The consequences of being colonial: Allee effects in metapopulations of seabirds

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ABSTRACT

Most seabirds live in large colonies. This fact signifies that there is an advantage in living and breeding together. Four explanations are put fore ward for this colonial behaviour, more birds have: (1) a reduced per capita predation of chicks in colonies, (2) a better anti-predator defence, (3) a more efficient foraging in temporally patchy environments and (4) sex ratios that are more likely to be close to one. These factors induce a strong Allee-type density-dependent relation, a positive relation between density and population growth rate at low density. Nevertheless, these Allee effects are generally ignored in seabird population studies. Therefore we study the consequences of introducing Allee-type density-dependent relations in a spatially explicit metapopulation model for the Common Tern (*Sterna hirundo*). Simulations show that Allee effects might be responsible for a 20-fold decline in the recolonization distances, causing patches and parts of metapopulations to effectively become more isolated. This leads to long recolonization times of empty breeding patches which consequently cause slower metapopulation expansion and recovery. Additionally, we show that the typical early warning signals, that show that a population is near its critical threshold induce by Allee effects, is less pronounced in colonies that are part of a metapopulation. Hence, we offer some simple equations to estimate critical densities and thresholds in a colony.

1. Introduction

Being top predators, seabirds play an important ecological role in the marine ecosystem, and their populations are frequently used as an indicator of coastal ecosystem health (Boyd et al., 2006; Heslenfeld and Enserink, 2008; Parsons et al., 2008). Coastal areas and estuaries offer important breeding habitats for seabird species. In recent decades, however, human activities have disturbed natural breeding sites along many coasts (Burger, 1984; Brinker et al., 2007; Oro et al., 2009). In addition to this, climate change might affect the seabird populations (Gremillet and Boulinier, 2009; Wolf et al., 2010). Here, changing environmental conditions and food availability might force seabird species to find new breeding grounds. As a result, many seabird species are endangered and protected. To facilitate decisions on seabird conservation, it is important to understand the life cycle and metapopulation dynamics of this important species group.

Most seabird species breed in large colonies. The fact that these birds prefer living in colonies suggests that there is an advantage in breeding together. The literature puts forward four reasons for such advantage:

- *Diluting effect.* In colonies more chicks are present for the same number of predators, which reduces the risk of an individual chick being predated (Krebs and Davies, 1978; Siegelcausey and Hunt, 1986; Serrano et al., 2005).
- *Anti-predator defence.* A group of birds forms a better early warning system than an individual, so birds have to spend less time being alert (Krebs and Davies, 1978; Becker and Ludwigs, 2004). Also, group defence against predators is more successful than individual defence (Becker, 1984; Cavanagh and Griffin, 1993; Whittam and Leonard, 2000).
- *Foraging efficiency.* Higher food intake per chick is expected among birds in colonies because many foraging parents discover food patches faster than solitary birds. The foraging behaviour of adults that have discovered a food patch attracts others, which is especially important when the location of food patches is variable (Buckley, 1997).
- *Finding mates.* At very low densities, couple formation is less efficient because the sex ratio is more likely to deviate from one (McCarthy, 1997; Verboom et al., 2001; Schmickl and Karsai, 2010).

The effects of these four density-dependent factors induces a decrease in the per capita growth rate at low density, which is called the Allee effect (Serrano et al., 2005; Taylor and Hastings, 2005). However, when colonies become crowded this effect disappears

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and local food shortages and intra-specific competition become dominant (Hunt et al., 1986; Mallord et al., 2007). The result is that the per capita growth rate has a maximum at intermediate colony densities (Te Marvelde et al., 2009). If Allee effects are strong and the per capita growth rate of seabirds at a low density is negative, this induces alternative stable states at the population level, individual populations below a certain threshold will go extinct and above this threshold they will grow to equilibrium (Wang et al., 1999; Van Nes and Scheffer, 2003; Scheffer et al., 2009). The expected alternative stable equilibria due to Allee effects raises questions about the consequences of Allee effects for the metapopulation dynamics and conservation of these seabirds because these Allee effects will hamper the recolonization and colonization of empty patches. This is especially important because we expect large distribution shifts due to climate change, in which colonization of new breeding habitat is a key process.

Recently a few studies have reveal the presence of Allee-type density-dependence in seabirds (Oro et al., 2006; Te Marvelde et al., 2009; Votier et al., 2009). Nevertheless, these Allee effects are generally ignored in seabird population studies (see e.g. Schroder et al., 1996; Oro and Ruxton, 2001; Jenouvrier et al., 2005; Gremillet and Boulinier, 2009) and no systematic research has yet explored the effects of Allee-type density-dependent relations and alternative stable equilibria on seabird metapopulation dynamics. Additionally, for nature managers it might be important to learn whether seabird populations are near a critical threshold, a density below a population cannot survive. Therefore, we systematically explore the ecological consequences of low reproduction potential at low densities using a metapopulation model that simulates the population dynamics of the Common Tern, a seabird that has a circumpolar distribution, and breeds in temperate and sub-Arctic regions of *Europe, Asia* and east and central *North America*. We specifically ask: (1) how do Allee effects affect the recolonization success of empty breeding habitat patches and patch clusters and (2) how can we detect critical thresholds and equilibria in seabird colonies?

2. Model

We used the demographic stochastic metapopulation model METAPOP (Van Apeldoorn et al., 1998; Schippers et al., 2009) to simulate the population dynamics of the Common Tern in several artificial landscapes consisting of patches of identical size. In our model we simulate the populations dynamics of females distinguishing 5 age classes. The life history events within a year are: chick loss due to Allee effects, between patch dispersal, survival and reproduction (Fig. 1). These life history events are described in detail in the following sections.

