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# Modelling the spatial dynamics of a recovering species: the Grey Heron *Ardea cinerea* in France

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In many countries, the implementation of measures to protect declining species has led to the recolonization of some areas by bird species within their historic range. There is, however, a lack of quantitative tools for exploring and projecting such large-scale dynamics. Here, we present an approach that makes use of both census and habitat suitability data and integrates them into a spatially explicit model of colonization dynamics (cellular automaton). The Grey Heron *Ardea cinerea*, which has recently recolonized much of France following legal protection measures, was used as a focal species. Data analysis allowed us to quantify the positive effects of habitat quality on the probability of colonization, and to uncover both positive and negative density-dependent colony settlement processes. Projective simulations then allowed us to determine an inflection point in global colonization dynamics and predict a significant reduction in the colonization rate during the next 50 years. This makes it possible to project the spatial distribution of the species at different timescales, and to estimate the carrying capacity of France for the species (around 1500 colonies).

Keywords: cellular automaton, colonization dynamics, CORMAS, habitat suitability, species distribution.

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In response to biodiversity loss, legal measures have been developed and enforced in several countries with the objective of reducing or reversing the negative effects of human activities on the dynamics of particular species. These measures have led to the re-colonization by some bird species to areas within their historic ranges (e.g. Yeatman-Berthelot & Jarry 1995). Although projective modelling methods are extensively used in conservation biology (Beissinger & McCullough 2002), there is a lack of quantitative tools for projecting the trends of large-scale species recovery. In particular, the dynamics of declining species or populations are generally assessed by considering the effects of extrinsic (e.g. temporal environmental variation) or intrinsic (e.g. genetic deterioration, demographic stochasticity) sources of variation of demographic rates, without explicit representation

of spatial heterogeneity. Although local ecological conditions play a key role in determining the presence or absence of a species in a given area, there is growing evidence that many ecological communities are not saturated and that their species richness is constrained more by the availability of potential colonists than by local ecological processes (Foster 2001). The colonization of a new breeding area by a species will depend on various factors, including the availability and proximity of dispersing individuals, the dispersal ability of the species and the extent to which establishment and subsequent reproduction is successful (Sakai et al. 2001). Limiting factors at any step can effectively preclude the species from (re)colonizing an area. Thus, understanding (re)colonization dynamics requires investigating the factors related to both the speed and the range of colonization at a large spatial scale. This requires not only examining species characteristics (e.g. growth, dispersal), but also the pattern of spatial heterogeneity of the landscape. Whereas the amount of suitable habitat is an important predictor of a species' abundance in a particular region, the spatial arrangement of the habitat (e.g. randomly distributed or aggregated) is another crucial determinant of colonization dynamics that is often ignored.

Modelling is a widely used tool in conservation management. Over the past two decades, researchers have developed a set of techniques designed to examine management problems (such as reserve design or species reintroduction strategies) using simulation models. On the basis of a set of specified ecological, demographic and environmental parameters, models can integrate

biological and non-biological processes and average stochastic population / community / ecosystem trajectories to produce quantitative estimates that may be related to abundance, distribution or persistence (Beissinger & McCullough 2002, Morris & Doak 2002). Of the approaches used to model single species dynamics, most are based on a very fine description of species demography, as exemplified by matrix population models (Caswell 2001) or individual-based models (Judson 1994), which generally consider populations structured according to age, sex or other functional characteristics. These models require very precise demographic data to simulate population dynamics and they are generally spatially implicit, even when considering large-scale, fragmented populations (Casagrandi & Gatto 1999). Among these approaches, various methods nevertheless allow an explicit representation of space. Individual-based models, for example, allow the characteristics of each individual to be tracked through time (including its location within a grid cell). Here, we choose to use cellular automata to model the recolonization dynamics of the Grey Heron *Ardea cinerea*. In cellular automata, the dynamics of ecological entities are considered through a spatial grid in which step rules are defined at the scale of each single spatial cell according to its state and the state of neighbouring cells (Rhode 2005). Here, because the colonization dynamics are described at the scale of the colony (each colony being defined according to its geographical location and not by the individuals that compose it), a simulation based on a uniform dissection of the space (as in cellular automata) was more convenient to use than a simulation based on individuals distributed within the space (as in individual-based models).

