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BIODIVERSITY RESEARCH

Land use drivers of species re-expansion: inferring colonization dynamics in Eurasian otters

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ABSTRACT

Aim Land use intensity has been recognized as one of the major determinants of native species declines. The re-expansion of species previously constrained by habitat degradation has been rarely investigated. Here, we use site occupancy models incorporating imperfect detection to identify the land use drivers of the re-expansion of the Eurasian otter (*Lutra lutra*).

Location Czech Republic.

Methods We applied multi-season occupancy models to otter presence–non-detection data collected in three national surveys (1992, 2000, 2006) at 552 sites (11.2 × 12 km grid cells). Model parameters included site occupancy, colonization and extinction probabilities, and detection probability at a sub-site level. We modelled changes in occupancy over time as a function of agricultural, urban and industrial land use and change in the extent of agricultural land use.

Results Under the best fitting model, occupancy was estimated to be 34.6% in 1992, 51.3% in 2000 and 83.7% in 2006. Detection probability was neither perfect nor constant. Occupancy probability in 1992 was negatively related to land use gradients. Colonization was more likely to occur where a reduction in agricultural land was larger. Variation in extinction and colonization rates along land use gradients resulted in increased occupancy in industrial and especially urban landscapes. Conversely, occupancy remained almost unchanged along agricultural gradients.

Main conclusions Dynamics of otter expansion were strongly associated with the two main patterns of the rapid environmental transition that has taken place in the Czech Republic since the early 1990s. Results show that a reduction in intensive agricultural land use led to an increase in otter distribution, providing evidence of the impact of agricultural land use on stream ecosystems. Moreover, otters recolonized urban and industrial landscapes, probably as a result of extensive reduction in water pollution from point sources. Our results suggest that active conservation of otter populations should focus on restoration of freshwater habitat at large scales, especially in agricultural landscapes.

Keywords

Detection probability, land use intensity, multi-season occupancy models, recolonization process, species distribution, stream habitat.

INTRODUCTION

Habitat loss, fragmentation and habitat degradation caused by human activities are considered one of the main threats to native species diversity. Landscape modification for agriculture and urbanization typically causes habitat loss and degradation for many species (e.g., Kerr & Deguise, 2004).

Several studies have investigated the determinants and spatial patterns of species decline (e.g., Fuller *et al.*, 1995; Channell & Lomolino, 2000; Rodriguez & Delibes, 2002; Skelly

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et al., 2003). Ecological drivers of spreading populations have recently been the focus of intensive research, mainly in the field of invasion biology (e.g., With, 2002; Bonter *et al.*, 2010; Kadoya & Washitani, 2010). Exotic invaders and generalist native species have been reported to benefit from urbanization processes and other human-induced environmental changes (e.g., McKinney, 2006; Chiron *et al.*, 2008; Strubbe & Matthysen, 2009). Conversely, the causal factors of the re-expansion of threatened species have been rarely assessed, although several species recoveries have been observed (Swenson *et al.*, 1998; Pacheco & McGregor, 2004; Davies *et al.*, 2005; Pascal *et al.*, 2005; Marcelli & Fusillo, 2009).

For some species historically harvested or persecuted by humans, the reasons for recent recovery of populations are clear. Most populations of large carnivores in North America and Europe have increased after the mid-1900s in response to legal protection and favourable management (Linnell *et al.*, 2001). However, recolonization processes are less obvious for species that have suffered as a result of habitat degradation rather than persecution and harvesting.

Two main hypotheses could be proposed for explaining large-scale recolonization processes in species sensitive to habitat degradation, both related to habitat improvement driven ultimately by socio-economic changes. First, species recover in response to a reduction in agricultural land use and the associated increase in native vegetation that results in decreased habitat fragmentation and degradation. Second, species recolonize human-dominated landscapes, because changes in human activities and specific practices result in an improved quality of habitat. Because changes in habitat quality can be difficult to detect and measure, this hypothesis could be evaluated indirectly by modelling temporal variation in a species response to gradients of land use intensity (e.g., proportion of urban land).

The Eurasian otter (*Lutra lutra*, L., 1758) is a semi-aquatic mammal species (Carnivora: Mustelidae), which has shown a recent re-expansion across most European countries (e.g., Marcelli & Fusillo, 2009; Clavero *et al.*, 2010), after a sharp contraction of range distribution from the 1950s to the 1980s. Considering the habitat specialization of the otter and its top position in the freshwater trophic web, it could be argued that human-induced habitat degradation was the main cause of decline in otter populations. Effects of bioaccumulative pollutants on individual otters from industrial, urban and agricultural activities have been suggested as the proximate causes of the negative trends in populations (e.g., Roos *et al.*, 2001). However, several forms of stream habitat degradation induced by land use intensity (Allan, 2004) could be linked to the decline in otter populations.

Despite extensive survey datasets that have become available over recent decades, few studies have focused on anthropogenic impacts on otter distribution at large scales (e.g. Barbosa *et al.*, 2001; Robitaille & Laurence, 2002; Marcelli & Fusillo, 2009; Clavero *et al.*, 2010). Previous studies overlooked the problem of false absences in otter presence–absence data, or failed to deal with it (but see Marcelli & Fusillo, 2009), reflecting a wider neglect of the issue of imperfect species detection in species distribution modelling (see review in Kéry, 2011). False absences may lead to biases in estimates of occupancy parameters and their relationships with landscape factors (MacKenzie *et al.*, 2006), resulting in misleading ecological inference. Moreover, until recently, anthropogenic effects on otter populations have been assessed with data collected at a single point in time. Despite the popularity of a static approach, robust inferences require estimates of occupancy dynamics and an explicit assessment of the effects of temporal variation in purported causal factors (MacKenzie *et al.*, 2006). Recently, otter data collected at different points in time have been used to investigate re-expansion dynamics in Italy (Marcelli & Fusillo, 2009) and Spain (Clavero *et al.*, 2010). However, these studies neither estimated changes in occupancy as a function of changes in the environment nor accounted for false absences. Temporal differences in false absence rates can severely bias inferences from diachronic datasets (MacKenzie *et al.*, 2006).

