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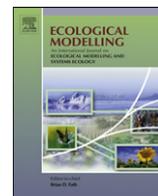
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Towards optimized population control efficiency in space and time: A modelling framework adapted to a colonial waterbird

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ABSTRACT

The double-crested cormorant is a native North American waterbird that recently underwent a dramatic population expansion. Population control efforts in the USA and Canada attempt to mitigate cormorant damages to natural resources and aquaculture. However, there is currently no coordination among the various stakeholders involved in management activities as well as no attempt to optimize population control efficiency. In this paper, we present for the first time a spatially explicit stage-structured metapopulation model parameterized for the cormorant. We developed simulation tools to get insights into the efficiency gain that can be expected from a better planning of management activities in both space and time. A case study is presented, in which we randomized where (on which colonies) and when (which years) a pre-determined amount of management activities would occur on 4 or 8 of 16 active colonies arranged on a 4×4 or 2×8 spatial grid over a period of 8 years, including 2 or 4 management years. We calculated two indices measuring the location of management activities, namely the average date of management years and the average degree of peripherality of colonies undertaking management, together with two indices measuring the resulting correlation of management activities, i.e., the degree of clustering of management activities both in space and time. Different spatio-temporal configurations of management activities generally yielded different metapopulation trajectories. Room for improving management efficiency increased with the intensity of management activities. However, the greatest efficiency gains are to be expected when colonies are far from carrying capacity, while the majority of management operations are undertaken when colonies are near or at carrying capacity. Locations of management activities in space and time appeared more important than resulting spatio-temporal correlations to explain the dispersion of metapopulation trajectories. When colonies were far from their individual carrying capacity, management was more efficient when applied earlier (a consequence of delayed reproductive maturity) and to more central colonies (due to greater immigration). The situation was more complex when colonies were closer to or at carrying capacity. Our modelling framework is flexible enough to allow more complex scenarios to be investigated in the future.

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1. Introduction

The double-crested cormorant (*Phalacrocorax auritus*, hereafter *cormorant*) is a large native North American piscivorous waterbird. The dramatic increase in cormorant abundance in recent decades (Wires and Cuthbert, 2006) has led to increased human-cormorant conflicts due to documented and alleged impacts on recreational fishing, aquaculture, vegetation, and competition with other colonial waterbirds (Taylor and Dorr, 2003).

Population control efforts were progressively implemented in the United States of America (USA) and Canada to mitigate these conflicts. Cormorant management techniques include harassment at roosting and breeding sites, culling of breeding and wintering cormorants, egg oiling to prevent hatching and re-laying, and nest destruction or removal. In Canada, cormorants are not federally protected, so management policy varies by province. In Ontario for instance, authorization to destroy nests of cormorants is issued on a case-by-case basis by the Ontario Ministry of Natural Resources (2006), but landowners may kill cormorants to protect their own property from cormorant damage without a permit. In the USA in 1998, the Aquaculture Depredation Order (AQDO; 50 CFR 21.47) allowed the lethal removal of cormorants at aquaculture facilities without a federal permit in 13 states. Since 2003, cormorants also have been managed under the Public Resource Depredation Order

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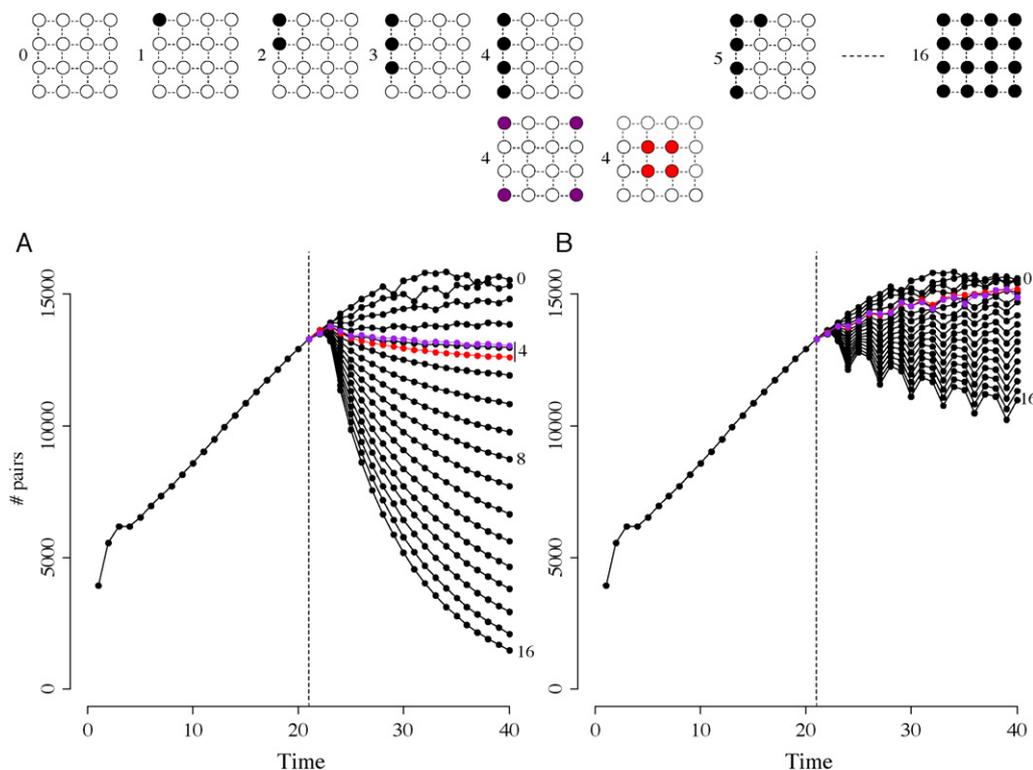


