LOCAL RECRUITMENT IN THE GREATER FLAMINGO: A NEW APPROACH USING CAPTURE–MARK–RECAPTURE DATA

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Abstract. Although the establishment of new individuals in the breeding component of a population is an essential feature of population regulation, only a few attempts have been made to test biological hypotheses about recruitment. Most previous studies rely on ad hoc calculations or are flawed with unwarranted assumptions about survival. We use a recently developed approach, based on capture–mark–recapture, in which analysis of local recruitment is similar to a time-reversed analysis of survival. The basic data set consists of capture histories viewed in reverse order, with initial capture at year of birth, and subsequent observations corresponding to years when the animal has bred. The model considers two essential components, the probability for any breeding individual to reproduce for the first time (β, the probability of first reproduction) and the probability of recapture (p), both conditional on survival. Contrary to previous attempts at modeling recruitment, the present approach does not assume an age at which breeding propensity stabilizes to a maximum value. The flexibility achieved allows the comparison of recruitment among groups within a population and also allows one to consider the effects of environmental variables, as well as interactions between such effects. Practically, the procedure starts from a global model, based upon the a priori knowledge of the biology of the species, and assesses its fit. Then more parsimonious models are selected using Akaike's Information Criterion and likelihood ratio tests. Finally, maximum likelihood estimates of model parameters are obtained with estimates of precision. We used a modified version of program RELEASE for goodness-of-fit tests, and program SURGE for iterative model fitting and the computation of likelihood ratio tests. We illustrate the method with the study of local recruitment of Greater Flamingos (*Phoenicopterus ruber roseus*) in the Camargue (southern France) between 1984 and 1994. We found additive effects of age and year to affect recruitment. Breeding propensity increased with age. Recruitment was noticeably higher in the year following an increase in mortality rate due to a particularly severe winter. Long-lasting effects of this increased mortality on recruitment were observed in the three following years. There was no evidence for an effect of sex or cohort (year of birth) on recruitment. However, sex, as well as time and age, affected recapture rates. We discuss the various advantages and limitations of the model for the study of local recruitment in long-lived species and mention some potential developments.

Key words: age-specific breeding probability; breeding propensity; capture–mark–recapture models; first reproduction; probability of; Greater Flamingo; local recruitment; Phoenicopterus ruber roseus; *population dynamics; reproduction; seniority probability.*
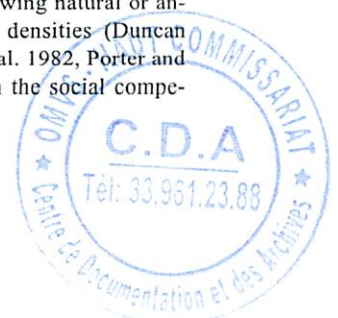
INTRODUCTION

Recruitment, the establishment of new individuals in the breeding component of populations, is a complex process, and is important both in population regulation (Birkhead and Furness 1985, Porter and Coulson 1987) and in life history theory (Lessells 1991, Roff 1992, Stearns 1992). Although natural selection is often thought to favor reproduction early in life (Charlesworth 1994), many species defer reproduction to a greater or lesser extent. For instance, long-lived birds often start to breed ≥1 yr after they have completed

their physiological maturation and growth (Dunnet 1991). Most explanations of delayed age at first reproduction assume a conflict between early reproduction and increase in reproductive competence with age (Brown 1987, Lessells 1991, Charlesworth 1994). Some authors have focused for instance on the importance of slow improvement of foraging skills with age (Lack 1968, Orians 1969, Ashmole 1971), whereas others considered social competition on breeding grounds, assuming a limited availability of breeding space (Coulson 1968). Previous studies demonstrated a decrease in age at first breeding following natural or anthropogenic reductions of colony densities (Duncan 1978, Potts et al. 1980, Coulson et al. 1982, Porter and Coulson 1987), in accordance with the social compe-

