Invasive species and anthropogenic habitat alteration are major drivers of biodiversity loss. When multiple invasive species occupy different trophic levels, removing an invasive predator might cause unexpected outcomes owing to complex interactions among native and non-native prey. Moreover, external factors such as habitat alteration and resource availability can affect such dynamics. We hypothesized that native and non-native prey respond differently to an invasive predator, habitat alteration and bottom-up effects. To test the hypothesis, we used Bayesian state-space modelling to analyse 8-year data on the spatio-temporal patterns of two endemic rat species and the non-native black rat in response to the continual removal of the invasive small Indian mongoose on Amami Island, Japan. Despite low reproductive potentials, the endemic rats recovered better after mongoose removal than did the black rat. The endemic species appeared to be vulnerable to predation by mongooses, whose eradication increased the abundances of the endemic rats, but not of the black rat. Habitat alteration increased the black rat’s carrying capacity, but decreased those of the endemic species. We propose that spatio-temporal monitoring data from eradication programmes will clarify the underlying ecological impacts of land-use change and invasive species, and will be useful for future habitat management.

1. Introduction

Invasive alien species and anthropogenic habitat alteration are the primary drivers of global biodiversity loss [1]. Invasive predators are the major cause of endemic prey extinction [2–5], and predicting the potential consequences of non-native predator species is essential to effectively mitigate their negative impacts. Furthermore, habitat alteration frequently occurs in combination with invasive species [6] and can change predator–prey systems in multiple ways [7], through direct effects on the predator and/or prey populations and by altering the intensity of predator–prey interactions [7]. Because the responses of a community with both native and invasive species depend on the intensities of these effects, each effect must be individually analysed to predict whether a particular management action will lead to the desired restoration outcome.

Ecosystems harbouring multiple alien species are now ubiquitous. Often, a non-native predator may interact with both non-native and native prey within an ecosystem [8]. In such a situation, predicting which type of prey will dominate following the removal of the non-native predator is crucial [8–11], because the response of the prey community to the predator removal is context-dependent [12–14]. Theoretical studies have indicated that eradicating...
non-native apex predators results in the outbreak of non-native prey and induces severe declines in native prey populations if the non-native prey are either superior competitors or are mesopredators of the native prey (termed the mesopredator release effect) [9]. Such an unwanted outcome occurs when top-down forces, rather than bottom-up forces, control the non-native prey populations [10,15]. Moreover, anthropogenic habitat alteration is likely to alter the relative advantage of native versus non-native competitors [16]. However, to the best of our knowledge, there have been no empirical studies demonstrating the outcome of predator eradication in such potentially context-dependent conditions.

Because invasive species abundance and anthropogenic habitat alteration often spatially correlate to one other, their effects on a population or community are difficult to distinguish. The eradication of invasive species in heterogeneous landscapes, however, could provide a unique opportunity to tease apart these factors at a large scale. In this study, we examined a predator–multiple-prey system consisting of an invasive predator undergoing eradication (the small Indian mongoose, *Herpestes auropunctatus*), a non-native prey species (the black rat, *Rattus rattus*), and two endemic prey species (the Amami spiny rat, *Tokudaia osimensis*, and the Ryukyu long-haired rat, *Diplothrix legata*) on Amami Island, southern Japan (figure 1).

The small Indian mongoose is an opportunistic predator [17] that poses a major threat to island endemics worldwide [18] and is ranked among the world’s 100 worst invasive species [19]. All three rat species are omnivores that depend on plant seeds and insects [20,21] and share the same guild on the island. The black rat is a highly noxious invasive species worldwide, whose impact is often associated with the decline or extinction of native rodents, flightless invertebrates, ground-dwelling reptiles, land birds and burrowing seabirds [22] caused by intraguild predation and/or competition. While there has been no evidence of intraguild predation and competition between native rats and the black rat, such interactions could threaten the conservation of native rats (figure 1). Endemic rat species on Amami Island have lower fecundity than black rats (see §2b), a trait that is generally adaptive in an island ecosystem with intense intraspecific competition [23]. The top-down forces imposed by mongooses on rat species [24] as well as other endemic species [25] appear to have been ameliorated by an island-scale eradication programme beginning in 2000.