Fig. 1. Schematic representation of the model and example of model application showing the dynamics of 16 colonies (4 rows \times 4 columns). Management is 80% of eggs oiled with no culling, starting at $T_m=21$, of a 40 year period. Part A has egg oiling occurring every year and part B egg oiling occurs every three years. All colonies are active and have a carrying capacity of $Kp=1000$. Each black curve represents the total number of breeding pairs in the metapopulation, with the number of managed colonies varying between 0 and 16 (the position of managed colonies is represented by a black dot in upper part, first row). We also show the dynamics of three '4 managed colonies' scenarios with alternative spatial designs: purple ($position_mg=1.44$, $SC=0.29$), black ($position_mg=1.32$, $SC=0.60$), and red ($position_mg=1.00$, $SC=0.88$). See text for details, including variable descriptions. Other parameter values were taken from the "main" analysis in Appendix A.

(PRDO; 50 CFR 21.48), which authorizes the lethal take of cormorants and egg-oiling or nest destruction by federal, state, and tribal officials without a permit in 24 states.

Management efforts, and the associated costs, are currently substantial in North America. In the USA during 2009, a total of 47,190 cormorants were killed and 32,296 nests oiled or destroyed (Terry J. Doyle, United States Fish and Wildlife Service, unpublished data). The total cost of the United States Department of Agriculture, Wildlife Services, cormorant control program in central New York State alone from 1998 to 2005 was approximately \$3.5 million (Shwiff et al., 2009).

Literature on insect pest management suggests that coordinated decisions among crop growers may improve returns (Byers and Castle, 2005; McKee, 2011). Optimization of management in space and time may be important to mitigate the impact of a pest (Zhang et al., 2010; McKee, 2011; Parsa et al., 2011). For mobile pests, management at large spatial scales may be more effective and preferable to the uncoordinated field-by-field approach (Vreysen et al., 2007). Despite the knowledge gained from other pest management experiences and theoretical models, there currently is no population-level management strategy for the cormorant.

Due to the ongoing and intensive nature of cormorant management in North America we explored a modelling framework that can be used to inform cormorant management strategies. Specifically, our aims were as follows: (i) to present a deterministic stage-structured metapopulation model parameterized for the cormorant. Our model represents a step beyond the works of Blackwell et al. (2002) who developed a single population model and Duerr (2007) whose metapopulation model, parameterized for cormorant colonies in the Lake Champlain, lacked an explicit spatial context which is necessary to accommodate distance-dependent dispersal

as evidenced in the closely related great cormorant (Henaux et al., 2007); (ii) as our model was designed to be an effective strategic and management decision tool, we also developed simulation tools to gain insight into the efficiency gain that could be expected from a better coordination of management activities in space and time; (iii) our modelling framework was applied to a case study in which we investigated the relative importance of the spatio-temporal location and degree of clustering of specific management activities on management efficiency.

2. Materials and methods

2.1. The model

2.1.1. Spatial structure

The spatial structure consists of a grid of $i=1$ to nr rows and $j=1$ to nc columns (all parameter definitions and values are given in Appendix A). Breeding colonies, when present, are located at grid intersections, and the number of breeding colonies $ncol$ ranges from 2 to $nr \times nc$ (Fig. 1). We assume the diameter of colonies to be negligible in comparison with the distance between colonies. The shortest distance between two rows or two columns corresponds to one unit of distance. All suitable habitats (colonies) are occupied at the beginning of the simulation (i.e., founding of new colonies is not allowed), but local extinction-recolonization dynamics may occur as a result of management activities.