2.1. Survival and density-dependent reproduction in a patch

The population dynamics of a patch of the common was based on Leslie models as published by Schroder et al. (1996) and Schippers et al. (2009). The state of each patch in the model is describes by a vector of five age classes, two juveniles and three adult age classes. We simulated age-structured reproduction and survival of females that is defined without Allee effect by the Leslie probability

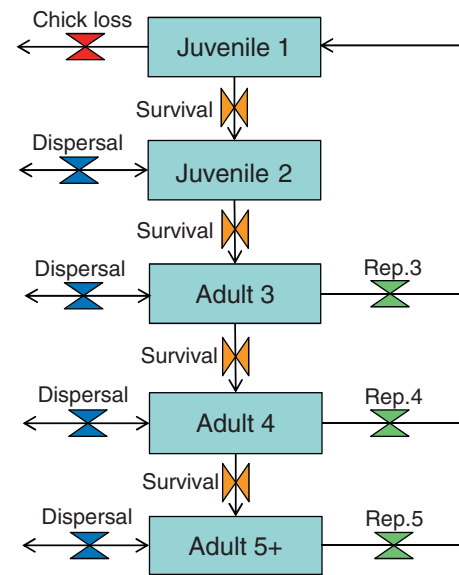|	J_1	J_2	A_3	A_4	A_{5+}	
J_1	0	0	$F_{3,d}$	$F_{4,d}$	$F_{5+,d}$	
J_2	S	0	0	0	0	matrix (1)
A_3	0	S	0	0	0	
A_4	0	0	S	0	0	
A_{5+}	0	0	0	S	S	

Fig. 1. Model scheme, representing population dynamical transitions of seabird females in a single patch. Rep. 3–5+ is the reproduction of adults of stage 3–5+. Dispersal is the in or out flux to other patches. Both dispersal and reproduction are density dependent. The chick loss is of the juvenile 1 stage is responsible for the Allee effects. All transitions are calculated in a demographical stochastic way.

J_1 and J_2 are the two juvenile age classes without reproduction A_3–A_{5+} are the adult age classes. $F_{3-5+,d}$ are the fecundity values of the adult age classes 3–5+ and S is the year to year survival. Fecundity value $F_{3-5+,d}$ represent the expected offspring (in females per female) that survive the first year and are determined by the density (d). The modelled offspring of each adult age class in a patch, however, is calculated stochastically from a Poisson distribution with the expected number of offspring $F_{3-5,d}$. Survival values of the matrix are probabilities and surviving animals are drawn from a Binomial distribution defined by the number of animals in each age group (J_{1-2} or A_{3-5}) and the survival probability S. So both recruitment and survival are calculated in a demographic stochastic way. We used a linear density-dependent recruitment function to account for intraspecific competition (Tavecchia et al., 2007). Here the $F_{i,0}$ is the fecundity for adult stage i at very low density and $f \cdot F_{i,0}$ is the fecundity at carrying capacity (K).

$$F_{i,d} = F_{i,0} - \left(\frac{A_t}{K}\right) \cdot (F_{i,0} - f \cdot F_{i,0}) \tag{1}$$

where, A_t is the total number of all adult age classes in a patch, K is the carrying capacity of a patch expressed as the number of adults of all age classes, f is factor that relates the fecundity at zero density to the fecundity at carrying capacity (K). We calibrate the factor f to have zero growth at carrying capacity, where the recruitment is just high enough to replace for the adult mortality. The calibrated value of f is 0.33. The fecundity and survival values originate from the work of Schroder et al. (1996) who studied the Common Tern in the Wadden sea area of the Netherlands (Table 1).

2.2. Loss rate due to Allee effects (L)

Chicks can be regarded as the vulnerable stage (Ezard et al., 2006) and the four Allee effect inducing mechanisms that are mentioned in the introduction will therefore likely affect the recruitment more than the adult survival. In the model structure, as described by matrix (1) and Eq. (1), recruitment at low population densities is per capita larger than at high densities. But we expect colonial birds to have a per capita disadvantage of living at low densities due to the Allee effects see e.g. (Te Marvelde et al.,

Table 1
Description of parameters used in the model.

Description	Symbol	Value	Unit[a]	Source[b]
Recruitment				
Fecundity of three-year-old adults at zero density	$F_{3,0}$	0.31	f f^{-1} year^{-1}	1
Fecundity of four-year-old adults at zero density	$F_{4,0}$	0.49	f f^{-1} year^{-1}	1
Fecundity of the five plus adults at zero density	$F_{5,0}$	0.63	f f^{-1} year^{-1}	1
Density dependent recruitment reduction at density K	f	0.33		3
Survival (all stages)	S	0.85	year^{-1}	1
Carrying capacity of a patch (female adults)	K	100	f patch^{-1}	4
Chick loss rate range juvenile stage 1	L	0–10	patch^{-1}	
Dispersal				
Probability to disperse of juvenile stage 2 at density K	$P_{k,j}$	0.4	year^{-1}	2
Probability to disperse of all adult age classes at density K	$P_{k,a}$	0.06	year^{-1}	2
Distance decay coefficient juvenile stage 2	α_j	0.034	km^{-1}	2
Distance decay coefficient of adults all stages	α_a	0.084	km^{-1}	2

[a] f, females.
[b] 1 = Schroder et al. (1996); 2 = Van der Hoorn et al. (1997); 3 = calibrated to have zero growth at K; 4 = Schippers et al. (2009).

2009). To account for this, we introduce a loss rate (L) representing the loss of chicks per patch per year due to all Allee mechanisms together. The leftover stage 1 juveniles ($\mathbf{J}_{1,L}$) after the Allee correction is as follows (see e.g. Boukal and Berec, 2009; Schippers et al., 2009; Eskola and Parvinen, 2010 for similar approaches):

$$J_{1,L} = \max(0, (J_1 - L)) \tag{2}$$

Here, L is the Allee effect inducing loss rate (chicks per patch per year) and $\mathbf{J}_1$ is the total number of juveniles of stage 1 in a patch as calculated by matrix (1) and Eq. (1). Note that the loss rate (L) is in fact density independent, but the consequences of L on per capita reproduction are strongly density-dependent. This is because at low densities R_t is low and the impact of L on per capita recruitment is relatively large whereas at high densities and large R_t the impact of L is relatively small.

The result of this mechanism is that below a certain density threshold no recruits survive and the population declines whereas above a density threshold the populations will grow.

2.3. Dispersal: probability to disperse

In population models dispersal consists of two phases: (1) the probability that an individual will leave the patch and become a disperser and (2) the interpatch movement using a connectivity matrix. We assume that the probability to leave a patch and disperse (P_D) increases with density (Travis et al., 1999; Hovestadt and Poethke, 2006; Schippers et al., 2011). We use a density-dependent relation according to Schippers et al. (2009) that resemble threshold based relations as used by Travis et al. (1999) and Hovestadt and Poethke (2006) to a large extend:

$$P_D = P_{D,K} \left(\frac{A}{K} \right)^3 \quad \text{and} \quad 0 < P \leq 1 \tag{3}$$

Here, $P_{D,K}$ is the dispersal probability at carrying capacity. Adults are especially site-faithful, whereas juveniles have more tendencies to disperse (Stienen and Brenninkmeijer, 1992). According to Van der Hoorn et al. (1997) who analyse ring data of the common tern, only 6% of the adults disperse, whereas 40% of the two-year-old juveniles disperse ($\mathbf{J}_2$, Fig. 1). Since these parameters were mostly measured in well established populations we use these dispersal values for $P_{D,K}$ (Table 1). We assume that all adult age classes have the same low dispersal probability of 6%.