The dominant tree species, *Castanopsis sieboldii* (Fagaceae), whose seeds are the major rat diet in winter [21,26], has a masting seed crop [27] that affects bottom-up regulation in the ecosystem [15]. The landscape of Amami Island has been altered by human activity, including urbanization, agriculture and forestry [28], and the spatial structure can be summarized by a simple gradient of habitat alteration (see §2b). These unique characteristics of Amami Island provide a good opportunity to understand landscape-scale trophic control on endemic and non-native prey species.

We collected data on the spatio-temporal patterns of relative abundance for the four species from 2002 to 2009 and estimated multiple factors, i.e. the top-down effects of the mongoose, anthropogenic habitat alteration and seed masting, that might affect the population growth rates of the endemic and non-native prey species.

We applied a Bayesian state-space model [29–31] to extract the relationship between the population growth rates and the various limiting factors on the three rat species, considering both process error and observation error. Process error is the stochastic fluctuation in population growth rate that cannot be explained by the deterministic relationship of the model. Observation error (measurement error) is that associated with the observation of the population [32]. We also evaluated the intraguild interactions (i.e. competition or intraguild predation) among the three rat species by assessing the lagged correlation between the process error at time $t$ and the relative abundance at time $t-1$. We tested the hypotheses that: (i) variation in the population growth rate among the three rat species can be explained by their different susceptibilities to predation, masting and anthropogenic habitat alteration; (ii) invasive predators, anthropogenic habitat alteration and their interactive effect suppress the endemic rat populations.
more than black rat populations; and (iii) bottom-up limitations are stronger on black rats than on endemic rat species.

2. Material and methods

(a) Study system

Amami Island (28°19' N, 129°22'E, 712 km²) is a subtropical island belonging to the Ryukyu Archipelago in southwesternmost Japan. The climate is warm and wet but seasonal. Annual mean temperature and annual precipitation are 21.6 °C and 2837.7 mm, respectively. The coldest and hottest months are January and July, respectively, with mean temperatures of 14.8 °C and 28.7 °C. The landscape of the island has been modified by human activities, such as forestry, agriculture and urbanization. Extensive clear-cut forestry for pulpwood production was conducted from the 1950s through the early 1990s [28], and most of the island's forests are secondary growth. Primary natural forest remains on only 3% of the island's area. There are over 60,000 residents on Amami Island, and sugar cane production is a major industry. Nine per cent of the island's vegetation has been converted to urban area and agricultural fields. The dominant non-agricultural vegetation is forest, and C. sieboldii is the dominant tree species in both natural and secondary forests. This tree produces a masting seed crop [27], and on Amami Island, consecutive island-scale lean crop (denoted 'LC' hereafter) years occurred in 2004 and 2005 [33].

The endemic Amami spiny rat (endemic to Amami Island) and Ryukyu long-haired rat (endemic to Amami Island and Ryukyu Island) have lower fecundity than the black rat. Litter sizes of the three species are 1–7, 2–5 and 2–10, respectively [21]. The breeding season of the Amami spiny rat is limited to October–December [21]. The Ryukyu long-haired rat is the largest native rat in Japan [21].

The small Indian mongoose was introduced in 1979, and it poses a significant predatory threat to the endemic vertebrates [24, 34]. Although the main diet of mongooses is insects and mammalian prey occupied only 20% of mongoose pellets on Amami Island [24], there is evidence that mongooses feed on rats. Abe [35] found that 24% of the stomach contents of mongooses was mammal tissue, most of which was black rat, probably because of its high abundance. The Amami spiny rat [36] and Ryukyu long-haired rat [37] were also found in mongoose stomach and in faecal contents.

