names can be found in Table 1.

estimated the deviation in relative abundance for each dT ($0 \leq dT \leq 30$ days) and selected the interval length with the smallest estimated deviation. Subsequently, we used the actual difference between the simulated relative abundance and that estimated with the Royle-Nichols model using the selected dT's to calculate a Goodness of Fit value per total sampling effort (i.e. the number of sampling points · study duration) and study duration:

$$GoF = 1 - \frac{\sum\left(\theta_1 \Big/ (\theta_1 + \theta_2) \; - \; \lambda_1/(\lambda_1 - \lambda_2)\right)^2}{\sum\left(\lambda_1/(\lambda_1 + \lambda_1) \; - \; \overline{\lambda_1/(\lambda_1 + \lambda_1)}\right)^2}, \tag{1}$$

where Θ_1 and Θ_2 are the estimated abundances and λ_1 and λ_2 are the actual abundances at locations 1 and 2, respectively. We also tested the tool using simulation data with different combinations of movement tortuosity ($\kappa = 0$, 1, 5, and 10), densities (0.3, 0.5, 3.8, 4.8, 11.5, and 14.4 individuals km^{-2}), numbers of sampling points (25, 50, 75, and 100 sampling points), and study durations (30, 60, and 90 days).

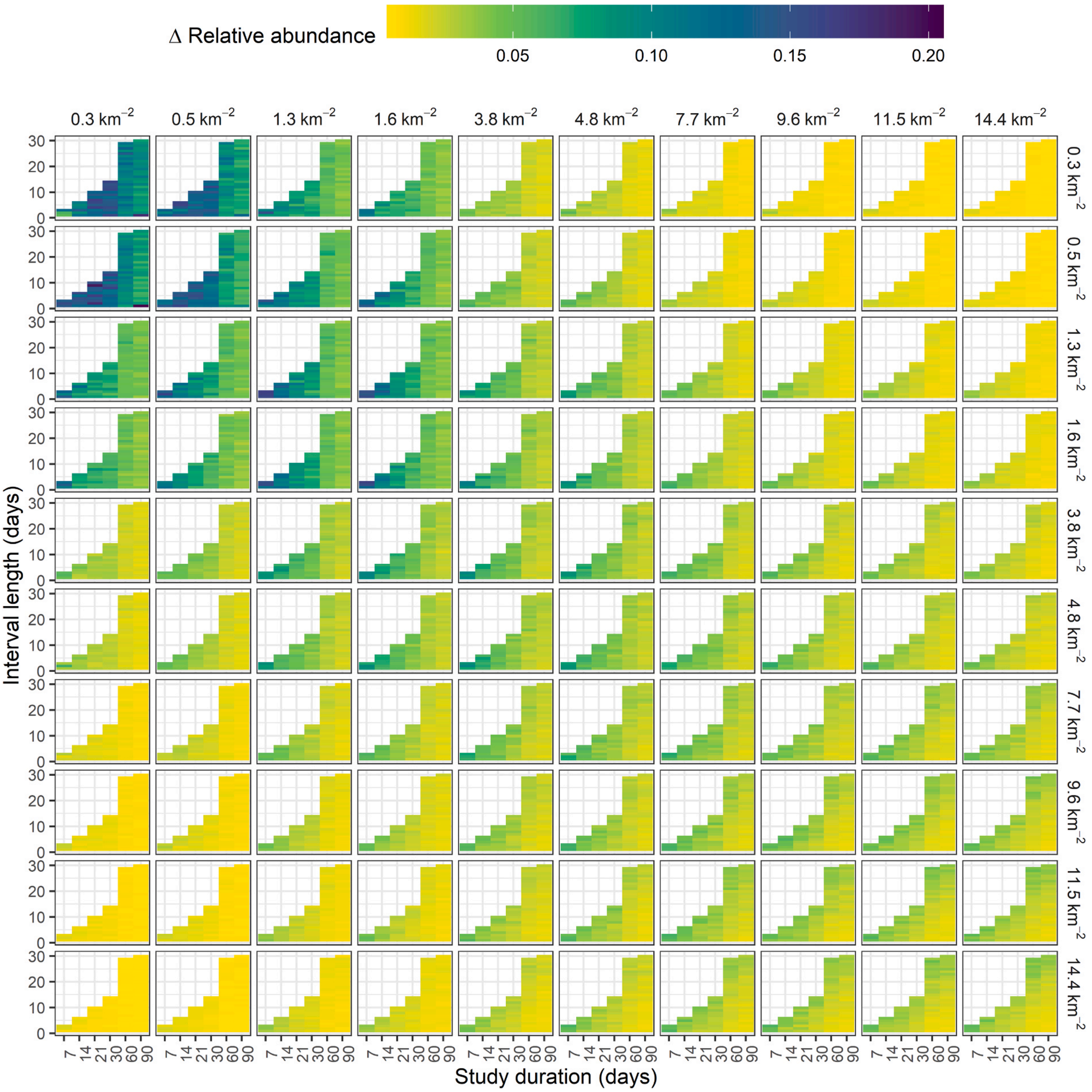

Fig. 2. Difference between actual relative abundance and that estimated with the Royle-Nichols model, per study duration (x-axis, in days), interval length (y-axis, in days), and combination of simulations with two different densities (rows and columns, individuals per km^2). In this figure, only results with 50 sampling points per simulation are shown. (See Fig. S3, S4, and S5 for results with 25, 75, and 100 sampling points, respectively).

