

## Investigating population dynamics and dispersal following a perturbation in population of Black-headed Gulls (*Chroicocephalus ridibundus*) with an integrated modeling framework: changes in dispersal patterns, but not causes

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## ABBREVIATIONS

**AE** : "Alive Elsewhere" - All colonies not monitored by Capture-Mark-Recapture, but monitored by direct visual counting.

**CMR** : Capture-Mark-Recapture

**IPM** : Integrated Population Model

**LR** : La Ronze - Name of the pond where the main colony is located

**SAT** : Satellite - All colonies monitored by Capture-Mark-Recapture and monitored by direct visual count, except the main colony on La Ronze pond.

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## 1. INTRODUCTION

### 1.1 *Spatially structured population*

The study of the spatio-temporal dynamics of populations has led to the identification of a broad range of population systems linked by flows of individuals (Hanski et Gaggiotti 2004; Thomas et Kunin 1999). These population systems are generally known as “spatially structured populations” (Thomas et Kunin 1999). The connectivity between populations is enabled by the phenomenon of dispersal (Clobert 2012; Greenwood et Harvey 1982). Dispersal is generally defined as the movement of an individual from its site of birth to its site of first reproduction (natal dispersal), or its movement between successive sites of reproduction (breeding dispersal) (Greenwood et Harvey 1982; Clobert 2012). When the dispersal between populations is low, the dynamics of populations depend mainly on the local survival and fecundity of individuals. Such systems have been more specifically termed “metapopulations” (Levins 1970; Hanski et Gaggiotti 2004). In contrast, when the dispersal between populations is high, emigration and immigration processes of individuals are key determinants of local population dynamics. Such systems correspond to Harrison’s definition of “patchy populations” (Harrison 1991).

Taking dispersal into account in population dynamics allows for a better understanding of ecological phenomena and interactions between populations, such as genetic processes (Hastings 1994) or epidemiological dynamics within local populations (May et Nowak 1994). Considering dispersal between populations has also led to major advances in understanding demographics (Thomas et Kunin 1999). The concept of metapopulation has notably provided insights into the causes, consequences and interactions of colonization and extinction events among subpopulations (Hanski et Gaggiotti 2004). For populations that persist over time, very simple theoretical models of metapopulations have for instance shown that even a low level of dispersal between subpopulations can stabilize population sizes and favor population viability (Gyllenberg, Söderbacka, et Ericsson 1993; Hastings 1993), a result that has also been empirically demonstrated in wild systems (e.g. Lecomte et al. 2004). This stabilizing effect seems to occur through both reinforcement and maintenance of subpopulations caused by the movement of individuals. For instance, immigration from surrounding populations can prevent the local extinction of a small, declining population by maintaining population size and enhancing genetic diversity. This phenomenon is known as the "rescue effect" (Brown et Kodric-Brown 1977). Therefore, comprehending dispersal, along with its causes and mechanisms, is crucial to understand the functioning of spatially structured populations.

### 1.2 *Evolutionary Causes and Mechanisms of Dispersal*

Dispersal is costly for individuals (Bonte et al. 2012). These costs can impact individual survival and reproduction. For example, dispersal may lead to reproductive costs like delays in finding mates or establishing territories (Bonte et al. 2012). Costs generally affect both survival and reproduction. These typically include energetic expenditures, increased predation risk during dispersal, or leaving a familiar habitat for an unknown and potentially unfavorable environment (Bonte et al. 2012). The benefits of dispersal must outweigh its cost to promote dispersal evolution. Whether it is natal dispersal or breeding dispersal, several evolutionary causes of dispersal have been identified. Bowler and Benton (2005) summarize these ultimate causes into three categories: reduced kin competition at the natal site, inbreeding avoidance, and habitat variability such as resource availability. Studies have

shown for instance that younger individuals often have a propensity to disperse further than older individuals, which can be attributed to the search for unsaturated territories or inbreeding avoidance (Aebischer 1995; Bowler et Benton 2005). However, the decision to disperse or not is also triggered by proximate factors such as habitat degradation or high level of competition with conspecifics (Bowler et Benton 2005). The choice to emigrate depends on the environment and the experiences of individuals over the course of their lifetime. Besides, physical condition and personality can also influence dispersal patterns, with some individuals being more inclined to take risks when dispersing than others (Clobert et al. 2009).

As all life-history parameters, dispersal is subject to natural selection and different evolutionarily stable dispersal strategies can emerge depending on the ecological context (Comins, Hamilton, et May 1980). The optimal dispersal strategy is the one that maximizes reproductive success and minimizes the probability of reproductive failure. When there is spatio-temporal variability in habitat quality, the “win-stay:lose-switch” strategy may be more advantageous than the pure philopatry strategy of “always stay” (Switzer 1993; Hendry, Castric, et Kinnison 2004). Empirical studies have shown that in many bird species, individuals tend to change locations following a year of poor reproductive success (Freer 1979; Burger 1982). The benefits of relocation after poor reproduction depend on the predictability of future reproductive success, thereby minimizing the risk of settling in an unfavorable environment (Switzer 1993; Burger 1982). In unpredictable environments, the costs of dispersal often outweigh the benefits, especially for species with strong habitat preferences (Clobert 2012). In this case, the probability to settle in an unsuitable habitat is high. Therefore, a dispersal strategy that integrates information about the future potential quality of other sites may be advantageous (Boulinier et Danchin 1997; Doligez et al. 2003). The information about the quality of a resource or habitat derived from the performance of other individuals, known as “public information”, can inform individuals beyond their personal experience, known as “private information”.

In summary, different dispersal strategies have emerged to cope with environmental variability. In this context, perturbation can be considered as extreme environmental variation. Understanding how the proximal causes of dispersal on which a strategy depends are affected by a strong, rare and punctual change in environmental conditions remains largely unexplored.

### **1.3 Impacts of Perturbations on Dispersal Patterns**

A “perturbation” in the context of population dynamics is an external event capable of significantly altering the system at various hierarchical levels, including the individual, population, and ecosystem (Oro et al. 2024a). According to this definition, any sudden environmental change with a large amplitude and limited duration corresponds to a perturbation. In this sense, anthropogenic activities and extreme meteorology are potential perturbations (Sergio, Blas, et Hiraldo 2018). Conversely, relatively frequent events with low amplitude should be called “disturbances” (Oro et al. 2024b). Disturbances can be often considered as inherent components of ecosystems, playing a crucial role in some ecological dynamics (Sergio, Blas, et Hiraldo 2018). For example, the role played by wildfires in certain ecosystem dynamics is now widely acknowledged (Bowman, Balch, et Artaxo 2009). On the contrary, a perturbation has the potential to drastically alter the functioning of a population.

Long-term demographic studies capable of quantifying population responses to a perturbation are scarce (Oro et al. 2024). And when such studies exist, the effect of perturbation is often assessed

through measurements of population size variation and rarely investigate the underlying changes in demographic parameters such as survival or dispersal (Oro, Jiménez, et Curcó 2012). This limitation leaves many unknowns regarding population responses to perturbation, particularly in terms of demographic traits. In addition, research on perturbation has so far focused on radical changes that persist over time, such as sudden habitat alterations or the introduction of a predator (Burger 1982; Payo-Payo et al. 2018; Chase 1991). The aim of such studies has been to understand the establishment of a new regime for the population in a new environment. For example, it was demonstrated how the construction of a dam led to a significant decline in the Greater flamingos (*Phoenicopterus roseus*) population on the Spanish coast presumably by affecting individual fecundity (Oro, Jiménez, et Curcó 2012), or how habitat modification negatively impacted the breeding site fidelity of Audouin's gulls (*Ichthyaetus audouini*) in a colony (Fernández-Chacón et al. 2013).

However, when studying the effect of a perturbation event, it is crucial to distinguish between the impact of the perturbation itself and any simultaneous changes in the environment it causes, in order to differentiate the two effects and identify those specific to the perturbation event. To do that it is necessary to study situations where the environment remains unchanged before and after the event. Only the study of a punctual perturbation can determine whether the population returns to its pre-perturbation equilibrium state, or if its functioning has been permanently altered, and how demographic processes and in particular dispersal strategies are affected by the occurrence of a major perturbation in the structure of the population.

#### **1.4 Demographic and Dispersal Responses of a Colonial Species to a Major Perturbation**

In this work, we analyzed an empirical case of perturbation in a patchy population of Black-headed Gulls (*Chroicocephalus ridibundus*) to understand how the demographic parameters and notably dispersal changed following a major and punctual perturbation affecting one of its larger subpopulations. The Black-headed Gull is a colonial bird species, gathering every year at breeding sites distinct from foraging grounds (Rolland, Danchin, et de Fraipont 1998; Danchin et Wagner 1997). In such systems, where nesting habitats are spatially discrete, subpopulations are clearly identifiable. Colonial species have been extensively studied to understand the causes and consequences of dispersal at the population level (Clobert 2012; Hanski et Gaggiotti 2004). Previous work on these species have notably shown that they exhibit strong conspecific attraction, which allows them to benefit from the advantages of colonial life, such as reduced predation pressure and access to information about feeding sites (Danchin et Wagner 1997). In addition to this conspecific attraction, some studies have shown that colonial birds may use this public information, such as average reproductive success of colonies, to guide their dispersal decisions (Blanchet, Clobert, et Danchin 2010; Boulinier et al. 2008; Acker et al. 2017). The reproductive success of locally breeding conspecifics could even be influential enough to outweigh an individual's own breeding experience when deciding whether to emigrate (Danchin, Boulinier, et Massot 1998).

Our studied population is situated in the Forez plain in central France. Every year, a dozen colonies of Black-headed Gulls settle in ponds managed by humans within a farmland landscape to breed. This population has been monitored through individual Capture-Marking-Recapture (CMR) and counts of breeding pairs for nearly 50 years. The dynamics of this population has been finely studied using data collected between 1986 and 2005 (Péron et al. 2010). This work has shown

that the population of the plain has gradually centered around one major colony, called la Ronze, which hosted between 3,000 and 5,000 breeding pairs at that time, representing 50% to 70% of the population. The high density of breeders in this colony resulted in high attractivity and high breeding fidelity. New breeders recruiting into this main colony have been shown to have delayed recruitment compared to those recruiting into other colonies because of intense competition for nests (Péron, Lebreton, et Crochet 2010). Thus, the main colony of la Ronze, by concentrating the majority of breeders, structured the overall population dynamics. In 2007, la Ronze pond was dried up for the first time since the gulls began to congregate on this site, preventing breeders from settling at this pond that year. This drastic, punctual, and localized suppression of the main colony provides the opportunity to describe the change in population dynamics and notably dispersal after a major and punctual perturbation.