In the Czech Republic, otters in 1992 were restricted mainly in the southern portion of the country (Toman, 1992). Since the early 1990s, the otter has expanded north-eastward, as evidenced by the raw survey data. Currently, the species occupies most of its historical range (Poledník *et al.*, 2007). Here, we analyse presence–absence (detection and non-detection) data collected in three national surveys in an effort to draw formal inferences about this expansion by using models that explicitly account for dynamic processes (i.e., colonization and local extinction) and imperfect detection (MacKenzie *et al.*, 2006). We incorporated two essential components of colonization processes: (1) immigration to vacant sites from previously established populations and (2) establishment of populations at these sites. We aimed to evaluate the hypothesis that a reduction in intensive agricultural land use was a driver of the re-expansion process and to assess if the effects of agricultural, urban and industrial land use on otter occupancy have decreased over time.

METHODS

Detection data

Spatio-temporal detection–non-detection data for the otter in the Czech Republic were gathered from three national surveys performed in 1992, 1997–2001 and 2006 (Fig. 1). Surveys consisted of searching for signs of otters, mainly spraints (otter faeces) but also tracks, on emergent substrates at stream sections, mainly under bridges. At least two locations were surveyed sequentially in each 11.2 × 12 km cell of the national grid system (S-JTSK) during one survey period by expert and trained surveyors. Grid cells constituted primary sampling sites and were classified as occupied when the presence of otters was detected (through identification of signs) in at least one sampling location within the cell.

Most data in the second survey were collected in 2000. We discarded the data collected in 2001 to reduce the time span. Data from 1997 to 99 were retained because they represented occupied

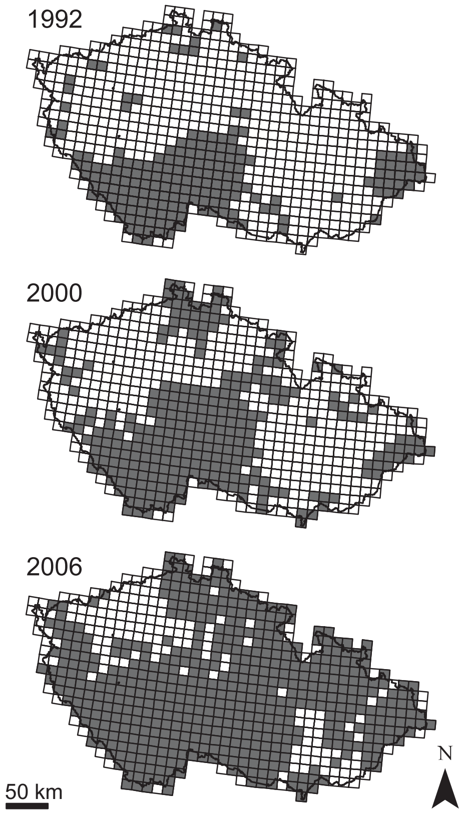

Figure 1 Observed expansion of the distribution of the Eurasian otter (*Lutra lutra*) from 1992 to 2006 in the Czech Republic. Data are from three surveys performed in 1992, 1997–2001 (data collected mostly in 2000) and 2006 across the entire country. The 11.2 × 12 km grid cells of the national grid system (S-JTSK) constituted primary survey sites. Grey cells are those with otters present, while white cells are those in which the species was not detected.

sites that have remained unchanged through recent times. Finally, we analysed 552 sampling sites, each surveyed at two to five locations in three time periods (henceforth 1992, 2000 and 2006), providing a total of 5777 survey locations (2.00, 3.63 and 4.82 locations/cell in 1992, 2000 and 2006, respectively).

Covariates used in models

We considered a set of landscape variables (Table 1) to evaluate model predictions of competing *a priori* hypotheses. We used the Corine Land Cover raster maps produced in 1990, 2000 and 2006 to quantify (1) the proportion of intensive agricultural land, (2) the proportion of urban land, (3) the proportion of total land occupied by industrial and commercial units, and mine and dump sites (henceforth 'industrial land') in the areas defined by the sampling sites and first-neighbours grid cells. In addition, we considered three variables that measured the difference in land proportion for each land use type between 1990 and 2000 and between 2000 and 2006 (Table 1). Overall, the raster datasets used were almost perfectly synchronous to the timing of the surveys.

Table 1 Codes and description of the variables considered for modelling occupancy dynamics of the Eurasian otter (*Lutra lutra*) in the Czech Republic

Variable code	Description
Agr	Proportion of intensive agricultural land in the area defined by a sampling site and first-neighbours (11.2 × 12 km grid cells) at year *t* (*t* = 1990, 2000, 2006)
Urb	Proportion of urban land in the area defined by a sampling site and first-neighbours (11.2 × 12 km grid cells) at year *t* (*t* = 1990, 2000, 2006)
Ind	Proportion of industrial land in the area defined by a sampling site and first-neighbours (11.2 × 12 km grid cells) at year *t* (*t* = 1990, 2000, 2006)
ΔAgr	Agricultural land use change ($\Delta\text{Ag} = \text{Agr}_t - \text{Agr}_{t+1}$)
ΔUrb	Urban land use change ($\Delta\text{Urb} = \text{Urb}_t - \text{Urb}_{t+1}$)
ΔInd	Industrial land use change ($\Delta\text{Ind} = \text{Ind}_t - \text{Ind}_{t+1}$)
LH	Proportion of lentic habitat in a sampling site
SOS	Sum of the stream order values in a sampling site
SOM	Mean of the stream order values in a sampling site
Con	Contagion variable (proportion of neighbouring otter detections around a sampling site)

We used the proportion of lentic habitat (i.e., lakes and fishponds) and two measures derived from a stream order classification (Strahler, 1957) to account for the density and quality of the aquatic habitat. A vector map 1:10,000 of lakes and ponds produced in 2004 (Masaryk Water Research Institute) was used to calculate the proportion of lentic habitat. The stream order variables were calculated by summarizing the mean and the sum of the stream order values of a raster map derived from a vector map 1:10,000 of the hydrographic network (Masaryk Water Research Institute). Habitat variables were calculated at the scale of the grid cell.