2.1.2. Local demography

Following Blackwell et al. (2002) and Duerr (2007) the breeding population consists of three age groups: year 1 subadults were juveniles produced during the previous breeding season, year 2

subadults, and a composite age class consisting of adults ≥ 3 years old. Below we describe the demography of colony i, j at time t (i, j, t indices are omitted in the equations).

Culling may occur before and/or after reproduction takes place, and the proportion of birds culled (cs) may be sex-specific. Because culling is suspected to impact primarily the males in both the breeding and nonbreeding grounds (Bedard, 1995; Strickland et al., 2011), our model assumes either an even or a female-biased sex-ratio. The hatching success is taken to be $h = 1 - eggD$, where $eggD$ is the proportion of eggs laid that do not hatch as a result of management activities. In this paper, we mainly consider egg oiling, as this is the most frequently used method (A. Guillaumet et al., unpublished data), and because it results in almost 100% of eggs that do not hatch (Shonk et al., 2004). Nest destruction, or predation due to disturbance, can easily be accommodated, but the proportion of eggs lost is more difficult to estimate, because a fraction of cormorants will re-nest and/or re-lay eggs (Duerr et al., 2007).

Density-dependent regulation is modelled using one of two methods. The first method is based on Frederiksen et al. (2001). The breeding proportion of year 2 subadults and adults ($b2$ and $b3$, respectively) are density-independent ($b(0)$ values) when the number of potential breeding pairs (pot_pairs) is below a given threshold thr_DDb , pot_pairs being calculated as $pot_pairs = b2(0) \times B2m + b3(0) \times B3m$, where $B2m$ is the number of year 2 subadult males and $B3m$ the number of adult males present. When $pot_pairs \geq thr_DDb$, breeding proportions take the form $b = b(0) \cdot e^{-DDb(pot_pairs - thr_DDb)}$, with DDb being the slope of the density-dependent relationship. Fertility coefficients ($f2$ and $f3$, see Appendix A) are density-independent ($f(0)$ values) when the actual number of breeding pairs (act_pairs) is below a given threshold thr_DDf , act_pairs being calculated as $act_pairs = b2 \times B2m + b3 \times B3m$. When $act_pairs \geq thr_DDf$, fertility coefficients take the form $f = f(0) \cdot e^{-DDf(act_pairs - thr_DDf)}$, with DDf being the slope of the density-dependent relationship. The number of juveniles produced ($B0$), is calculated as $B0 = h \times (b2 \times f2 \times B2m + b3 \times f3 \times B3m)$; $B0m = B0f = 1/2 \times B0$.

The first method does not guarantee that the number of breeding pairs will not exceed a certain value (Kp), which is the carrying capacity of the number of pairs (e.g., corresponding to the number of nest sites available). We thus implemented a second method, where the actual number of breeding pairs is calculated as $act_pairs = p_breed \times pot_pairs$, where p_breed , the proportion of pairs actually breeding, is 1 if $pot_pairs \leq Kp$, and (Kp/pot_pairs) otherwise. We also accommodated the possibility that the total number of individuals in the breeding colony after reproduction, summing over all age classes and sex (noted B), did not exceed a certain value Kb , a carrying capacity corresponding to the quantity of resources available around the colony. The potential number of juveniles produced (pot_B0), was thus calculated as $pot_B0 = p_breed \times h \times (b2(0) \times f2(0) \times B2m + b3(0) \times f3(0) \times B3m)$; $B0 = pot_B0$ (if $B < Kb$), but $B0 = pot_B0 - d$ (if $B \geq Kb$), where $d = B - Kb$ is the number of deaths necessary to keep $B \leq Kb$.

2.1.3. Dispersal

Following Lebreton et al. (2003), we assume a higher annual dispersal rate for pre-breeding dispersal (m_natal , for cormorants less than 3 years-old which is the usual age of first reproduction) than for cormorants aged 3+ years-old (m_breed). Although estimates available in the literature may not be generally applicable, as dispersal is a complex trait conditional on the interaction of individual, social and environmental causes (Martin et al., 2008), we used dispersal estimates described by Duerr (2007) and by Henaux et al. (2007) for the great cormorant as our references.

To account for potentially higher dispersal rates due to density-dependence effects (Doligez et al., 2003) or management activities (Duerr et al., 2007; Pope et al., 2007), natural dispersal rates of all

ages classes (except juveniles) can be augmented by the parameter psi_DD when $b < b(0)$ or $p_breed < 1$, psi_eggD when $eggD > 0$, and by psi_cs when $cs > 0$. Dispersing individuals are allocated to another colony with a probability inversely related to the distance to the source colony (e.g., Hansson et al., 2002). If the distance between the focal colony f and another colony g is $d_{f,g}$, the proportion of dispersing cormorants from f actually going to g is calculated as: $e^{-(d_{f,g}/2)} / \sum_{m \neq f} e^{-(d_{f,m}/2)}$, where the denominator is the sum (over $ncol - 1$) of the distances between the focal colony f and any other colony m of the metapopulation. We assume that the selection of a new breeding colony (dispersal) occurs between the end of the reproduction period and fall migration, at a period when cormorants frequently visit other colonies (Guillaumet et al., 2011).