We applied this accuracy estimation on the analyses performed on the data by Zwerts et al. (2024). Per species, we calculated N_{SE}, Δp, and Δr for all dT. Using the tool for estimating accuracy, we predicted how well the Royle-Nichols model should be able to provide correct results. The R-script to implement this selection of optimal interval length to other datasets is available at https://doi.org/10.5281/zenodo.10424188.

3. Results

3.1. Does interval length affect population comparisons?

As is common in camera-trapping studies, the sampling period per camera varied widely, ranging between just 1 and as many as 239 days per camera (due to Covid travel restrictions, some cameras have been deployed longer than three months). 447 camera traps had 7 or more recording days (average = 85 and SD = 49 recording days). Depending on the interval length, the total sampling effort thus differed greatly (Fig. S2).

Eleven of the examined species had a higher abundance in FSC- than in non-certified sites and two species were more abundant in non-certified than in FSC-certified sites, regardless of interval length. However, for 6 species, interval length qualitatively affected the abundance comparison between FSC- and non-certified sites (Fig. 1). These results demonstrate that the choice of interval length can indeed affect the outcome of comparisons using the Royle-Nichols occupancy model.

3.2. Does interval length affect the accuracy of the Royle-Nichols model?

The ability to detect correct relative abundances depended on the modeled densities, the study duration, the interval length, and the number of sampling points (i.e. camera traps; Fig. 2). Estimated relative abundances differed most from actual relative differences when densities were similar and low ($\lambda_1 = \lambda_2 = 0.3$ km^{-2}). Accuracy increased with study duration and with the number of sampling points (Fig. S3-S5). Accuracy was generally highest with intermediate sampling intervals. In case of low densities, small sampling