With increasing social awareness of the ecological threats posed by the mongoose, the local government began a control project in 1993. The Ministry of the Environment of Japan has been operating the mongoose eradication project since 2000 [28]. Mongooses have been trapped, and the population has declined dramatically. Fukasawa et al. [38] estimated that the mongoose population in 2000 was 6141 individuals (95% credible interval, CI: 5415–6817). In 2011, that population had declined to 196 (95% CI: 42–408). By-catches of both native and alien rats occur incidentally, and these data were used to estimate the relative abundances of the rat species. Both live traps and kill traps have been used to eradicate the mongooses. However, we analysed data from live traps only, because the use of kill traps was prohibited within the range of the endemic rats to avoid lethal by-catch, and thus by-catches of native rats are actually uncommon (mean annual number of kill-trap by-catches of Amami spiny rat and Ryukyu long were 1.25 and 5.38, respectively). Whether native or non-native, all rats captured in live traps were released.

(b) Dataset

In this study, we analysed data from April 2002 through to March 2010. The mongoose eradication project has recorded trapping effort and the number of mongooses and rats captured, including the locations and dates of all traps. Trapping effort was defined as the number of traps multiplied by the number of nights of trapping per year (called trap-days or TDs, hereafter). Annual TDs of live traps differed among years, ranging from 55,864 to 175,991 TDs per year (see the electronic supplementary material, figure S3). The total numbers of by-catches of black rat, Amami spiny rat and Ryukyu long-haired rat from April 2002 through to March 2010 were 6056, 1320 and 177, respectively. We pooled the number of live-trap catches in a fiscal year (from April to March) in each geographical grid cell of 1°30’ latitude and 1’ longitude, for a total of 159 grid cells × 8 years.

Spatio-temporal patterns of trapping effort are shown in the electronic supplementary material, figure S3. The habitat alteration index (HAI) was derived from vegetation maps using an ordination technique. First, we calculated the area ratios of primary natural forest, secondary forest, farmland and urban area for each grid cell using ArcGIS v. 10.0 (ESRI Inc., Redlands, CA, USA). Next, we performed detrended correspondence analysis (DECORANA [39]) for the four landform ratios. Axis I of the detrended correspondence analysis explained well the gradient of land-use activity (from native forests to urban areas; see the electronic supplementary material, figure S1), which was defined by a HAI. In 2004 and 2005, island-scale scarcity of C. sieboldii nuts occurred on Amami Island [33]. To estimate the effects of LC years, we considered a binary explanatory variable, representing 2004 and 2005 as the value 1. Data are deposited in the Dryad repository at http://datadryad.org/resource/doi:10.5061/dryad.2hb12.

(c) Bayesian state-space models

Bayesian state-space models have been used to analyse non-Gaussian and nonlinear ecological processes from time-series data [31, 40–42]. State-space models can be divided into state processes and observation processes. State process, denoted as \( n_t \) (\( t = 0, 1, \ldots, T \)), is an unobservable vector that expresses stochastic evolution of ecological states (e.g. relative population density). When analysing population dynamics, a first-order Markov process, \( n_t | n_{t-1}, \psi \) is applied generally. The observation process, denoted as \( y_n \), is an observable vector that is related to \( n_t \) but fluctuates with observation error. These processes have uncertainties, which are described as a set of three probability distribution functions (pdfs): \( g_t(n_t | n_{t-1}, \eta) \) state process pdf, \( g_0(n_0 | \nu) \) initial state pdf and \( f_t(y_t | n_t, \phi) \) observation process pdf,

where \( \eta, \nu \) and \( \phi \) are vectors of model parameters. In this study, we applied Bayesian state-space models to obtain the smoothed relative abundance of mongooses as an index of top-down effects and to estimate dynamics of the rat species.

(d) Relative abundance of mongooses

We regarded the relative abundance of mongooses as an index of top-down forces. Catch per unit effort (CPUE, number of captured individuals per capture effort) obtained by trapping is a population index often used for small mammals and is related to relative abundance [43–45]. However, the assumption of a linear relationship between them is valid only when the probability of capture is low [46], because probability of capture will saturate with increasing capture effort when the capture probability is near 1. In addition, the population index includes observation error, especially where the trapping effort or relative abundance were low, which may obscure the actual top-down effect. To filter such observation errors and to estimate the relative density of mongooses throughout all grid cells from the capture and effort data, we applied a Bayesian state-space...
model (appendix A). We defined the posterior median of the mongoose’s relative abundance as the mongoose predatory index, denoted \( M_i[t] \).