2.4. Dispersal: inter-patch connectivity

Dispersing individuals of seabirds prefer to disperse to nearby patches. The inter-patch connectivity, the probability that a dispersing animal will reach another patch is often described by a negative exponential relation (see e.g. Hanski, 1999, 2008). We use this exponential relation between inter-patch distance and connectivity $P_{i \to j}$ according to Hanski and Thomas (1994):

$$P_{i \to j} = \frac{K \ \exp(-\alpha \cdot d_{ij})}{\sum_{k=1}^{n} K \cdot \exp(-\alpha \cdot d_{ij})} \tag{4}$$

Here K is carrying capacity (nr of adults per patch of all age classes), d_{ij} is the distance between patch i and j (km), n is the number of patches in the population, k is the patch number of an individual population, α is the exponential parameter that determines the decrease in connectivity over the distance. Juveniles disperse farther than adults (Van der Hoorn et al., 1997), and therefore we calibrate two values for α, α_j for one-year-old juveniles and α_a for all the adults age classes, to fit the dispersal data of the common tern in the Netherlands (Van der Hoorn et al., 1997). The exponential model explains 92% of the variation for the juvenile for $\alpha_j = 0.034$ and 99% of the variation for the adults for $\alpha_a = 0.084$ (Table 1). Note that α_j is only used for the $\mathbf{J}_2$ age class (Fig. 1) since one-year-old juveniles do not return to their breeding ground (see also Table 1).

2.5. Model coherence

Here we the describe the exact calculation sequence of the model. Initially, before the time loop started, a connectivity matrix is calculate containing all between patch connectivity values $P_{i \to j}$ using Eq. (4). In the time loop, at the beginning of a year, the model starts with the calculation of the adult density in every patch, subsequently the three density dependent fecundity values of matrix 1 ($F_{3-5+,d}$), are calculated using Eq. (1). Then the survival and reproduction is calculated for the state vectors of all patches using matrix 1. After that, for all patches, the reduction in $\mathbf{J}_1$ is calculated using Eq. (2). Next, a new adult density is calculated and used to estimate the probability to disperse (P_D) of every patch using Eq. (3), then for each patch the number of dispersing animals is calculated as a binomial process using probability to disperse P_D and the amount of animals in the patch ($\mathbf{J}_2$, $\mathbf{A}_{3-5+}$). At the end of the year the dispersing animals of each patch are distributed over the other patches according to the connectivity matrix that was initially calculated. Note that a dispersing animal of a certain age class that disperse to another patch is added to the same age class of the new patch.

2.6. Breeding habitat patch configurations

To improve our understanding of processes, we work with an artificial patch distribution consisting of four squared clusters of breeding patches (Fig. 2). The inter-patch distance within the clusters is 15 km, a distance that is easy for the common tern to bridge (Van der Hoorn et al., 1997). The inter-cluster distances were varied
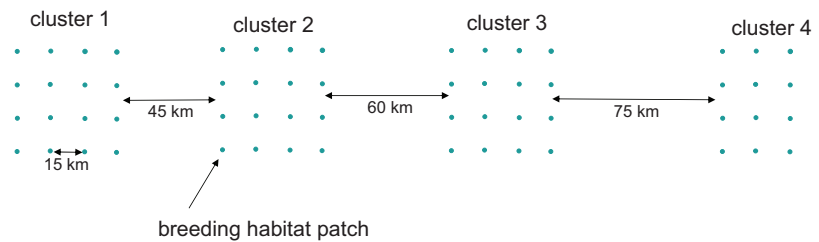
Fig. 2. Spatial layout of seabird breeding habitat patches as used in the model. There are four clusters consisting of 16 breeding habitat patches which can each accommodate 100 breeding females.

according to Fig. 2. The breeding patches have a carrying capacity of 100 adults each, which is a medium colony size for this seabird species in the Netherlands (Schippers et al., 2009, Fig. 2).

3. Simulation and results

The value of the loss rate (L) is relatively uncertain, because it is difficult to measure and because it is dependent on the accessibility of the colony to predators and whether temporary food patches are present in the vicinity of breeding grounds. Additionally, as we will see, L determines whether the model has alternative stable equilibria, so we can compare our results with more traditional approaches without alternative stable equilibria. Therefore, we especially focus on exploring the effect of L on growth, equilibria and population dynamics. For this, we use various spatial configurations starting with a single patch under deterministic conditions and subsequently adding spatial and stochastic complexity to the model. Finally, we explore the effects of L on metapopulation resilience and study the detection of critical thresholds.

3.1. Single patch analysis

Here we deterministically evaluate the intrinsic growth factor of the model at various levels of the loss rate (L) and assess the stable and unstable equilibria of a single patch without dispersal or colonization, assuming that the colonisation equals dispersal.

The loss rate (L) has a distinct effect on the intrinsic growth rate of the population (Fig. 3). When $L = 1$, there is negative growth (Fig. 3, growth factor < 1) at densities below 2. When $L = 8$ the population does not grow even at a density of 30 adults per patch. L also has important consequences for the growth rate at intermediate densities. The carrying capacity, the point at which the line L
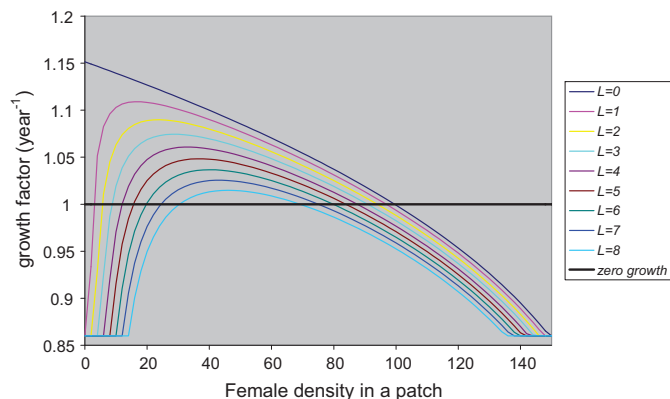
crosses the zero growth line, decreases by 30% as L increases from 0 to 8.