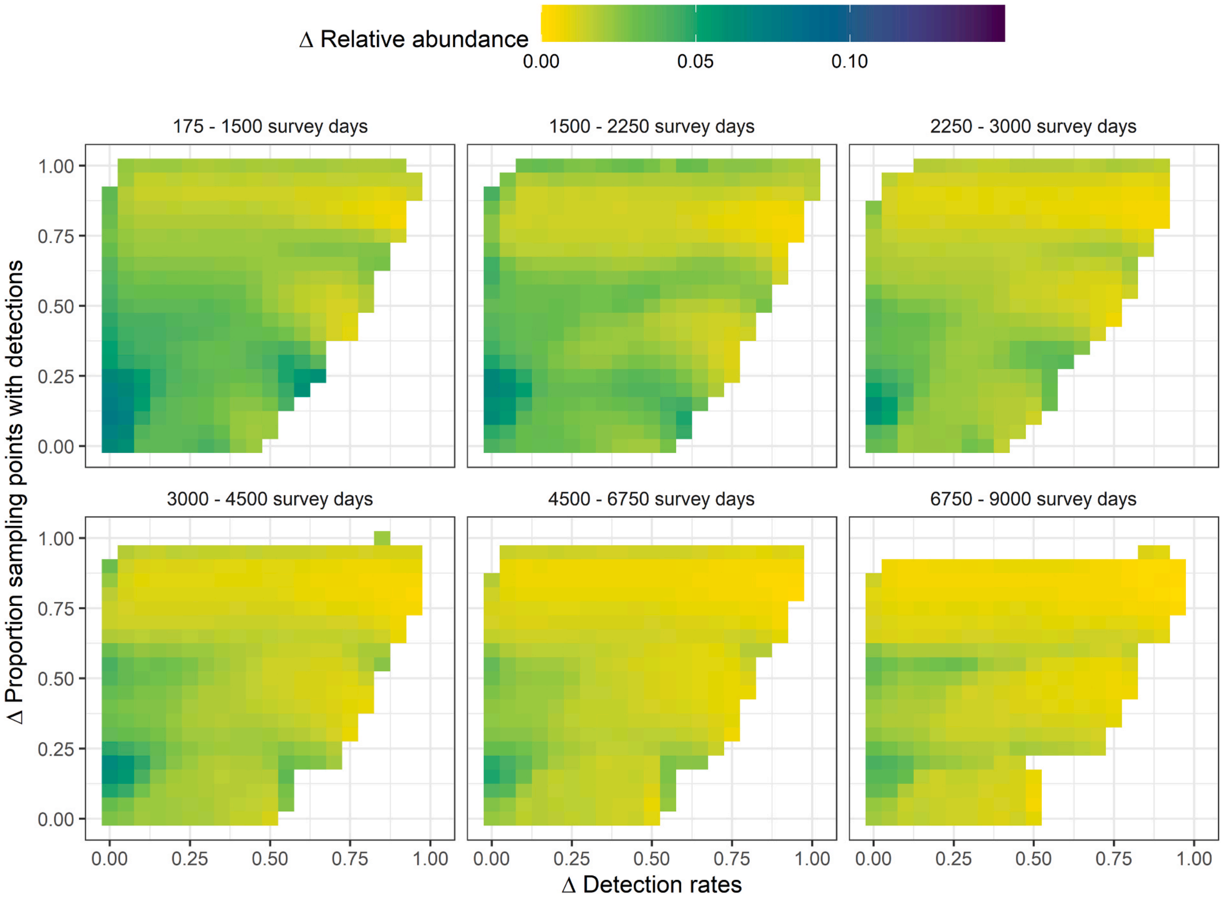

Fig. 3. Difference between the actual relative abundance and that estimated using the Royle-Nichols model per sampling effort (panels, in survey days), difference in detection rates (x-axes), and difference in the proportion of sampling points with detections (y-axes) between the compared simulations.

intervals result in zero inflation. Here, larger intervals provide higher accuracy. In contrast, in case of high densities, large sampling intervals result in the loss of absence data. Here, smaller sampling intervals provide higher accuracy.

Whereas actual densities are not available in empirical studies, emergent properties such as detection rates and proportions of cameras with detections can be easily derived from biomonitoring data. Variation in accuracy mainly depends on both differences in detection rates (Δr) and differences in the proportion of cameras with detections between locations (Δp; Fig. 3). In general, detection rate increases with density and interval length (Fig. 4). Interval length can only negatively affect detection rate when detections in the last, incomplete interval are omitted. For example, when the 1-day presence/absence vector of a sampling point is [0 1 1 0 0 0 0 0 0 1 1] and a 3-day interval length is used, the last two detections are omitted (becoming [1 0 0]). In this case, the detection rate decreases from $4/11 = 0.36$ when $dT = 1$–$1/3 = 0.33$ when $dT = 3$. Likewise, interval length can affect the proportion of sampling points (e.g. camera traps) with detections (p), if first detections by one or more sampling points are truncated. For example, in the case of [0 0 0 0 0 0 0 0 0 1 0], a detection is present at $dT = 1$, but not at $dT = 3$, as the last two days are omitted (as the vector becomes [0 0 0]). While the proportion of sampling points with detections increased with density and study duration (Fig. 4), study duration did not affect detection rate. Convergence of the Royle-Nichols occupancy model failed in 0.01 % of all cases, and only when both densities were low and $dT = 1$. In general, model convergence failed for long studies with many sampling points, showing that zero-inflation can be an issue in such analyses.

3.3. *Choosing the optimal interval length*

Comparing Royle-Nichols estimated relative abundance to actual relative abundance in simulations with $\kappa = 1$, goodness of fit ranged between 0.837 (7 day study with 25 cameras) and 0.995 (90 day study with 100 cameras; Fig. S6). Goodness of fit increased with total sampling effort. Tortuosity did not affect goodness of fit (Fig. S7).