We summarized, for a given primary site, information about species occurrence in the surrounding space by means of a contagion variable (Augustin *et al.*, 1996). Specifically, we calculated the proportion of neighbouring otter detections around a sampling site by weighting the contribution of each survey location with their inverse Euclidean distance to the centroid of a sampling site. Detections at the focal site were not included in the contagion calculation. Because we did not account for detection uncertainty when calculating the contagion, this variable should be considered as only an index of otter presence at neighbouring points.

All variables were calculated using ArcGIS 9.3 (ESRI, Redlands, CA, USA).

Modelling approach and parameters

We used multi-season occupancy models (MacKenzie *et al.*, 2006) to model changes in site occupancy of otters between the survey periods. This approach allows the estimation of detection probability from probabilistic descriptions of sequences of detection–non-detection data (detection histories) collected over multiple assessments (i.e., temporal or spatial replicates) at each sampling site during a defined survey season. Under this modelling approach, changes in site occupancy may occur between survey seasons but occupancy is assumed static among multiple assessments within a survey season. Changes in site occupancy are modelled as a first-order Markovian process (i.e., occupancy at time $t + 1$ is dependent upon occupancy at time t) by explicitly accounting for the processes of colonization and local extinction. A maximum likelihood modelling procedure then relies on detection history data to estimate site occupancy, colonization, extinction and detection probabilities (MacKenzie *et al.*, 2003).

We summarized records of otter detection (1) and non-detection (0) collected at the survey locations within each site (grid cell) for each survey period (1992, 2000 and 2006) into detection histories (e.g. 001 101 111). Thus, we considered the spatially replicated surveys at each site as repeated assessments suited to the occupancy modelling framework. Models used in our analyses contain four specific parameters:

ψ_{i1992}, initial occupancy probability; the probability that a site (11.2×12 km cell) is occupied by the otters during the first survey period (1992).

γ_{it}, local colonization probability; the probability that an unoccupied site in the period t is occupied by the otters in the period $t + 1$.

ε_{it}, local extinction probability; the probability that an occupied site in the period t is unoccupied by the otters in the period $t + 1$.

p_{it}, detection probability; the probability that otter sign is found at a survey location of a site in the period t, given presence of otters at the site.

Model fitting and predictions

We evaluated *a priori* hypotheses about the processes of occupancy and colonization by modelling site-specific parameters as linear functions of site-specific covariates using the logistic link. We used the change in agricultural land use proportion as a predictor of site colonization. To account for decrease in the impact of land use on otter occupancy over time, we tested for the effects of the proportion of agriculture, urban and industrial land use on the occupancy probability in 1992, and on the colonization probability in 1992 (i.e., between 1992 and 2000) and in 2000 (i.e., between 2000 and 2006).

Model selection based on Akaike's information criterion (AIC; Burnham & Anderson, 2002) was performed to rank competing models in terms of their ability to describe the data. We used Akaike weights to assess the relative likelihood of each model fitting the data and the relative importance of anthropogenic and habitat factors. A model that summarized the data well, relative to the number of parameters in the model, had a small AIC and a high Akaike weight (Burnham & Anderson, 2002).

All models were run using the program PRESENCE 3.0 (Hines, 2010). Variables were z-transformed to standardize means and variances. Predictor variables used in analyses were not highly collinear ($r < 0.37$).

Detection probability

We built a single general model with variables most likely to explain probability of detection. We expected that density of otter sign would be higher in areas of high-quality habitat as a consequence of a higher population density. Therefore, we included stream order sum and the proportion of lentic habitat as predictors. Furthermore, we tested the prediction that persistence and detectability of signs were lower in large streams by adding the mean stream order as a covariate. We also specified a year effect and its interaction with habitat covariates.

Initial occupancy

We predicted occupancy probability in 1992 to be negatively related to the proportion of agricultural, urban and industrial land, as a result of local extinctions in landscapes dominated by human activities during the previous declining phase. Response to (natural) variation in habitat quality was accounted for by including the proportion of lentic habitat and the stream order sum in the models. We expected that otters were confined to landscapes with dense networks of aquatic habitats and high availability of potential food resources. We also expected that otter populations in areas with a high proportion of lentic habitat are more resilient to anthropogenic effects because of high food concentration in fishponds. This effect was tested by adding single interaction terms between each land use covariate and the lentic habitat variable.

Model selection for occupancy in 1992 was performed in a single-season model analysis (MacKenzie *et al.*, 2006) to limit the number of competing models in the multi-season analysis. We ranked single-season models obtained from all possible combinations of covariates for initial occupancy. Covariates for detection probability described above were included. Then, we parameterized initial occupancy in the multi-season models with the covariates selected in the single-season analysis.