The equilibrium analysis shows clear stable equilibria (solid lines in Fig. 4) and an unstable equilibria (dashed line, Fig. 4). Between the solid and the dashed line, the population is growing, whereas elsewhere the population is declining. For instance, when $L = 3$ and the density is 40 the population grows to the stable equilibrium line at a density of 90 (Fig. 4, point 1). When $L = 6$ and the density is 10, the population goes extinct (Fig. 4, point 2). When L is larger than 9 no survival is possible (Fig. 4, point 3). Finally, when densities are greater than the stable equilibrium, the growth is negative and densities diminish to the stable equilibrium line (Fig. 4, point 4). It is clear in Fig. 4 that L is responsible for two alternative stable equilibria in the model: the stable equilibrium (solid line) and the zero line. Note that the zero equilibrium at $L = 0$ differs from that at higher values of L. Clearly, extinct populations cannot grow when $L = 0$, but when the density is a bit higher the population will grow to the density of 100. When $L = 5$ we need a density of at least 18 animals to get a growing population.

As stated earlier, our model is in fact a demographic stochastic model in which Leslie matrix survival fractions are used as probabilities and recruitment is drawn from a Poisson distribution. Nevertheless, the deterministic model explains the behaviour of the stochastic model to a large extent. We also calculated Fig. 4 with the stochastic version of a single patch model (not shown). The average quasi-equilibrium line roughly matches the stable equilibrium, while the 50% extinction isocline roughly matches the unstable equilibrium line of Fig. 4.
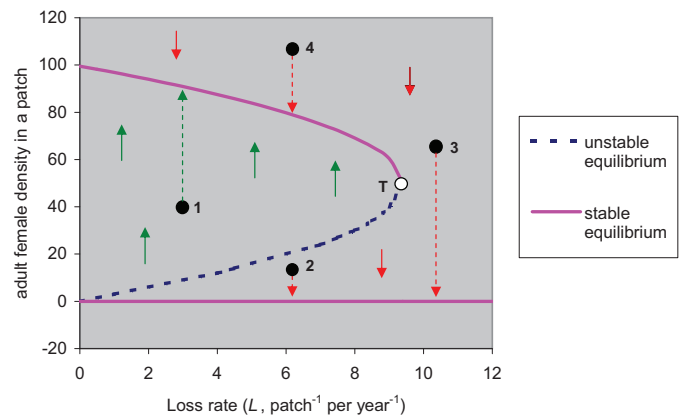

Fig. 3. Deterministic growth factors of a seabird population in response to adult female densities. Lines describe various levels of loss rate (L). Note that if the growth factor is greater than 1, the population is growing, whereas below 1 the population is declining. Loss rate (L) describes the loss of chicks per patch and is responsible for the alternative stable states in the model. At a growth factor of 0.86 all chicks are lost and the adult survival determined the population decay.

Fig. 4. Deterministic alternative stable states at various levels of the loss rate (L). There are two stable equilibria (solid lines) and one unstable equilibrium (dashed line). Arrows indicate that the population is growing or declining. What happens depends on the initial state of a population and the loss rate (L). Point 1 will grow to equilibrium at a constant value of L. Point 4 will decline to equilibrium, the population, however, will go extinct when initialized at points 2 and 3. The loss rate (L) describes the loss of chicks per patch and is responsible for the alternative stable states in the model. Point T indicates the critical threshold. For values of L above this threshold the population will not survive.
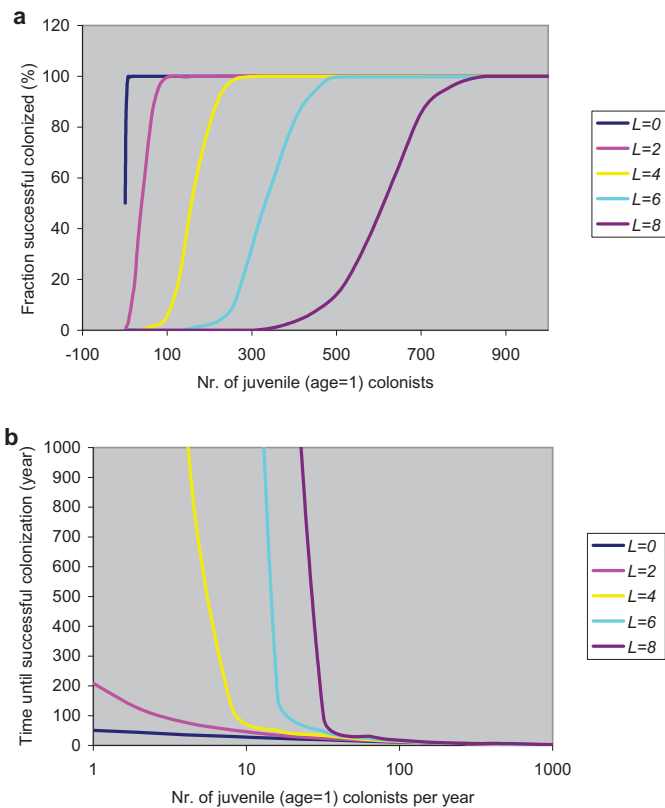
Fig. 5. Colonization success of a cluster of 16 patches. (a) The probability of a successful colonization as a result of a single colonization event. (b) The average time until a successful colonization results from a yearly colonization event. The loss rate (L) describes the loss of chicks per patch and is responsible for the alternative stable states in the model.

3.2. Analysis of a single cluster

We saw in the preceding section that the introduction of the loss rate (L) results in alternative stable equilibria in our seabird model. Consequently, patches will likely go extinct when they are below the unstable equilibrium line. This raises the question of whether empty patches or a cluster of patches can be colonized and how many animals are needed for a successful start-up of a cluster of patches. Therefore we initialize the METAPOP model with a single cluster of 4×4 empty patches with an inter-patch distance of 15 km (see a single cluster as described in Fig. 2). We first evaluate the probability for the population to start up as a result of a single colonization event at various levels of the loss rate (L). Subsequently, we evaluate the period required for the population to start up as a result of a yearly colonization event. We assume that cluster that eventually reach half the carrying capacity (=800 adults) is considered to be started up subpopulation.

