

## MODELING DISPERSAL WITH CAPTURE–RECAPTURE DATA: DISENTANGLING DECISIONS OF LEAVING AND SETTLEMENT

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**Abstract.** Increasing habitat fragmentation has led population ecologists to consider dispersal as a key process for population functioning and persistence. However, due to logistic and methodological problems, dispersal rates within fragmented populations have rarely been estimated, leaving many unanswered questions about the role of dispersal and the factors affecting dispersal.

Recently developed multistrata capture–recapture models allow the estimation of dispersal probabilities from the analysis of recaptures or recoveries of marked individuals. Despite their undoubted efficiency at estimating dispersal rates, their contribution to the investigation of dispersal processes at the individual level is presently limited by a lack of flexibility in their parameterization. In this paper, a new parameterization of these models is presented in which the probability of leaving the site of origin and the probability that an emigrant settles on a given recipient site are modeled separately.

This parameterization is then used to address the influence of local perturbations on site fidelity and settlement decisions of emigrants in a subdivided population of Black-headed Gulls, *Larus ridibundus*.

The parameterization introduced here accurately describes dispersal probabilities whenever they result from a two-step decision-making process (i.e., when choice of a settlement site only occurs after a decision has been made to leave the current site). Furthermore, this parameterization permits investigators to disentangle hypotheses about these two components of dispersal behavior.

**Key words:** *Black-headed Gull; dispersal; habitat perturbation; Larus ridibundus; multistrata capture–recapture; settlement probability; site fidelity.*

### INTRODUCTION

The habitat of many species is naturally fragmented or has become fragmented as the result of the expansion and intensification of human land use. It is thus often relevant to consider populations as collections of subpopulations in heterogeneous environments rather than continuous entities in homogeneous environments (Pulliam and Danielson 1991, Hanski 1998, Thomas and Kunin 1999). In this paradigm, dispersal is a key process that influences habitat occupancy (Hanski and Gilpin 1991, Holt 1997), population stability (Gadgil 1971, Vance 1984, Thomas 2000), and the potential for adaptation to local conditions (Kawecki 1995, Holt 1996). A considerable number of theoretical predictions concerning the influence of dispersal on the distribution of individuals (e.g., Levin 1976, Pulliam 1988) and genes (e.g., Wright 1943, Weir and Cockerham 1984, Rousset 1997; reviewed in Slatkin 1987) within subdivided pop-

ulations has therefore been produced. The evolution of dispersal has also been widely studied on theoretical grounds (e.g., Van Valen 1971, Hamilton and May 1977, Hastings 1983, Levin et al. 1984, Olivieri et al. 1990, McPeck and Holt 1992, Perrin and Mazalov 1999; reviewed in Johnson and Gaines 1990, Dieckmann et al. 1999, Clobert et al. 2001).

In spite of the importance of these theoretical predictions for conservation and evolutionary studies (Leimar and Norberg 1997), dispersal rates of individuals within subdivided populations have rarely been estimated. This leaves many questions about the role of dispersal and the factors affecting dispersal unanswered. The lack of an empirical counterpart to the huge body of theoretical studies is largely due to logistic and methodological problems (Ims and Yoccoz 1997, Bossart and Prowell 1998, Bohonak 1999). The analysis of data from capture–recapture studies involving several geographic localities holds great potential for the direct study of dispersal in animal populations (Nichols et al. 1993). It almost invariably requires the use of statistical models that take into account the probability of recapture of a marked individual (Lebreton et al. 1992). Multistrata capture–recapture models allow the estimation of dispersal probabilities from the analysis of recaptures or recoveries of marked individuals (Arnason 1973, Brownie et al. 1993, Schwarz et al. 1993). These models can

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also be used to determine the factors that influence dispersal probabilities (Nichols and Kendall 1995, Spindelov et al. 1995). Recent applications of these models have shown that between-patch dispersal is associated with intrinsic factors such as sex (Lindberg et al. 1998) as well as with extrinsic factors like weather conditions (Hestbeck et al. 1991), patch size (Hanski et al. 2000), or subpopulation productivity (Spindelov et al. 1995).

Despite the undoubted efficiency of existing multistrata models at estimating dispersal rates, their contribution to investigations of dispersal processes at the individual level is presently limited by a lack of flexibility in their parameterization. In multistrata models, dispersal is described by a single parameter (i.e., the probability of movement between two given sites during a given time interval). However, it is often natural to view a dispersal event as the result of a multi-step behavioral process that should be described using at least two probabilities: (a) the probability of leaving a given site (i.e., the complement of the site fidelity), and (b) the probability of settling on a given recipient site, conditional on the former probability (Lidicker and Stenseth 1992, Ims and Yoccoz 1997, Forero et al. 1999, Hanski et al. 2000, Clobert et al. 2001). These two components of dispersal could be affected by different factors. The decision to leave a site appears to be influenced by local factors such as the degree of relatedness with potential local mates (Daniels and Walters 2000), the degree of prevalence of parasites (Brown and Bomberger Brown 1992), or by individual proximate factors like sex (Greenwood 1980), age (Greenwood and Harvey 1982), and breeding success (Aebischer et al. 1995, Forero et al. 1999). These factors could prove to be irrelevant for the settlement decision of emigrants. Higher scale factors such as landscape structure (Matthysen et al. 1995, Gustafson and Gardner 1996), relative habitat patch size (Spindelov et al. 1995, Hanski et al. 2000), or relative subpopulation densities (Smith and Peacock 1990, Reed and Dobson 1993) are more likely to influence the distribution of emigrants among potential recipient sites. Furthermore, the most recent advances in the theoretical study of the evolution of dispersal strategies distinguish these two components of dispersal. For example, some theoretical models consider the evolution of dispersal strategies in which the decision to leave and the settlement decision of emigrants are influenced by local densities (Ruxton and Rohani 1998, Metz and Gyllenberg 2001), while others investigate the evolution of dispersal strategies in which only the decision to leave is density dependent (Travis et al. 1999).

Explicit modeling of the hierarchical decision rules underlying movement of individuals within a metapopulation is therefore necessary to disentangle the factors influencing the decision to leave from those influencing the settlement decision of emigrants. In this paper we present a new parameterization of multistrata

capture–recapture models that permits distinction between these two components of dispersal.