The strong dispersal links between subpopulations demonstrated by Péron et al (2010) are expected to enhance the resilience of this patchy population to such perturbations over the medium to long term. In our case, we predicted that the immediate effect on the population, over the few years following the perturbation, would be a decrease in fidelity to the main colony due to the loss of conspecific attraction. Additionally, the massive movement of breeders from the main colony to satellite colonies could also have affected the fidelity of other colonies. Indeed, the arrival of experienced breeders is likely to increase competition in the satellite colonies, causing the departure of other previously established breeders. However, in the longer term, beyond a few years, we expected the pre-perturbation dynamics to be largely restored, mainly through the attraction effect of conspecifics, with the reformation of a large colony either on la Ronze or at a new pond.

Here, we leverage this long-term study of the Black-headed Gull and capitalize on the methodological advancements of integrated population models (IPM) to enhance parameter estimation by integrating different data sets (Kéry et Schaub 2012). Integrated population models represent a methodological advancement for estimating demographic parameters (Schaub et Kéry 2022) as they allow population trends, survival, fecundity, and movement probabilities between colonies to be inferred altogether. Thus, by comparing demographic parameters before and after the drying of the pond hosting the main colony, we aim to determine how the dispersal dynamics of this patchy population have changed in the face of such a major and punctual perturbation.

## 2. MATERIAL AND METHODS

### 2.1 *Study species and population*

The Black-headed Gull is a medium-sized, highly gregarious and opportunistic bird species. It occupies a wide range of wetland habitats, including lakes, rivers and coastal areas. This species has a diverse diet consisting of insects, fish, and invertebrates, and can also scavenge human refuse (Vernon 1972). Black-headed gulls generally start breeding at the age of two years. Although the species can nest in isolated pairs, the majority of pairs are found in colonies ranging from a few to several thousand pairs. Breeding pairs are highly territorial, often displaying aggressive behaviors towards intruders within close proximity to their nest (JD Lebreton et Landry 1979; Péron et al. 2010). Clutch size usually consists of 2-3 eggs, with both parents involved in incubation and chick-rearing (Lebreton et Landry 1979).

The Forez plain in central France (45.66N, 4.16E) hosts a patchy population of Black-headed

Gulls, which nest in human-managed ponds within a farmland landscape. Within this network of nearly 300 ponds, approximately 95 have been occupied by gulls at least once since 1976. From the beginning of the monitoring in 1976 until 2007 (see Fig. 1), the population was relatively stable, with approximately 6,000 breeding pairs nesting annually in the plain. However, in 2007, la Ronze pond, which hosted the main colony of the plain, was drained for one year, preventing the gulls from nesting at the site that year. Following this event, the population experienced a dramatic decline, with nearly half of the breeding pairs lost. Since then, the numbers have not recovered, and the population continues to decline.

## 2.2 Data collection

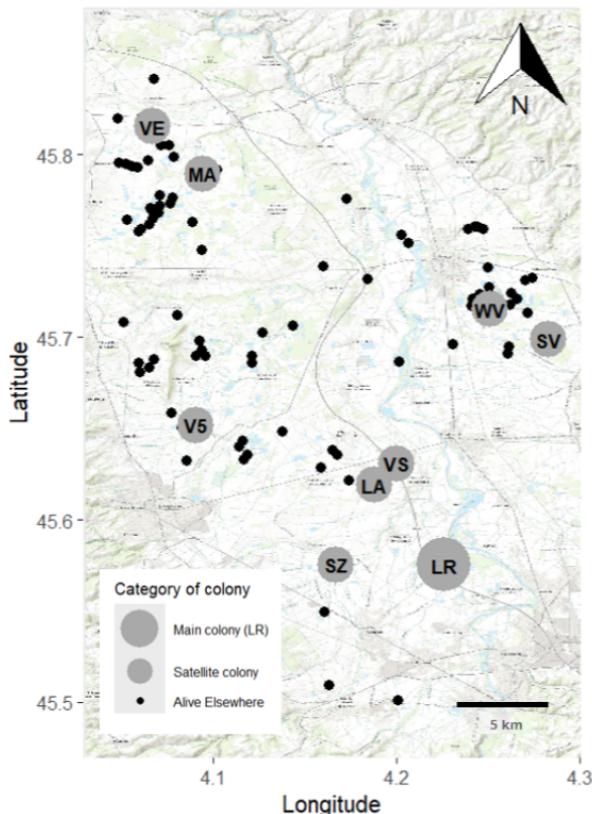
We used two types of data collected from 1986 to 2019: Capture–Mark–Recapture (CMR) data and breeding population counts (number of breeding pairs at colonies).

Prefledging young birds have been captured by hand and have been ringed at the colonies with metal and alphanumeric rings (Table 1). In certain years, some adult birds have also been captured and ringed using a cannon net in ploughed fields and landfills surrounding the colonies (Table 1). Resighting efforts have been conducted annually on breeding birds using a telescope to read rings from a floating hide. Nine colonies have benefited from these resighting efforts (Fig. 1): the largest colony established on la Ronze pond, coded LR, and eight other monitored colonies, referred to as satellite colonies SAT. Only the main colony LR benefited from continuous observation efforts over the years. For the SAT colonies, ring readings were not conducted for all breeding years. Over the entire study period, the CMR data consists of 33,285 individually ringed birds and 6,030 resightings of breeders on the study colonies (Table 1).

Every year, an aerial survey has been conducted to locate all occupied colonies in the plain. Then, on the ground, the number of breeding pairs in each located colony has been determined through direct visual counting. In May, after triggering a general alarm in the colony, all individuals flying over the site were counted. All the individuals counted in the colonies have been considered to be breeders. One-year-old individuals, which are not yet breeding, visit the breeding colonies only very occasionally. Two counting methods have been used depending on the size of the colony. The first method estimated the number of pairs by multiplying the number of observed breeders by a fixed ratio of 0.7 (Grosbois 2001). This method was applied for all satellite colonies. For the large LR colony, visual count methods were unreliable before 2007 due to the very high number of breeders. Instead, a method based on the ratio between ringed and unringed birds and the probability to read a ring on a detected bird was used (Grosbois 2001). However, this second method could not be applied between 2001 and 2006. During this period, direct colony counts indicated rather stable population numbers. For these six years, it was therefore decided to replicate the value found in 2000 to conserve the information on colony stability as already done in Périon et al (2010). From 2007 onwards, the size of the LR colony was considered small enough to be estimated using the direct counting method.

## 2.3 Description of the model

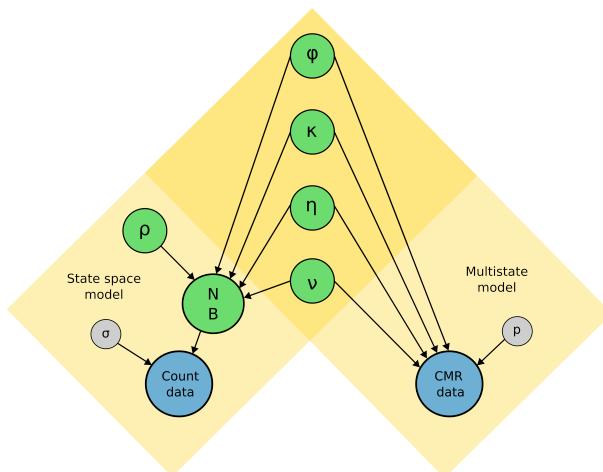
We used an Integrated Population Model (IPM) to model the dynamics of the Black-Headed Gull population (Schaub et Kéry 2022). This approach allows data at individual and population levels to be



**Figure 1.** Spatial configuration of the black-headed gull population colonies in the Forez plain between 1986 and 2019. Colonies are represented with gray circles. Three types of colonies are represented : the large circle is the main colony LR, mid-sized circles are the colonies monitored by Capture-Mark-Recapture (satellite colonies), and the small circles are colonies that were occupied but not monitored by Capture-Mark-Recapture, collectively forming the "Alive Elsewhere" colony.

**Table 1.** Summary of ringing effort (number of individuals ringed) and ring resighting effort (number of individuals visually controlled) for each colony and period: before the perturbation (1986-2006), shortly after the perturbation (2007-2010), and a few years after the perturbation (2010-2019).

Colony	Ringing Effort			Reading Effort		
	1986-2006	2007-2010	2011-2019	1986-2006	2007-2010	2011-2019
La Ronze	22907	496	775	3018	158	491
Les Marquants	2399	303	175	368	54	166
La Verchère	929	0	0	289	17	0
Vallon 5	186	0	0	118	0	0
La Vergnat Sud	0	0	274	2	10	115
Les Champs Blancs	0	54	3	0	51	3
Sury	0	309	21	0	331	61
Vieux Ouest	0	193	684	0	204	425
La Sausée	0	0	291	0	0	149
Alive Elsewhere	29442	41	224	0	0	0
<b>Total</b>	<b>29442</b>	<b>1396</b>	<b>2447</b>	<b>3795</b>	<b>825</b>	<b>1410</b>



**Figure 2.** Directed acyclic graph of the Integrated Population Model (IPM) used to model the demographics of the studied population of Black-Headed Gull. The graph illustrates the different components of the model and how the datasets provide information on demographic parameters and population abundance. The sub-models are represented as yellow rectangles and labeled with the model structure. Demographic parameters are shown as green circles, observation parameters as gray circles, and data is represented by blue circles. Arrows indicate the dependencies between the datasets and the parameters they inform on. Node notations: phi = survival; kappa = recruitment; eta = natal dispersal; nu = breeding dispersal; rho = fecundity; p = recapture probability; sigma = the observation error; N = number of prebreeders; B = Number of breeders. Figure adapted from Margalida et al. (2020)

analyzed jointly in a single statistical framework, which allows the sharing of information between the different datasets. The central element of an IPM is a matrix population model, which links demographic parameters to variations in population size. Our IPM used two datasets: (i) multi-state CMR data and (ii) counts of breeding pairs (Fig. 2). No data on fecundity was available. Within this framework, full error propagation through the model is possible under the assumption that the two datasets are independent, although IPMs have been shown to be robust to non-independence of CMR and population count data (Abadi et al. 2010). Here, non-independence between our capture-mark-recapture (CMR) data and our survey data was considered negligible.

## **2.4 Patchy population model**

### **2.4.1 The colonies**

Our model included nine colonies monitored by CMR. Resighting effort was continuously carried out at the largest colony, La Ronze (abbreviated as LR). Other colonies benefited from discontinuous resighting efforts : Les Marquants, MA; La Verchère, VE; Vallon 5, V5; La Vergnat Sud, VS; Les Champs Blancs, LA; Sury, SV; Vieux Ouest, WV; La Sausée, SZ. These smaller colonies are referred to as satellite colonies (SAT). Not all the Forez gull colonies could be monitored by the ringing programme. Nevertheless, the number of individuals on these colonies not monitored by CMR is known from counts. In order to integrate these colonies into the model, we defined an "Alive Elsewhere" (AE) state, which groups together all colonies not monitored by CMR that ecologically belong to the population.