The Grey Heron, which has recently undergone a rapid recovery in France following the introduction of legal protection measures, was used as a focal species to study the dynamics of recolonization. Breeding colonies of the Grey Heron (ranging from 1 to 1000 breeding pairs; Marion 1997) are generally located near shallow water and the size of the foraging area can reach 40 km around the colony (Marion 1989). The European breeding population of the Grey Heron has shown a moderate increase since the early 20th century (<5% per year; EBCC 2009), and a large part of this increase is explained by the strong increase of the French population (Marion et al. 2000). Owing to hunting and habitat destruction pressures, the French population was

pushed to the brink of extinction during the 19th century. In 1974, the species became protected, resulting in a rapid increase in the number of colonies from 29 in 1962 to 653 in 1994 (Marion 1997). This dramatic recovery has several ecological and socio-economic consequences. Because of its piscivorous habits, the species is regarded as a pest by aquacultural interests in several countries (Hughes et al. 1999). Thus, it is important to identify areas where the species is likely to reach high density and hence interfere with human activities. This requires that the speed and pattern of colony spread be quantified at a large spatial scale.

To examine the pattern of species recovery in relation to environmental quality, we combined colony counts with a habitat suitability index, allowing us to obtain quantitative insights into the joint effects of habitat properties and local colony density on the probability of new colony settlement in a particular area at a fine spatial scale. A stochastic cellular automaton model integrating these data allowed us to make qualitative and quantitative inferences on: (i) the speed of recolonization; (ii) the expected spatial distribution of colonies in 80 years; and (iii) an estimation of the maximum number of colonies at a regional / national scale.

## METHODS

### Species census and habitat suitability data

Colony counts have been conducted at irregular intervals since 1962 (censuses were conducted in 1962 in Brittany only, and from 1974 to 2000 over the whole French territory, see Table 1). These census data suggest that the Grey Heron is re-establishing itself over most of its historical range. Although the censuses were designed to be as exhaustive as possible (census occurred between May and July; Marion 1997), data on both number of colonies and colony size are considered minimum estimates as: (i) some colonies may have been missed by observers and (ii) non-synchronous breeding in the Grey Heron may not allow total colony size to be estimated with a single count. These errors are not expected to affect our results greatly, as missing colonies may lead to an underestimation of the number of colonies but do not bias colony trend (Marchant et al. 2004).

In addition to census data, previous studies allowed a habitat suitability index (hereafter called HS) to be developed for the species at the scale of the French territory (Boisteanu 2006). This integrated index has been

computed by Ecological Niche Factor Analysis (ENFA) (Hirzel et al. 2002) and describes, for each  $10 \cdot 10 \text{ km}^2$ , the potential for a breeding colony to occur in that square. ENFA is a statistical approach based on ecological niche theory (Hutchinson 1957), which is used to define the eco-geographical variables that characterize the presence of a species. This method does not use information from sites where the species is absent, in contrast to other methods (e.g. Generalized Linear Models), which need both presence and absence data. The use of presence-absence data may lead to false negative effects of the characteristics of areas where the species is absent, especially in species that do not use all suitable habitats. ENFA is therefore considered to be the most appropriate method with which to study expanding species (Hirzel et al. 2001). Studies of colonial nesting herons have shown that a breeding site must offer suitable materials to build the nest, be accessible to feeding areas within the foraging range, and provide protection against predators (Fasola & Alieri 1992, Hafner 2000). Here, we used an index covering the whole French territory, based on variables characterizing the foraging habitat of the species only (most variables were related to the presence or proximity of freshwater). In each grid square, the HS value depended on the distances between the centre of the square and the coast, the closest river, as well as on the lengths of ditches, estuaries and rivers (classified as permanent, non-permanent, natural,  $> 50 \text{ m}$  wide,  $10\text{--}50 \text{ m}$  wide,  $< 10 \text{ m}$  wide) within three buffers (1, 5 and 10 km around the centre of the square). All data used to compute HS were collected in 1994. The computation of HS through ENFA was validated using the Boyce index (Boyce et al. 2002, Boisteanu 2006, Hirzel et al. 2006). More details on the HS computation and source data are available in IGN (1996), Boisteanu and Marion (2006) and Boisteanu (2006).