The level of L has a large effect on the number of colonists needed for successful colonization (Fig. 5a). When L is zero, one colonist is enough to have a 50% probability for a cluster to start up. This value increases strongly with the value of L: when L is 2 we need 48 birds, when $L = 4$ we need 160 birds, and when $L = 8$ we need 640 birds to have a 50% probability for the cluster to start up.

Usually patch colonisations are no single events but occur on a more frequent basis, with surviving colonists from the past helping to build up the population (Fig. 5b). Here we use the average time to start up a population as a measure because theoretically all populations will start up if we wait long enough. When we have 8 colonists per year and $L = 0$, we must wait on average 30 years to have a successful growing population. When $L = 2$ this increases to

52 years, when $L = 4$ this value is 129. For higher values of L this rises to more than 1000 years. This implicates that there is a minimum threshold of colonists per year to have a successful colonization.

3.3. Dynamics of a multi-cluster metapopulation

To evaluate the effect of the loss rate (L) at the metapopulation level we first did several simulations to evaluate initial conditions and disturbances at levels of L between 0 and 10. We do this in the breeding habitat configuration as described in Fig. 2 that consists of four equally sized clusters of breeding patches with increasing inter-cluster distances.

In the first series of simulations, we start the metapopulation with every patch at carrying capacity (100 adults of age 5+ per patch, Fig. 6a). Results show that when $L = 9$ and 10 the metapopulation goes extinct. For values of $L \leq 8$ all metapopulations survive, however, the quasi equilibrium values are lower at higher values of L. Note that these results are consistent with the stable equilibrium line of Fig. 4.

In the second series of simulations we initialize one patch at carrying capacity leaving all of the other patches empty. The patch at carrying capacity is located in the upper left corner of cluster 1. Results show that only at low values of L are the populations able to expand (Fig. 6b) and reach all clusters. Patterns of population increase correspond to the expansion over the clusters: a period of strong increase corresponds with fast expansion within a cluster, whereas stagnation of growth represents a period in which the population "tries" to bridge the gap between two clusters. Clearly low L values induce fast within-cluster and between-cluster expansion and vice versa. When $L = 0$, all patches are occupied within 130 years; when $L = 4$ this takes roughly the whole simulation period of 1000 years. When $L = 5$ or 6, the initialized patch survives for 1000 years, but the populations are unable to expand from their single patch. At L values higher than 6, the population goes extinct during the simulation period.

In the third series of simulations we initialize the whole first cluster at carrying capacity, leaving all of the other clusters empty. Results roughly match those of the second series (compare Fig. 6b and c). Here, however, simulations with higher values of L perform better. For instance, simulations with L values of 5 and 6 are now able to cross the 45 km gap to the next cluster, whereas in the preceding series they were unable to bridge the 15 km to the next patch.

In the fourth simulation series we start with all patches at carrying capacity. After 100 years, we disturb the most isolated cluster 4 by removing all of the birds and look at the recolonization of this cluster while varying the loss rate (L) between 0 and 10. Results show that only when L is less than 5 the populations are able to recover to the old population levels indicating that under these conditions the populations are able to recolonize cluster 4 within the simulation time (Fig. 6d).

3.4. Colonization time and distance between clusters

The previous section showed that it takes time for a population to bridge the distance between clusters. However, the previous section's results are from single simulations. This calls for a systematic investigation of the relation between the inter-cluster distances and the time required to bridge the inter-cluster gap. For this, we define a spatial configuration consisting of two 4×4 clusters with the same dimensions as in Fig. 2. We start our simulation at carrying capacity in one of the clusters and measure the time it takes until successful colonization of the other cluster is achieved. We do this for various inter-cluster distances and take the average value of 100 simulations as our measure of the colonization time.
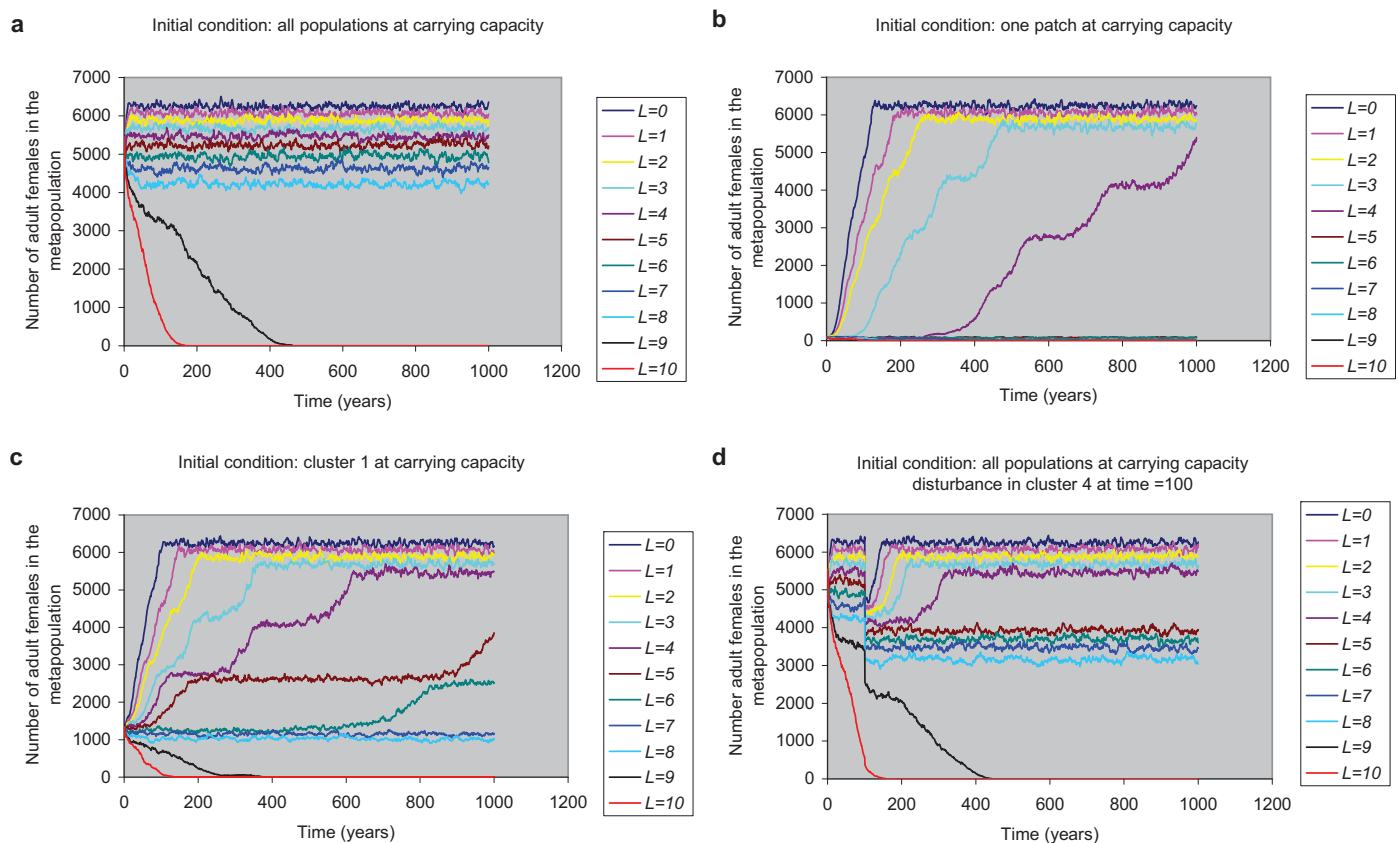
a