### **2.4.2 The demographic parameters**

The population model we used was a reproductive stage-classified matrix population model (Caswell 2001). This population model was inspired by the population model developed by Péron et al (2010) on the same population. Our population model was female-centered and was built to fit prebreeding census data. It included two life stages: 1) prebreeders, noted  $P_s$ , corresponding to individuals born on the site  $s$  that have not yet reproduced, and 2) breeders, noted  $B_s$ , corresponding to individuals that reproduce on site  $s$  for the current year. The relationship between these two stages were governed by five demographic processes: (i) survival, (ii) reproduction, (iii) recruitment to reproduction, (iv) natal dispersal and (v) breeding dispersal (Fig. 3).

(i) Annual apparent Survival probability We distinguished two age classes for survival probability (Grosbois 2001; Péron 2009). We estimated the survival probability of juveniles (between fledging and the age of 1 year) and the survival probability of adults (after the age of 1 year). Adult survival and juvenile survival were modeled with random year effects to take account for inter-annual variation of survival probabilities :

$$\text{logit}(\phi_{ad,t}) \sim \text{Normal}(\bar{\phi}_{ad}, \sigma_{\phi_{ad}}^2)$$

Where  $\bar{\phi}_{ad}$  is the mean survival and  $\sigma_{\phi_{ad}}^2$  is the temporal variability of  $\phi_{ad,t}$ .

$$\text{logit}(\phi_{juv,t}) \sim \text{Normal}(\bar{\phi}_{juv}, \sigma_{\phi_{juv}}^2)$$

Where  $\overline{\phi_{juv}}$  is the mean survival and  $\sigma_{\phi_{juv}}^2$  is the temporal variability of  $\phi_{juv,t}$ .

#### (ii) Reproduction

The fecundity of the population is defined as the average number of chicks produced by a female. Because the largest colony (LR) was suspected to have higher fecundity than the other colonies, fecundity was modeled differently for LR and the other colonies (Péron et al. 2010).

#### (iii) Recruitment

The probability of transition from being a prebreeder to being a breeder is defined as recruitment probability. Here, we assumed all individuals were recruited during the 2nd summer, meaning that the recruitment probability was set to 1 for individuals aged 2 or more, based on what is known of the biology of the species (Grosbois 2001; Péron 2009). We also assumed that, once they have recruited, individuals remain in the breeder stage, even though they may not actually breed in some years. Skipping reproduction appears to be rare among gulls (Pugesek et Wood 1992; Pyle et al. 1997).

#### (iv) Natal dispersal

Natal dispersal is defined as the transition from the birth site to the site of first reproduction. In our model, natal dispersal was modeled to happen during the year of first reproduction. Because prebreeders are not present on the colonies, their detection is impossible before their first reproduction. Consequently, all movements between birth and first reproduction were summarized by this single transition. The probability of staying on the birth site corresponded to natal fidelity.

#### (v) Breeding dispersal

From one year to another, dispersal between breeding colonies was modeled by a transition probability. The probability of staying on the same site as the previous year corresponded to breeding fidelity.

$$B_{s,t+1} = \sum_i P_{i,t} \cdot \phi_{ad} \cdot \eta_{i,s} \cdot \kappa + \sum_j B_{j,t} \cdot \phi_{ad} \cdot \nu_{j,s}$$

$$P_{s,t+1} = B_{s,t} \cdot \rho_{class(s)} \cdot \phi_{juv} + P_{s,t} \cdot \phi_{ad} \cdot (1 - \kappa)$$

$B_{s,t}$  : number of breeders in colony  $s$  in year  $t$

$P_{s,t}$  : number of prebreeders in colony  $s$  in year  $t$

$\phi_{juv}$  : annual survival rate of individuals aged 0 to 1 year

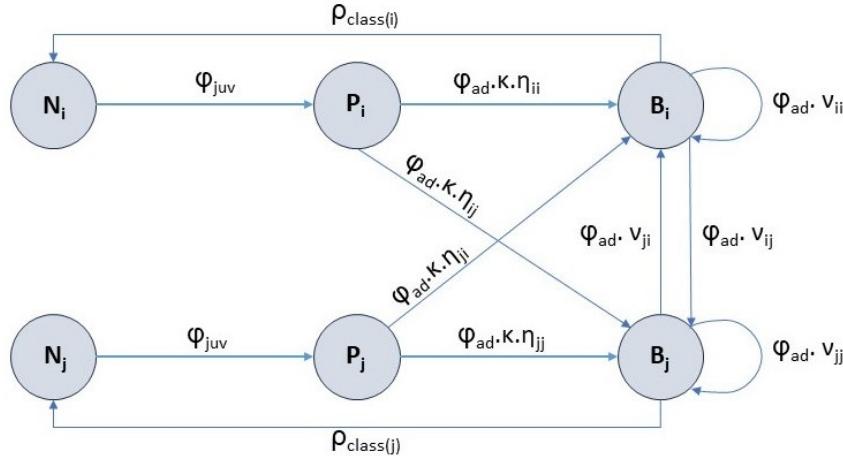
$\phi_{ad}$  : annual survival rate of individuals older than 1 year

$\kappa$  : probability of recruitment (probability of a prebreeder to transition into a breeder)

$\eta_{i,j}$  : probability of reproducing for the first time in colony  $j$  given that the individual was born in colony  $i$

$v_{i,j}$  : probability of reproducing in colony j given that the individual previously bred in colony i

$\rho_{\text{class}(s)}$  : fecundity (number of females per pair). This parameter depends on the colony class (main colony or satellite colony)



**Figure 3.** Life-cycle graph for the population model. The nodes refer to breeders (B) and prebreeders (P) and the nestling (N) in two connected colonies i and j. Parameters are defined in the main text.

#### 2.4.3 Integration of colonies not monitored by CMR

Not all the Forez gull populations could be monitored by the ringing programme. Nevertheless, the number of individuals on these colonies not monitored by CMR are known from counts. In order to integrate these colonies into the model, we define an "Alive Elsewhere" (AE) site which groups together the all non-tracked sites that ecologically belong to the population. The AE site is then included in the design of the CMR analysis. The probability of detecting individuals from this site is zero. In this way, individuals that leave the monitored sites to settle permanently on non-monitored sites, is distinguishable from mortality.

#### 2.4.4 Modeling extinction-colonization dynamics

Some ponds were not occupied continuously over time. Such extinction-colonization dynamics were identified with certainty during the monitoring in the field. To model these dynamics, in years when a colony was reported as extinct by the counts, both natal dispersal and breeding dispersal to this colony were set to zero. We then normalized the other dispersion parameters so they still summed to 1. This assumed that the birds from the newly extinct colony all dispersed to the other colonies and remained in the population, and that the proportionality in dispersal parameters between the remaining colonies was maintained.

#### 2.5 Multistate capture-recapture modeling

The CMR data was analyzed using a multistate model. CMR data was summarized into capture histories, corresponding to the sequence of observed states of an individual over time. Our CMR

data comprised 31 states between which individuals could transition between years (Table 2). With three life-stages (nestling, prebreeder and breeder) and ten “colonies”, the states of the nestling were coded from 1 to 10 according to their colony of birth, breeders were coded from 11 to 20 according to the colony where they breed, and pre-breeders were coded from 21 to 30 according to their colony of birth. State 0 corresponded to dead individuals (Table 2).

**Table 2.** Codification of the states. The dead state, coded with the value 0, is not represented in this table.

Colony	Code	Reproduction Stage		
		Nestling	Breeder	Prebreeder
La Ronze	LR	1	11	21
Les Marquants	MA	2	12	22
La Verchère	VE	3	13	23
Vallon 5	V5	4	14	24
La Vergnat Sud	VS	5	15	25
Les Champs Blancs	LA	6	16	26
Sury	SV	7	17	27
Vieux Ouest	WV	8	18	28
La Sausée	SZ	9	19	29
Alive Elsewhere	AE	10	20	30

Transition probabilities between two successive states depended on demographic processes that can be described in a square matrix whose dimension is the number of states. For the sake of clarity, the transition matrix presented here shows an example for a population with two colonies, i and j. Rows represent the state at time t, and columns represent the state at time t+1. Based on the same demographic processes as in the population model described above, our transition matrix  $\psi_t$  for two colonies takes the following form:

$$\psi_t = \left( \begin{array}{c|ccccc|cc} & \mathbf{N}_{i,t+1} & \mathbf{N}_{j,t+1} & \mathbf{B}_{i,t+1} & \mathbf{B}_{j,t+1} & & \mathbf{P}_{i,t+1} & \mathbf{P}_{j,t+1} \\ \hline \mathbf{N}_{i,t} & 0 & 0 & 0 & 0 & & \phi_{juv} & 0 \\ \mathbf{N}_{j,t} & 0 & 0 & 0 & 0 & & 0 & \phi_{juv} \\ \mathbf{B}_{i,t} & 0 & 0 & \phi_{ad}\gamma_{i,i} & \phi_{ad}\gamma_{j,i} & & 0 & 0 \\ \mathbf{B}_{j,t} & 0 & 0 & \phi_{ad}\gamma_{i,j} & \phi_{ad}\gamma_{j,j} & & 0 & 0 \\ \mathbf{P}_{i,t} & 0 & 0 & \phi_{ad}\eta_{i,i}\kappa & \phi_{ad}\eta_{j,i}\kappa & \phi_{ad}(\sum_k \eta_{s,k})(1-\kappa) & 0 & 0 \\ \mathbf{P}_{j,t} & 0 & 0 & \phi_{ad}\eta_{i,j}\kappa & \phi_{ad}\eta_{j,j}\kappa & 0 & \phi_{ad}(\sum_k \eta_{s,k})(1-\kappa) & \end{array} \right)$$

However, the states of all individuals are usually not known in CMR studies. Our ability to assign an individual to a state thus depends on an observation process, which hides the biological process described by the transition matrix. The detection of a state was modeled with a specific probability depending on the reproductive stage of the state and the year of observation. For nestlings and prebreeders, the states were never observed during the monitoring, so their detection probability was set to 0. Similarly, because no observation effort was carried out in the AE state, detection probability for breeders in AE was also set to 0. For the sake of clarity, the detection matrix presented here shows an example for a population with two monitored colonies, i and j, and for one year t (see

matrix). The detection matrix  $s$  is as follows:

$$p_t = \left( \begin{array}{c|c|c|c|c|c} \mathbf{N}_{i,t} & \mathbf{N}_{j,t} & \mathbf{B}_{i,t} & \mathbf{B}_{j,t} & \mathbf{P}_{i,t} & \mathbf{P}_{j,t} \\ \hline 0 & 0 & p_i & p_j & 0 & 0 \end{array} \right)$$