2.1.4. Migration and overwinter survival

Overwinter survival rate is calculated as $s \times (1 - cw)$, where s is the natural survival rate, and cw is the probability of being culled in the non-breeding area. The model accommodates three migration strategies: (1) no migratory connectivity; cw does not depend on the spatial position of the breeding colony; (2) parallel migration; cw may vary according to the longitude, i.e., each column j may have a different cw_j ; (3) migratory divide; two different cw_j are allowed, one for each side of the migratory divide. We assume that all individuals (including first years) come back to the breeding colonies, so that non-breeders contribute to deplete the resources, affecting the B/Kb ratio (see above).

2.2. Simulations

We simulated $4 \times 4 = 16$ active colonies over a period of 8 years. For each simulation, we started by picking at random the colonies that would undergo management; 4 or 8 colonies were selected in this way (variable = nb_col_mg). We calculated SC , an index of spatial correlation of management, inversely related to the average geographic distance between managed colonies (the more clustered the managed colonies, the higher the index). We also calculated $position_mg$, the average position of managed colonies on the grid, as follows: (i) we gave each colony an index of peripherality; and (ii) $position_mg$ was calculated as the average peripherality of managed colonies. The index of peripherality was 1 for the four central colonies, 1.44 for the four most peripheral (corner) colonies, and 1.20 for the remaining eight colonies (Fig. 1). These values derived from the dispersal transition matrix (D) for each colony: $\max(D)$ was used as a proxy for the peripherality, the rationale being that more central colonies will distribute their migrants more evenly among neighboring colonies, yielding a lower $\max(D)$ value as elements of D sum up to 1. The resulting indices were adjusted so that the value for central colonies was 1.

Next, we picked at random 2 or 4 years of the 8 years simulated during which management would be applied on the randomly selected colonies (variable = nb_yr_mg). We calculated TC , an index of temporal correlation of management, inversely related to the average number of years between management years (the more clustered the management years, the higher the index). We also calculated $date_mg$ as the average of the management years, taking higher values when management occurred later during the study period. Finally, we assigned the severity of management activities (sev_mg) among two options: low (culling in summer = 0.1, and egg oiling = 0.4), or high (culling in summer = 0.2, and egg oiling = 0.8). We calculated the number of breeding pairs at the end of the simulation period as an estimate of the total metapopulation size (variable = $metapop_size$).

We thus investigated 8 different scenarios of management intensity ($2nb_col_mg$ values \times $2nb_yr_mg$ values \times $2sev_mg$ values). Each scenario was investigated by performing a series of 500

Table 1
Results of model selection for two response variables measuring the dispersion of metapopulation size values (*metapop_size*) at the end of the simulation: *rge.metapop_size* is the range of *metapop_size* values, and CV the coefficient of variation of *metapop_size*.

Response variable	Simulation factor	Explanation	t-value	P-value
<i>rge.metapop_size</i>	<i>nb.col.mg</i>	# colonies managed	3.02	<0.01
	<i>nb.yr.mg</i>	# years of management	1.41	0.16
	<i>sev.mg</i>	Severity of management activities	3.24	<0.01
	<i>DD.meth</i>	Density-dependence method	2.95	<0.01
	<i>disp</i>	Dispersal magnitude	1.70	0.09
	<i>log(inits)</i>	log of initial population size	14.72	<0.001
$\log(100 \times CV + 1)$	<i>nb.col.mg</i>	# colonies managed	5.83	<0.001
	<i>nb.yr.mg</i>	# years of management	1.85	0.07
	<i>sev.mg</i>	Severity of management activities	5.55	<0.001
	<i>DD.meth</i>	Density-dependence method	3.21	<0.01
	<i>log(inits)</i>	log of initial population size	-20.59	<0.001

simulations. To assess the sensitivity of the results to initial population size and to the choice of a specific density-dependent model and dispersal values, simulations for the 8 different management intensity scenarios were run for: (1) both density-dependent methods (*DD.meth*); (2) for two combinations of dispersal values (*disp*): low and high (see Appendix A for values); and (3) for initial population size (*inits*) drawn from a Poisson distribution with parameter $\lambda = 10, 50, 100, 200, 500$ or 1000. In practice, each sex and age category of each colony received an average of λ individuals at $t=1$; the number of potential pairs at $t=1$ was inferior to the carrying capacity Kp in all but the last scenario ($\lambda = 1000$). Altogether, we thus conducted 8 (management intensity) \times 6 (initial population sizes) \times 2 (density-dependent methods) \times 2 (dispersal magnitude) = 192 run of 500 simulations. Each run yielded a vector ($n=500$) of each explanatory factor (*SC*, *position.mg*, *TC*, *date.mg*) and the resulting vector ($n=500$) of the response variable (*metapop_size*).