Colonization and extinction

In all models, colonization was allowed to vary with year and the contagion variable (except one without contagion). We predicted colonization probability to increase with the number of potential immigrants in the surrounding space as indexed by the contagion variable. Raw data suggested that extinction rates would be low, especially between 2000 and 2006. Thus, we modelled extinction probability in 1992 (i.e., between 1992 and 2000) as a function of only the contagion variable and in 2000 (i.e. between 2000 and 2006) as a constant. We expected extinction probability to decrease with increase in contagion, because of the potential ‘rescue effect’ (Brown & Kodric-Brown, 1977) from neighbouring populations.

We developed competing models for describing the establishment process in terms of environmental suitability. We initially considered eight environmental covariates (land use and habitat factors) for colonization and extinction parameters. However, consideration of a model set containing all possible combination of eight covariates for both parameters would have been ill-advised (e.g., Burnham & Anderson, 2002). We thus focused on models containing single land use factors for colonization probability, and used model selection to identify important land use predictors of colonization *a priori*, which we considered to be the primary focus of our analysis. One group of models described the effects of gradients in land use intensity (i.e., proportion of urban, industrial and agricultural land) on colonization probability. We predicted negative relationships between land use proportion and colonization probability. The second group tested for land use changes as determinants of the re-expansion process. Because urban and industrial land proportion increased across the survey periods, while intensive agriculture decreased, we considered only change in agricultural extent as a determinant of site colonization. We predicted colonization events to be more frequent in landscapes where a decrease in cultivated area was larger. We tested for effects of habitat factors on colonization by adding the proportion of lentic habitat, the stream order sum and an interaction term between each land use factor and the proportion of lentic habitat to the land use models.

Using the hierarchical approach outlined above, our total model set included 25 multi-season *a priori* models.

A posteriori modelling

We also conducted *a posteriori* exploratory modelling by adding other land use covariates for colonization probability to the favoured single land use model(s) identified by the *a priori* AIC analysis (Buij *et al.*, 2007). Furthermore, we modelled effects of land use on the extinction probability to develop a full mechanistic description of temporal changes in occupancy along each land use gradient.

Rate of change in occupancy along land use gradients

To examine the recolonization of human-dominated landscapes and to identify how the effects of land use on otter occupancy decreased over time, we plotted the rate of change in occupancy (λ_t) as a function of land use proportion for each transition time (1992–2000 and 2000–06). Occupancy in 2000 and 2006 was estimated from the occupancy estimated in 1992 using a formula from MacKenzie *et al.* (2006):

$$\psi_{t+1} = \psi_t\,(1 - \varepsilon_t\,) + (1 - \psi_t\,)\,\gamma_t$$

Then the rate of change in occupancy from years t to $t + 1$ to describe increase or decrease in occupancy:

$$\lambda_t = \psi_{t+1}\,(\,\psi_t\,)^{-1}$$

The rate of increase in λ_t with land use proportion indicates to what extent the effect of land use on otter occupancy decreased over time.

Model suitability

We used the approach described by MacKenzie & Bailey (2004) to test the fit of the single-season models for initial occupancy. We compared the Pearson χ^2 of the best model with the distribution of χ^2 values based on 1000 parametric bootstrapping replicates and estimated the overdispersion parameter $\hat{c}$.

No procedures currently exist to estimate $\hat{c}$ for multi-season occupancy models. Thus, we assessed the multi-season model selected to summarize the data, by subtracting the observed proportion of grid sites where the presence of otters was detected from that predicted by the model (Watson *et al.*, 2008). We obtained the predicted proportion from

$$\psi\,p^*$$

where

$$p^* = 1 - (1 - p\,)^{\mathrm{k}}$$

is the probability of detecting the presence of otters at least once among k surveys within the sampling site.

RESULTS

Model selection for initial occupancy

Parametric bootstrapping did not indicate any evidence of lack of fit of single-season models for initial occupancy ($\chi^2 = 0.751$, P-value = 0.481, $\hat{c} = 0.648$). The best fitting model included additive effects of all potential predictors and an interactive effect between the proportion of the lentic habitat and the urban land use. The Akaike weight for this model was 0.975, indicating a very low degree of uncertainty and similar importance of natural and anthropogenic factors (see Appendix S1 in Supporting Information). According to *a priori* predictions, otter occupancy probability decreased with each increasing agricultural, urban and industrial land proportion, and increased with the amount of lentic and stream habitat. The coefficient of interaction between urban land use and lentic habitat was positive; thus, as the amount of lentic habitat increased, the effect of urban land use on occupancy decreased (Fig. 2).

Model selection for colonization

The four top multi-season models ($\Sigma w_i = 0.97$) all included the level of change in agricultural land as a predictor of colonization probability (Table 2). The mean proportion of agricultural land declined from 46.4% in 1992 to 38.7% in 2006. As predicted, colonization was more likely to occur in areas where the reduction in intensive agriculture was larger, in both transition periods (Fig. 3). Agricultural land proportion appeared to be more important than urban and industrial land in terms of AIC (Table 2). Under the Model 8, beta estimates for agricultural proportion were −0.46 (95% CI: −0.74, −0.17) in 1992 and −0.41 (95% CI: −0.70, −0.13) in 2000. However, there was no evidence within this model set that land use proportions were supported as shown by the AIC weights of zero (Table 2). Models received null or negligible additional support in terms of AIC when habitat factors were accounted for (Table 2).

A posteriori models for colonization and extinction

Four *a posteriori* multi-season models were considered following the original analysis. Change in agriculture proportion was the most important determinant of site colonization based on single land use *a priori* models. We explored the possibility that after this effect was accounted for, urban and industrial land use prove to be important. Agricultural land proportion was not included as a predictor because it was correlated to its change in time (ΔAgr). Then, we added single land use covariates for the extinction probability in 1992. According to AIC, these more complex models were more supported by the data (Table 3).