tition hypothesis (Coulson 1968). Another condition that may lead to deferred reproduction is a trade-off between current reproductive effort and subsequent reproduction, growth, or survival (Charlesworth 1994). Survival of younger birds might be more sensitive to increased reproductive effort (Lack 1954) and such a fitness cost of early reproduction could delay age at first breeding. For instance, several studies of long-lived species found interspecific differences in age at first breeding that they related to differences in post-breeding survival and reproductive effort (Mills 1973, Wooler and Coulson 1977). Studies of lifetime reproductive success (Clutton-Brock 1988, Newton 1989) provide evidence that various hypotheses can accommodate the large *inter*specific variation in age at first breeding. Variability in recruitment at the *intra*specific level requires, on the other hand, an understanding of the underlying behavioral mechanisms (Porter 1990). However, most analyses of the recruitment process in natural populations so far have been hindered by a lack of appropriate statistical approaches (Clobert and Lebreton 1991, Dunnet 1991). A suitable method should provide ways for testing various hypotheses about recruitment, including environmental effects, and allow comparisons between groups of individuals.

In most previous studies (Austin and Austin 1956, Harrington 1974, Williams and Joanen 1974, Lloyd and Perrins 1977, Wooler and Coulson 1977, Duncan 1978, Finney and Cooke 1978, Harris 1981, Coulson et al. 1982, Nelson 1983, Serventy and Curry 1984, Rattiste and Lilleleht 1986, Weimerskirch and Jouventin 1987, Gratto 1988, Brooke 1990, Spendelow 1991, Thompson et al. 1994), recruitment has been equated with the age distribution of first-time breeders, without correction for variation in survival rate and/or probability of capture. However, a bird observed breeding for the first time might have bred previously. Clobert and Lebreton (1991) attributed this observed lack of formal analysis to the difficulty in obtaining separate estimates of the proportion of breeders and of survival and return rates, and emphasized the need for formal models. First attempts to model recruitment (Barrat et al. 1976, Chabrzyk and Coulson 1976, Lebreton 1978, Mougin et al. 1986) were based on simple ratio estimates of age-specific breeding probabilities from recaptures or resightings, and considered adult survival to be constant. More recently, two types of models have been proposed for the study of age-specific recruitment. Lebreton et al. (1990) proposed *transversal* models of recruitment for the analysis of data collected at one or several points over time, but without information on individual fate over time. Clobert et al. (1994; see also Clobert et al. 1990) developed *longitudinal* models to estimate age-dependent recruitment from individual recapture histories of animals marked when young, considering that the probability of capture of an individual differs before and after the first recapture as a breeder. Both models depend on some critical assumptions whose biological
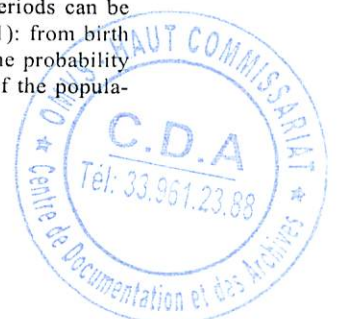
relevance may be limited, namely that survival rates are identical for breeders and non-breeders, that survival rates are not year specific and that recapture probabilities are not age specific. In addition, the statistical models of Lebreton et al. (1990) and Clobert et al. (1994) essentially focus on the influence of age on recruitment and do not allow testing for the influence of other factors that potentially affect recruitment, such as the prevailing environmental conditions during growth, or the environmental conditions during the current breeding season. Finally, as it is most often difficult to estimate the non-breeding part of the population, all recruitment models proposed so far assumed that there is an age at which every animal still alive breeds or at least an age at which breeding propensity, i.e., the probability that an animal that has already bred will breed again (Cooke et al. 1995), becomes maximum.

The new statistical approach we present here (Pradel 1996) represents a radical change in the way in which capture histories can be studied. Capture histories are read *from the last observation backward through time* rather than from the first observation onwards as is usually done. In this way, when an animal ceases to be observed as a breeder, it may be reproducing for the first time or may have reproduced earlier without being detected. Recruitment thus becomes the main target of the analysis. Furthermore, this approach is also more general than previous methods in that no survival assumptions are required, and the a priori hypothesis of a stabilization in the recruitment rate after a certain age does not have to be made, but can now be tested. Finally, this approach provides more flexibility by allowing different aspects of recruitment to be analyzed directly. We first describe the general procedure and then illustrate the approach through a case study of local recruitment at the natal colony in the Greater Flamingo (*Phoenicopterus ruber roseus*).