Many seabird species are colonial (Kharitonov and Siegel-Causey 1988). They thus occur in subdivided populations and are adequate biological models for the study of dispersal (e.g., Spindelov et al. 1995). To illustrate the parameterization introduced here, we applied it to the study of breeding dispersal within a subdivided population of a colonial seabird species: the Black-headed Gull, *Larus ridibundus* L.

## METHODS

### *The classical multistrata model*

Multistrata capture–recapture models (Arnason 1973, Brownie et al. 1993, Schwarz et al. 1993) are an extension of the Cormack–Jolly–Seber model (Cormack 1964, Jolly 1965, Seber 1965), which was designed to estimate mortality using recaptures (or resightings) of marked individuals. The Cormack–Jolly–Seber model describes the transition between the state “alive” and the state “dead.” Multistrata models handle more complex information. They can be used when the state “alive” is further stratified according to nonpermanent states like breeding success (Nichols et al. 1994) or breeding sites (Nichols et al. 1993). In the capture–recapture literature, these states or sites are often referred to as strata. The general model, in which all parameters are strata and time dependent (Arnason 1972, 1973, Schwarz et al. 1993), can be viewed as a matrix extension of the single-stratum Cormack–Jolly–Seber model. In this model the transitions between strata are modeled as first-order Markov processes. The basic parameters are:

$\phi_i^{RT}$  = the probability that an individual alive in stratum  $R$  at occasion  $i - 1$  is alive and in stratum  $T$  at occasion  $i$ .

$p_i^R$  = the probability of recapture at occasion  $i$  of a marked animal alive and in stratum  $R$  at that occasion.

It is possible to compute the following parameters:

$S_i^R = \sum_T \phi_i^{RT}$ ; the probability that an individual alive in stratum  $R$  at occasion  $i - 1$  survives until occasion  $i$ .

$\psi_i^{RT} = \phi_i^{RT}/S_i^R$ ; the probability of being in stratum  $T$  at occasion  $i$  for an individual that was in stratum  $R$  at occasion  $i - 1$  and that survived until occasion  $i$ .

Under the hypothesis that survival between occasion  $i - 1$  and occasion  $i$  depends only on the stratum at occasion  $i - 1$ ,  $\psi_i^{RT}$  is the probability of transition between  $R$  and  $T$  conditional on survival (Hestbeck et al. 1991, Brownie et al. 1993, Schwarz et al. 1993, Nichols and Kendall 1995). Because  $\psi_i^{RT}$  is conditional on survival, it follows that  $\sum_T \psi_i^{RT} = 1$ .

We will hereafter refer to this parameterization of multistrata capture–recapture models as the  $v$ -parameterization.

TABLE 1. Structure of the model used to build the simulated data set.

Parameter	Notation	Effect		
		Time (2 levels)	Site (3 levels)	Time × Site
Survival	$S$	...	...	...
Recapture	$p$	...	...	...
Probability of leaving	$\pi$	<b>X</b>	...	...
Settlement	$\mu$	...	<b>X</b>	...
Movement	$\psi$	<b>X</b>	<b>X</b>	...

Notes: Under the  $\pi\mu$ -parameterization, the above model structure corresponds to model  $S4/p4/\pi3/\mu2$  of Table 2. Under the  $\psi$ -parameterization, the above model structure corresponds to model  $S4/p4/\psi1$  of Table 2. The presence of an effect is indicated by **X**.

It is possible to model the variations of  $\psi_i^{RT}$  in a statistical framework very similar to a generalized linear model (e.g., Spendelov et al. 1995):

$$\psi_i^{RT} = f(b_0 + \sum_j b_j x_{ij}^{RT}). \tag{1}$$

In this equation,  $f(x)$  is a link function, the  $x_{ij}^{RT}$  s are the values taken by a set of continuous and/or categorical explanatory variables, and the  $b_j$  s are the coefficients linking the variations in  $\psi_i^{RT}$  to the variations in the explanatory variables. Capture-recapture models allow estimation of these coefficients.

*A two-step parameterization*

In the case where strata are sites,  $\psi_i^{RT}$  describes the probability of leaving site  $R$  together with the probability of settlement on site  $T$  in the time interval between two capture occasions. However, the factors influencing the probabilities of leaving can be different from the factors influencing the probabilities of settlement of emigrants on potential recipient sites. It is also possible that the same factors influence these two components of dispersal differently. In such situations, one can model dispersal by considering that the variations of the probability of leaving and of the probability of settlement are related to the variations of explanatory variables through distinct generalized linear models. We define:

$\pi_i^R = \sum_{T \neq R} \psi_i^{RT}$ : the probability of leaving stratum  $R$  between occasion  $i - 1$  and occasion  $i$  for an individual known to be alive at occasion  $i$ . This is the complement of site fidelity.

$\mu_i^{RT} = \psi_i^{RT}/\pi_i^R$ : the probability of settling in stratum  $T$  between occasion  $i - 1$  and occasion  $i$  for an individual known to be alive at occasion  $i$  and known to have left stratum  $R$  between occasion  $i - 1$  and occasion  $i$  (for  $T \neq R$ ). Under the hypothesis that there is no additional mortality during dispersal,  $\sum_{T \neq R} \mu_i^{RT} = 1$ .

Note that the definitions of  $\pi_i^R$  and  $\mu_i^{RT}$  given here are adequate whenever dispersal is viewed as a behavioral phenomenon occurring at the individual scale. At the population scale  $\pi_i^R$  and  $\mu_i^{RT}$  can be viewed, respectively, as emigration and immigration probabilities.

Models in which the probabilities of leaving and the probabilities of settlement on the potential recipient

sites are related to different explanatory variables or are differently related to the same explanatory variables can now be explicitly designed by defining two distinct generalized linear models:

$$\pi_i^R = f(b'_0 + \sum_j b'_j x'_{ij}{}^R) \tag{2}$$

$$\mu_i^{RT} = f(b''_0 + \sum_j b''_j x''_{ij}{}^{RT}). \tag{3}$$

Since  $\psi_i^{RT}$  is the product of  $\pi_i^R$  and  $\mu_i^{RT}$ , designing such a model using the  $\nu$ -parameterization implies expressing the product of the right hand sides of Eq. 2 and Eq. 3 in the form of a generalized linear model similar to Eq. 1. This may be nontrivial or even impossible.