Initial condition: all populations at carrying capacity

b

Initial condition: one patch at carrying capacity

c

Initial condition: cluster 1 at carrying capacity

d

Initial condition: all populations at carrying capacity
disturbance in cluster 4 at time =100

Fig. 6. Single simulations with the full stochastic model having a spatial layout according to Fig. 2. (a) The simulation starts with all patches at carrying capacity. (b) The simulation is initialized having the upper left patch of Fig. 2 at carrying capacity whereas all of the other patches are empty. (c) Cluster 1 is initialized at carrying capacity whereas the other clusters are empty. (d) Simulation starts with all patches at carrying capacity; after 100 years there is a disturbance in cluster 4 that removes all of the birds. Fast increase events correspond with expansion in a cluster, relatively stable periods between these events represent periods in which the seabirds could not successfully colonize the next cluster. Note that it takes more time to bridge the gap at higher L values and at higher inter-cluster distances.

At $L = 0$, the relation between the inter-cluster distance and colonization time increases gradually to a distance of 250 km; it takes on average 200 years to bridge this gap (Fig. 7). Thereafter, a strong increase is registered in colonization time: at an inter-cluster distance of 300 km more than 1000 years is needed to bridge the gap. As the value of L increases, the distance at which a gradual increase occurs diminishes. At $L = 6$ and 7 the steep part of the curve already starts at a distance of 30 and 15 km, respectively (Fig. 7). At $L = 8$, the population is unable to bridge a gap of 15 km (not shown in Fig. 7).
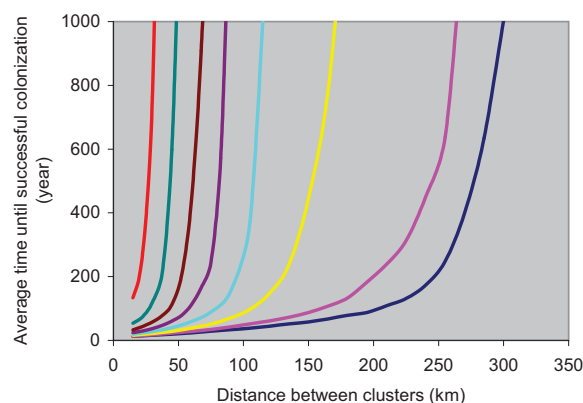

Fig. 7. Time until successful colonization of an empty cluster from another cluster in relation to the inter-cluster distance. The two clusters have 16 patches (Fig. 2) and one cluster is initialized at carrying capacity. Note that L has a large impact on the colonization potential of seabird species.

3.5. Population stability and resilience

The loss rate (L) determines the resilience of populations. Therefore, we study the dynamics at two values of loss rate: $L = 6$ in the relatively stable part of the curve and $L = 8.5$ near the catastrophic shift (see Fig. 4). We did two series of 20 simulations at these L levels in the configuration as described in Fig. 2, starting with each patch at carrying capacity. In one a disturbance that halves the population at all patches at year 200. In another we introduce noise in the birth rate parameter at year 200 with a coefficient of variation (standard deviation/mean) of 30%.

When the L value is near the critical threshold ($L = 8.5$), the population is relatively unstable and a large-scale disturbance or an increase in environmental stochasticity could cause extinction of the whole metapopulation. At $L = 6$ the metapopulation is resilient enough to tolerate the disturbance and the increased variation (Fig. 8a and b).

3.6. On the detection of critical thresholds

For nature managers dealing with seabird populations it is interesting to learn whether populations are near the critical threshold (T in Fig. 4). Recent research reveals that populations near the critical threshold have increased standard deviations and temporal autocorrelations, because near the threshold the decrease in the growth-density relation is less steep (Van Nes and Scheffer, 2007; Scheffer et al., 2009) (compare $L = 0$ and $L = 8$ in Fig. 3 at the point at which the lines cross the zero growth line the second time). Clearly this should be the case in the deterministic models of a single patch.
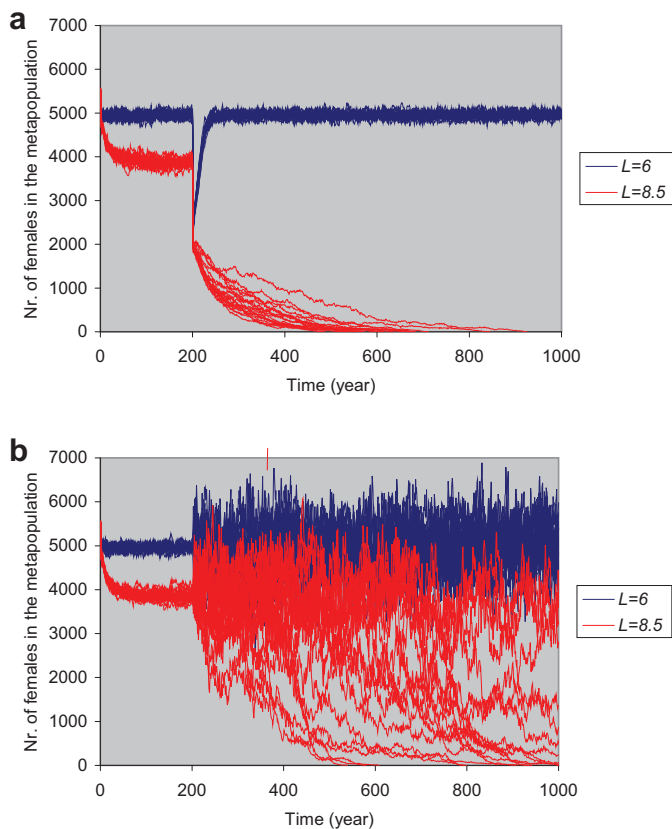
Fig. 8. Effects of disturbance and increased variation on the survival of a metapopulation as described in Fig. 2. Both figures show 20 independent simulations. (a) There is a 50% disturbance in all patches at year 200. (b) We introduce 30% variation in the birth rate parameter at year 200. Note that near the critical threshold ($L=8.5$) the population is less resilient than farther away from this threshold ($L=6$).