We estimated accuracy of the Royle-Nichols models' results shown in Section 3.1. For some species, the deviation from the actual relative abundance varied greatly between different interval lengths (Table 1; Fig. 5; Fig. S8). The interval lengths at which the estimated deviation from actual relative abundance was minimized ranged between 1 and 29 days (Table 1). The estimated deviation corresponding to these interval lengths varied between 0.019 and 0.042 (with an average estimated deviation of 0.027). In contrast, the estimated deviation ranged between 0.023 and 0.049 (with an average of 0.036), when the standard interval length of one day was used.

When we used the species-specific interval lengths that minimized estimated deviation (Fig. 6), we found the following results. In seven species, FSC-certification positively affected abundance ($Z > 1.96$). These are all large species. Two of these species are critically endangered (African forest elephant and Western gorilla), one is endangered (Chimpanzee), and two are near-threatened (White-bailed duiker and Yellow-backed duiker), due to habitat destruction and bush meat hunting. In thirteen species (of which eleven least concern, one vulnerable (Mandrill), and one near threatened (Bay duiker) IUCN-status), FSC-certification had no significant effect. In one species (Emin's pouched rat), FSC-certification negatively affected abundance ($Z < -1.96$). Emin's pouched rats are easily tamed and are held as exotic pets. A comparison between these results to those produced with the arbitrarily chosen 1-day interval showed

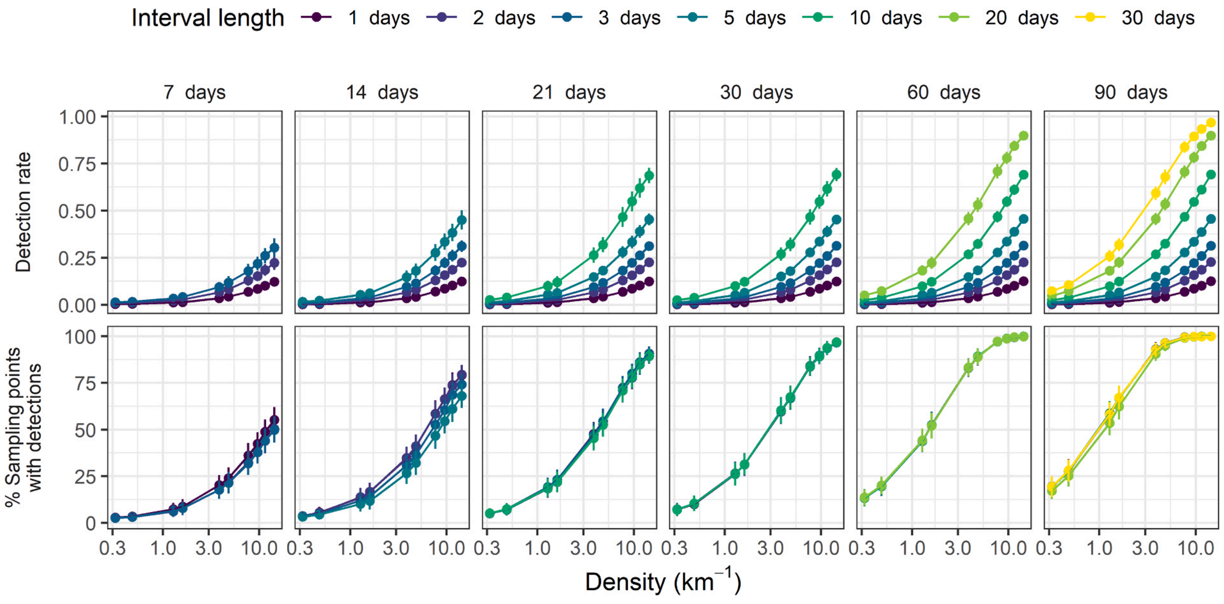

Fig. 4. Average detection rates (the average number of presence recordings in the presence/absence matrix; top panels) and percentages of sampling points (e.g. camera traps) with detections (bottom panels) per density (x-axes), study duration (columns), and interval length (colors). Bars indicate SD.