A CAPTURE–MARK–RECAPTURE MODEL FOR TESTING BIOLOGICAL HYPOTHESES ABOUT LOCAL RECRUITMENT

Link between breeding history and capture history

The sampling scheme considered hereafter is that of a capture–mark–recapture (CMR) study carried out at a single breeding site, where individuals are marked as young and recaptured (or resighted) as breeding adults. The data are summarized in capture histories where the first observation corresponds to the year of birth and subsequent observations correspond to years when the animal is known to have bred. Thus, the model deals exclusively with local recruitment and in its present form does not address the problem of natal dispersal of birds born in the Camargue. Three periods can be distinguished in a capture history (Fig. 1): from birth to the first observed breeding attempt, the probability of joining the reproductive component of the popula-

1	0	0	0	1	0	1	1	0	0	0	0

↑ birth

←———→ PERIOD 1 (during which recruitment has occurred)

←———→ PERIOD 2 (during which breeding has been observed)

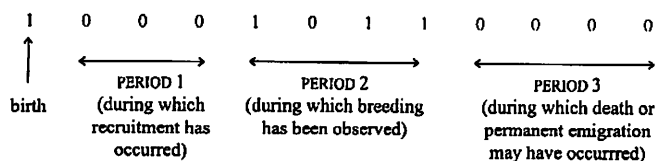←———→ PERIOD 3 (during which death or permanent emigration may have occurred)

FIG. 1. Link between life history and capture/sighting history. Numbers above horizontal arrows represent capture events.
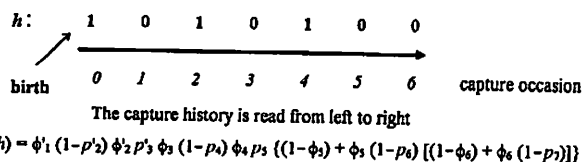
tion typically increases with age; from the first to the last observed breeding attempt when the animal is alive and breeds (during which period breeding propensity may increase with age); finally, death (or permanent emigration) may occur at some point after the last observed breeding attempt. Information about recruitment is thus found in the first period and information about breeding propensity in the second period.

To extract the information about recruitment (Fig. 2), Clobert et al. (1994) use "a special case of a survival and recapture model for several data sets" that contrasts the capture rates during the first period (which rates should be relatively low because not all animals have started to breed) to those during the other periods. Their model "links the probabilities of capture with age-specific breeding probabilities" (see Clobert et al. 1994 for details). Because this model is essentially a survival model, it involves assumptions about survival, and because age-specific breeding probabilities are not directly accessible, factors affecting recruitment can only be interpreted indirectly. The approach by Pradel (1996), however, was specifically designed for the study of recruitment, although not exclusively in relation to reproduction. The method relies on two parameters (Fig. 2), the seniority probability and the recapture rate. When the model is applied to breeding animals, the seniority probability, denoted γ, corresponds to the probability that an animal breeding on a given occasion has already bred at least once. Within the framework of the study of breeding recruitment, we will consider instead the complementary event, the probability that the animal is breeding for the first time, and its associated probability (hereafter called probability of first reproduction), denoted β ($\beta = 1 - \gamma$). Details regarding the computation of β are presented in the Appendix. The probability of first reproduction reflects recruitment whereas the capture rate, apart from capture effort, reflects breeding propensity. Both parameters can be tested against potential covariates by means of built-in constraints. Moreover, because only the first two periods of capture histories (when an animal is by definition alive) are modeled, no assumption on survival is needed.

As stated in the introduction, the core idea behind Pradel's model is to look at the capture histories backwards, from right to left (Fig. 2). Going along a capture history in this way, one may ask when an animal ceased to be a breeder and becomes an immature. Here is an example of how this idea may be formalized using seniority probability (γ) and capture rate (p). The capture history 1010100 where the first 1 represents birth (occasion 0), will be read: the animal was last caught at occasion 4, it was not recruited at 4, was not captured at 3, was not recruited at 3, was captured at 2, and was not seen earlier than 2. The last phrase can be further expanded as: the animal was recruited at occasion 2 or was not recruited at 2, was not captured at 1 and was recruited at 1. The associated probability is therefore $\gamma_4(1 - p_3)\gamma_3 p_2[(1 - \gamma_2) + \gamma_2(1 - p1)(1 - \gamma_1)]$. The same logic of computing probabilities is used in survival analysis of CMR data (Fig. 3). Indeed, recruitment models with this approach are to a large extent formally equivalent to survival models (for proof and limitations see Pradel 1996). This equivalence is important as it allows the use of pre-existing software