The model that incorporated the urban proportion as a covariate for extinction probability received the highest support and was the best model of the entire set. This model summarized the data reasonably well. Deviations between predicted and observed proportion of sites where otters were detected were 0.02, 0.028 and 0.058 across the three surveys. Estimates of slope parameters for initial occupancy, colonization and extinction probability under this model are shown in Table 4. Colonization probability tended to decrease as a function of both urban and industrial land. Overall, effects of urban and industrial land uses on colonization probability in 1992 and 2000 were smaller than on occupancy probability in 1992 (Table 4). Confidence intervals largely bounded zero for the effect of urban land proportion on colonization in 2000. In contrast, a negative effect of industrial land proportion on colonization was evident in 2000 (CI 95% exclude 0), but not in 1992. Extinction probability in 1992 increased as a function of urban land use. Contagion effects were evident for both colonization and extinction parameters, and coefficient signs were as expected (Table 4).

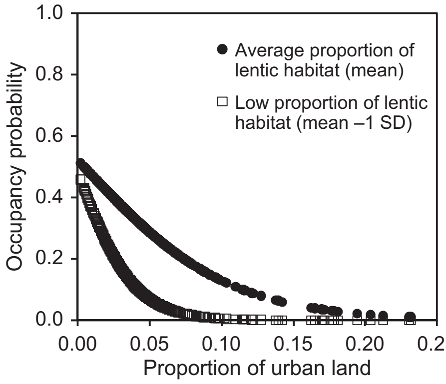

Figure 2 Predicted probability of site occupancy by the Eurasian otter (*Lutra lutra*) as a function of interaction between the proportion of urban land and the proportion of lentic habitat in the Czech Republic in 1992.

The lower-ranked models (Models 4 and 5 in Table 3) did not evidence effects of agricultural land use variables on local extinction (CI 95% included 0). However, there was some support for the effect of the industrial land on extinction probability in the model ranked second ($\hat{\beta} = 0.94$; 95% $\mathrm{CI}: 0.21,\ 1.67$). Under the best multi-season model, mean estimates of colonization rates were 0.46 in 1992 and 0.75 in 2000; extinction rate decreased from about 0.38 to 0.08. As a result, occupancy increased considerably in 2006 (Table 5).

According to estimated rates of occupancy change, otter occupancy increased on sites located in highly industrialized landscapes between 1992 and 2000. A large expansion in urbanized areas occurred in the second transition period (2000–06). Conversely, the rate of change in occupancy remained relatively constant along the agricultural gradient (Fig. 4).

Estimates of detection probability

Estimates from the best multi-season model indicated that otter detectability was not constant among survey locations. Detection probability tended to be inversely related to the stream order mean, but this effect was pronounced only in the first survey. Probability of detection was higher on sites with a higher proportion of lentic habitat in the second and third surveys. We found no evidence for the effect of the stream order sum (Table 4).

Yearly p estimates differed among years, with the highest value in 1992 (Table 5). However, actual otter detection at the level of a grid site is given by $[1-(1-p_i)^n]$, where n is the number of survey locations within a grid site. So the probability of detection at the level of a primary sampling site ranged from 0.88 ± 0.015 (SE) for $n = 2$, to 1 ± 0 (SE) for $n = 5$. Consequently, average occupancy probabilities (Table 5) were only slightly higher than the proportion of sites including at least one otter detection (i.e., naïve estimates of occupancy).

DISCUSSION

Heterogeneity in detection probability

By applying multi-season occupancy modelling, we accounted for variation in detection probability, while addressing hypotheses about expansion of Eurasian otters in the Czech Republic. The probability of otter detection was high (0.65–0.81), and on average, a minimum number of about three survey points were required to be 95% certain the species was

Table 2 Model selection results for the colonization (γ) and extinction (ε) probabilities of the Eurasian otter (*Lutra lutra*) in the Czech Republic (1992, 2000 and 2006). Presentation of parameterizations of initial occupancy (ψ_{1992}) and detection (p) probabilities was omitted, being kept constant among models in the forms ψ_{1992} (Agr + Urb × LH + Ind + SOS), p(Y + LH + SOS + SOM). All models for γ and p included interaction terms between year (Y) and covariates. Given are the relative difference in AIC values compared to the top ranked model (ΔAIC), the AIC weights (w), the −2 log-likelihood values (−2LL) and the number of parameters (np)

No.	Model	ΔAIC	*w*	−2LL	np
1	γ(Y + Con + ΔAgr), ε(Y + Con)	0	0.482	4893.44	28
2	γ(Y + Con + ΔAgr + SOS), ε(Y + Con)	0.69	0.341	4890.13	30
3	γ(Y + Con + ΔAgr + LH), ε(Y + Con)	3.49	0.084	4892.93	30
4	γ(Y + Con + ΔAgr + LH + SOS), ε(Y + Con)	3.84	0.071	4889.28	32
5	γ(Y + Con + ΔAgr × LH), ε(Y + Con)	7.49	0.011	4892.93	32
6	γ(Y + Con + ΔAgr × LH + SOS), ε(Y + Con)	7.84	0.001	4889.28	34
7	γ(Y + Con + Agr + SOS), ε(Y + Con)	30.8	0.000	4920.24	30
8	γ(Y + Con + Agr), ε(Y + Con)	31.54	0.000	4924.98	28
9	γ(Y + Con + Ind + SOS), ε(Y + Con)	32.6	0.000	4922.04	30
10	γ(Y + Con + Ind), ε(Y + Con)	33.26	0.000	4926.70	28
11	γ(Y + Con + Ind × LH + SOS), ε(Y + Con)	33.62	0.000	4915.06	34
12	γ(Y + Con + Ind × LH), ε(Y + Con)	33.83	0.000	4919.27	32
13	γ(Y + Con + Agr × LH + SOS), ε(Y + Con)	34.35	0.000	4915.79	34
14	γ(Y + Con + Urb), ε(Y + Con)	34.88	0.000	4928.32	28
15	γ(Y + Con + Urb × LH), ε(Y + Con)	35.32	0.000	4920.76	32
16	γ(Y + Con + Agr × LH), ε(Y + Con)	35.36	0.000	4920.80	32
17	γ(Y + Con + Agr + LH), ε(Y + Con)	35.4	0.000	4924.84	30
18	γ(Y + Con + Urb + SOS), ε(Y + Con)	35.52	0.000	4924.96	30
19	γ(Y + Con + Ind + LH), ε(Y + Con)	35.98	0.000	4925.42	30
20	γ(Y + Con + Ind + LH + SOS), ε(Y + Con)	36.03	0.000	4921.47	32
21	γ(Y + Con + Urb × LH + SOS), ε(Y + Con)	37.13	0.000	4918.57	34
22	γ(Y + Con + Urb + LH), ε(Y + Con)	38.83	0.000	4928.27	30
23	γ(Y + Con + Urb + LH + SOS), ε(Y + Con)	39.45	0.000	4924.89	32
24	γ(Y + Con), ε(Y + Con)	46.67	0.000	4937.41	26
25	γ(Y), ε(Y + Con)	114.31	0.000	4944.11	24