(e) Modelling rat dynamics and observations

We incorporated the indices of top-down forces of the invasive predator (\( M \)), habitat alteration (HAI), their interaction (HAI \( \times M \)) and bottom-up forces (LC) on rat populations into a density-dependent stochastic population model and implemented it as a Bayesian state-space model to estimate the model parameters. As the state process, we applied the Gompertz population dynamics and observations. When

\[
\text{observation} = \text{relative abundance} \times \text{trapping effort}.
\]


As the state process, we applied the Gompertz population dynamics and observations. When

\[
\text{observation} = \text{relative abundance} \times \text{trapping effort}.
\]

\[
\text{conditional on the observed time-series data } y_{i,t-1}. \text{ Denoting the prior pdf of the model parameters as } \pi(\theta), \text{ the joint posterior pdf can be written as}
\]

\[
\pi(y_{i,t-1}, \theta | y_{i,t-1}) \propto \pi(\theta)\pi(y_{i,t-1} | \theta) \int_{\theta} g(\theta | n_0, \nu, \psi) \left\{ \sum_{t=1}^{T} g(n_{t-1} | \nu, \psi) \right\}. \]


Posterior samples were obtained by Gibbs sampling using WinBUGS v. 1.43 [51]. For all parameters of the three rat species, we used vague prior distributions to make inferences using only information from the data: \( N(0, 1000) \) for \( a, b \), and \( Uniform(0, 100) \) for \( a, \sigma_\text{tr}, a_\text{tr}, a_\text{t}, \text{ and } \sigma_\text{tr}. \) Note that setting 1.001 (not 1) as the upper bound of the uniform priors is a rule of thumb to avoid a numerical overflow of the WinBUGS posterior summaries were derived from three-chain Gibbs sampling for 1 000 000 iterations after discarding 1 000 000 samples as ‘burn-in’. The posterior summaries of all the parameters are shown in the electronic supplementary material, table S1 and the posterior densities are shown in the electronic supplementary material, figures S4–S6.

As a proxy of mongoose predation, we used the posterior median of mongoose relative abundance estimated by the state-space model. To evaluate the extra variation derived from uncertainty in estimated relative abundance, we iteratively estimated the rat models 50 times using randomly selected posterior samples of mongoose relative abundance, instead of the posterior median. The models with randomly selected posterior samples yielded results that were qualitatively consistent with those of the model with a posterior median (see the electronic supplementary material, figure S7). We concluded our result was robust to the uncertainty owing to using an estimate of mongoose relative abundance.

(g) Detecting intraguild interactions

To detect intraguild interactions among the rat species, we evaluated the posterior Pearson’s correlation coefficient between relative process error from year \( t - 1 \) to \( t \), \( \rho[I[t] + \alpha[I[t-1] + e[I[t-1], 1]] \) and the relative abundance of another species in year \( t - 1, n_{t-1} \). The correlation coefficient was calculated for each of the posterior samples. Although including interspecific interactions in the process model is desirable in a statistical sense, such modelling was not used here, because the posterior probability failed to converge.

3. Results

From 2002 to 2009, mongooses were removed from Amami Island, and the annual CPUE decreased from 14.8 to 0.32 (figure 2b). Temporal patterns of the CPUEs of native and non-native rats responded differently to the mongoose decline. While the CPUE of the endemic rat species increased exponentially, a similar increase was not found in the black rat. With low levels of anthropogenic habitat alteration, the CPUE of the two endemic rat species increased faster ...
Habitat alteration positively affected black rats, and the 95% CI fell above 0, whereas the effects on the two native rat species tended to be negative, and the 90% CIs fell below 0 (table 1 and the electronic supplementary material, table S1). The effects of masting and the interaction of the invasive predator and habitat alteration were not significant for any of the rat species.

Figure 3 shows the carrying capacity of the three rat species along the gradient of habitat alteration. The carrying capacity of the black rat increased with increasing anthropogenic habitat alteration, but inverse patterns were observed for the Amami spiny rat and the Ryukyu long-haired rat; their carrying capacities were higher in natural forests.