To account for temporal variation in observation effort on the monitored colonies, detection probabilities were modeled with an annual random effect:

$$\text{logit}(p_{s,t}) \sim \text{Normal}(\bar{p}_s, \sigma_{p_s}^2)$$

We fitted the multistate CMR data using an m-array formulation, which allows for a faster model convergence by reducing dataset dimensions (Schaub et Kéry 2022). However, this requires converting capture histories into an m-array format, which summarizes the capture histories of all individuals in a matrix showing the number of recaptured birds in one year and state (columns) according to the year and state in which they were last captured (rows). Each m-array row  $m_{s,t}$  is modeled by a multinomial distribution with parameters  $\pi_{s,t}$  (probability of capture history fragment for state  $s$  at capture occasion  $t$ ) and  $R_{s,t}$  (number of individuals in state  $s$  released on a given date). For detailed guidance on using m-array in CMR data analysis, see Schaub and Kéry's work (2022).

$$m_{s,t} \sim \text{Multinomial}(\pi_{s,t}, R_{s,t})$$

Where  $\pi_{s,t}$  is the probability of obtaining each fragment of the capture history, specific to a state  $s$  and an occasion of capture  $t$ , and  $R_t$  the number of individuals in a given state released on the given date.  $m_{s,t}$  is the observed number of recaptured individuals released in state  $s$  at the occasion  $t$ .

## 2.6 Population count modeling

Population count data was analyzed using a state-space formulation (Royle et Kéry 2007). The number of breeding pairs in each colony and each year was modeled using a normal distribution centered on the observed count value. The observational error  $\sigma_{obs,s,t}$  was modeled as the product of the observed count value and an error  $\sigma_i$  specific to the counting method  $i$ . In this way, the observation error was proportional to the colony size to account for differences in survey precision between small and large colonies.

$$\text{CountedPairs}_{s,t} \sim \text{Normal}(B_{s,t}, \sigma_{obs,s,t}^2)$$

$$\sigma_{obs,s,t} = B_{s,t} * \sigma_i$$

Where  $\text{CountedPairs}_{s,t}$  is the observed number of breeders on the colony  $s$  in year  $t$ ,  $B_{s,t}$  is the estimated number of breeders in colony  $s$  in year  $t$ ,  $\sigma_{obs,s,t}$  is the observational error specific to a colony  $s$  in year  $t$ ,  $\sigma_i$  is the error specific to the counting method  $i$ .

## 2.7 Investigation of the perturbation

The model was applied for the three periods around the perturbation, i.e. the drying up of LR pond in 2007, where the main colony was located: (i) before the perturbation, from 1986 to 2006, (ii) a transitional period post-perturbation, from 2007 to 2010, and (iii) a post-perturbation period, from

2011 to 2019. In order to assess the demographic dynamics specific to each of these periods, survival, fecundity, and dispersal parameters were estimated independently for each period.

### **2.8 Assessment of the performance of the model on simulated data**

To ensure that our model provides unbiased estimates on simulated data, we constructed simulated datasets and ran our model on them. Demographic parameters were chosen based on estimates commonly found in the literature specific to our species and population (notably Péron et al. 2010). Five colonies were simulated, including one without ringing effort to mimic the state "Alive Elsewhere" (AE). We generated a CMR dataset from the transition matrix (see  $\psi_t$ ) and a count dataset from the population model equation (see Fig.3) from a simulated population dynamics over 20 years. The number of ringed individuals per year and per colony were similar to those of the real dataset. The detection probability was set to follow a uniform distribution ranging from 0.2 to 0.4. Our integrated population model provided accurate estimates of population parameters on this simulated data. The model yielded unbiased results, allowing us to proceed to the analysis of the real data.

### **2.9 Implementation**

All calculations, including the joint likelihood calculation and statistical inferences, were performed in a Bayesian framework, with JAGS software (Plummer 2003) using R v4.3.1 (R Core Team 2023) and the jagsUI package (Kellner et Meredith 2024). We ran three chains, running for 60,000 iterations following a 10,000-iteration burn-in period to ensure convergence, with a thinning interval of 20. Convergence was assessed through visual inspection of the MCMC chains and the Gelman–Rubin convergence statistic (Gelman, Carlin, et Stern 2014). All results are reported with means and 95% Bayesian credible intervals.

We used non informative priors for all parameters (Appendix 1). The model required a prior for the population sizes of each colony during the first year for both breeders and prebreeders. For the breeders, we used uniform priors with bounds set at plus or minus 80% the observed count values. For the prebreeders, because they could not be observed and thus counted, we used an estimation of the number of prebreeders based on the proportion of prebreeders and breeders at equilibrium from a stable stage distribution, using a matrix population model (Schaub et Kéry 2022). The demographic parameters used for this parameterization were derived from previous estimates of the demographic rates of the species (Péron et al. 2010). From these estimates, we used uniform priors with bounds set at plus or minus 80% of these values.

### **2.10 Complementary analyses**

To quantify the heterogeneity in the distribution of breeders between colonies before and after the perturbation, we calculated the Gini coefficient applied to the colony sizes of occupied ponds. The Gini coefficient is a measure of the inequalities among the values of a frequency distribution. A Gini coefficient of 0 indicates complete equality, whereas a Gini coefficient of 1 indicates the maximal inequality among values, characterized by a single non-zero value. Additional analyses were performed on the outputs of the model. To investigate the role of conspecific attraction in structuring dispersal before and after the perturbation, we tested for a correlation between estimates of natal or breeding dispersal and estimates of colony size. A Spearman correlation coefficient was

computed on the posterior distributions of fidelity or settlement probabilities and of the number of breeders in colonies, to build a distribution of correlation coefficient. We used the same approach to test the relationship between natal fidelity and breeding fidelity.

### **3. RESULTS**

#### ***3.1 Variation in population sizes***

From 1986 to 2006, the breeding population size decreased by 42% (32%-51%), from 8,711 (7,209-10,952) pairs to 4,783 pairs (4,157-5,487) (see Fig.4). In 2007, the year of the drying of la Ronze pond, the population decreased by 2,016 (1,332-2,747) breeders, representing a 45% (32%-51%) decline in a single year. From 2007 to 2019, the population continued its decrease, reaching 2,097 pairs (1,745-2,585) across the entire plain in 2019.

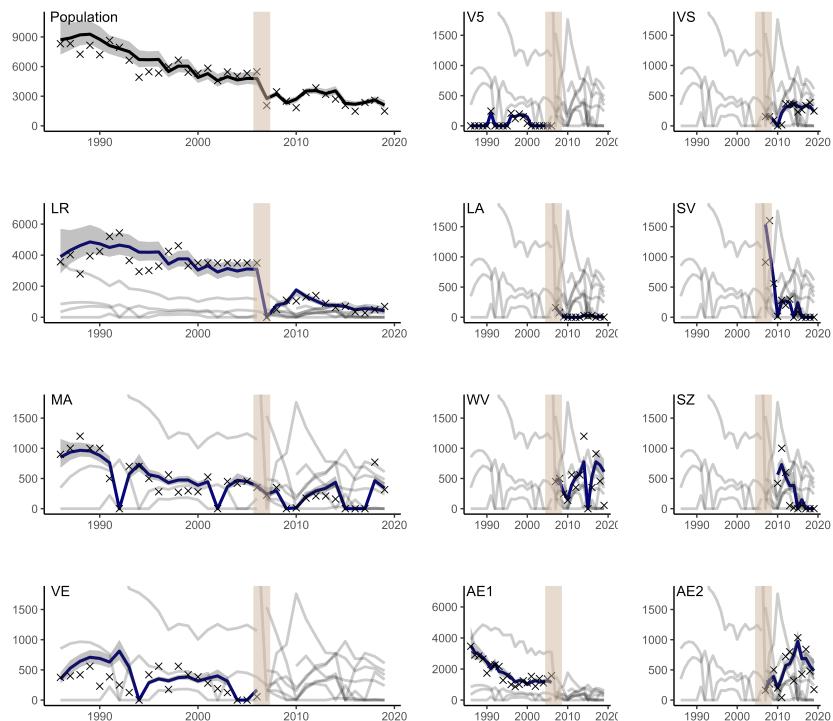
The LR colony declined from 4,006 (2,825-5,690) pairs in 1986 to 2,582 (2,582-3,638) pairs in 2006. In 2007, no adults reproduced on LR as the pond was dry. From 2008 just after the perturbation to 2012, the LR colony increased in numbers, reaching 1,723 pairs (1,357-1,886). Yet, after 2012, the colony started to decline, reaching 421 pairs (338-525) only in 2019. Apart from 2007, the LR colony has always been occupied. All other ponds had intermittent occupation.

The heterogeneity in the distribution of breeders between colonies, quantified using the Gini coefficient applied to the colony sizes of occupied ponds, sharply decreased after the perturbation in 2007 (Appendix 2).