The assumption that survival depends only on departure stratum still remains under the  $\pi_i^R$  and  $\mu_i^{RT}$  parameterization but movement is now split into two distinct probabilities that can be estimated and modeled separately. Hereafter, we will refer to this parameterization of multistrata capture-recapture models as the  $\pi\mu$ -parameterization. The  $\pi\mu$ -parameterization can be used with available programs after transformation of capture histories, as described in the Appendix.

*Validation of the  $\pi\mu$ -parameterization by the analysis of simulated data*

In order to validate the accuracy of estimates obtained under the  $\pi\mu$ -parameterization and the identifiability of the parameters involved, 18 000 three-strata, seven-occasions capture histories were simulated with the program SCR (R. Choquet, *unpublished program*). For this simulation, the probability,  $\pi_i^R$ , of leaving site  $R$  (where  $R = A, B,$  and  $C$ ) was considered time dependent (two levels: C1 and C2). The probability,  $\mu_i^{RT}$ , of settling in site  $T$ , given departure from site  $R$ , was considered to be dependent on the departure and the settlement sites. This parameter structure is summarized in Table 1.

*Breeding dispersal in a subdivided Black-headed Gull population*

We used the  $\pi\mu$ -parameterization to investigate breeding dispersal in a population of the Black-headed Gull in central France (Lebreton 1981). We considered three

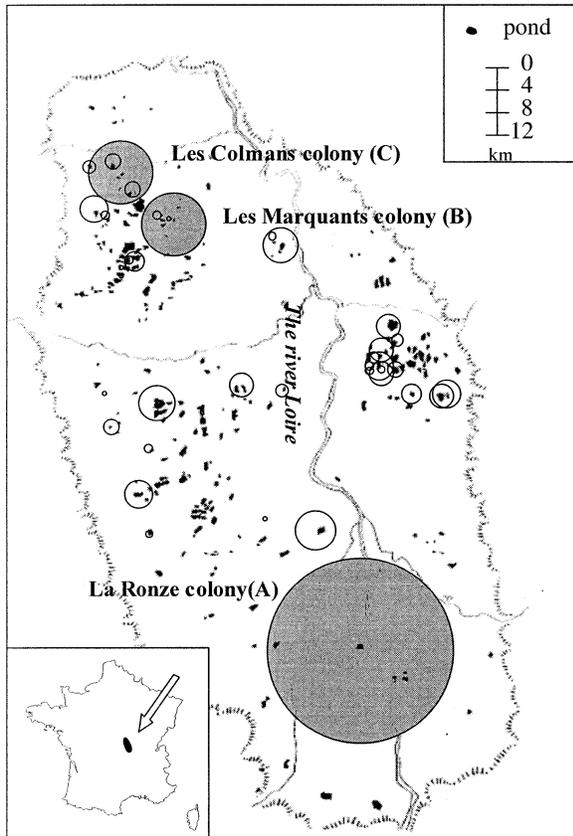


FIG. 1. Black-headed Gull colonies in the Forez plain in central France. Each circle indicates the presence of a colony during the period 1994–2000. The perimeter of each circle indicates the mean population size of the corresponding colony over the 1994–2000 period. The shaded circles indicate the colonies considered in the present study. The insert at the bottom left indicates the geographical position of the Forez plain.

breeding colonies settled on ponds: “La Ronze,” hereafter referred to as site A; “Les Marquants,” hereafter referred to as site B; and “Les Colmans,” hereafter referred to as site C (Fig. 1). Sites B and C are very close together and relatively remote from site A (Fig. 1). These sites harbor colonies of contrasting sizes and differ in terms of stability of environmental conditions. Site A harbors a large colony, ranging from 3000 to 4600 pairs over the period 1994–2000, and invariably exhibits water levels permitting colony settlement. Sites B and C harbor smaller colonies, ranging from 280 to 700 pairs and from 300 to 665 pairs, respectively, over the period 1994–2000. Sites B and C are occasionally subject to human-controlled droughts during the breeding season, thereby preventing colony settlement. Within the period 1994–2000, colony C experienced a drought in 1997 and colony B in 1998. The dynamics of this population is described in Grosbois (2001).

Droughts may affect probability of leaving without necessarily influencing the probability of settlement in

the different recipient colonies. Interannual instability of local habitat has been identified as a potentially important proximate factor of colony desertion in the Black-headed Gull (Creutz 1967) and more broadly in Larids (McNicholl 1975). Empirical observations suggest that the underlying mechanism in Black-headed Gulls involves habitat selection strategies based on assessment at the beginning of the breeding season of the quality of the colony site occupied during the previous breeding season (Nef 1961). According to this hypothesis the probability of leaving a colony should increase when a drought renders the local habitat unsuitable for breeding. Alternatively, individuals may respond to drought by skipping reproduction until suitable conditions are restored.

A drought affecting a given colony may also influence the probability that emigrants settle on this colony during the next year. The settlement decisions of emigrants may rely on the evaluation, through prospecting behavior, of the breeding success in the potential recipient colonies during the previous breeding season (Boulinier and Danchin 1997, Danchin et al. 1998). Under this hypothesis, settlement probability is expected to be lower the year following a drought event.

In addition to the effects of droughts, variations in intercolony distance and colony-specific ecological conditions (e.g., colony size) may influence probability of leaving and settlement probability. We do not intend to address specifically the effects of distance and colony size in the present study because three colonies is obviously not a sufficient number for such an investigation. Instead, we aim at detecting the differences between colonies in probability of leaving and probability of settlement that do not result from the differences in the drought regime affecting the colonies.

In summary, the  $\pi\mu$ -parameterization was used: (1) to test the predictions concerning the influence of droughts on colony fidelity (probability of leaving) and/or on settlement probability; and (2) to assess the differences in probability of leaving and/or settlement probability that remain after the effects of the droughts have been taken into account.

The most complex model considered in the analysis includes, for each parameter type, all of the factors considered as potentially important. This model is denoted  $S0/\pi0/\mu0$  (see Table 2 for model notation).