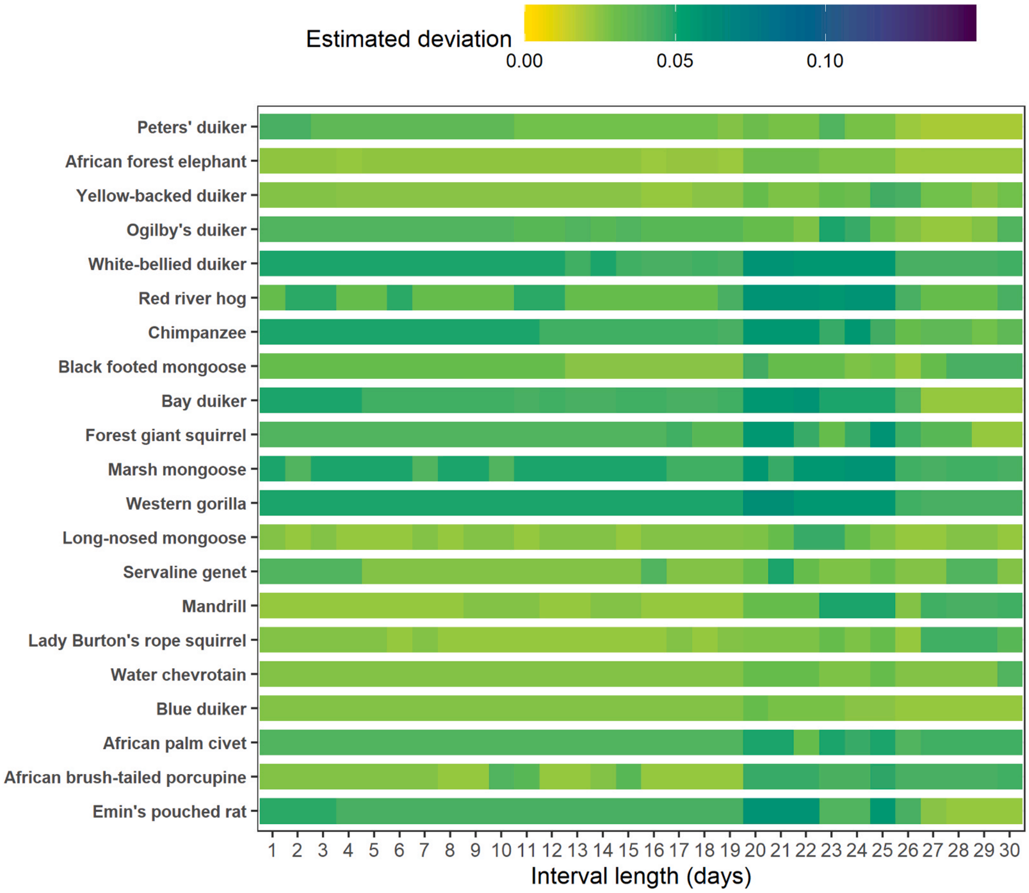

Fig. 5. Estimated deviation from the actual relative abundance per species and interval length. Latin species names can be found in Table 1.

that models with species-specific interval lengths resulted in more significant outcomes (Fig. 6). That is, for most species, the z-value estimated with the 'optimized Royle-Nichols model' was further from zero than those estimated using a 1-day interval. For example, with the 1-day interval, we observed no difference in chimpanzee and Western gorilla abundance between FSC- and non-certified logging concessions. Yet, with the optimized interval length, chimpanzee and Western gorilla abundances were significantly higher in FSC- than in non-certified logging concessions. With the 1-day interval, we found no significant effects for seventeen species and a significantly higher abundance in FSC-certified sites for four species, compared to non-certified sites. The model with species-specific, optimized sampling intervals thus yielded less conservative results.

4. Discussion

Choosing the length of sampling intervals is a necessary step in applying discrete models (such as the Royle-Nichols model) to continuous survey data, but guidelines on optimizing this choice had been lacking. Selecting short intervals (i.e., 1 day) may lead to zero inflation (Denes et al., 2015) and very low detection probabilities, which can be difficult to estimate, while selecting large intervals might result in the absence of zeros in the occupancy data, leading to the inability to detect differences in a species' abundance between areas. Series of detections combined with non-detections give more insight into the differences in abundances between sites, where sites with higher abundances of individuals have more detections and fewer non-detections over time compared to sites with lower numbers of individuals. Using sampling intervals that are too large will remove these differences in detections between sites. In addition, non-detections at sampling points with detections are needed in order to estimate the detection probability, which also gives insight in the probability that, at sampling points with non-detections only, individuals have been present but have not been recorded. Choosing the wrong interval length may result in an incorrect comparison between two locations, and can lead to erroneous management decisions.