#### ***3.2 Variation in demographic parameters induced by the perturbation***

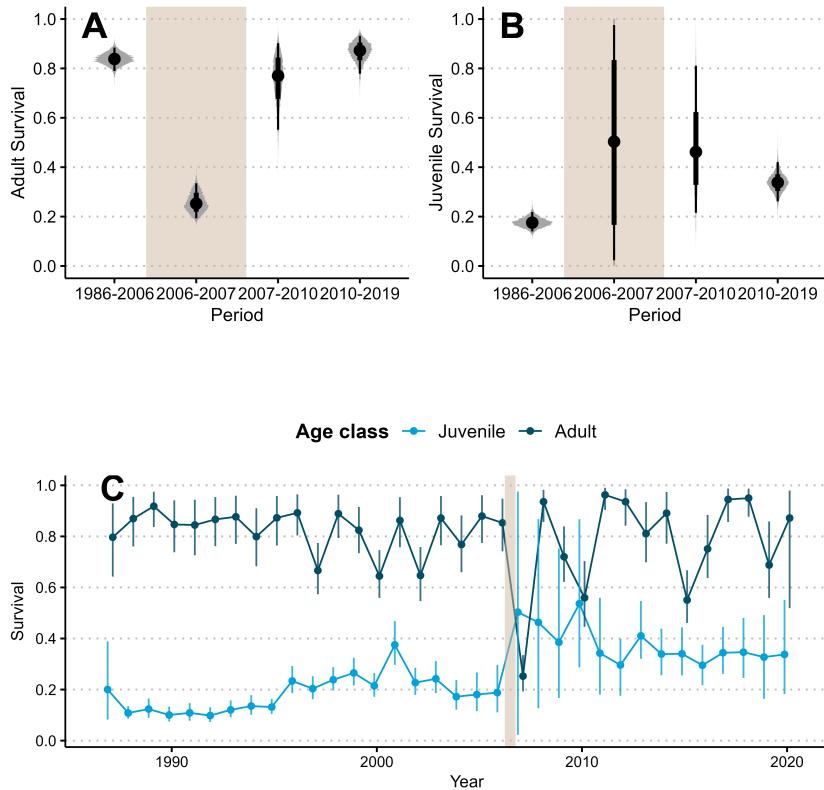
Posterior mean and 95% credible interval of all demographic parameters estimated by the IPM are reported in the appendix 3. Annual survival estimates for adults were equivalent before and after the perturbation, with a mean survival of 0.84 (0.79-0.88) between 1986 and 2006, and 0.87 (0.78-0.93) between 2010 and 2019 (Fig. 5). Adult survival was much lower the year of the perturbation, with a mean adult survival of 0.25 (0.19-0.33) between 2006 and 2007. Adult survival was estimated at 0.76 (0.55-0.90) the years immediately following the perturbation, in 2007-2010. Mean juvenile survival was higher after the perturbation than before the perturbation, with a mean juvenile survival of 0.18 (0.14-0.22) between 1986 and 2006, and 0.34 (0.26-0.42) between 2010 and 2019. Mean juvenile survival estimates could not be estimated precisely in the year of the perturbation and the following short term period, with a mean juvenile survival of 0.50 (0.02-0.97) in 2006-2007, and 0.48 (0.22-0.81) in 2007-2010 (Table 4). The interannual variation in survival showed a progressive increase in juvenile survival between 1986 and 2006 (Fig. 5). Besides, in addition to the year of perturbation in 2007, interannual variation in survival revealed particularly low adult survival estimates, below 0.60, in 2010 and 2015. Fecundity was estimated at 0.97 (0.91-1.00) for LR colony and 0.96 (0.87-1.00) for the satellite colonies in 1986-2006. These values were constrained by the upper bound of their prior distributions and cannot be interpreted.

Breeding fidelity of individuals occupying the LR colony was inferior after the perturbation, with a value estimated at 0.98 (0.97-0.99) in 1986-2006, and 0.59 (0.51-0.66) in 2010-2019 (Appendix 3). The same difference was observed for natal fidelity of individuals born at LR colony, with a value estimated at 0.75 (0.65-0.82) in 1986-2006, and 0.24 (0.15-0.36) in 2010-2019. Although the 95% credible intervals overlap, both breeding fidelity and natal fidelity for the MA colony, the only other



**Figure 4.** Estimated number of breeders (colony size) on the colonies monitored by CMR (Capture-Mark-Recapture) from 1986 to 2019. Lines represent the posterior means in each year for colony size (blue line) and the total population size (black line), with 95% credible intervals in gray. Crosses correspond to the raw breeder counts data. The vertical band marks the perturbation that occurred at la Ronze in 2007. The colony code is written in the upper left corner. All colonies are represented in shaded lines within each plot.

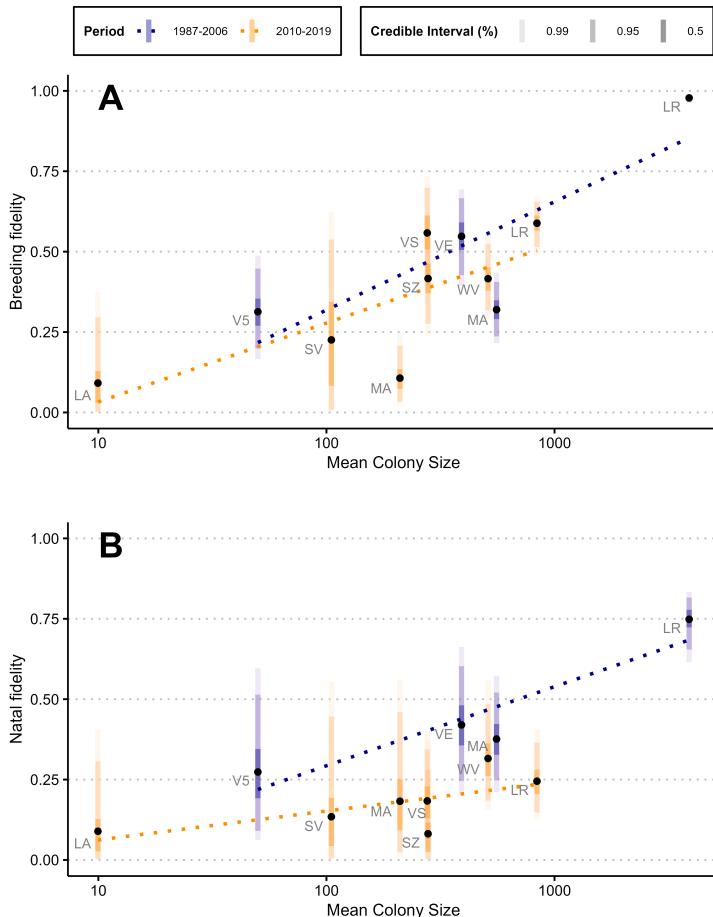
colony that was monitored before and after the perturbation, seemed lower in the years following the perturbation (Appendix 3).



**Figure 5.** Annual survival rates for juvenile and adult Black-headed gulls in the population of the Forez plain. The vertical band marks the perturbation that occurred at la Ronze in 2007. A : Posterior distribution of the mean survival rate for adults for the four study periods. B : Posterior distribution of the mean survival rate for juveniles for the four study periods. C : Interannual variation of survival rates from 1986 to 2019, with mean and 95% Bayesian credible intervals. Values for adults are in dark blue and values for juveniles are in light blue

### 3.3 Relationships between fidelity and mean colony size

Spearman's correlations between the posterior distributions of breeding fidelity and mean colony size were positive for both periods: 0.62 (0.40–0.80) in 1986–2006 and 0.77 (0.46–0.96) in 2010–2019 (Fig. 6). No differences were found between the periods. Spearman's correlations between natal fidelity and mean colony size were positive for the pre-perturbation period, with a value of 0.75 (0.20–1.00) in 1986–2006. For the post-perturbation period, despite the mean correlation coefficient being 0.48, the correlation was not statistically different from 0 according to the 95% credible interval (−0.11–0.93). No differences in the relationship were found between the periods.



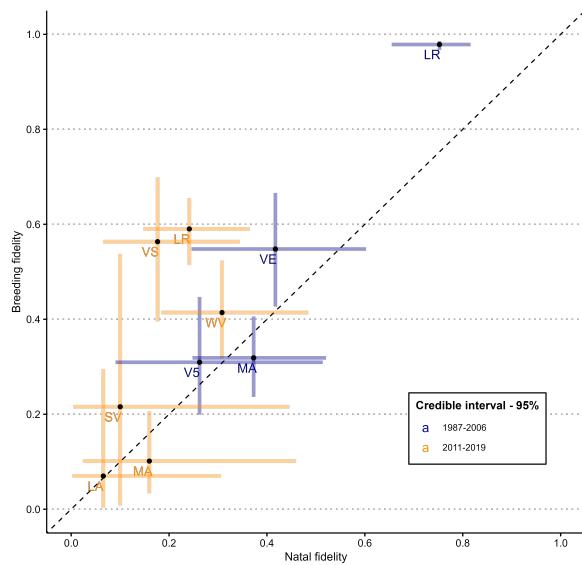
**Figure 6.** Breeding and natal fidelity in relation to the colony size in the Black-headed gull population of the Forez plain. Results are shown for two periods: before the perturbation in blue (1986-2006) and after the perturbation in orange (2010-2019). The lines are the result of a regression specific to each period. Colony sizes are log-transformed. A : Breeding fidelity. B : Natal fidelity. Intervals represent 99%, 95% and 50% Bayesian credible intervals of fidelity.

### 3.4 Relationships between breeding fidelity and natal fidelity

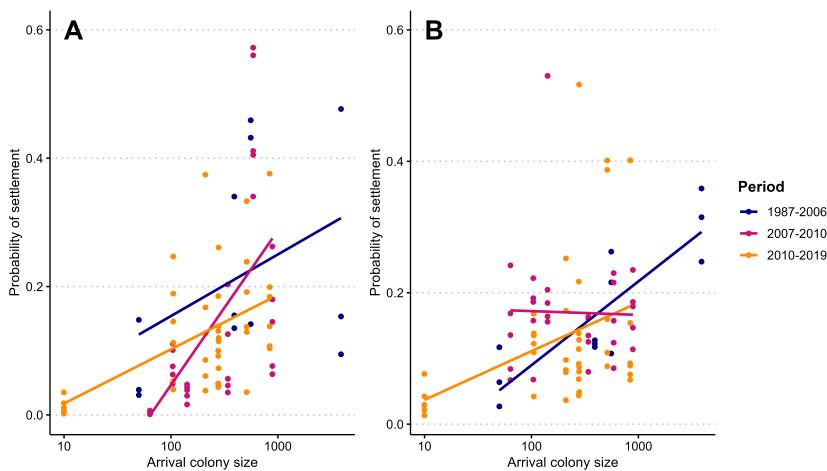
Spearman's correlations between the posterior distributions of breeding fidelity and natal fidelity were only strictly positive for the pre-perturbation period, with a value of 0.77 (0.20-1.00) in 1986-2006 (Fig. 7). For the post-perturbation period, despite the mean correlation coefficient being 0.30, the correlation was not statistically different from 0 according to the 95% credible interval (-0.39-0.82). No differences in the relationship were found between the periods.

### 3.5 Relationships between settlement probability and mean colony size

For breeding dispersal, Spearman's correlations between the posterior distributions of settlement probabilities and of the size of the colony of arrival were positive for all periods (Fig. 8): 0.44 (0.14-0.69) in 1986-2006, 0.65 (0.49-0.78) in 2007-2010 and 0.46 (0.30-0.62) in 2010-2019 (Fig 8).