Previous analyses have shown that the capture probability in this population varies with resighting effort, which differs among occasions and colonies (Clobert et al. 1985). However, measures of resighting effort in B and C were not available for every year of the study. For this reason, the model describing the variations of recapture probability included a year effect, a colony effect, and the interaction between year and colony. In addition, since individuals may respond to drought by skipping reproduction, and since the probability of recapture of nonbreeders equals zero, the probabilities of recapture in sites B and C were set to zero during

TABLE 2. Model structure and notation.

Model structure	Notation
$\text{Logit}(\chi) = b_0 + b_1 \text{ colony} + b_2 \text{ drought} + b_3 \text{ colony} \times \text{drought}$	$\chi^0$
$\text{Logit}(\chi) = b_0 + b_1 \text{ colony} + b_2 \text{ drought}$	$\chi^1$
$\text{Logit}(\chi) = b_0 + b_1 \text{ colony}$	$\chi^2$
$\text{Logit}(\chi) = b_0 + b_1 \text{ drought}$	$\chi^3$
$\text{Logit}(\chi) = b_0$	$\chi^4$

Notes: A generic parameter corresponding to  $S$ ,  $\pi$ , or  $\mu$  is represented by  $\chi$ . The coefficients of the linear relationship between the logit of parameter  $\chi$  and the different explanatory variables considered in the model are represented by  $b_j$  ( $j = 1, 2, 3, 4$ ).

drought-years (1998 for B and 1997 for C). For probabilities of survival, leaving, and settlement, the modeling of time variations aimed at exploring the effects of the droughts. For probabilities of survival and leaving, the time intervals were pooled according to two categories (Fig. 2). The time intervals ending with a drought event (type D time intervals: 1996–1997 for colony C and 1997–1998 for colony B) were distinguished from all the other time intervals (type ND time intervals). For settlement probabilities the time intervals were pooled according to three categories (Fig. 2). Settlement probabilities on a given colony were set to zero for time intervals ending with a drought event on this colony. These time intervals are 1996–1997 for colony C and 1997–1998 for colony B. In order to address the effect of previous year conditions on settlement probability, settlement parameters applying to time intervals starting with a drought event on the recipient colony (type D intervals: 1997–1998 for colony C and 1998–1999 for colony B) were distinguished from those applying to time intervals that neither start nor end with a drought event on the recipient colony (type ND intervals). In addition, a colony effect and the interaction between colony and type of interval (D or ND) were included in the modeling of probabilities of survival, leaving, and settlement.

For all parameter types except recapture probability, reduced models were considered as alternatives to the most complex model (Table 2). The structure for settlement probability deserves further comment. A col-

ony effect on settlement probability corresponds to variation in both departure and recipient colony. On the other hand, when settlement probabilities of individuals that left a given colony do not differ among the potential recipient colonies (structure 3–4 in Table 2), the migration pattern is identical to the “island model” (Nichols and Kendall 1995). When only three sites are considered, this corresponds to  $\mu_i^{RT} = \mu_i^R = 0.5$ .

The procedures of selection among alternative models in multistrata capture-recapture analysis are hindered by the lack of appropriate goodness-of-fit tests (Lebreton and Pradel 2002). As a consequence, when there is over dispersion, one may erroneously conclude that an effect is significant when it is not (inflated type I error). If a modified form of Akaike’s Information Criterion,  $AIC_c$  (Burnham and Anderson 1998), is used for model selection, a general rule to avoid inflated type I error is to consider two models with  $AIC_c$  differing by less than two points as describing the data equally well. If a unique model has to be chosen among several models within two  $AIC_c$  points, the model with the lowest number of parameters should be preferred (parsimony principle; Lebreton et al. 1992). There is an alternative way of accounting for the model selection uncertainty: parameter estimates can be derived from more than one single model by model averaging using  $AIC_c$  weights (Burnham and Anderson 1998). Comparisons between pairs of estimates can then be carried out using a Z test that allows for their covariance structure (Lebreton et al. 1992). These two ways

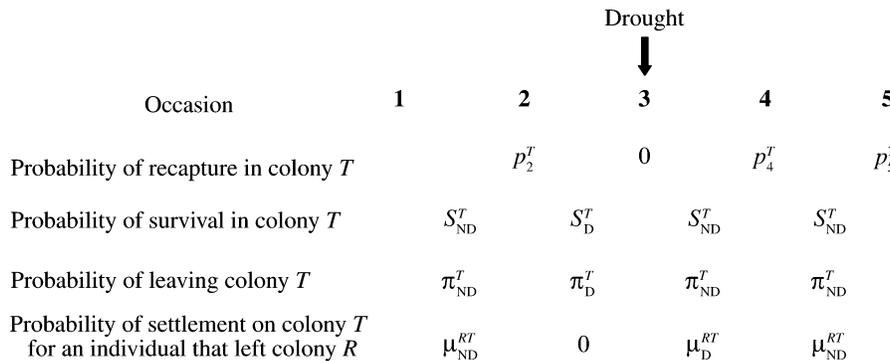


FIG. 2. The temporal structure of the model used to analyze Black-headed Gull data. The letter D represents time intervals ending with a drought event: ND represents all the other time intervals.

TABLE 3. Comparison of the estimates of movement probabilities obtained under two distinct parameterizations in the analysis of the simulated data set.

Occasion type	Expected values					Estimates				
	$\psi$ -parameterization		$\pi\mu$ -parameterization			$\psi$ -parameterization		$\pi\mu$ -parameterization		
	$\psi^{AB}$	$\psi^{AC}$	$\pi$	$\mu^{AB}$	$\mu^{AC}$	$\psi^{AB}$	$\psi^{AC}$	$\pi$	$\mu^{AB}$	$\mu^{AC}$
C1	0.045	0.015	0.06	0.75	0.25	0.049 (0.002)	0.014 (0.002)	0.063 (0.002)	0.775 (0.013)	0.225 (0.013)
C2	0.090	0.030	0.12	0.75	0.25	0.092 (0.001)	0.027 (0.002)	0.120 (0.003)	0.775 (0.013)	0.225 (0.013)

Note: Estimates of movements from only one site (site A) are given. Standard errors are reported in parentheses.

of dealing with model selection uncertainty were used at different stages of the modeling procedure in the present study.