Our study showed that the common choice to segment the study duration into as many sampling units as it contains days, to retain as much information as possible, is not always the best. Rather, the optimal interval length and number may differ between species within a study, and depends on rarity. Furthermore, we found that interval length can impact the outcome and accuracy of the Royle-Nichols model's results. Re-analysis of camera-trapping data from a field study (Zwerts et al., 2024) revealed that the choice of interval length can even affect the direction of relationships. Thus, interval length should not be standardized at a given value, but be carefully

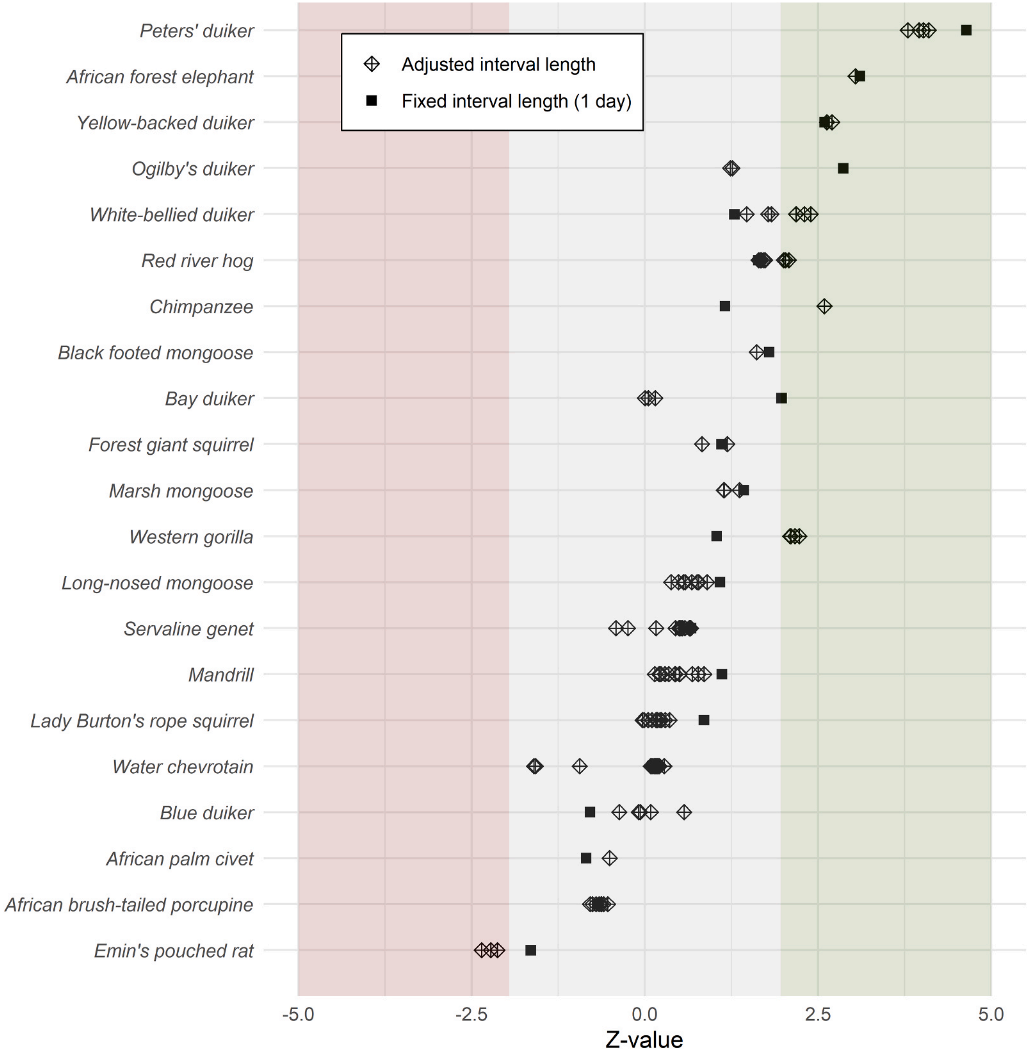

Fig. 6. *:* Comparison of species' abundances between concessions in the Republic of Congo and Gabon with and without FSC certification, for 21 mammalian species. Z-values, resulting from the Royle-Nichols abundance model using the adjusted interval length (i.e. the interval length that corresponds to the lowest estimated deviation given the data; diamonds) or the commonly used fixed interval length (1 day; squares), indicating whether a species is estimated to be more abundant in FSC-certified forests than in non-FSC concessions (green area, $Z > 1.96$), more abundant in non-FSC than in FSC-certified concessions (red area, $Z < -1.96$), or equally abundant in both FSC and non-FSC concessions (grey area, $-1.96 \leq Z \leq 1.96$).

chosen based on the properties of the data.