### Data analysis

Our aim was to determine the joint effects of local habitat properties and local colony density on the probability of new colony settlement in a particular area. We used a  $100 \cdot 100$  grid to represent the French territory. Each cell corresponded to a  $10 \text{ km} \cdot 10 \text{ km}^2$  ( $10 \text{ km}$  corresponds approximately to the mean minimum distance between colonies in France in 1994; Marion 1994).

To address the problem of irregular intervals between colony censuses, 4-year time steps were used to describe the dynamics of colony settlement. Two 4-year intervals were available in our dataset (interval between the 1981 and 1985 censuses and between the 1985 and 1989 censuses). The number of observed new colony establishments within the 4-year intervals in each cell

Table 1. Numbers of colonies and breeding pairs of Grey Herons counted in France between 1974 and 2000.

Year	No. of colonies	No. of pairs	Reference
1974	72	3383	Marion (1991)
1981	189	10 092	Marion (1991)
1985	301	13 458	Marion (1991)
1989	460	20 027	Marion (1991)
1994	653	26 343	Marion (1991)
2000	872	c. 35 000	L. Marion unpubl. data

the hollow square of cells immediately surrounding the focus cell (eight cells),  $C_2$  refers to the number of colonies in the hollow square separated by one cell from the focus cell (16 cells), etc. The year  $t$  (1981 or 1985) was added as a qualitative control variable.

We used generalized linear models (GLM, McCullagh & Nelder 1989) to investigate statistical relationships between NewC and explanatory variables. The variance of NewC was assumed to follow a Poisson in the GLM. The best models were selected by starting from a full model with all explanatory variables described above (including second-order density variables  $C_x^2$ ). Several starting models were considered, by pooling or not pooling the empty squares located at different distances from the focus cell, for the  $C_x$  and  $P_x$  variables (40 different starting models). Then, for each starting model, variables were sequentially removed according to the Akaike information criterion (AIC, Akaike 1987).

(NewC) was used as a dependent variable in statistical analyses. Two types of explanatory variables were used in the analysis to explain the number of new colonies between time  $t$  and  $t + 4$ . First, habitat variables describing the habitat suitability of a

central cell ( $HS_0$ ) and the mean suitability of its eight neighbouring cells ( $HS_1$ ) were computed for each cell, and assumed to be constant through time. The second type of variable described the number of colonies ( $C_x$ ) and the total number of breeding pairs ( $P_x$ ) in the focus cell and its eight neighbouring cells at time  $t$ . The subscript  $x$  denotes the distance to the central cell ( $x$  varies from 0 to 10). For instance,  $C_0$  refers to the number of colonies already present at time  $t$  in the focus cell,  $C_1$  refers to the number of colonies in

As a complement to the GLM approach, we performed a hierarchical partitioning analysis (MacNally 2000). This method uses all models in a regression hierarchy to distinguish those variables that have high independent correlations with the dependent variable. It was run using 10 explanatory variables:  $HS_0$ ,  $HS_1$ ,  $C_0$ ,  $C_{1-5}$ ,  $C_{6-10}$ ,  $P_0$ ,  $P_{1-5}$ ,  $P_{6-10}$ ,  $(HS_0 \cdot C_{0-5})$  and  $(HS_0 \cdot P_{0-5})$ . The last two variables allowed the effect of the interaction between HS and numbers (and sizes) of close colonies on colony settlement probability to be examined. Hierarchical partitioning enabled us to determine whether each explanatory variable had an independent effect on colony settlement (after having removed the effect due to interactions or correlation with other variables). This method allowed us to confirm the qualitative results obtained with the GLM. All analyses were conducted using the R 2.8.1 software package (R Development Core Team 2008).

### Spatially explicit projection model

A two-dimensional stochastic cellular automaton was used to project the dynamics of colonization for the Grey Heron. The automaton was run in the CORMAS freeware environment (Bousquet et al. 1998). The space was described by a 100 · 100 grid (each cell corresponding to a 10 · 10 km<sup>2</sup> in France). Only cells located within the French territory were considered in the cellular automaton, and no information on habitat suitability and colony distribution in neighbouring countries was considered, which may distort the model projection near the borders. Each spatial cell had two attributes: its habitat suitability value (HS), assumed to be constant through time, and the number of Heron colonies (C) located in the cell at time t. In each time step (4 years), the expected number of new colonies in each cell i (NewC<sub>i</sub>(t)) was computed as a function of HS<sub>i0</sub>, HS<sub>i1</sub>, C<sub>ix</sub>(t) and C<sub>ix</sub><sup>2</sup>(t) according to the estimates provided by the most parsimonious GLM (see Results). The integer number of new colonies was therefore drawn from a Poisson distribution of expectation NewC<sub>i</sub>(t). The model was synchronous (i.e. in each time step, cells were updated simultaneously).