A) CLOBERT ET AL.'S MODEL

h: 1   0   1   0   1   0   0

birth   0   1   2   3   4   5   6   capture occasion

The capture history is read from left to right

$\Pr(h) = \phi'_1 (1-p'_2) \phi'_2 p'_3 \phi_3 (1-p_4) \phi_4 p_5 \{(1-\phi_5) + \phi_5 (1-p_6) [(1-\phi_6) + \phi_6 (1-p_7)]\}$

B) PRADEL'S MODEL

h: 0   1   0   1   0   0

←——————

0   1   2   3   4   5   6   capture occasion

The capture history is read from right to left

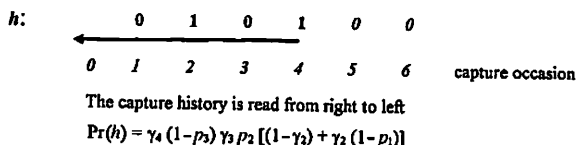$\Pr(h) = \gamma_4 (1-p_3) \gamma_3 p_2 [(1-\gamma_2) + \gamma_2 (1-p_1)]$

FIG. 2. Alternative parameterizations for the study of recruitment from capture histories (row of 0's and 1's labeled h). In the Clobert et al. (1994) model for the study of recruitment, p' = capture rate before recruitment, p = capture rate after recruitment, ϕ' = survival probability before recruitment, ϕ = survival probability after recruitment; p and p' are further related to the age-specific breeding probabilities. In Pradel's (1996) model, p = capture rate, and γ = seniority probability, i.e., the probability that an individual has bred at least once before. Subscripts refer to occasion (for capture probability) or starting occasion (for survival probabilities).

A)

Capture occasions

t_1 t_2 t_3 ...t_k

ϕ_1 ϕ_2 ...ϕ_k
survival rates

p_1 p_2 p_3 ...p_k
capture rates

B)

Capture occasions

$t_1...$ t_{k-2} t_{k-1} t_k

$\gamma_1...$ γ_{k-1} γ_k
seniority rates

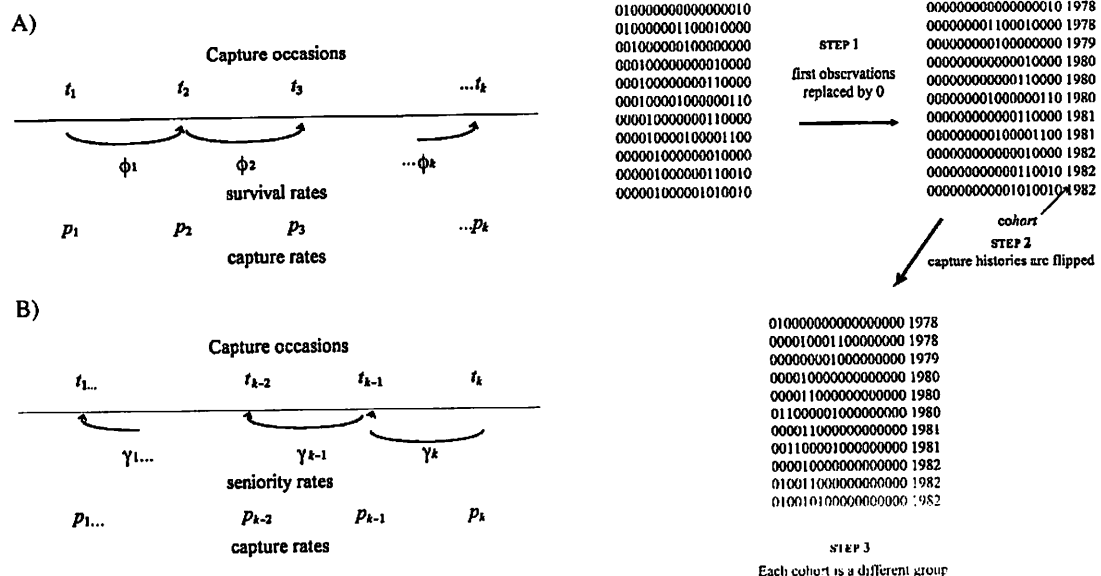$p_1...$ p_{k-2} p_{k-1} p_k
capture rates

FIG. 3. Formal equivalence of survival (A) and recruitment (B) models. (A) p_1 is not estimable; (B) p_k is not estimable. When data are read backward, first reproduction is equivalent to death; seniority probability is equivalent to survival probability.