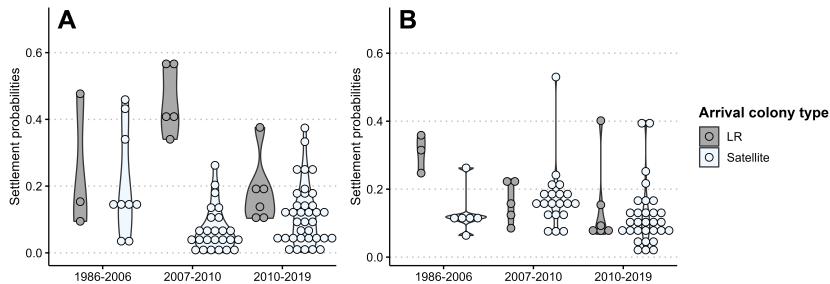
**Figure 7.** Breeding fidelity in relation to natal fidelity for the monitored colonies of Black-headed gulls in the population of the Forez plain. Results are shown for two periods: before the perturbation in blue (1986-2006) and after the perturbation in orange (2010-2019). Intervals represent 95% Bayesian credible intervals.



**Figure 8.** Probability of settlement given that individuals do not remain on the same site, in relation to the arrival colony size, for the monitored colonies of Black-headed gulls in the population of the Forez plain. Results are shown for three periods: before the perturbation in blue (1986-2006), shortly after the perturbation in pink (2007-2010), and a few years after the perturbation in orange (2010-2019). The lines are the result of a regression specific to each period. Colony sizes are log-transformed. A : Breeding settlement. B : Natal settlement.

No differences in the relationships were found between the periods.

For natal dispersal, Spearman's correlations between the posterior distributions settlement probabilities and the arrival colony size were positive for two periods: 0.72 (0.45–0.93) in 1986–2006, 0.31 (0.11–0.51) in 2010–2019. Between 2007 and 2010, the correlation did not differ from 0 in 2010–2019 (mean 0.05 and 95% interval -0.29–0.38). No differences in the relationship were found between the periods.



**Figure 9.** Probability of settlement given that individuals do not remain on the same site, in relation to the arrival colony type (LR colony or Satellite colony), and the period : before the perturbation (1986-2006), shortly after the perturbation (2007-2010), and a few years after the perturbation (2010-2019), for the monitored colonies of Black-headed gulls in the population of the Forez plain. A : Breeding settlement. B : Natal settlement.

### 3.6 Relationships between settlement probability and the arrival colony type

For both breeding and natal dispersal, there is no evident difference of probability of settlement on LR pond and SAT ponds both in 1986–2006 and in 2010–2019 (Fig.9). Just after the perturbation, in 2007–2010, the probability of settling on LR pond was notably higher than on a SAT pond, with values between 0.35 and 0.55 for LR pond and values between 0.01 and 0.26 for SAT pond. For first breeders, the probability of settling on LR pond pond or SAT pond remained equivalent, with values between 0.08 and 0.25.

## 4. DISCUSSION

### 4.1 The perturbation induced an exceptional dispersal response, leading to a new population structure and dynamics.

#### 4.1.1 A definitive loss of breeders at the population level

The perturbation on the pond occupied by the main colony had immediate major consequences on the population structure and the dispersal dynamics between the colonies. Because no breeders were able to settle on the pond that hosted the main colony, three non-exclusives responses might have been expected: 1) breeders skipping reproduction in the year of the perturbation, which is an expected response for long-lived species (Sanz-Aguilar et al. 2011), 2) breeders settling elsewhere temporarily on the plain, or 3) breeders permanently emigrating from the population. In the year of the perturbation, no increase in breeder numbers in the nearby colonies nor unusual pond colonization was observed. The drying of LR pond instead coincided with a massive drop of 4,060 breeders at the

scale of the entire breeding population, representing 45% (32%-51%) of the breeding population size. This decline in the exact year of the drying provides initial evidence in favor of the hypothesis of a mass departure of individuals from the population. This mass departure is further confirmed by a major drop in the apparent survival at the population scale. While the apparent survival rate of adults was estimated at around 0.84 (0.79–0.88) in the years before the perturbation, it dropped to 0.26 (0.19–0.33) in the year of the perturbation. Because long-lived species like Black-headed Gulls (van Dijk et al. 2012) invest more in survival than in fecundity (Stearns 1976), and because the drying of the pond is unlikely to increase adult mortality, the considerable decrease estimated in survival can most likely be explained by an event of permanent emigration out of the plain. On its own, such an extremely low apparent adult survival rate would have implied an even more pronounced population decline in the year of the drying of LR pond, but this effect has been mitigated by the recruitment of prebreeders and probably, to some degree, by background immigration. To our knowledge, such large-scale permanent emigration events have never been documented in colonial bird species, likely because such situations of temporary site unavailability are rare. Two cases of the displacement of breeders after a short, strong perturbation have been reported in the literature, but neither was followed by a dispersal response to a distant location. In a small colony of California gulls (*Larus californicus*), the arrival of a predator following the draining of a reservoir induced the relocation of breeders and caused a small proportion of adults (15%) not to return to the breeding site in subsequent years (Chase 1991). In Canada, after springtime shooting at one of their two colonies, 92% of a large population of Double-crested cormorants (*Phalacrocorax auritus*) shifted temporarily to a very close site, on an island less than 5 km away (Cairns, Dibblee, et Daoust 1998). Besides strong perturbation, it was noted that the accumulation of repeated disturbances could also lead to the progressive abandonment of a breeding site by the breeders in Audouin's gulls (*Ichthyaetus audouinii*) (Fernández-Chacón et al. 2013).

The permanent emigration event in our study population in response to the perturbation lasted only one year. LR pond was recolonised the year just after the drying. The number of individuals breeding on this site increased over four years, then stabilized at a third of the number breeding on the site before the perturbations. After the perturbation, the probability of settlement of experienced breeders was higher on LR pond than in the satellite ponds, with values between 0.35 and 0.55 for LR pond and values between 0.01 and 0.26 for satellite ponds. This difference in attractiveness between sites was not observed for first-year breeders, indicating that the increase in numbers on LR after the drying was mainly driven by the recolonization of experienced breeders. This observation bears some similarity with studies investigating the colonization dynamics of Audouin's gull, where colonizers were also found to be mostly experienced breeders. (Payo-Payo et al. 2017). However, in our case, it was the recolonisation of a pond where previous colonies were characterized by high fecundity, and not the colonization of a previously unoccupied pond. Indeed, a large proportion of the population (54%) nested on LR pond the year before the perturbation. The information of the former site quality must have been known by some experienced breeders, which could explain their rapid return to the site. Thus, this response to the perturbation may suggest that Black-headed Gulls memorize the quality of sites. Alternatively, experienced individuals may be sensitive to different environmental features than 'naive' individuals, for example, better assessing the intrinsic quality of the site or being less influenced by the presence of conspecifics.

#### 4.1.2 A new population structure and dynamics after the perturbation

The perturbation occurred in the context of a declining population, which experienced a decrease of 42% over 20 years even before the perturbation. After the perturbation, a decline with a similar trend was observed, with a decrease of 25% over 12 years. In parallel to the population decline, the number of occupied ponds has gradually diminished from around thirty colonies in 1986 to around ten colonies in 2019 (see Appendix 3). Several hypotheses can be put forward to explain this persistent decline in the population. One probable reason is the diminishing availability of food resources. The gulls living in the Forez plain seemed to feed mainly on earthworms at the start of the study (Francesiaz et al. 2017). Changes in farming practices in France have caused a considerable drop in the earthworm biomass per hectare (Pérès et al. 2011; Vauthier 2012). However, the lack of precise information on changes in the diet of the Black-headed Gull in our population does not allow to confirm this hypothesis. Another non-exclusive explanation could be the opening and closing of landfill sites in the region. For some vertebrates, rubbish dumps can provide food resources that may improve body condition, reproductive performance, and survival rate, significantly influencing their population dynamics (Plaza et Lambertucci 2017). This has notably been demonstrated for other gull species related to Black-Headed Gulls (Delgado et al. 2021; Egunez et al. 2018). In particular, a large landfill located less than ten kilometers from the main colony LR was heavily used by Black-headed Gulls before its closure in 1998. Hundreds of birds were captured and marked there during the monitoring program. The closure of this landfill might have triggered the decline of the population.

While the perturbation did not seem to have changed the demographic trend of the population, the distribution of breeders in the occupied ponds has changed radically after the perturbation. Quantified using the Gini coefficient of inequality, the spatial heterogeneity in colony sizes began to fall sharply after the perturbation, meaning a more homogenous distribution of breeders among colonies. Few studies have examined variations in colony size heterogeneity over time, and those that have tried have found that spatial and temporal patterns of colony sizes were rather unpredictable (Brown, Brown, et Roche 2013), and seemed very specific to each population system. In our case, the absence of factors that promote the aggregation of individuals on the same site, such as a concentration of resources ('landfill hypothesis') may have contributed to a redistribution of breeders that is close to an homogenous distribution.

Besides this new population structure, the flow of individuals between colonies increased after the perturbation, as suggested by the reduction in natal and breeding philopatry rates. For example, breeding fidelity at pond MA, which was a continuously monitored satellite pond, significantly decreased from a rate of 0.32 (0.24–0.41) in 1986–2006 to 0.11 (0.03–0.21) in 2010–2019. Thus, the population appears to have shifted to a more dynamic dispersal regime and a more homogeneous population structure than before the perturbation.

### 4.2 New dynamics but unchanged proximal causes of dispersion

#### 4.2.1 Causes of dispersal

As seen before, the study of dispersal parameters allowed us to characterize a change in dispersal dynamics. Our results showed that breeding fidelity was positively correlated with colony size. The degree of philopatry can be affected by colony size, the number of colonies, and the space between subpopulations in spatially structured populations (Hanski et Gaggiotti 2004). For seabird species that

exhibit high philopatry (> 80%; Coulson 2016), correlation between breeding fidelity and colony size was hardly found. The relative size of the colony in relation to the total population seems to be a better indicator of philopatry (Aebischer 1995). In our case, for all periods between 1986 and 2019, the relationship between breeding fidelity and absolute colony size was sufficiently strong to be directly detected. In our study population, the size of the colony seemed to be a major factor in the decision to disperse. We found no difference in the strength of this relationship between the periods before and after the perturbation. This suggests that the perturbation did not alter the effect of colony size on philopatry.

Additionally, concerning natal fidelity to the sites, values were lower than breeding fidelity. This is a common result for birds, where first breeders often have a greater propensity to disperse than experienced breeders (Thompson et Hale 1989; Aebischer 1995; Winkler et al. 2004). Nevertheless, within our study system, we observed a correlation between natal and breeding fidelity, indicating that the factors influencing the decision to leave the birthplace or previous breeding site were similar.