Estimates from the GLMs were implemented as fixed values in the spatial model. Alternatively, to assess the sensitivity of model projections to uncertainty in GLM estimates, we computed 95% confidence intervals by running simulations with variable input parameters. In each trajectory, each parameter (i.e. HS<sub>i0</sub>, C<sub>ix</sub>(t), etc.) was drawn from a Gaussian distribution with expectation set as the mean value of the parameter, with one standard deviation provided by the GLM output.

The values of NewC<sub>i</sub> at time zero were initialized according to the actual distribution of colonies in 1981. Both NewC<sub>i</sub>(0) and HS<sub>i0</sub> were imported from a Geographic Information System file using the ARC-VIEW GIS 3.2 software (Environmental Science Research Institute 1992). The colonization dynamics of Grey Herons in France were investigated by running 300 Monte Carlo iterations of the model over a fixed time horizon of 20 time steps (corresponding to 80 years).

### RESULTS

The GLM analysis suggested that the colonization of a given cell is influenced to a greater extent by the number of surrounding colonies than by their sizes (i.e. all variables of colony sizes (P<sub>x</sub>) were removed by standard AIC-based model selection procedures, see Appendix

S1 in Supporting Information). The quantitative effects of explanatory variables on the number of new colonies per time unit are summarized in the following equation, obtained from the GLM analysis (most parsimonious model):

$$\begin{aligned} \log(\text{New}C_{i0}(t+1)) = & \sum_{x=0}^1 \alpha_x HS_{ix} + \sum_{x=0}^3 \beta_x C_{ix}(t) \\ & + 0.4 \sum_{x=4}^5 C_{ix}(t) - 0.018 \left( \sum_{x=0}^5 C_{ix}(t) \right)^2 \\ & - 0.0007 \left( \sum_{x=6}^{10} C_{ix}(t) \right)^2 - 5.4 \end{aligned}$$

where

$$\alpha = [0.042 \quad -0.037] \quad \beta = [0.83 \quad 0.58 \quad 0.52 \quad 0.44] \quad (1)$$

This model included explanatory variables related to the habitat (HS<sub>ix</sub>) and to the presence of existing colonies (C<sub>ix</sub>), at different distances x from the focal cell i (detail in Table 2). All retained variables had a significant influence on the number of new colonies. The model explained 13.2% of the total variance in colony settlement and a goodness-of-fit test based on model deviance analysis indicated that the model adequately fitted the data (P > 0.05).

As expected, the statistical model indicated that local colonization dynamics are positively influenced by habitat suitability in the focal cell (HS<sub>i0</sub>) and by the presence of nearby colonies (C<sub>i0</sub>, C<sub>i1</sub>, C<sub>i2</sub> and C<sub>i4-5</sub>). However, the negative estimates associated with the second-order terms (which correspond to the square of the number of colonies within a 100-km radius) indicated a negative effect of colony density beyond a certain threshold. Unlike the habitat suitability in the focal cell (HS<sub>i0</sub>), the quality of surrounding cells (HS<sub>i1</sub>) exhibited a negative influence on colonization dynamics (see Discussion).

The qualitative results reported above were confirmed by the hierarchical partitioning analysis, which indicated that all explanatory variables had a significant independent effect on the probability of cell colonization, although each variable explained only a very small proportion of variance (< 1%). In agreement with the GLM, the analysis showed that colonization was influenced to a greater extent by the number of surrounding colonies (0.32% of variance) than by their sizes (0.1% of variance). Furthermore, although HS<sub>0</sub> had a significant effect on colonization, it explained a small

proportion of variance (0.08%), as compared with the interaction between  $HS_0$  and  $C_{0-5}$  (0.43%).