MacKenzie and Royle (2005) recommended surveying many sampling points for a short period when dealing with rare species. In contrast, they recommended surveying few sampling points for long periods when dealing with common species. In general, the Royle-Nichols model predicted relative abundances more reliably when studies were longer, average densities were higher, and differences in densities between areas were larger. In practice, however, study length and number of sampling points are constrained by the availability of equipment, labor, and battery power (Zwerts et al., 2021). We recommend an increase in the number of sampling points over an increase in study duration (Fig. S6). Other studies have also provided guidelines and tools to optimize this choice (e.g., Beaudrot et al., 2019; Kays et al., 2020; Zwerts et al., 2021). Study setups may not always be ideal, but may still provide reasonable results when their limitations are considered and sensible choices are made when analyzing the data.

Our study has several limitations. One limitation that is generic to the Royle-Nichols model is that it assumes demographic and geographic closure. To meet this assumption, we restricted the study duration in our simulations to a maximum of 90 days. A second limitation of our study is that we used simulated data, which generally do not reflect the complexity of animal movement. In most species, individuals constrain their movements to ranges much smaller than the survey area, which may lead to concentrations of detections at a subset of the sampling points, with some sampling points detecting many animals and others few or none. With increasingly skewed numbers of detections across sampling points, the need to replicate over space rather than time increases. Such constrained movements of individuals change the patterns that we found, but the need for interval length selection remains the same. Our results indeed show that, regardless of the turning behavior of individuals, the interval length selected with our tool provides a better fit than using the standard 1-day interval (Fig. S7). Third, a large disadvantage of models using count data (including presence-absence data, such as the Royle-Nichols model; MacKenzie et al., 2002; O'Connel et al., 2011; Steenweg et al., 2018) is that collected data is pooled into segments. Such pooling decreases the amount of information we can use from the collected data. Other methods that do not have this drawback are time-to-detection models (Guillera-Arroita et al., 2011; Henry et al., 2020; Emmet et al., 2021; Priyadarshani et al., 2022; Pautrel et al., 2024). Yet, these models require a larger number of parameters than models relying on count data, which can be problematic to estimate (Pautrel et al., 2024).

This study demonstrated that the choice of interval length plays a pivotal role in the accuracy of detecting abundance differences. It may have far-reaching implications for the assessment of conservation efforts, as there is no one-size-fits-all solution. In general, an interval length should be selected that maximizes the survey effort as well as the differences between areas in detection rates and proportion of sampling points with detections. The optimal interval length is inherently context-dependent, and may depend on many factors, such as the species' behavior, the spatial and temporal scales of the study, and the intricacies of the used modelling techniques. Hence, we advocate to carefully select interval length (for example, by using the tool that we provided) and to implement a well-designed sampling strategy.

Our study focused on how well the Royle-Nichols model can estimate relative differences in abundance between sites. We do not address estimation of absolute abundances, as these estimations vary to a very large extent and are far more unpredictable than relative abundance estimations (Fig. S9). We therefore do not recommend using the Royle-Nichols model, with or without our tool, to assess absolute abundances of species in a study region.

For the future, we suggest developing systematic frameworks for interval length choice. In such frameworks, interval length choice (or data segmentation in general) can be adapted across diverse ecological contexts. Developing these frameworks requires further research. For example, we need to further investigate how interval length selection interacts with different species and different environmental conditions. Future studies could also explore integrating advanced statistical techniques and machine learning algorithms to automate the selection process. An accurate assessment of species abundance can increase the effectiveness of conservation initiatives. Hence, the careful selection of interval length is a linchpin in the evaluation of such conservation initiatives.

CRediT authorship contribution statement

Monique de Jager: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Marijke van Kuijk:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Joeri A. Zwerts:** Writing – review & editing, Writing – original draft, Data curation. **Patrick A. Jansen:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Monique de Jager, Marijke van Kuijk, and Patrick A. Jansen, reports financial support was provided by the graduate school Production Ecology and Resource Conservation (PE&RC). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04065.

Data availability

The R-script is available at Zenodo (https://doi.org/10.5281/zenodo.10424188), as is the camera trapping data (https://zenodo.org/records/10061155).

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