Once they have decided to disperse, individuals have to select a new pond to breed on. In our population, the probability of settlement on ponds was also correlated to colony size for both first-time breeders and experienced breeders. Conspecific attraction has been documented frequently in birds (Buxton et al. 2020), particularly for colonial species (Danchin et Wagner 1997). Nesting where the density of conspecifics is high increases reproductive output due to reduced predation pressure and access to information on feeding sites. (Danchin et Wagner 1997). Thus, the phenomenon of conspecific attraction, by directing individuals towards sites where they benefit most from the advantages of colonial life, is a mechanism that motivates both the departure from the original colony and the choice of the new colony. In addition to conspecific attraction, it has been strongly suggested that the performance of other individuals may also influence settlement choice in species related to the Black-headed Gull, in particular the Black-legged Kittiwake (*Rissa tridactyla*) (Boulinier et al. 2008). Due to the absence of data on reproductive success in our population, it was not possible to test this other proximal cause of preferential settlement.

The relationship between colony size and probability of settlement was found for both periods. No difference in the strength of this relationship has been detected between the periods before and after the perturbation. Moreover, the probability to settle on LR pond or satellite ponds also seemed equivalent after the perturbation. Therefore, as for site fidelity, the importance of conspecific attraction in the choice of a new colony does not seem to have been affected by the perturbation. Thus, the reduced colony sizes following the perturbation, along with the persistent relationship between breeding fidelity and settlement with colony size, seem to be the key factors driving the observed decrease in fidelity post-perturbation and explain the perceived increase in dispersal dynamics.

#### 4.2.2 Causes of permanent emigration

The apparent survival rate we estimated in our model is the difference between actual survival rate and permanent emigration rate out of the Forez population. Mean survival was very close before and after the perturbation, with a value of 0.84 (0.79–0.88) in 1986–2006 and 0.87 (0.78–0.93) in 2010–2019. These average apparent survival values reflect equivalent permanent emigration rate in both periods. The absence of a difference in permanent emigration between the two periods indicates that the impact of the perturbation was temporary and did not persist. The population

rapidly returned to its pre-perturbation permanent emigration rate.

Contrary to the period before the perturbation, the apparent survival rate fell below 0.60 in several years (2010 and 2015) after the perturbation, suggesting a difference in the stability of emigration between the periods. Before the perturbation, emigration seemed relatively stable. This stability was likely due to LR Pond, which always hosted more than 50% of the breeding population, never drying up and always being available for breeders to settle on. After the perturbation, the population was more evenly distributed among the colonies. As a result of this new spatial distribution, a large number of breeders settled on ponds that were subject to punctual drying (see Appendix 4). Thus, the difference in the stability of permanent emigration between the periods might be simply explained by this new spatial organization of the population.

Although juvenile survival is expected to be more prone to interannual variations than adult survival for this long-lived species (van Dijk et al. 2012; Péron 2009; Grosbois 2001), the long-term trends we observed in juvenile survival can also be interpreted in terms of permanent emigration of prebreeders. Unlike adults, the increased apparent survival rate we observed in juveniles suggest a lower level of permanent emigration after the perturbation than before. The loss of individuals caused by the perturbation could have induced a reduction of competition for nesting sites in the plain colonies and eventually favored the local recruitment of prebreeders that may have previously dispersed when the competition was high. Indeed, Black-headed Gulls experience strong competition, particularly for nesting sites (Jean-dominique Lebreton 1987). It has been demonstrated that less experienced breeders settle on nest sites with lower elevation above the water level, making the nests more vulnerable to water level changes and waves (Lebreton 1987). This explanation is reinforced by the fact that the juvenile local survival was already increasing before the perturbation and was concomitant to the observed decline in the population the years before the perturbation.

This decreased permanent emigration of young individuals may even have a visible impact on the age structure of the population. In a population of Audouin's gull, the sudden arrival of predators induced a differential dispersal and a change in age structure (Payo-Payo et al. 2018). Analysis of CMR data should help evaluate this hypothesis of a potential impact on the age structure of our population.

### **4.3 Limits and Perspectives**

#### *4.3.1 Benefits of the integrated modeling approach*

In populations studied at relatively small spatial scales or with highly mobile individuals, emigration and immigration become important processes for the local dynamics of the population (Thomas et Kunin 1999; Hanski et Gaggiotti 2004). In our patchy population, it was crucial to differentiate between dispersal within the population and dispersal outside of the population, i.e. permanent emigration. The use of the "Alive Elsewhere" site in an integrated population model allows for this differentiation. Our IPM enables the quantification of the flow of breeders moving to colonies not monitored by CMR by integrating the size of these unmonitored colonies. This advantage of integrated population modeling has provided a fine understanding of dispersal processes within the population and the changes of permanent emigration from the population, and thus enabled subtle questions about dispersal to be addressed.

#### 4.3.2 Model validation

The use of IPMs to study the demography of wild populations is now widespread (Schaub et Kéry 2022; (Bled et al. 2017; Schaub et Kéry 2022). However, methodological improvement is ongoing, and major advancements are still being made (Schaub et Kéry 2022; Abadi et al. 2010; Nater 2024). Notably, research into goodness-of-fit testing of integrated models in general, and IPMs in particular, has been limited (Plard, Turek, et Schaub 2021). Currently, no straightforward model validation procedure that can be applied to any IPM is available (Newman et al. 2014). Like any parametric model, our IPM is based on assumptions. For example, our multi-state CMR sub-model assumes homogeneity of survival and recapture probabilities between individuals (Pradel, Wintrebert, et Gimenez 2003). However, the integration of several datasets requires other major assumptions, such as the independence of datasets (Abadi et al. 2010; Schaub et Kéry 2022). One way of evaluating our model would be to carry out Posterior Predictive Checks (Andrew Gelman, Meng, et Stern 1996). This involves simulating a dataset using the estimates from the model, and comparing it to the real dataset on which the model was fitted. The comparison can be made graphically, using discrepancy measures and statistical tests (Schaub et Kéry 2022). This model validation process is the next step in the project.

#### 4.3.3 Limits on hidden parameters

IPMs enable the estimation of hidden parameters in a demographic model (Schaub and Kéry 2022). A hidden parameter is one that is estimated without explicit data (Schaub and Kéry 2022). In our model, the only demographic process that did not benefit from direct information input was fecundity. Since all other demographic parameters could be directly estimated, fecundity values were inferred from population size variations not explainable by other demographic processes, such as survival or recruitment that were explicitly informed by the data in our IPM. Besides, as in all spatially structured populations, individuals can immigrate into the population and influence its size. For our population, immigration was considered negligible. This means that in our model, fecundity and immigration are combined, and cannot be distinguished. Additionally, it has been shown that the estimation of hidden parameters within IPMs can be prone to bias (Nater 2024). The hidden parameter might capture a large portion of the residual variance including observation errors. In our case, we chose to retain a constrained prior for fecundity to keep fecundity values within biologically plausible ranges (Grosbois 2001; Péron 2009). However, this modeling choice did not allow for a comparison of fecundity between the colonies. One solution to improve the quality of fecundity estimates would be to include direct reproductive information. Data on the proportion of occupied colonies that completely failed to reproduce is available. Such information on fecundity, although degraded, may be integrated into the IPM to improve fecundity estimates and the overall estimates of the model, and should therefore be explored in the near future.

### 5. Conclusion

The perturbation had immediate impacts on the population structure and dynamics of the Black-headed Gulls. The drastic decrease in breeders and the sudden drop in adult survival rates provided strong evidence of mass emigration caused by the perturbation. Nonetheless, the permanent emigration event was temporary, as the colony was quickly recolonized by experienced breeders. The

perturbation did not change the underlying causes of dispersal, such as conspecific attraction, which remained a major factor in philopatry and settlement decisions. Combined with the maintenance of conspecific attraction as a proximate cause of dispersal, the new population structure, characterized by a more homogeneous distribution of breeders across smaller colonies, seemed to be sufficient to explain the new dispersal patterns following the perturbation. The reduced competition, caused by the mass event of permanent emigration of experienced breeders, may explain the observed decrease in juvenile permanent emigration. This study highlights that a strong change in population dynamics pattern may mask a strong maintenance of the population dynamics mechanisms, suggesting that perturbation effects should always be studied through demographic parameters like survival and dispersal.

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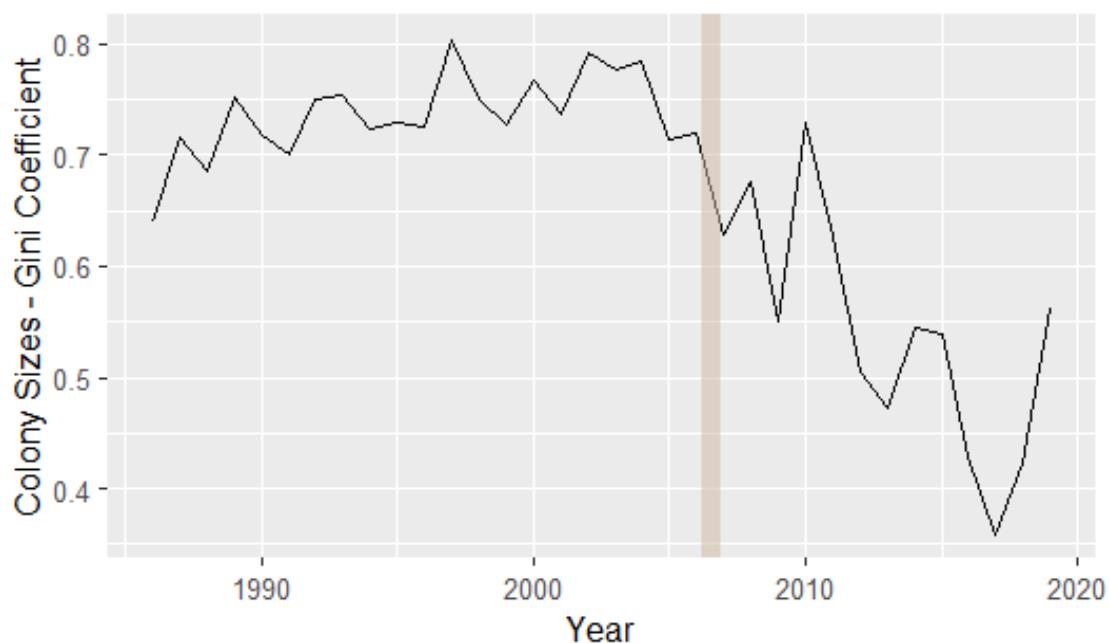
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## APPENDIX

Parameter	Prior
Mean survival	$\phi \sim \text{Uniform}(0,1)$
Standard deviation survival	$\sigma_\phi \sim \text{Uniform}(0.0001,1)$
Number female fledging per pair	$\rho \sim \text{Uniform}(0,1)$
Breeding dispersion from a colony	$\eta \sim \text{Dirichlet}(1,1,\dots,1)$
Natal dispersion from a colony	$v \sim \text{Dirichlet}(1,1,\dots,1)$
Observation error - Method 1	$\sigma_{\text{obs},1} \sim \text{Uniform}(0,0.15)$
Observation error - Method 2	$\sigma_{\text{obs},2} \sim \text{Uniform}(0,0.3)$