Another difficulty encountered in the analysis of multistrata capture–recapture data is the large number of models that can arise from consideration of all possible combinations of explanatory variables by parameter type. In order to achieve an efficient model selection while computing a minimum number of alternative models, two series of selection subprocedures were performed, each of which combined three independent subprocedures (one for each parameter type). In the first series, each subprocedure considered reduced structures for the target parameter type while the most complex structure was retained for all other parameter types. A model was obtained by combining the structures selected for each parameter type. This model is referred to as the composite model. In the second series, each subprocedure considers all the models differing by one step (in which one effect only has been removed or added) from the composite model for the target parameter type while the structure of the composite model was retained for all other parameter types. We will hereafter refer to the set of models explored in this series as the neighborhood of the composite model. The selection criterion applied for the two series of selection procedures combined the minimum AIC<sub>c</sub> and the parsimony principle.

Capture histories of 1375 adult gulls resighted as breeders on the three colonies (A, B, and C) from 1994 to 2000 ( $k = 7$ ) were analyzed using program MARK1.9 (White and Burnham 1999) after a modification of multisite capture histories (see the Appendix).

TABLE 4. Comparison of the fit and parsimony achieved in the modeling of the simulated data using the  $\psi$ -parameterization or the  $\pi\mu$ -parameterization.

Parameterization	Model	Deviance	Np†	AIC <sub>c</sub>
$\psi$	S4/p4/ $\psi$ 1	3129.67	9	91 451.60
$\pi\mu$	S4/p4/ $\pi$ 3/ $\mu$ 2	3128.73	7	91 447.36

Note: See Table 2 for model notation.

† Np = number of parameters.

RESULTS

Validation of the  $\pi\mu$ -parameterization by the analysis of simulated data

Two capture–recapture models were fitted to the simulated data. In the first, the classical  $\psi$ -parameterization was used, whereas in the second, the  $\pi\mu$ -parameterization was used. The model built with the  $\pi\mu$ -parameterization provides estimates close to the values used to simulate the data (Table 3). Moreover, this model has a lower AIC<sub>c</sub> value than the one that used  $\psi$ -parameterization (Table 4). This reduction of the AIC<sub>c</sub> is due to a reduction in the number of parameters and a slightly better fit (i.e., lower deviance; Table 4).

Breeding dispersal in a Black-headed Gull subdivided population

In the composite model, survival was constant, probability of leaving and settlement probability varied among colonies (model S4/ $\pi$ 2/ $\mu$ 2; Table 5). The model selected after the second step of model selection (investigation of the neighborhood of the composite model), was model S4/ $\pi$ 2/ $\mu$ 4 with constant survival and settlement probabilities and colony-related variations in probability of leaving (Table 6). However all models but one in Table 6 had an AIC<sub>c</sub> value differing by less than two from the AIC<sub>c</sub> of model S4/ $\pi$ 2/ $\mu$ 4. To account for the resulting uncertainty in model selection, parameter estimates have been derived by model averaging across all models in Table 6. The following a posteriori hypothesis tests are based on comparisons of these estimates. Unless otherwise noted, the tests are two sided. When a given estimate was involved in several tests, significance levels were corrected using the Dunn-Sidak method (Sokal and Rohlf 1995:241).

Droughts did not seem to affect survival in colony B ( $S_{ND}^B$  vs.  $S_D^B$ :  $Z = -0.58$ ,  $P = 0.28$ ; Fig. 3) or in colony C ( $S_{ND}^C$  vs.  $S_D^C$ :  $Z = -0.60$ ,  $P = 0.27$ ; Fig. 3). There were no significant differences between survival probabilities in the different colonies during the ND intervals ( $S_{ND}^B$  vs.  $S_{ND}^C$ :  $Z = -1.33$ ,  $P = 0.09$ ;  $S_{ND}^A$  vs.  $S_{ND}^B$ :  $Z = 0.75$ ,  $P = 0.23$ ;  $S_{ND}^A$  vs.  $S_{ND}^C$ :  $Z = -0.63$ ,  $P = 0.26$ ; Fig. 3). Dunn-Sidak-adjusted significance levels are 0.017, 0.025, and 0.05, respectively.

TABLE 5. Selection of the composite model.

Model	Deviance	Np†	AIC <sub>c</sub>
<b>Survival probability</b>			
S0/π0/μ0	283.7	32	2495.4
S1/π0/μ0	284.6	31	2494.2
S2/π0/μ0	285.3	30	2492.9
S3/π0/μ0	290.5	29	2496.0
<b>S4/π0/μ0</b>	<b>291.0</b>	<b>28</b>	<b>2494.4</b>
<b>Site-fidelity probability</b>			
S0/π0/μ0	283.7	32	2495.4
S0/π1/μ0	285.0	31	2494.6
<b>S0/π2/μ0</b>	<b>285.5</b>	<b>30</b>	<b>2493.0</b>
S0/π3/μ0	306.5	29	2512.0
S0/π4/μ0	329.8	28	2533.2
<b>Settlement probability</b>			
S0/π0/μ0	283.7	32	2495.4
S0/π0/μ1	284.6	30	2492.1
<b>S0/π0/μ2</b>	<b>285.7</b>	<b>29</b>	<b>2491.2</b>
S0/π0/μ3	294.9	27	2496.2
S0/π0/μ4	295.1	26	2494.4
<b>Composite model</b>			
<b>S4/π2/μ2</b>	<b>295.1</b>	<b>23</b>	<b>2488.2</b>

Notes: The selected structure for each parameter is highlighted in bold type. The composite model combines the structures selected for each parameter type. The structure of recapture probability does not appear in the model notation because it is the same in all models.

† Np = number of parameters.

There was also no evidence that the droughts on colonies B and C increased the probability of leaving these colonies ( $\pi_{ND}^B$  vs.  $\pi_B^B$ :  $Z = -0.19$ , one-tailed  $P = 0.21$ ;  $\pi_{ND}^C$  vs.  $\pi_D^C$ :  $Z = -0.24$ , one-tailed  $P = 0.20$ ; Fig. 4). Probability of leaving was found to vary significantly among colonies, independently of the drought events, and was found to be lower for the largest colony (A) ( $\pi_{ND}^A$  vs.  $\pi_{ND}^C$ :  $Z = -2.63$ ,  $P = 0.004$   $H_0$ :  $\pi_{ND}^A$  vs.