The most parsimonious GLM model (see Equation) was implemented into our cellular automaton as a transition rule. As the first step, our simulations starting from the actual situation of colony occurrence in 1981 were compared with the actual situations in 1985, 1994 and 2000. Simulated results were in good agreement with real colony counts in terms of spatial distribution. A generalized linear mixed model was used to analyse the correlation between projected and observed numbers

of colonies in each cell while accounting for spatial autocorrelation (cell coordinates considered as random effect variables). The regressions were highly significant ( $P < 10^{-4}$ ) for the years 1985 ( $R^2 = 38\%$ ), 1994 ( $R^2 = 15\%$ ) and 2000 ( $R^2 = 12\%$ ; Fig. 1).

Rapid colonization of eastern France occurred first, followed by the establishment of a connection between the eastern and western populations, and colonization of northern France. In a second step, colonies settled in the Mediterra-

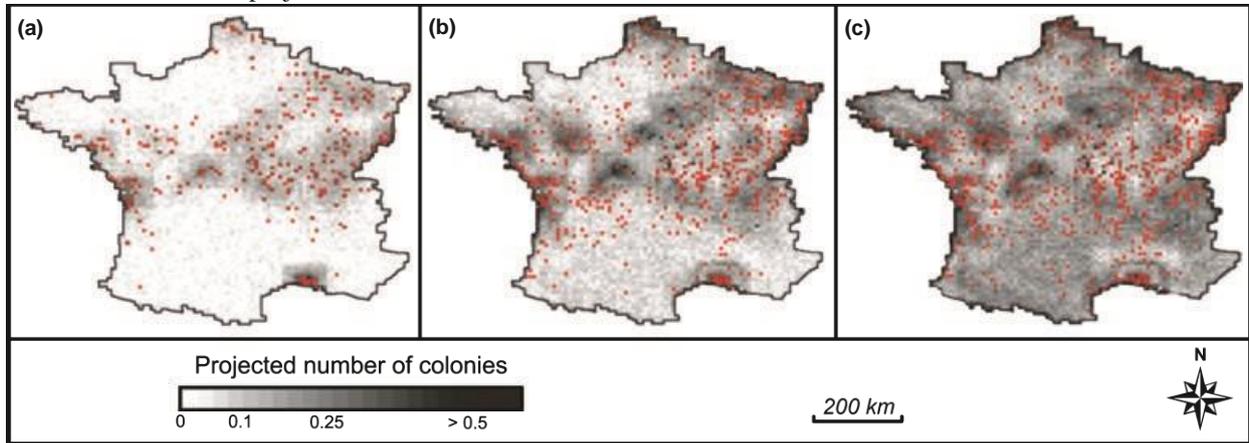


Figure 1. Comparison of observed and projected colony distributions. The grey scale indicates the projected number of colonies in each cell (expressed as the mean number of colonies per cell). Actual colonies are indicated by red dots. Due to the time step used in the model, and the irregularity of census intervals, projected years do not correspond exactly to census years. (a) Projected and real distributions for the year 1985. (b) Projected distribution for the year 1993, real distribution for the year 1994. (c) Projected distribution

Table 2. Estimates of the coefficients of the best regression model (GLM) obtained to predict local numbers of new colonies of Grey Heron per time unit.

(t)1	Estimate	se
Intercept	5.3641	0.3801
$C_0$	0.8261	0.1388
$(C_{0-5})^2$	0.0185	0.0023
$HS_0$	0.0418	0.0106
$HS_1$	0.0371	0.0102
$C_1$	0.5738	0.0622
$C_2$	0.5146	0.0579
$C_3$	0.4360	0.0559
$C_5$	0.3961	0.0423
$(C_{6-10})^2$	0.0007	0.0003

nean (southeastern) area. Simulations projected a lower colony density in southwest France (Fig. 1).

Long-term projections predicted a decline in the number of new colony establishments and stabilization

of the number of breeding colonies (Fig. 2). Predicted values of the number of colonies were used to fit a logistic growth model (method presented in Sparks et al. 2008), which yielded an equilibrium number of colonies of approximately 1500. Furthermore, simulations uncovered a temporal decrease in the mean habitat quality of newly colonized cells (Fig. 2), with stabilization at  $HS = 80$ , corresponding to a decrease of 7.4% compared with the situation in 1981. for the year 2000, real distribution for the year 2001.