None of the pairwise correlations between the process error of a particular species and the precedent relative abundance of another species was significant (table 2). In particular, the correlation between the black rat and Amami spiny rat or Ryukyu long-haired rat was small, indicating no detectable effect of invasive black rats on native rat species.

4. Discussion

Although eradication of invasive predators occasionally results in an outbreak of another invasive species [8,9, 52–54], the occurrence of such an indirect effect is context-dependent [14,55]. In our case, populations of two endemic rat species rapidly increased with the decline of invasive mongooses, whereas that of the invasive black rat did not. A Bayesian state-space model clearly showed the different susceptibilities of the rat species to top-down forces and anthropogenic habitat alteration.

The reason that black rats did not break out in response to mongoose eradication seems simple; the predation impact of the mongoose on the black rat was much lower than on the native rats (table 1). This result is not surprising, as there are many cases in which the biological control of black rats by introduced mongooses has failed [56]. Although rodents are one of the major foods of mongooses, and are frequently found in mongoose stomachs in their invaded ranges [57,58], including on Amami island [35], the top-down pressure on the black rat population appeared to be trivial. This result might be owing to microhabitat segregation of the mongoose and black rat (ground-dwelling versus arboreal nesting) [59], and/or to some unknown adaptive behaviour against mongoose predation that has not been acquired by the endemic rats, which have not coexisted with mammalian predators on the islands until recently.

The extent to which the interactive effects of invasive species and habitat degradation threaten biodiversity in nature is an important issue in ecology and conservation biology [6,60,61]. Our analysis revealed that habitat alteration can decrease the carrying capacity of endemic rats and halt the recovery of endemics from suppression by an invasive predator (figure 3), but the interaction effect with predatory impact was not significant (table 1). This finding is consistent with those of previous studies focusing on the interaction effects of invasive species and habitat alteration [62,63]. Importantly, as habitat alteration intensified, the relative rank of the carrying capacity of the black rat increased (figure 3), probably because the black rat can eat agricultural crops and rubbish, which are abundant in human-dominated landscapes, whereas endemic rats are purely forest-dwellers. Thus, the natural
deviations. (Online version in colour.)

Figure 3. Posterior means of log-scale carrying capacity for the three rat species along the land-use gradient. Error bars indicate posterior standard deviations. (Online version in colour.)

Table 1. Posterior mean (95% credible interval, CI) of the population growth coefficients for the three rat species.

<table>
<thead>
<tr>
<th>variable</th>
<th>black rat</th>
<th>Amami spiny rat</th>
<th>Ryukyu long-haired rat</th>
</tr>
</thead>
<tbody>
<tr>
<td>invasive predator (mongoose)</td>
<td>0.0144 (−0.00403, 0.0303)</td>
<td>−0.401 (−0.732, −0.143)</td>
<td>−0.176 (−0.445, 0.0434)</td>
</tr>
<tr>
<td>anthropogenic habitat alteration</td>
<td>0.125 (0.0293, 0.244)</td>
<td>−0.242 (−0.562, 0.0129)</td>
<td>−0.471 (−1.03, 0.0467)</td>
</tr>
<tr>
<td>invasive predator × anthropogenic habitat alteration</td>
<td>0.00505 (−0.00349, 0.0134)</td>
<td>−0.0701 (−0.182, 0.0311)</td>
<td>0.0732 (−0.0404, 0.208)</td>
</tr>
<tr>
<td>bottom-up factor (lean crop year)</td>
<td>−0.199 (−2.48, 1.72)</td>
<td>1.19 (−1.01, 3.50)</td>
<td>−2.31 (−7.76, 3.39)</td>
</tr>
</tbody>
</table>

*a* Significant effect whose 95% CI does not overlap with zero.

*b* Marginal effect whose 90% CI does not overlap with zero.

Table 2. Posterior mean and 95% credible interval (CI) of Pearson’s correlation coefficient between process error and the precedent relative abundance.