AIC, Akaike's information criterion.

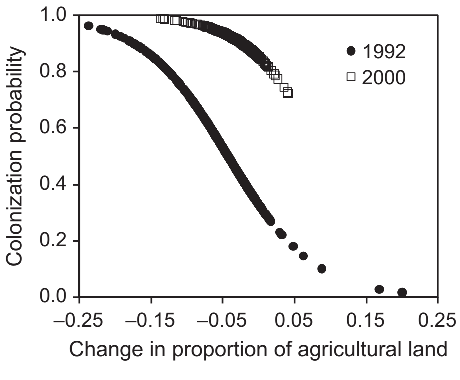

Figure 3 Predicted probability of site colonization by the Eurasian otter (*Lutra lutra*) in 2000 and 2006 as a function of the difference in proportion of agricultural land between 1990 and 2000 and between 2000 and 2006 in the Czech Republic.

absent. However, even low levels of false absences may bias the results of conventional habitat models, especially when the same variables explain the spatial variation of both occupancy and detection rates (Gu & Swihart, 2004). This situation occurred in our study for the lentic habitat variable and emphasized the importance of accounting for detection probability.

Spatial variation in local density of otters could explain the main patterns of heterogeneity in detection probability we observed. The lower detection rates in the second and third survey may reflect lower density of otters in recently recolonized areas. Moreover, it could be argued that density of otters, and thus detectability, increased with lentic habitat density because of the trophic importance of fishponds for otters in terms of fish accessibility and concentration (Kranz & Toman, 2000). Other factors could explain the decrease in detection rates with the stream order. Survey sites along large streams may be difficult to explore, and may be more exposed to climatic and hydraulic agents, which can facilitate the decay or washing of spraints.

Factors affecting otter sign detection during surveys at small spatial or temporal scales have been recently explored with occupancy models (Fusillo *et al.*, 2007; Jeffress *et al.*, 2011). However, ignoring non-detection issues for otters was prevalent up to recent times. To our knowledge, our study is the first attempt to account for detection probability of otters

Table 3 AIC analysis of *a posteriori* models for the colonization (γ) and extinction (ε) probabilities of the Eurasian otter (*Lutra lutra*) in the Czech Republic (1992, 2000 and 2006). Models were developed by adding other land use factors to the best *a priori* model (Model 6). Given are the relative difference in AIC values compared to the top ranked model (ΔAIC), the AIC weights (*w*), the −2 log-likelihood values (−2LL) and the number of parameters (np)

No.	Model	ΔAIC	*w*	−2LL	np
1	γ(Y + Con + ΔAgr + Urb + Ind), ε(Y + Con + Urb)	0.00	0.926	4861.99	33
2	γ(Y + Con + ΔAgr + Urb + Ind), ε(Y + Con + Ind)	5.41	0.062	4867.40	33
3	γ(Y + Con + ΔAgr + Urb + Ind), ε(Y + Con)	10.06	0.001	4874.05	32
4	γ(Y + Con + ΔAgr + Urb + Ind), ε(Y + Con + ΔAgr)	10.93	0.000	4872.92	33
5	γ(Y + Con + ΔAgr + Urb + Ind), ε(Y + Con + Agr)	11.96	0.000	4873.95	33
6	γ(Y + Con + ΔAgr), ε(Y + Con)	21.45	0.000	4893.44	28

AIC, Akaike's information criterion.

Table 4 Beta estimates and 95% confidence intervals (CI) from the AIC best-ranked model of occupancy (ψ), colonization (γ), extinction (ε) and detection (*p*) probabilities of the Eurasian otter (*Lutra lutra*) in the Czech Republic (1992, 2000 and 2006)