We also performed two control analyses replicating these 192 run of 500 simulations, while modifying two other types of parameters: (1) 16 active colonies were arranged in 2 rows of 8 colonies (instead of 4×4); and (2) we used a different source of (higher) survival values (Appendix A).

2.3. Statistical analyses

For each run of 500 simulations, we first calculated the range of the response variable *metapop_size* ($rge.metapop_size$ = difference between maximum and minimum *metapop_size* values) as a measure of the impact of the different management strategies (larger dispersion implies a larger potential to improve management efficiency). Using the standard deviation of *metapop_size* instead of *rge.metapop_size* yielded similar results (not shown). However, since standard deviation may scale proportional to the mean (e.g., Lande, 1977), we also calculated the coefficient of variation of *metapop_size* (CV = standard deviation/mean) as a normalized measure of dispersion.

Both *rge.metapop_size* and CV were used as new (independent) response variables to identify, using linear models, which of the simulation factors were driving the dispersion of *metapop_size* values: number of colonies managed (*nb.col.mg*), number of years of management (*nb.yr.mg*), severity of management activities (*sev.mg*), density-dependence method (*DD.meth*), dispersal magnitude (*disp*), and initial population size (*inits*). Both CV and *inits* were log-transformed prior to analyses to increase linearity ($\log(100 \times CV + 1)$ and $\log(inits)$, respectively). We used a backward + forward stepwise selection procedure and AIC criterion to select the best model. Because the assumptions of linear models (normality of residuals and homoscedasticity) were rejected at the usual significance level (5%), we also conducted non-parametric analyses to check the robustness of our conclusions (Wilcoxon

rank-sum tests for binary variables, generalized additive models for $\log(inits)$). As conclusions were identical, we only provide the results of linear models.

The role of explanatory factors was then evaluated as follows. First, for each simulation run we built a full (linear) model for *metapop_size* containing *date.mg*, *position.mg*, *SC*, *TC* and the interaction between *SC* and *TC*. We calculated the coefficient of determination R_{full}^2 and Student's *t*-test values for each these five covariates. Second, we built a model containing only location variables *date.mg* and *position.mg* and calculated the coefficient of determination R_{loc}^2 ; the statistic $R_{full}^2 - R_{loc}^2$ gave us the unique contribution due to the correlation of management activities in space and time. Third, we used Student's *t*-test values, estimated from the full model, as five new (independent) response variables to investigate, using linear models, which of the simulation factors were responsible for the negative or positive influence of each explanatory factor on *metapop_size*, using the same stepwise selection procedure as described above (Appendix B for further details). Modelling and statistical analyses were performed with R version 2.7.2 (© The R Foundation for Statistical Computing).

3. Results

The range of the response variable *metapop_size* (variable = *rge.metapop_size*) was 0–3268 (mean of *rge.metapop_size* = 712, $SD = 629$, $n = 192$). *Rge.metapop_size* was strongly positively correlated with initial population sizes (Table 1, Fig. 2), with the latter being strongly positively correlated with final metapopulation sizes (Pearson correlation coefficient on log–log scale, $r = 0.99$, $P < 0.001$). In addition, the range of *metapop_size* increased with the intensity of management activities (Table 1: *nb.col.mg* and *sev.mg*; although retained in the best model, *nb.yr.mg* did not reach significance), and was also influenced by the density-dependence method.

The coefficient of variation of *metapop_size* varied from 0 to 7.54% (mean of $CV = 3.07$, $SD = 1.88$, $n = 192$). Although CV and *rge.metapop_size* were impacted by the same simulation factors (Table 1), CV (unlike *rge.metapop_size*) was negatively correlated with initial population sizes (Fig. 2C).

Our candidate explanatory factors explained a fraction of this dispersion. The coefficient of determination of the full model (R_{full}^2) was 28.3% on average ($SD = 24.0$, range = 0.4–93.2, $n = 192$), while $R_{full}^2 - R_{loc}^2$, the unique contribution due to the correlation of management activities in space and time (*SC*, *TC* and *SC* \times *TC*) was only 4.0% on average ($SD = 6.9$, range = 0.0–41.9).