But is this also true if this patch is part of a metapopulation? Here interacting populations might mask this effect. To answer this question, we study population patterns and the coefficient of variation (CV = the standard deviation divided by the mean) in two cases: (1) a single patch that is part of a metapopulation as described in Fig. 2 with all patches occupied and (2) a single patch that is not part of a metapopulation in which we assume that dispersal always equals recolonization, which resembles the non-spatial approach of Van Nes and Scheffer (2007) and Scheffer et al. (2009).

At L values near the critical threshold ($L=8.5$) we see higher temporal autocorrelations and fluctuations than at low L values (Fig. 9a and b). Additionally, we see that autocorrelations and variations are generally larger in the nonspatial case. An increase of the loss rate (L) results, as expected, in an increase of the coefficient of variation (CV) from about 0.07 when $L=0$ to 0.14 when $L=8$ (Fig. 9c). However, the steepest increase and highest variation is found for a single patch that is not part of a metapopulation.

4. Discussion

4.1. Analysing main results

Or results show that the introduction of Allee-type density-dependence had large consequences for the survival and recolonization ability of seabirds. The reason for these results can be found in the fact that these effects induces alternative stable equilibria at the local level, significantly reducing the probability of achieving successful colonization at the metapopulation level

(Amarasekare, 1998; Taylor and Hastings, 2005). If Allee effects are strong, growth is only possible when density levels at a patch exceed a certain minimum. Therefore, a few colonists are often insufficient to start up a population whereas small populations are more vulnerable for extinction. Our results show that at low values of loss rate (L) our seabird species is able to bridge inter-cluster distances 20 times larger than at high values of L. This means that at high values of L, patches are effectively more isolated than would be expected when taking distance as an isolation measure. Furthermore, we see that the last part of the distance–colonization time relation is very steep (Fig. 7). For instance, when $L=0$ the birds on average bridge a gap of 100 km in 40 years and 200 km in 90 years, but they need more than 1000 years to bridge a gap of 300 km. This finding is crucial because our calculations suggest asymptotic relations between distance and colonization time, meaning that above a certain distance it is virtually impossible for a population to bridge a gap. This points to clear-cut distance thresholds that are strongly affected by the loss rate (L). These results are very important in the light of climate change, because large species distribution shifts are expected and colonization of new breeding habitat will be crucial for species survival (Gremillet and Boulinier, 2009). Clearly both nonspatial approaches (e.g. Schroder et al., 1996; Jenouvrier et al., 2005) and straightforward spatial approaches that do not take Allee effects into account (e.g. Oro and Ruxton, 2001; Gremillet and Boulinier, 2009) may overestimate the viability and sustainability of seabird metapopulations.

4.2. Isolation of a mobile bird

It seems strange that one of the world's most mobile species groups could suffer from isolation. This is because seabirds are generally site-faithful and tend to return to their previously used nesting area (Becker et al., 2001; Spendelow et al., 1995; Van der Hoorn et al., 1997). Only the few birds that do not return to their original breeding site and nest instead at an alternative location, can be regarded as dispersing animals. Furthermore, dispersal distances are low compared to the large distances the birds can fly (Stienen et al., 2009). For example, the median dispersal distance of juveniles of the common tern is 20 km and that of adults is 8 km (Van der Hoorn et al., 1997), whereas the winter domicile for the Dutch populations is in Africa, roughly 4000 km away from their breeding grounds. In addition, this study shows the isolation that result from Allee effects. So both the birds' limited dispersal and Allee effects determine the degree of effective isolation of breeding grounds and thus determine the metapopulation structure of a seabird population. The fact that the dispersal of these animals is very conservative might also be the result of Allee effects because dispersal is risky when there are strong Allee effects. Here we expect strong selection for conservative dispersal (see e.g. Travis and Dytham, 2002; Fowler, 2009).