Parameter	Variable	*β*	SE	95% CI lower	95% CI upper
ψ_{1992}	Intercept	−0.82	0.136	−1.08	−0.55
	Agr	−0.69	0.130	−0.94	−0.43
	Urb	−0.64	0.201	−1.04	−0.25
	Ind	−0.69	0.236	−1.15	−0.22
	LH	1.54	0.281	0.99	2.09
	SOS	0.57	0.158	0.26	0.88
	Urb × LH	0.99	0.304	0.40	1.59
γ_{1992}	Intercept	−0.07	0.232	−0.52	0.39
	Con	1.85	0.446	1.15	2.56
	ΔAgr	−0.70	0.358	−0.96	−0.44
	Urb	−0.35	0.624	−0.70	0.01
	Ind	−0.12	0.133	−0.40	0.16
γ_{2000}	Intercept	2.50	0.321	1.62	3.37
	Con	2.89	0.182	1.66	4.11
	ΔAgr	−0.81	0.192	−1.44	−0.18
	Urb	0.25	0.143	−0.13	0.62
	Ind	−0.62	0.265	−1.13	−0.12
ε_{1992}	Intercept	−1.05	0.299	−1.64	−0.46
	Con	−1.53	0.361	−2.14	−0.92
	Urb	1.02	0.311	0.40	1.63
ε_{2000}	Intercept	−2.93	0.313	−3.63	−2.22
p_{1992}	Intercept	1.65	0.186	1.29	2.02
	LH	0.00	0.084	−0.20	0.19
	SOS	−0.03	0.051	−0.55	0.49
	SOM	−0.93	0.099	−1.49	−0.37
p_{2000}	Intercept	0.65	0.103	0.48	0.81
	LH	0.37	0.054	0.16	0.57
	SOS	0.20	0.264	−0.13	0.53
	SOM	−0.22	0.169	−0.56	0.13
p_{2006}	Intercept	0.75	0.085	0.64	0.85
	LH	0.14	0.283	0.03	0.25
	SOS	−0.03	0.176	−0.19	0.14
	SOM	−0.11	0.084	−0.27	0.06

AIC, Akaike's information criterion.

Table 5 Year-specific estimates (mean) and standard errors of occupancy (ψ), colonization (γ), extinction (ε) and detection (*p*) probabilities under the AIC best-ranked model of occupancy dynamics of the Eurasian otter (*Lutra lutra*) in the Czech Republic. Naïve estimates of occupancy (proportion of sampling sites including at least one otter detection) are given in for comparison. Data are from three surveys (1992, 2000 and 2006) performed at 552 11.2 × 12 km grid cells

Parameter	Mean	Standard error	Naïve occupancy
ψ_{1992}	0.3465	0.0453	0.3134
ψ_{2000}	0.5127	0.0510	0.4656
ψ_{2006}	0.8370	0.0398	0.7699
γ_{1992}	0.4582	0.0485	
γ_{2000}	0.7500	0.0388	
ε_{1992}	0.3845	0.0692	
ε_{2000}	0.0803	0.0270	
p_{1992}	0.8073	0.0376	
p_{2000}	0.6503	0.0347	
p_{2006}	0.6771	0.0196	

AIC, Akaike's information criterion.

over large temporal and spatial extents using dynamic occupancy modelling.

Land use and habitat correlates of otter persistence

The occupancy pattern of 1992 may be considered the turning point of a steady decline in the Czech otter populations protracted over some decades since the 1950s (Hájková *et al.*, 2007), a time when the species was still widespread. Our model selection analysis showed that the residual distribution was strongly associated with landscapes with a lower extent of agricultural, urban and industrial land. These results suggest that multiple anthropogenic impacts on freshwater habitats drove local extinctions of otter populations in the Czech Republic. Numerous studies document statistical associations between land use metrics similar to those used in this work and indicators of stream ecological integrity. Urban and agricultural land uses and human activity at the landscape scale impact habitat and water quality of freshwater ecosystems via numerous and complex pathways (Allan, 2004). Significant changes in biological assemblages are associated with developed land, including decreased density and diversity of fishes (Allan, 2004), the basis of otter nutrition.

Dramatic environmental changes underlie the strong relationships we found between otter site occupancy in 1992 and land use metrics. By the 1950s and 1960s, industrial development in the Czech Republic shifted greatly towards a heavy and energy-producing industry under inefficient technologies, leading to an enormous increase in the exploitation of natural resources (Bičík *et al.*, 2001). At the same time, urbanization increased and agriculture was marked by a huge period of intensification; pesticides and fertilizers were intensively used until the end of the 1980s (Young *et al.*, 2004). Biodiversity of freshwaters was significantly reduced by high acidification and eutrophication (Petřík *et al.*, 2007).

Our analysis showed that persistence of otters was not only linked to a gradient of habitat degradation from low to high land use intensity. According to *a priori* predictions, otter occupancy probability increased with both increasing amount of stream habitat (weighted for stream order) and increasing proportion of lentic habitat. These findings suggest the importance of food availability and landscape connectivity for otter persistence when human pressure on habitat is high. The importance of lentic habitat for otters in the Czech Republic is straightforward. A high fraction of lentic ecosystems in the Czech Republic include fishponds managed for commercial fish production. Because of high resource availability, fishponds are profitable habitats for otters and support high population densities (Kranz & Toman, 2000). The interactive effect of urban land use and lentic density further underscores the importance of fishpond areas for persistence of otter populations when human pressure is high.

Re-expansion process: mechanisms and context

Occupancy of 11.2 × 12 km grid cells by otters increased from 34.6% in 1992 to 51.3% in 2000 and to 83.7% in 2006. The mechanisms of this expansion were very different between the two transition periods. The level of turnover in occupancy was relatively high between 1992 and 2000, with extinction and colonization rates of 0.38 and 0.46, respectively. Between 2000 and 2006, the extinction rate was very low and the colonization rate increased to 0.75.