<table>
<thead>
<tr>
<th></th>
<th>Amami spiny rat</th>
<th>Ryukyu long-haired rat</th>
<th>black rat</th>
</tr>
</thead>
<tbody>
<tr>
<td>process error</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amami spiny rat</td>
<td>0.154 (−0.324, 0.524)</td>
<td>0.143 (−0.238, 0.478)</td>
<td>−0.133 (−0.366, 0.109)</td>
</tr>
<tr>
<td>Ryukyu long-haired rat</td>
<td>0.247 (−0.108, 0.557)</td>
<td>0.303 (−0.207, 0.693)</td>
<td>0.00120 (−0.233, 0.232)</td>
</tr>
<tr>
<td>black rat</td>
<td>0.133 (−0.0399, 0.304)</td>
<td>0.125 (−0.161 − 0.398)</td>
<td>0.0415 (−0.183, 0.269)</td>
</tr>
</tbody>
</table>

Figure 3. Posterior means of log-scale carrying capacity for the three rat species along the land-use gradient. Error bars indicate posterior standard deviations. (Online version in colour.)

Our state-space modelling of rat species explicitly considered top-down and bottom-up effects, as well as anthropogenic habitat alteration and density dependence. However, we did not include diffusion processes of populations because of the failure of parameter convergence in Gibbs sampling. However, it seems reasonable to assume that diffusion from more favourable to less favourable sites is common, and this could reduce the difference in apparent population growth rates between sites with different environmental conditions. Thus, our model probably underestimated the environmental effects, and the qualitative conclusions are unlikely to change.

When attempting to eradicate invasive species, the monitoring of not only invasive species under eradication but also native and other non-native species is essential to evaluate ecosystem recovery [11]. We showed that it is possible to estimate from monitoring data the strength of interspecific interactions and extrinsic factors that may limit the dynamics of multiple species if the monitoring system is properly designed in space and time. This knowledge offers valuable insights into ecosystem management. In the case of Amami Island, we have shown clearly that to conserve the Amami spiny rat, not only is eradication of mongooses required, but also the protection of natural and secondary forests, and an outbreak of the invasive black rat is unlikely to occur. Beyond the current eradication attempt, the approach presented here will help decision-making in adaptive management of communities and ecosystems composed of complex interaction webs that include multiple alien and native species.

 forests remaining on Amami Island appear to be a core area for the restoration of the endemic rat species. Fortunately, these forests are located far from the release point of the mongoose, and the predatory impact of the invasive mongoose has been relatively low thus far [34]. If the central area of the top-down control by mongooses had overlapped with the natural forests, then the endemic rat species might have been more threatened. The spatial distributions of habitat alteration and invasive species, and their overlap, are important to predict how these drivers will impact native species.

We found little evidence for intraguild interactions (i.e. intraguild predation and competition) among rat species (table 2). This lack appeared to be an important factor that enabled the endemic rats to recover after the mongoose removal, with no apparent effects of the black rat. While many studies have examined the mesopredator release effects of invasive rats on seabird colonies [12], evidence for predation on insular rodents by invasive rats is quite limited [64]. The predatory impact of the black rat on Amami Island is also unlikely to be a major limiting factor on endemic rat populations. As for interspecific competition, many pre–post eradication surveys revealed a competitive impact of black rats on island-endemic small mammals [64,65], but we found no such evidence. Dietary segregation, spatial segregation [66] and temporal resource variation [67,68] may explain the lack of competitive interactions among rodent species.

When attempting to eradicate invasive species, the monitoring of not only invasive species under eradication but also native and other non-native species is essential to evaluate ecosystem recovery [11]. We showed that it is possible to estimate from monitoring data the strength of interspecific interactions and extrinsic factors that may limit the dynamics of multiple species if the monitoring system is properly designed in space and time. This knowledge offers valuable insights into ecosystem management. In the case of Amami Island, we have shown clearly that to conserve the Amami spiny rat, not only is eradication of mongooses required, but also the protection of natural and secondary forests, and an outbreak of the invasive black rat is unlikely to occur. Beyond the current eradication attempt, the approach presented here will help decision-making in adaptive management of communities and ecosystems composed of complex interaction webs that include multiple alien and native species.
Appendix A. Bayesian smoothing for the relative abundance of mongooses

To estimate the relative density of mongooses throughout all grid cells from the capture and effort data, we applied a Bayesian state-space model. Although the relative abundance of mongooses is thought to be determined by intrinsic growth rate, diffusion and removal by humans, we used a convenient approach that considered only a spatio-temporal autoregressive process with spatially structured process error [69].