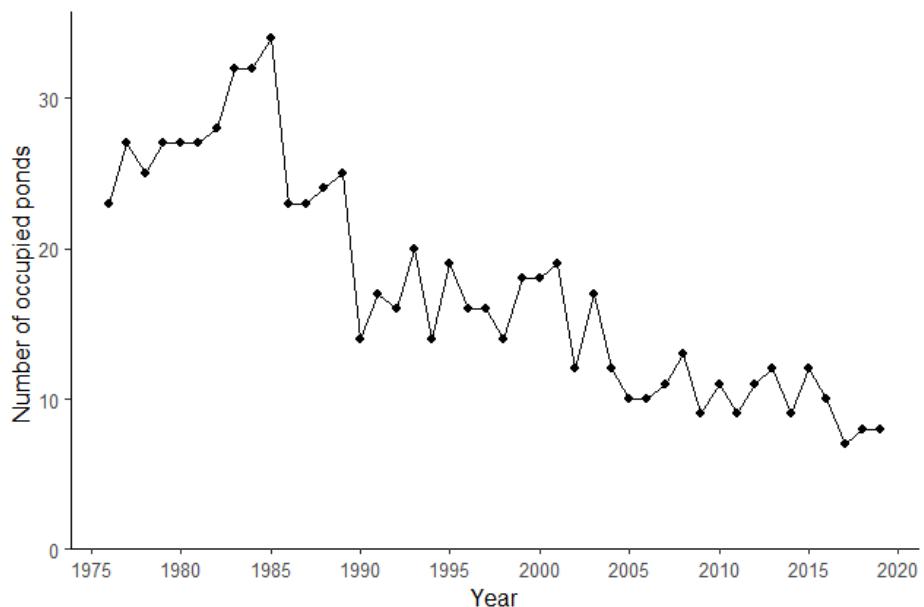
Appendix 1. Priors used for the parameters of the Integrated Population Model. All priors are considered as noninformative, except for observation errors. Method 1 is based on multiplying the number of observed breeders with a fixed ratio. Method 2 is based on the ratio between ringed and unringed birds and the probability to read a ring on a detected bird. Method 1 is expected to have an observation error of less than 15% and method 2 is expected to have an observation error of less than 30%.



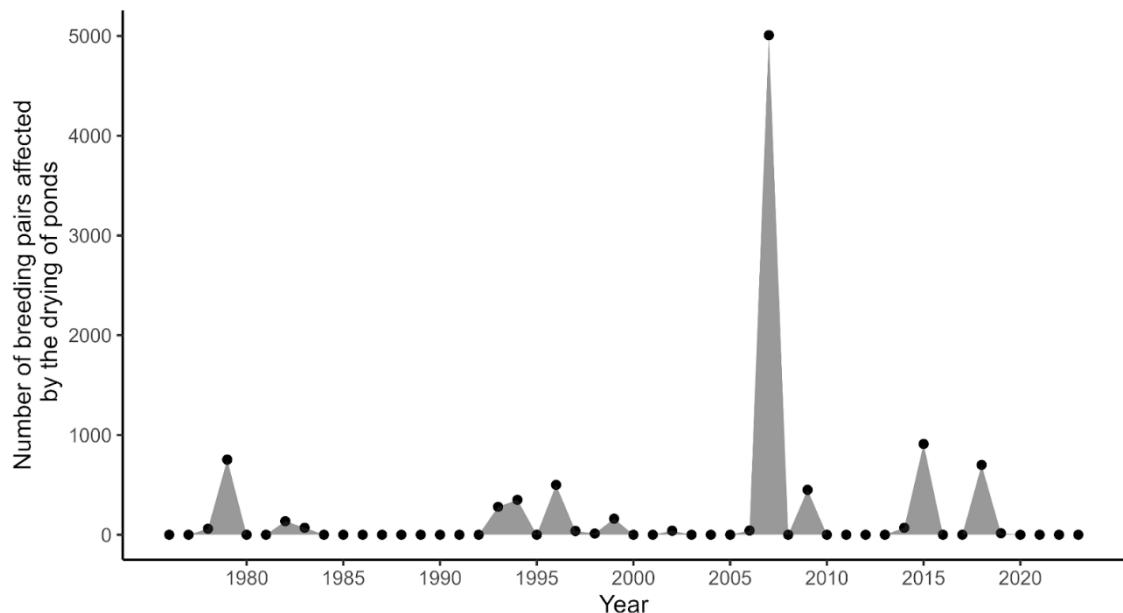
Appendix 2. Gini coefficient applied to the number of breeders of occupied colonies of Black-headed Gulls (*Chroicocephalus ridibundus*) from the population occupying the Forez plain, for each year between 1986 and 2019. The vertical band marks the perturbation that occurred at la Ronze pond in 2007.

Definitions	1986-2006		2007-2010		2010-2019	
	Est.	CI (95%)	Est.	CI (95%)	Est.	CI (95%)
Mean survival of adults	0.84	[0.79,0.88]	0.76	[0.55,0.90]	0.87	[0.78,0.93]
Standard deviation survival of adults	0.70	[0.42,0.97]	0.83	[0.51,0.99]	0.89	[0.68,1.00]
Mean survival during the first year	0.18	[0.14,0.22]	0.48	[0.22,0.81]	0.34	[0.26,0.42]
Standard deviation survival during the first year	0.54	[0.37,0.79]	0.54	[0.04,0.98]	0.32	[0.03,0.81]
Number of female fledging per pair in LR	0.97	[0.91,1.00]	0.08	[0.00,0.66]	0.18	[0.00,0.90]
Number of female fledging per pair in SAT	0.96	[0.87,1.00]	0.00	[0.00,0.01]	0.63	[0.24,0.90]
Breeding fidelity in LR	0.98	[0.97,0.99]	0.68	[0.49,0.90]	0.59	[0.51,0.66]
Breeding fidelity in MA	0.32	[0.24,0.41]	0.23	[0.08,0.45]	0.11	[0.03,0.21]
Natal fidelity in LR	0.75	[0.65,0.82]	0.24	[0.05,0.54]	0.24	[0.15,0.36]
Natal fidelity in MA	0.38	[0.25,0.52]	0.19	[0.01,0.52]	0.18	[0.02,0.46]

Appendix 3. Posterior mean and 95% credible interval of some demographic parameters estimated by the IPM. Results are shown for three periods: before the perturbation (1986-2006), shortly after the perturbation (2007-2010), and a few years after the perturbation (2010-2019).



Appendix 4. Number of occupied ponds over the years by Black-headed Gulls (*Chroicocephalus ridibundus*) in the Forez plain, between 1976 and 2019.



Appendix 5. Number of breeding pairs of black-headed gulls affected by the drying of ponds in the Forez plain each year during the study period. Dots represent the number of breeding pairs on a pond in the year before it was dried up.

# Investigating population dynamics and dispersal following a perturbation in population of Black-headed Gulls (*Chroicocephalus ridibundus*) with an integrated modeling framework: changes in dispersal patterns, but not causes

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## ABSTRACT

In spatially structured populations, dispersal is a key driver of population dynamics. Dispersal strategies, the decision to change breeding site and the choice of where to settle next, are influenced by the ecological context that individuals encounter, in particular spatio-temporal environmental variability. Perturbation can be considered as extreme environmental variation. How dispersal is affected by the occurrence of a strong, punctual perturbation remains largely unexplored. In this paper, we analyzed an empirical case of perturbation in a patchy population of black-headed gulls (*Chroicocephalus ridibundus*), where the pond that had historically hosted the main breeding colony for decades was dried out for one year. Using an integrated population model to analyze breeding population counts and capture-mark-recapture data before and after the perturbation, we sought to understand how the demographic parameters and notably dispersal changed following the sudden and punctual loss of the main colony. We found a drastic reduction in the number of breeders caused by a massive permanent emigration of adults in the year of the perturbation. The perturbed colony was quickly recolonised by experienced breeders. After the perturbation, a new population structure emerged, characterized by a more homogeneous distribution of breeders across smaller colonies and an increased flow of individuals between colonies. The perturbation did not alter the main underlying cause of dispersal, conspecific attraction, which remains a major factor explaining philopatry and settlement decisions. This study highlighted that a strong change in the population dynamics pattern may mask a strong maintenance of the underlying mechanisms, suggesting that perturbation effects should always be studied through demographic parameters such as survival and dispersal.

**Keywords :** Demography / Perturbation / Dispersal / Integrated Population Model / Spatially structured population

## RÉSUMÉ

Dans les populations structurées spatialement, la dispersion apparaît comme un processus clé des dynamiques de population. Les stratégies de dispersion, la décision de changer de site de reproduction et le choix du prochain site d'installation, sont influencés par le contexte écologique auquel les individus sont confrontés, en particulier la variabilité spatio-temporelle de l'environnement. Une perturbation peut être considérée comme une variation environnementale extrême. Savoir comment la dispersion est affectée dans le cas d'une perturbation ponctuelle de la population reste une question largement inexplorée. Dans ce travail, nous avons analysé un cas empirique de perturbation dans une population de Mouettes rieuses (*Chroicocephalus ridibundus*), où l'étang qui avait historiquement accueilli la principale colonie pendant des décennies a été asséché pendant un an. En utilisant un modèle de population intégré permettant d'analyser conjointement les comptages de reproducteurs et les données de capture-marquage-recapture avant et après la perturbation, nous avons cherché à comprendre comment les paramètres démographiques et notamment la dispersion ont changé suite à la perte soudaine et ponctuelle de la colonie principale. Nous avons constaté une réduction drastique du nombre de reproducteurs causée par une émigration massive et permanente d'adultes au cours de l'année de la perturbation. La colonie perturbée a été rapidement recolonisée par des reproducteurs expérimentés. Après la perturbation, une nouvelle structure de population est apparue, caractérisée par une distribution plus homogène des reproducteurs au sein de colonies plus petites et un flux accru d'individus entre les colonies. La perturbation n'a pas modifié la principale cause sous-jacente de la dispersion, l'attraction conspécifique, qui reste un facteur majeur expliquant la philopatrie et les décisions d'établissement sur de nouveaux sites. Cette étude a mis en évidence le fait qu'un changement important dans la dynamique de la population peut masquer un maintien important des mécanismes sous-jacents, suggérant que les effets de perturbation devraient toujours être étudiés à travers des paramètres démographiques tels que la survie et la dispersion.

**Keywords :** Démographie / Perturbation / Dispersion / Modèle Intégré de population / Population Spatialement Structurée