Local extinctions were more frequent in highly urbanized and industrialized landscapes from 1992 to 2000. At the same time, colonization was lower in highly urbanized areas, but it was weakly negatively related to industrial land. As a consequence, occupancy of otters along the urban gradient remained relatively unchanged in 2000 with respect to 1992. On the contrary, the net balance of extinction and colonization resulted in an increase in occupancy in the highly industrialized areas. However, between 2000 and 2006, colonization of industrialized areas greatly slowed down, but a large colonization of urbanized landscapes occurred. Overall, these dynamics reflect a reduction over time of the impacts generated by the urban and industrial areas on otter populations. This reduction in anthropogenic effects on otters has likely been mediated by a reduction in pollutant loads and recovery of water quality in freshwater systems. By the 1990s, the political and economic changes in the context of the post-socialist transition induced a general improvement in environmental conditions of the Czech regions (Langhammer, 2010). Improvement in surface water quality was the result of the decrease and changes in industrial production and the intensification of wastewater treatment plants (Petřík *et al.*, 2007). Improved policies and technological advances led to a significant drop in sulphur emission levels from lignite-burning power plants, which led to recovery of surface waters (Křeček & Hořická, 2001). However, acidification in many sites has not been significantly improved, particularly in the northwest region of the Czech Republic (Petřík *et al.*, 2007). This severely impacted area remains unoccupied by otters, and largely contributed to the highest values of industrial land measured at vacant sites in 2000. This situation may explain the strong negative relationship between colonization and industrial land predicted by our models between 2000 and 2006.

Overall, effects of agricultural land use on otter populations were persistent and higher than those of urban and industrial origin. After a small increase in agriculture dominated

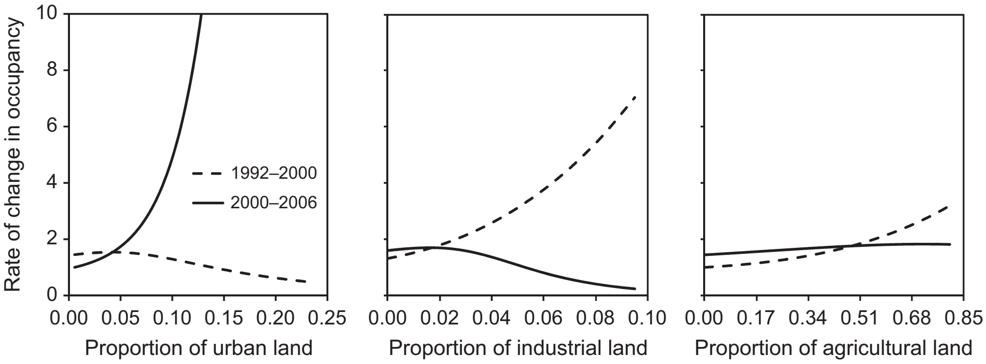

Figure 4 Estimated rates of change in probability of site occupancy by the Eurasian otter (*Lutra lutra*) between 1992 and 2000 and between 2000 and 2006 along gradients of urban, industrial and agricultural land use in the Czech Republic.

landscapes from 1992 to 2000, the rate of change in occupancy remained relatively constant along the agricultural gradient, providing evidence that otters were less able to recolonize highly agricultural landscapes. These patterns resemble trends of agrochemical use (Petřík *et al.*, 2007) and nitrate concentration in stream water (Langhammer, 2010), suggesting again that water pollution could have influenced the establishment of otters.

Similar to the Czech pattern, re-expanding otters in Italy were able to recolonize urbanized landscapes rather than intensive agricultural landscapes (Marcelli & Fusillo, 2009). It could be argued that the degradation of physical habitat in urban streams tends to be more localized than the degradation induced by agricultural land use (Allan, 2004). As a consequence, the control and treatment of point source pollution in urbanized areas could be sufficient to allow recovery of freshwater ecosystems and recolonization by otters. In contrast, the recovery of physical habitat and control of diffuse pollution in streams draining highly agricultural landscapes may be more difficult because require fundamental changes in agricultural activity and management practices (e.g., Myers *et al.*, 1985).

Substantial landscape changes occurred in the Czech Republic in the period 1990–2000. The main landscape change process was unanimously the transition of intensive agriculture to grasslands, due mainly to land abandonment (e.g., Bičík & Jeleček, 2009; Václavík & Rogan, 2009). This process continued throughout the 2000s. Given the relatively persistent impacts of agriculture on freshwater habitats in the Czech Republic (Langhammer, 2010), it is not surprising that local colonization by otters was spatially associated with local reduction in cultivated land. This mechanistic description of the colonization process highlights the beneficial effects of the transition of agricultural land to native vegetation on stream ecosystems and otter populations. Beyond the recovery of water condition in streams, reduction in cultivated land could have favoured otter colonization by allowing the recovery of structure and width of riparian vegetation corridors. Riparian cover is important for otter ecology, because it provides habitat for resting and protection from human threats (Kruuk, 2006).

Contagion effects clearly showed that the re-expansion process was also shaped by spatial factors, as a result of immigration from neighbouring populations.

CONCLUSION

Measures of temporal changes in agricultural land cover and dynamic occupancy modelling enabled us to strengthen the large body of exploratory evidence of the negative impact of agricultural land use on stream biota. Previous studies have largely relied on static descriptions of spatial variation in landscapes, mainly to model responses in macroinvertebrate and fish assemblages (see review in Allan, 2004). Similar analyses have been used to test negative effects of agricultural land use on otter occurrence (Marcelli & Fusillo, 2009; Clavero *et al.*, 2010) at large spatial scales. However, the impact of intensive agriculture on otter populations has not been fully recognized.

We showed that the dynamics of otter expansion in the Czech Republic were strongly associated with the two main patterns of the rapid environmental transition that has taken place in the country since the early 1990s. The re-expansion was directly related to reduction in intensively cultivated land. Moreover, otters appear to have responded to the reduction in water pollution from point sources by recolonizing urbanized and industrialized landscapes.

Our results suggest that active conservation of otter populations should focus on restoration and protection of aquatic and riparian habitat at large scales. Beyond the control of point source pollution of urban and industrial origin, the restoration and management of riparian buffers aimed at improving water quality (e.g., Haycock & Muscuttb, 1995) and stream habitat in highly agricultural landscapes are valuable options for conservation of otter populations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Table of model selection results for the occupancy probability of the Eurasian otter in 1992.

BIOSKETCH

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