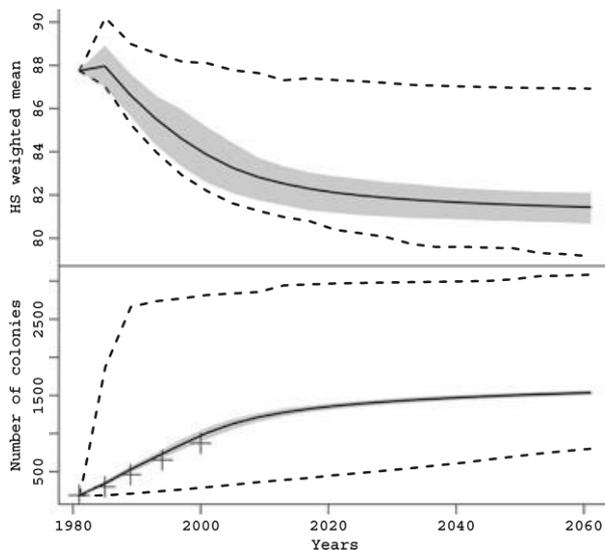


Figure 2. Projected number of Grey Heron colonies and mean habitat suitability: the upper panel is the projected mean habitat suitability value of newly established colonies. The lower panel presents the overall projected number of colonies. The shaded band denotes the 95% confidence interval obtained from the simulation model (i.e. when assuming that model parameters have fixed values equal to their mean values). Dashed lines denote the 95% confidence interval obtained when assuming variable values of model input parameters (see Methods). Plus symbols indicate observed numbers of colonies.

## DISCUSSION

The spatial integration of census and habitat suitability data allowed us to compare the effects of different ecological processes related to the spatial extension of the species range: (i) habitat choice, (ii) establishment of new colonies close to existing colonies and (iii) negative density dependence.

The probability of establishment of new colonies in a given area (10-km cell) increases with the ‘quality’ of this area (HS). However, the mean HS of surrounding cells has a negative effect on the probability of new colony establishment to the central cell. This pattern is partly explained by the process of habitat selection, in which a given area is more attractive if other nearby areas are of lower quality. Previous studies on biological invasions have shown that range expansion can be driven by various modes of dispersal, such as neighbourhood diffusion or long-distance dispersal (e.g. Shigesada et al. 1995). Depending on the spatiotemporal scale considered, any realistic mode of dispersal might greatly affect species distribution, especially during the invasion phase. In the Grey Heron, foraging generally

occurs within 40 km of the breeding colony (Marion 1989), and the establishment of new colonies is expected to depend on this threshold distance. In agreement with this prediction, our analysis indicates that the probability of new colony settlement in a given area (central cell) increases with the presence of nearby colonies, and that this effect progressively decreases as the distance between existing colonies and the central cell increases (see  $b$  coefficients in Equation 1). At the scale of France, our dynamic results are clearly consistent with a diffusion process in which new colony settlement occurs near already existing colonies, leading to spatial aggregations of colonies.

The feeding territories of Herons exhibit individual variation, but are constrained by their gregarious breeding behavior (Marion 1989). Typically, colonies grow until they reach the carrying capacity of the environment (Kushlan et al. 2005). The present analysis nevertheless indicates that the probability of establishment of a new colony is influenced by the number of existing colonies and not by their size. This result is related to: (i) the long time step of the analysis, (ii) the rapid growth of the Heron population within the study period and (iii) the existence of spatial variation in local carrying capacities and the use of the HS index in statistical models, which has been shown to be correlated with local carrying capacity (Boisteau 2006). The creation of new colonies is a positively density-dependent process, occurring through juvenile dispersal. However, the analysis shows that very high local colony densities tend to slow down colonization rate until equilibrium is reached, in which no new colony settlement occurs. This process occurs at a regional scale (compatible with the foraging distance of the species). The limitation of the species’ growth at a larger spatial scale should depend on the availability and distribution of suitable habitats. According to our simulations, at the scale of France, the rate of colonization will slow down around the year 2010 and the number of colonies should stabilize to 1500–2000 within the next few decades (Fig. 2). Thus, although these quantitative inferences are subject to large uncertainties, results strongly suggest that the last phase of the colonization process (i.e. regulation) has already started.

Another determinant of the probability of new colony settlement is the suitability of the habitat (HS). Comparisons of hierarchical partitioning analyses including or excluding the interaction factor between colony density and HS indicated that the quality of

habitat increases the probability of colonization of a cell only if colonies are present within a 50 · 50-km area. Thus, although heron species are capable of long-distance dispersal (e.g. Cattle Egrets *Bubulcus ibis* colonized North America by crossing the Atlantic, Arendt 1988), our results indicate that even highly suitable habitats are not attractive if too distant from existing colonies.