The explanatory power of each factor is examined in Fig. 3, showing the histograms of Student's *t*-test values. Most *t*-values for *SC* and *SC* \times *TC* are in between -2 and $+2$ (non-significance thresholds), suggesting that these factors are generally not

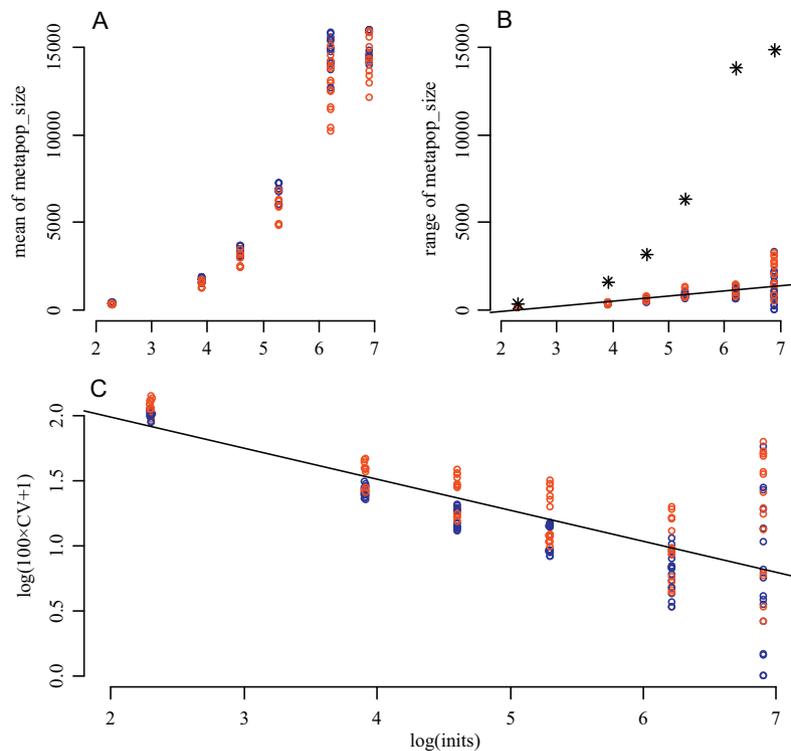


Fig. 2. Dispersion of metapopulation size values at the end of the simulation as a function of initial population sizes on a log scale (2.3–6.9 ↔ $\lambda = 10$ –1000). A) average metapopulation size. Each dot represents the mean of *metapop_size* ($n = 500$) for each of the 192 runs; for illustrational purpose, low severity of management activities (i.e., low egg-oiling and culling values) is in blue, while high severity is in red. B) Range of metapopulation size. Each blue or red dot represents the range of *metapop_size*, i.e., the difference between maximum and minimum values of *metapop_size* for each of the 192 runs (variable = *rge.metapop_size*); the stars show the mean of *metapop_size* for each of the six initial population sizes (compare with A). The range of *metapop_size* increases with severity of management activities and initial population sizes (black line is fitted simple linear regression; see Table 1 for multivariate regression), but the mean of *metapop_size* increases faster with initial population sizes than its range. This is illustrated by the coefficient of variation of *metapop_size* (CV) which decreases with initial population sizes (C).

important. *T*-values for *date_mg*, *position_mg* and *TC* are slightly skewed towards negative values and positively correlated, the latter likely because they are strongly influenced by initial values. Larger initial values generally resulted in a more negative impact of these factors on the total metapopulation size (Fig. 3). The variable *inits* was by far the most significant simulation variable selected by the stepwise regression for *date_mg* ($F_{1,188} = 344.2$, $P < 0.001$) and *position_mg* ($F_{1,187} = 160.7$, $P < 0.001$); hence the very strong correlation between *t*-values for *date_mg* and *position_mg* (Pearson's correlation coefficient $r = 0.79$). For *TC*, *inits* was also the most significant variable ($F_{1,187} = 94.4$, $P < 0.001$), but other simulation factors also played an important role, particularly the dispersal magnitude (*disp*: $F_{1,187} = 55.3$, $P < 0.001$) and the number of colonies managed (*nb_col_mg*: $F_{1,187} = 30.9$, $P < 0.001$); hence the lower correlation between *t*-values for *TC* on one hand, and *t*-values for *date_mg* or *position_mg* on the other hand ($r = 0.35$ – 0.44). Stepwise regression results are detailed in Appendix B.