TABLE 6. Neighborhood of the composite model.

Model	Deviance	Np†	AIC <sub>c</sub>
<b>Survival probability</b>			
S2/π2/μ2	290.7	25	2487.9
S3/π2/μ2	293.5	24	2488.7
<b>S4/π2/μ2</b>	<b>295.1</b>	<b>23</b>	<b>2488.2</b>
<b>Site fidelity probability</b>			
S4/π1/μ2	294.8	24	2490.0
<b>S4/π2/μ2</b>	<b>295.1</b>	<b>23</b>	<b>2488.2</b>
S4/π4/μ2	340.4	21	2529.4
<b>Settlement probability</b>			
S4/π2/μ1	294.3	24	2489.4
S4/π2/μ2	295.1	23	2488.2
<b>S4/π2/μ4</b>	<b>303.0</b>	<b>20</b>	<b>2489.9</b>
<b>Final model</b>			
<b>S4/π2/μ4</b>	<b>303.0</b>	<b>20</b>	<b>2489.9</b>

Notes: The selected structure for each parameter type is highlighted in bold type. The final model combines the structures selected for each parameter type. The structure of recapture probability does not appear in the model notations because it is the same in all models.

† Np = number of parameters.

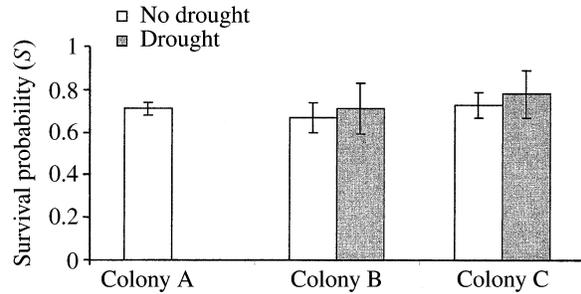


FIG. 3. Estimates ( $\pm 1$  SE) of survival probabilities ( $S$ ). Estimates are given for each colony. Estimates applying to time intervals ending with a drought event are distinguished from estimates applying to other time intervals; see Fig. 2.

$\pi_{ND}^B$ :  $Z = -2.15$ ,  $P = 0.016$   $\pi_{ND}^B$  vs.  $\pi_{ND}^C$ :  $Z = 0.19$ ,  $P = 0.42$ ; Fig. 4). Dunn-Sidak-adjusted significance levels are 0.017, 0.025, and 0.05, respectively.

Probability of settlement on a given colony after this colony experienced a drought was not significantly lower than during a normal year ( $\mu_{ND}^{AB}$  vs.  $\mu_D^{AB}$ :  $Z = 0.28$ , one-tailed  $P = 0.19$ ;  $\mu_{ND}^{BC}$  vs.  $\mu_D^{BC}$ :  $Z = 0.20$ , one-tailed  $P = 0.21$ ;  $\mu_{ND}^{CB}$  vs.  $\mu_D^{CB}$ :  $Z = 0.28$ , one-tailed  $P = 0.19$ ; Fig. 5). The comparison between  $\mu_{ND}^{AC}$  and  $\mu_D^{AC}$  is not given because the time interval starting with a drought event on colony C also ends with a drought event on colony B. The probabilities of settlement on colony B and colony C of individuals that left colony A were therefore set, respectively, at 0 and 1 at this time interval (Fig. 2).

For individuals leaving colony A, the probability of settlement on B (and therefore on C) did not differ significantly from 0.5 ( $\mu_{ND}^{AB}$  vs. 0.5:  $Z = 0.28$ ,  $P = 0.19$ ; Fig. 5). On the other hand, for individuals leaving colony B, the probability of settlement on C (and therefore on A) was significantly different from 0.5 ( $\mu_{ND}^{BC}$  vs. 0.5:  $Z = 2.11$ ,  $P = 0.017$ ; Fig. 5). Individuals leaving colony B were more likely to settle on colony C than on colony A. Although point estimates indicate a tendency for individuals leaving colony C to settle on colony B rather than on colony A, the probability of settlement on B or A did not differ significantly from 0.5 ( $\mu_{ND}^{CB}$  vs. 0.5:  $Z = 1.17$ ,  $P = 0.12$ ; Fig. 5).

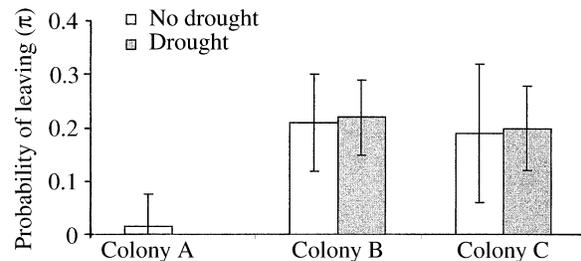


FIG. 4. Estimates ( $\pm 1$  SE) of probabilities of leaving ( $\pi$ ). Estimates are given for each colony. Estimates applying to time intervals ending with a local drought event are distinguished from those applying to other time intervals; see Fig. 2.

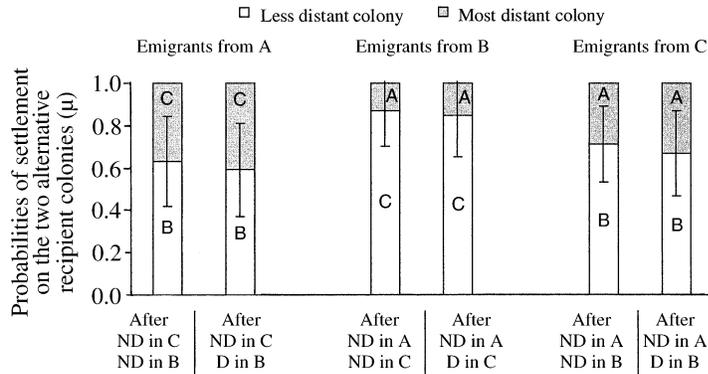


FIG. 5. Estimates ( $\pm 1$  SE) of probabilities of settlement ( $\mu$ ). Estimates are given for each departure colony, each recipient colony, and each time interval type (D for time intervals starting with a drought event on the recipient colony, ND for other time intervals; see Fig. 2).