The process model describes spatio-temporal change in the relative abundance of mongooses. Letting \( m[i, t] \) be the log-scale relative abundance of mongooses in year 1, 2, \( \dot{\ldots} \), \( T \) at site \( i = 1, 2, \dot{\ldots} , J \), we used a first-order autoregressive process as follows:

\[
m[i, t + 1] = m[i, t] + r + \mu_m[i] + \omega_m[i, t] + \epsilon_m[i, t],
\]

where \( r \) is the apparent mean log population growth rate, \( \mu_m[i] \) is the spatially structured process error, \( \omega_m[i, t] \) is the temporally structured process error and \( \epsilon_m[i, t] \) is the unstructured process error. The spatio-temporal structure of the process error allows us to accommodate the heterogeneous population dynamics mediated by intrinsic growth and removal. The spatial structure of \( \mu_m[i] \) was expressed by a Gaussian Markov random field [48, 49]:

\[
\mu_m[i] | \mu_m[\ldots] \sim N \left( \frac{\sum_{i \in \mathcal{N}[i]} \mu_m[i]}{|\mathcal{N}[i]|}, \frac{\sigma^2_{\mu}}{|\mathcal{N}[i]|}, \right)
\]

where \( \mu_m[i] \) is the overall mean of \( \mu_m[i] \) and \( \sigma_{\mu}^2 \) is spatial heterogeneity. For \( \mu_m[i] \), a Gaussian Markov random field with conditional variance \( \sigma_{\mu}^2 \) was used in the same manner as \( \mu_m[i] \).

The observation model describes the stochastic relationship between the number of mongooses captured \( C_{m[i, t]} \) and the relative abundance \( m[i, t] \). We assumed that the mean number of mongooses captured, \( \lambda_m[i, t] \), is proportional to mongoose relative abundance and to exponentiated trapping effort, with fluctuation owing to local environmental conditions. \( \lambda_m[i, t] \) can thus be described as follows:

\[
\lambda_m[i, t] = \exp(m[i, t])E[i, t]^\alpha \exp(\epsilon_m[i, t]),
\]

where \( E[i, t] \) is capture effort \((\times 1000)\), \( b_m \) is an exponent corresponding to the saturation of capture probability with increasing capture effort and \( \epsilon_m[i, t] \) is an overdispersion term owing to local environmental fluctuations expressed as a Gaussian distribution with mean 0 and variance \( \sigma_{\epsilon_m}^2 \). The observed number of captures was assumed to follow a Poisson distribution with mean \( \lambda_m[i, t] \).

Posterior samples were obtained by Gibbs sampling using the WinBUGS v. 1.43 [51]. Vague prior distributions were used for all the model parameters: \( N(0, 1000) \) for \( r \) and \( \mu_m \), \( \text{Uniform}(0, 1.001) \) for \( \sigma_{\omega_m} \) and \( \text{Uniform}(0, 100) \) for \( \sigma_{\epsilon_m} \), \( \text{Uniform}(0, \sigma_{\mu}) \) for \( \sigma_{\mu} \), \( \text{Uniform}(0, \sigma_{\omega_m}) \), \( \text{Uniform}(0, \sigma_{\epsilon_m}) \), and \( \text{Uniform}(0, \sigma_{\epsilon_m}) \). Note that setting 1.001 (not 1) as the upper bound of the uniform prior is a rule of thumb to avoid a numerical overflow of the WinBUGS. The posterior summaries were derived from three-chain Gibbs sampling for 100,000 iterations after discarding 100,000 samples as ‘burn-in’. We defined the posterior median of \( \exp(m[i, t]) \) as the mongoose predatory index, denoted \( M[i, t] \).

References