The two control analyses yielded similar results and so are not detailed. For instance, the coefficient of variation of the response variable *metapop_size* remained around 3%: (mean = 3.08, SD = 1.88 for the 2×8 spatial design, mean = 2.88, SD = 2.12 for the “higher survival” control). Both R_{full}^2 and $R_{full}^2 - R_{loc}^2$ were also very similar: for the 2×8 spatial design, $R_{full}^2 = 29.7\%$ on average (SD = 25.0), $R_{full}^2 - R_{loc}^2 = 3.8\%$ (SD = 6.5); for the “higher survival” control, $R_{full}^2 = 29.1\%$ (SD = 22.6), $R_{full}^2 - R_{loc}^2 = 4.3\%$ (SD = 7.8). The main difference between treatments was observed when colonies were close to or at carrying capacity. In particular, while management was more efficient when applied later for the main analysis and 2×8 control, the reverse was generally observed for the “higher survival” control (Fig. 3, Appendices B and C).

4. Discussion

In this paper, we presented a metapopulation model parameterized for the double-crested cormorant, a species subjected to population control efforts in the USA and Canada. As an example of application, we designed a simulation study to provide insight into the efficiency gain that could be expected from a better planning and coordination of management operations. For every run of simulations (for a total of 192) we manipulated where (on which colonies) and when (which years) a pre-determined amount of management activities would occur, while all other parameters were kept constant. In turn, this choice determined how correlated the management activities were both in space and time.

We observed a non-null dispersion of metapopulation size values at the end of the simulation period for all but 2 runs, indicating that in the vast majority of situations different spatio-temporal configurations of management activities yielded different metapopulation trajectories. The most important source of dispersion was initial population sizes (Table 1). Although absolute dispersion increased with initial population sizes (Fig. 2B), the coefficient of variation followed an inverse trend (Fig. 2C). Arguably, the largest efficiency gains are thus to be expected when colonies are far from carrying capacity, while the majority of management operations are undertaken when colonies are near or at carrying capacity. We also found that both absolute and normalized dispersion significantly increased with the number of colonies managed and the severity of management operations, i.e., proportion of eggs oiled and cormorant culled (Table 1, Fig. 2). In other words, room for improving management efficiency increases with intensity of management activities.