## DISCUSSION

### *Breeding dispersal in a subdivided Black-headed Gull population*

Our analysis failed to detect any influence of drought on the probability of leaving. This might be due to a lack of statistical power because the data set contains only two drought events. Nevertheless the estimated changes in colony fidelity during a drought year were very small. The human-controlled droughts are unpredictable perturbations: the occurrence of such a drought event during a given breeding season gives no information on the probability of occurrence of a similar perturbation in the following year. Theoretical studies (e.g., Switzer 1993) as well as empirical evidence gathered on colonial seabirds (e.g., Burger 1982) suggest that this type of perturbation should not trigger decision of permanent emigration. However, the model we used distinguishes only two responses of individuals occupying a colony to a drought event: strict fidelity, which involves skipping reproduction until suitable conditions are restored, and emigration to breed at a different colony. There may be two types of emigration: individuals may either permanently emigrate, or temporarily emigrate to another colony and return to their previous colony when suitable conditions are restored. The model we used does not distinguish between these two types of emigration. To do so would require modeling transitions between sites dependent not only on the site occupied the year before, but also on the site occupied at least two years before. Hestbeck et al. (1991) developed such "memory" multisite models using the  $\psi$ -parameterization. Further studies should focus on whether such models can be adapted to the  $\pi\mu$ -parameterization.

Fidelity to the colony that never experienced drought during the study period (colony A) was high relative to fidelity to colonies that experienced at least one drought during the study period (colonies B and C), even when favorable local conditions were met for colony settlement. Occasional droughts may therefore contribute to the general quality of colonies, which in turn may influence habitat selection decisions in any

year. Breeding success may also be higher in colony A than in colonies B and C in years when favorable environmental conditions are met. Unfortunately we have insufficient information on breeding success in the different colonies to address this hypothesis. Another possible explanation for the comparatively high fidelity in colony A is its size, per se, which may lead to high fidelity through conspecific attraction phenomena (Forbes and Kaiser 1994).

Failure to detect any influence of drought on the probability of settlement in the next breeding season suggests that the settlement decision in a given breeding season does not depend strongly on information gathered through prospecting the year before. However, the role of prospecting behavior in settlement decisions has mainly been documented in "naïve" first time breeders (Halley et al. 1995, Schjorring et al. 1999; but see Danchin et al. 1998). Prospecting may be less important for the settlement decisions of experienced breeders, which may mainly rely on individual experience (Switzer 1993).

Our results concerning settlement probability suggest that an individual leaving one of the two small colonies is more likely to settle on the other small colony than on the more distant and larger colony. This suggests a negative relationship between the probability of moving to a given recipient colony and the remoteness of this colony. Distance may be associated with a decrease in the probability of detecting potential recipient sites (e.g., Fahrig and Paloheimo 1988), or an increase in direct costs of dispersal (increased risk of death; Gadgil 1971, Hanski et al. 2000). This seems unlikely in the present study. Black-headed Gulls can travel thousands of kilometers during migration, and the maximum distance between the colonies considered here is <40 km. However, Black-headed Gulls are also known to be central place foragers, and could benefit from the familiarity with the feeding habitat in the vicinity of their colony. This is probably associated with higher efficiency in finding food sources (Prévot-Julliard and Lebreton 1999). If the results of the present study reflect an effect of distance on dispersal, this probably involves costs

associated with loss of familiarity. Alternatively, the comparatively low probability of settlement on the large colony could reflect stronger competition for the acquisition of a nest site on this colony.

The estimates of survival probability obtained in the present analysis are lower than those found in other survival analyses in the same population. Prévot-Julliard et al. (1998) obtained an estimate of adult survival equal to 0.9 for birds breeding in colony A. However this previous analysis was performed using models that took into account a transient effect (an "excess" of individuals resighted only once). This transient effect could result from heterogeneity in local survival (individuals establishing in the colony for a short period only) and/or from heterogeneity in capture rates (Pradel et al. 1997). If not taken into account, a transient effect is likely to induce negative biases in survival estimates (Prévot-Julliard et al. 1998). The main purpose of the present analysis was to illustrate the use of  $\pi\mu$ -parameterization and to the separate site-fidelity probabilities and settlement probabilities. For the sake of clarity, we did not design our models to take into account these transient effects. This omission could explain our low estimates of survival probabilities.

#### *General discussion*

The parameterization of multisite capture-recapture models presented here allowed us to build statistical models that are more realistic and account more efficiently for the ecological and behavioral processes underlying dispersal. First, it seems clear that the  $\pi\mu$ -parameterization describes movement among sites more accurately whenever they result from a two-step decision-making process (i.e., when choice of a settlement site only occurs after a decision has been made to leave the current site). Furthermore, this parameterization offers the possibility of separately testing effects on (a) the probability of leaving a given site, and (b) the probability of settling on another site, conditional on having left the current site. Because the  $\pi\mu$ -parameterization permits a mechanistic description of movement patterns while the  $\psi$ -parameterization permits only a phenomenological description, we believe that this method is more effective in addressing hypotheses about movements in conservation, evolutionary biology, and behavioral ecology studies.

The analysis of the Black-headed Gull data set did not involve the modeling of emigration and immigration probabilities as functions of continuous explanatory variables. Potentially highly relevant factors of variation of dispersal in metapopulations may include distances between subpopulations, relative areas of the habitat patches (e.g., Hanski et al. 2000), and relative densities of the subpopulations (e.g., Doncaster et al. 1997). Spendelov et al. (1995), using the  $\psi$ -parameterization, have tested the effects of distances and local densities on movement probabilities. They built ultra-structural models in which parameter variations are

constrained by logit-linear relationships with these continuous explanatory variables. It should be possible to build models using the  $\pi\mu$ -parameterization in which probability of leaving and settlement probability are constrained in the same way.