During the second half of the 20th century, urbanization has resulted in the almost complete destruction or degradation of wetlands in France and Europe (Finlayson & Vandervalk 1995, Marion et al. 2000). However, due to the lack of empirical data on the temporal variation in habitat suitability (due either to changes in habitat characteristics or to changes in the species behaviour), HS was considered constant in our analysis. This assumption is not expected to affect our results because: (i) our index is only based on the presence of freshwater and the proximity of the sea, for which no substantial changes are expected to occur within 80 years; and (ii) global absolute changes in HS are not expected to greatly affect the projected spatial distribution of colony occurrence (depends only on the relative values of HS for different locations) or the equilibrium number of colonies (depends mainly on the balance between negative and positive density-dependent functions). Empirical results suggest that at high density, the Grey Heron becomes less demanding with respect to environmental quality, and will establish colonies in sub-optimal areas (Marion 1997). We obtained similar results with our simple model (assuming a constant decision rule for colony settlement and constant HS). This suggests that the observed decrease in quality of colonized sites does not necessarily imply a change in Heron behaviour, but may occur only as a consequence of the lack of good quality vacant sites.

Although based on simple, empirical relationships, we believe that the present model provides reliable short-term estimation of the future colonization dynamics of Grey Herons in France. The analysis showed that most of the factors of growth limitation occur at a local or regional scale (corresponding to a 50-km-radius area). Equations used to characterize these processes were based on the situations observed between 1981 and 1989, in which local colony densities were very heterogeneous. Estimates based on such local situations of high and low densities may therefore accurately model dispersal and intraspecific competition

and provide unbiased projections of colonization dynamics at a larger scale.

In the context of (re)colonizing species potentially causing ecological or economic problems, spatial model projections may help define management priorities: (i) at an interspecific level, by determining among colonizing species those that are the most likely to spread rapidly and/or reach the highest densities; and (ii) at an intraspecific level, by identifying specific areas where local management actions are needed. In the present case, this could be achieved by comparing the projected distribution of Grey Heron colonies with the distribution of human activities that are likely to interfere with the species (e.g. farming, fishing). Areas with high Heron densities and high densities of fish-farming may, for example, be identified as areas of concern where preventative and protective actions should be implemented.