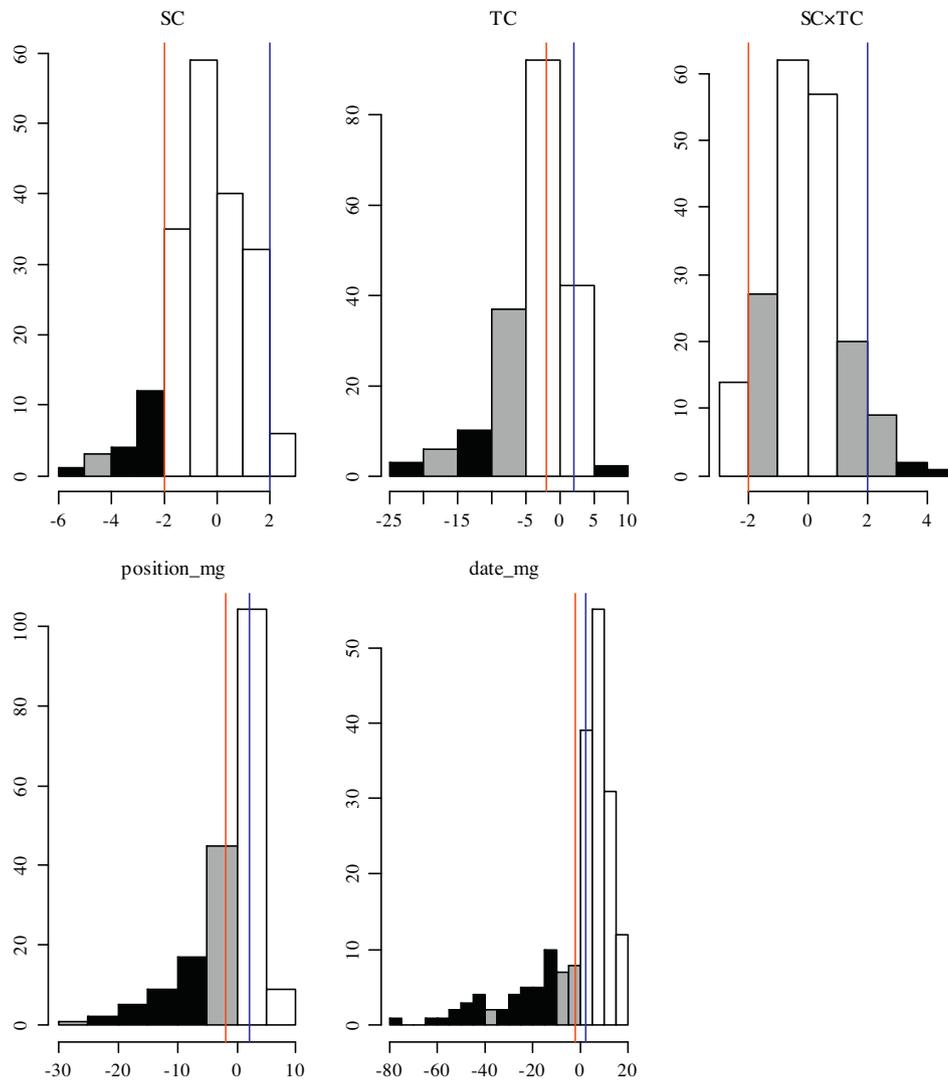


Fig. 3. Role of spatio-temporal design in explaining the variance of metapopulation size. For each of the 192 runs (500 simulations each): (i) we used the metapopulation size at the end of the simulation as our response variable and recorded a set of five explanatory factors, namely the spatial and temporal location (*position_mg*, *date_mg*) and correlation (*SC*, *TC*, and their interaction) of management activities; (ii) we used a linear model to determine Student's *t*-test values for each explanatory factor. Student's *t*-test values corresponding to our main analysis are represented in the histograms. Non-significance thresholds $[-2; 2]$ are indicated by vertical lines. The importance of initial values (*inits*) is highlighted by bar colors: white for small initial values (mean of *inits* < $Kp/3$), black for large initial values (mean of *inits* > $2 \times Kp/3$), and grey for intermediate initial values; see text and Appendices A and B for details.

We further attempted to identify which spatio-temporal configurations were the most efficient. A comprehensive analysis of the mechanisms involved was beyond the scope of this study, so we restrict ourselves to some simple hypotheses. Coefficients of determination suggested that actual locations of management activities in space and time (*position_mg* and *date_mg*) were more important than resulting spatio-temporal correlations (*SC*, *TC* and *SC* × *TC*). When colonies were small and far from their individual carrying capacity, management was more efficient when applied earlier and to more central colonies (Fig. 3). Later management appears less efficient because it allows more time for the colonies to go through the steep phase of exponential population growth. Juveniles produced early become breeding adults, and the difference in age structure is not entirely counterbalanced by subsequent treatments. For the spatial dimension, peripheral colonies tend to receive a smaller fraction of the dispersing birds than more central colonies for purely geographical reasons. For instance, in the case where all colonies send out a same amount of dispersing birds, the four most peripheral colonies receive each $\sim 5.1\%$, and the four central colonies each 7.5% , of those dispersing birds (4×4 design).

Hence, when regulation is essentially due to management activities (colonies far from carrying capacity), the population control is more efficient when management occurs on central colonies that grow faster owing to larger immigration.

The situation was more complex when colonies were close to or at carrying capacity, when population regulation is an interplay between natural density-dependence and anthropic disturbance. The fact that more, potentially counter-acting, factors were involved could account for the smaller relative impact of the spatio-temporal design (Fig. 2C). In our main design and the 2×8 control, the management was generally more efficient when applied later and to more peripheral colonies and, all else being equal, when management years and managed colonies tended to be clustered together (Fig. 3, Appendix C). Highly non-linear effects appear in the “higher survival” control, as illustrated by the date of management. Again, management was more efficient when applied earlier for small initial values (colonies far from carrying capacity), but in this scenario this was true also for large (but not intermediate) initial values (Appendix C).

Of course, choices made in this paper to keep the model and the simulation design reasonably simple and tractable may have influenced our results to some extent. Caution should be exercised when trying to reach conclusions beyond the strict simulation conditions we used here. However, our modelling framework is flexible enough to allow additional sophistication of the model as well as more complex, real-life scenarios to be investigated in the future. For instance, future versions of the model could accommodate the possibility of density-dependent survival (Frederiksen and Bregnballe, 2000; but see also Frederiksen et al., 2001) and the possibility that cormorants, particularly first-time breeders, use public information to select a breeding colony (Henaux et al., 2007). More realistic scenarios may include irregular spatial grids with unequal spacing between active colonies, and the fact that different colonies may have different carrying capacities and/or be at different stages of their dynamics.

Because the number of such possible simulations is almost infinite, we believe that our simulation tools could find their most relevant application during the preparation of strategic management plans at local or regional scales, when managers and scientists can use real-life estimates of spatial parameters while simultaneously assessing the consequences of uncertainty in other model parameters. The model could be used to evaluate management intensity and structure to optimize desired outcomes, but management intensity could also be tuned relative to risk of undesirable management outcomes such as colony extirpation or metapopulation collapse. Because the model has been parameterized using a wide array of intra-, but also inter-specific data (great cormorant: see Appendix A), not necessarily relevant to actual local or regional context, our modelling tools would be especially valuable when incorporating feedback from monitoring programs within an adaptive management setting (e.g., Lyons et al., 2008).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2012.03.028>.

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