4.3. Different mechanisms contributing to the Allee effect

We mentioned four mechanisms responsible for Allee effects and alternative stable equilibria in the population dynamics of seabirds. These are: (1) the dilution of predation risk at higher densities, (2) better early warning and group defence in colonies, (3) more efficient foraging because of information exchange among foraging adults and (4) sex ratios are more likely to deviate from one at low densities. The first two mechanisms relate to the presence of predators. However, predation risk is not everywhere the same. For instance, terrestrial predators like foxes and common rats, which form a major threat to chicks (Keitt et al., 2002; Mulder et al., 2009; Igual et al., 2006; Stienen and Brenninkmeijer, 2006; Russell et al., 2009; Towns et al., 2009), cannot reach a coastal islands that serve as seabird breeding habitat. Here, predatory
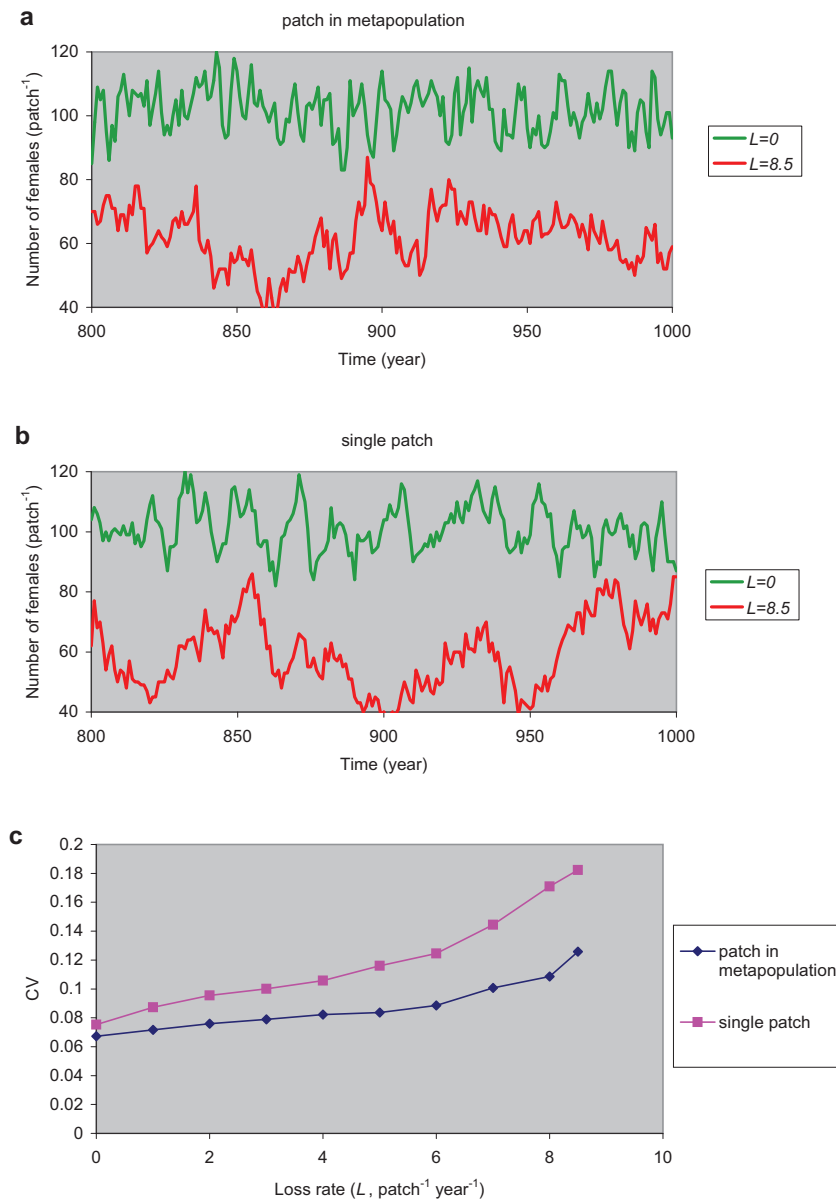
Fig. 9. Population fluctuations as effected by the loss rate (*L*). (a) A patch in the metapopulation as defined in Fig. 2 starting with all patches at carrying capacity. (b) A single patch starting at carrying capacity. (c) The effect of *L* on the coefficient of variation (CV = standard deviation/mean) in both cases.

losses are determined only by predatory birds. This implies that controlling access of terrestrial predators to potential breeding sites is a key measure to increase the start-up probability of potential colonies. The third mechanism relates to information exchange among adults; here diving activity of conspecifics and the typical white plumage of most seabirds may help individuals to locate temporal food patches, like shoals of fish. When temporal and patchy food areas are a major food source this will likely contribute to the density-dependence causing Allee effects. But when food patches are not temporal and patchy, single birds are as effective as groups and we expect no density-dependent effects of this mechanism (Buckley, 1997). The fourth mechanism is the simple fact that a bird's chances of reproduction is smaller at low densities because here the sex ratio is expected to deviate from one. This effect is always present but is more important at low bird numbers. The fact that three out of four mechanisms are determined by local conditions like predation pressure, nest location and food type means that the alternative stable equilibria of a colony are

probably highly determined by local breeding conditions and are therefore highly variable depending on seabird species and colony location.

4.4. On the detection of critical thresholds

From a management perspective, it is interesting to learn whether a colony is near its critical thresholds. Our simulations show that the population level near the critical threshold can be large, so managers may have no clue that they are close to a catastrophic shift. Like Scheffer et al. (2009) and Van Nes and Scheffer (2007), our simulation reveals that populations near the critical threshold showed increased autocorrelation in time increases resulting in slower recovery from perturbations. However this signal is weak, meaning that a manager needs long-term and good quality data to pick up this signal. Moreover, our results show that an increase in variation as well an increase in autocorrelation near the critical threshold is less pronounced in populations that are

part of a metapopulation. Here, dispersing and colonizing animals dampen population fluctuations. Furthermore, it is important to know not only whether the population is near the critical threshold but also whether a population is close to an unstable or stable equilibrium. These thresholds can be estimated using simple differential equations to mimic the alternative equilibria of the matrix model (see ESM Appendix A).

The critical threshold value of the loss rate (L) is then (see ESM Appendix A)

$$L_{\text{crit}} = \frac{r \cdot K}{4c}, \tag{5}$$

where r is the relative growth rate (year^{-1}), K is the carrying capacity of the population and c is a conversion factor that relates juvenile to adult loss, here this value is 0.38.

The unstable equilibrium population value is (see ESM Appendix A),

$$N_{\text{crit}} = \frac{K}{2r} \left(r - \sqrt{\left(r^2 - \frac{4 \cdot r \cdot c \cdot L}{K} \right)} \right), \tag{6}$$

whereas the stable equilibrium is (see ESM Appendix A),

$$N_{\text{stab}} = \frac{K}{2r} \left(r + \sqrt{\left(r^2 - \frac{4 \cdot r \cdot c \cdot L}{K} \right)} \right) \tag{7}$$

Although these formulas are straightforward, it is difficult to precisely estimate the parameters. The estimation of loss rate (L) is especially difficult because it is a composite value describing all of the mechanisms inducing Allee effects. When predation is the dominant mechanism, L can be replaced by the chick loss due to predation in a patch. Nevertheless, these relatively simple equations may provide a rough picture of the colony state and whether it is endangered.

5. Conclusion

We show here that alternative stable equilibria induced by Allee effects might be responsible for a twenty fold decline in the recolonization distances in seabird population, causing patches and parts of metapopulations to effectively become more isolated. This leads to long recolonization times of empty breeding patches which consequently cause slower metapopulations expansion and recovery. Ignoring these Allee effects may lead to serious overestimation of the sustainability, viability and mobility of seabird colonies and metapopulations. Consequently, straightforward network evaluation methods and metapopulation studies that do not take Allee effect into account overestimate the viability and sustainability of seabird populations. These results are especially important because we expect large distribution shifts due to climate change, in which colonization of new breeding habitat is a key process.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2011.05.022.

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