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## REFERENCES

- Akaike, H. 1987. Factor analysis and AIC. *Psychometrika* 52: 317–332.
- Arendt, W.J. 1988. Range expansion of the Cattle Egret (*Bubulcus ibis*) in the Greater Caribbean Basin. *Colon. Waterbirds* 11: 252–262.
- Beissinger, S.R. & McCullough, D.R. 2002. *Population Viability Analysis*. Chicago: University of Chicago Press.
- Boisteau, B. 2006. *Rôle de la structure du paysage dans la distribution spatiale et la régulation des colonies de reproduction chez le Héron cendré (Ardea cinerea) et modélisation de son expansion future*. PhD thesis, Rennes 1 University of Rennes.
- Boisteau, B. & Marion, L. 2006. Landscape influence on the Grey Heron colonies distribution. *C. R. Biol.* 329: 208–216.
- Bousquet, F., Bakam, I., Proton, H. & Le Page, C. 1998. Cormas: common-pool resources and multi-agent systems. *Lect. Notes Artif. Intell.* 1416: 826–838.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. 2002. Evaluating resource selection functions. *Ecol. Modell.* 157: 281–300.
- Casagrandi, R. & Gatto, M. 1999. A mesoscale approach to extinction risk in fragmented habitats. *Nature* 400: 560–562.
- Caswell, H. 2001. *Matrix Population Models*, 2nd edn. Sunderland, MA: Sinauer Associates.
- EBCC. 2009. Trends of common birds in Europe, 2008 update, computation procedure and data quality control in details. The European Birds Census Council. <http://www.ebcc.info/> (accessed 13 February 2009).
- Environmental Science Research Institute. 1992. ArcView GIS 3.2. <http://www.esri.com/> (accessed 13 February 2009).
- Fasola, M. & Alieri, R. 1992. Conservation of Heronry Ardeidae sites in North Italian agricultural landscapes. *Biol. Conserv.* 62: 219–228.
- Finlayson, C.M. & Vandervalk, A.G. 1995. Wetland classification and inventory – a summary. *Vegetation* 118: 185–192.
- Foster, B.L. 2001. Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. *Ecol. Lett.* 4: 530–535.
- Hafner, H. 2000. Heron nest site conservation. In Kushlan, J.A. & Hafner, H. (eds) *Heron Conservation*: 201–218. Midsomer Norton: Academic Press.
- Hirzel, A.H., Helfer, V. & Merilä, F. 2001. Assessing habitat suitability models with a virtual species. *Ecol. Modell.* 145: 111–121.
- Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology* 83: 2027–2036.
- Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Modell.* 199: 142–152.
- Hughes, B., Bevan, R.M., Bowler, J.M., Still, L., Cars, D.N., Marquiss, M., Hearn, R.D. & Bruce, J.H. 1999. *Feeding Behaviour of Fish-Eating Birds in Great Britain*. London: DETR.
- Hutchinson, G.E. 1957. Concluding remarks. In *Cold Spring Harbor Symposium on Quantitative Biology*, vol. 22: 415–427. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.
- IGN. 1996. *BDCarthage – Version 2.4*. Paris: Institut Géographique National.
- Judson, O.P. 1994. The rise of the individual-based model in ecology. *Trends Ecol. Evol.* 9: 9–14.
- Kushlan, J.A., Hancock, J. & Thelwell, D. 2005. *The Herons*. Oxford: Oxford University Press.
- MacNally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – ‘predictive’ and ‘explanatory’ models. *Biodivers. Conserv.* 9: 655–671.
- Marchant, J.H., Freeman, S.N., Crick, H.Q.P. & Beaven, L.P. 2004. The BTO Heronries census of England and Wales 1928–2000: new indices and a comparison of analytical methods. *Ibis* 146: 323–334.
- Marion, L. 1989. Feeding and colonial breeding are not necessarily mutually exclusive spatial occupation systems: the case of the grey heron (*Ardea cinerea*). *J. Anim. Ecol.* 58: 693–710.
- Marion, L. 1991. *Inventaire National des héronnières de France 1989*. Rennes: Museum National d’Histoire Naturelle de Paris.
- Marion, L. 1994. *Le Héron cendré*. In Yeatman-Berthelot, D. & Jarry, G. (eds) *Atlas des oiseaux nicheurs de France*: 2–5. Paris: Société Ornithologique de France.
- Marion, L. 1997. *Les populations de Hérons cendrés en Europe et leur impact sur l’activité piscicole*. In Clergeau, P. (ed.) *Oiseaux à risques*: 85–100. Paris: INRA.
- Marion, L., Ulenaers, P. & van Vesseem, J. 2000. *Hérons in Europe*. In Kushlan, J.A. & Hafner, H. (eds) *Hérons Conservation*: 1–31. Midsomer Norton: Academic Press.
- McCullagh, P. & Nelder, J.A. 1989. *Generalized Linear Models*. London: Chapman & Hall/CRC.
- Morris, W.F. & Doak, D.F. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sunderland, MA: Sinauer Associates.
- R Development Core Team. 2008. *R: A Language and Environment for Statistical Computing*. V. 2.7.2. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org> (accessed 13 February 2009).
- Rhode, K. 2005. Cellular automata and ecology. *Oikos* 110: 203–207.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O’Neil, P., Parker, I.M., Thompson, J.N. & Weller, S.G. 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 32: 305–332.
- Shigesada, N., Kawasaki, K. & Takeda, Y. 1995. Modeling stratified diffusion in biological invasions. *Am. Nat.* 146: 229–251.
- Sparks, A.H., Esker, P.D., Bates, M., Dall’Acqua, W., Guo, Z., Segovia, V., Silwal, S.D., Tolos, S. & Garrett, K.A. 2008. *Ecology and Epidemiology in R: Disease Progress over Time*. <http://www.apsnet.org> (accessed 24 April 2009).
- Yeatman-Berthelot, D. & Jarry, G. 1995. *Nouvel Atlas des oiseaux nicheurs de France (1985–1989)*. Paris: Musée National d’Histoire Naturelle.

## SUPPORTING INFORMATION

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

Appendix S1. AIC-based model selection for examining the influence of habitat suitability, and colony and breeding pair densities on colony settlement.

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