The  $\pi\mu$ -parameterization presents advantages from a computational and statistical point of view. For many situations, the  $\pi\mu$ -parameterization leads to a description of dispersal patterns involving a smaller number of parameters, as illustrated by the analysis of the simulated data set. This may prove advantageous when dispersal patterns are not the only parameters of interest. Effects on other parameters will then be tested in the framework of a more parsimonious model than with the  $\psi$ -parameterization, leading to increased power (Lebreton et al. 1992). Furthermore, the optimization function of the multistrata model with the  $\psi$ -parameterization may lead to numerical problems when transitions between strata are rare, because the estimates of the transition probabilities are very close to zero (Spendelov et al. 1995). This is often the case when the states are distinct sites and transition probabilities describe movements between sites. By separating the two components of movement probability, the  $\pi\mu$ -parameterization will lead to estimates further from this boundary, as illustrated by the analysis of the simulated data set.

Finally, the  $\pi\mu$ -parameterization can be generalized to all those cases in which a transition process can be split into its components. For example, capture-recapture models have been recently used to study trade-offs between current and future reproduction (Nichols et al. 1994, Viallefont et al. 1995, Cam et al. 1998). The level of reproductive effort invested can result from a two-step decision process: deciding whether to breed, and conditional on the decision of breeding, deciding the amount of resources to allocate to reproduction (e.g., whether to invest in 1, 2, or more offspring). The probability associated with the first decision may depend on local intrasexual competition while that associated with the second may be affected by resource availability. The  $\pi\mu$ -parameterization would allow such hypotheses to be tested.

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APPENDIX

The  $\mu\pi$ -parameterization has not been implemented in any software program. However, it is possible to build such a model using a software program designed to use the  $\psi$ -parameterization (MARK1.9 or MSSURVIV1.2). Here we show how to build  $\mu\pi$  models using program MARK. First, capture histories should be modified to contain dummy occasions (equal in number to the actual number of occasions minus 1) and non-observable strata (equal in number to the observable ones). A classical multisite capture–recapture history for five capture occasions is **A0BBC** for example. In this notation an individual is released in site A, is recaptured at occasions 3 and 4 in site B and in site C at the last occasion. To decompose  $\psi_i^{RT}$  into its two components  $\pi_i^R$  and  $\mu_i^{RT}$ , one adds a dummy occasion (i.e., a column of zeros) after each real recapture occasion, except the last. The above capture history becomes **A00B0B0C**. Each original time interval is now divided into two intervals: the interval between a real occasion (hereafter referred to as O1 type) and a dummy one (hereafter referred as to O2 type), and between the dummy occasion and the next real occasion.

Next, an additional non-observable state for each site is added. Individuals are allowed to enter these states only on dummy occasions. Let these non-observable states be denoted a, b, and c. Consider the matrix and vectors containing the parameters of  $\pi\mu$ -models. The probability of recapture during a dummy occasion is set to zero (i.e., no observations). The vector  $P_{O2}$  containing the capture probabilities applying to dummy occasions can be written as

$$P_{O2} = \begin{pmatrix} A & 0 \\ B & 0 \\ C & 0 \\ a & 0 \\ b & 0 \\ c & 0 \end{pmatrix}$$

During real occasions, capture probabilities are set to one in strata a, b, and c but are not fixed for the observable strata A, B, and C. The vector  $P_{O1}$  containing the capture probabilities applying to real occasions can be written as follows:

$$P_{O1} = \begin{pmatrix} A & p_i^A \\ B & p_i^B \\ C & p_i^C \\ a & 1 \\ b & 1 \\ c & 1 \end{pmatrix}$$

The survival/transition probability matrix  $T_{O12}$  applying to a time interval starting with a real (O1 type) occasion and finishing with a dummy occasion (O2 type) can be written as shown at the bottom of the page ( $\tau$  is used here for the parameters that describe transitions between strata).

$S^R$  is the survival probability in site  $R$  ( $R = A, B,$  and  $C$ ) and  $\tau_i^{Rr}$  ( $R = A, B, C$  and  $r = a, b, c$ ) corresponds to the probability,  $\pi_i^R$ , of leaving a site  $R$ .

The survival/transition probability matrix  $T_{O21}$  applying to a time interval starting with a dummy (O2 type) occasion and finishing with a real occasion (O1 type) can be written as

$$T_{O21} = \begin{matrix} & A & B & C & a & b & c \\ \begin{matrix} A \\ B \\ C \\ a \\ b \\ c \end{matrix} & \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & \tau_i^{aB} & \tau_i^{aC} & 0 & 0 & 0 \\ \tau_i^{bA} & 0 & \tau_i^{bC} & 0 & 0 & 0 \\ \tau_i^{cA} & \tau_i^{cB} & 0 & 0 & 0 & 0 \end{pmatrix} \end{matrix}$$

In this matrix, the survival probabilities are set to 1 in all strata.  $\tau_i^{rT}$  ( $r = a, b, c;$  and  $T = A, B, C$ ) corresponds to  $\mu_i^{rT}$  (where  $R = A, B, C,$  and  $T = A, B, C$ ), the probability of settlement in a given recipient site, conditional on  $\pi_i^R$  (i.e., for individuals known to have left the previous site). Use of this model is currently limited to situations with three sites because the available software programs for multisite analyses (MSSURVIV1.2 and MARK1.9; Brownie et al. 1993, White and Burnham 1999) do not optimize the likelihood function under the constraint that movement probabilities add up to 1. Use of this constraint will allow consideration of situations with more than three sites and the use of ultrastructural models in which dispersal probability depends on external covariates such as distance between sites. For this reason, it might also be useful to consider the use of a Lagrange function in the optimization procedure (R. Choquet, *personal communication*).

$$T_{O12} = \begin{matrix} & A & B & C & a & b & c \\ \begin{matrix} A \\ B \\ C \\ a \\ b \\ c \end{matrix} & \begin{pmatrix} S_i^A(1 - \tau_i^{Aa}) & 0 & 0 & S_i^A \tau_i^{Aa} & 0 & 0 \\ 0 & S_i^B(1 - \tau_i^{Bb}) & 0 & 0 & S_i^B \tau_i^{Bb} & 0 \\ 0 & 0 & S_i^C(1 - \tau_i^{Cc}) & 0 & 0 & S_i^C \tau_i^{Cc} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \end{matrix}$$