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01000000000000010
01000001100010000
00100000100000000
00010000000010000
00010000000110000
00010000100000110
00010000000110000
00010000100001100
00000100000010000
00000100000110010
00000100001010010
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STEP 1
first observations
replaced by 0
⟶

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00000000000000010 1978
00000001100010000 1978
00000000100000000 1979
00000000000010000 1980
00000000000110000 1980
00000001000000110 1980
00000000000110000 1981
00000000100001100 1981
00000000000010000 1982
00000000000110010 1982
00000000001010010 1982
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cohort
STEP 2
capture histories are flipped

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01000000000000000 1978
00001000110000000 1978
00000000100000000 1979
00001000000000000 1980
00001100000000000 1980
01100000100000000 1980
00001100000000000 1981
00110000100000000 1981
00001000000000000 1982
01001100000000000 1982
01001010000000000 1982
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STEP 3
Each cohort is a different group

FIG. 4. Preparation of the capture–mark–recapture data for an analysis of recruitment.

cohort 1978
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01000000000000000
00001000110000000
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cohort 1979
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00000000100000000
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cohort 1980
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00001000000000000
00001100000000000
01100000100000000
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cohort 1981
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00001100000000000
00110000100000000
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cohort 1982
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00001000000000000
01001100000000000
01001010000000000
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designed for survival analysis, such as program SURGE (Pradel and Lebreton 1991) used hereafter.

Preparation of the data

To take advantage of the correspondence just mentioned between survival and recruitment analyses, data must be prepared in a specific way (Fig. 4). First, the observation corresponding to year of birth is removed from all capture histories and this information is kept separately (since age is an important factor in recruitment). Second, capture histories are reversed. Third, each cohort is made a different group. Then first reproduction becomes equivalent to mortality and estimates of seniority probability are obtained in the guise of survival probability. However, it must be noted that, because the capture histories have been reversed, the estimates of seniority probabilities will be obtained in reverse order, starting from the oldest animals. Apart from this, the recruitment analysis proceeds exactly as a survival analysis, with the identification of a general starting model that fits the data and proceeding to simpler models by eliminating the nonsignificant effects and interactions between effects. We refer the reader to the monograph of Lebreton et al. (1992) for the generalities about CMR methodology and restrict our discussion to the points specific to the study of recruitment.

Goodness-of-fit test

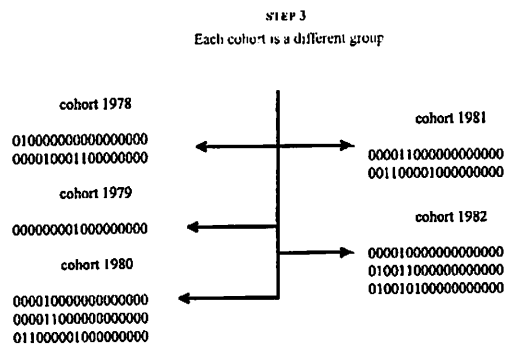Goodness-of-fit tests assess whether a model correctly describes the data. In CMR, robust and well-studied goodness-of-fit tests are available only for a few models. One such model is the Interval-Specific Survival and Capture model known as the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965). In this model, changes in survival or capture probabilities over intervals are generally thought of as temporal variations. However, when a single cohort is considered, changes among individuals may also result from the aging process. Since we know that the probability of first reproduction should strongly depend upon age, we will test the fit of the Interval-specific First Reproduction and Capture (IFRC) model on each cohort separately using the data prepared according to Fig. 4.

Separating age, time, and cohort effects

When considering only one cohort, there is no possibility of separating the respective effects of age and time on probabilities of first reproduction and capture rates. For instance, we cannot know whether, apart from expected variation with age, there are more or less favorable years for recruitment. This important question
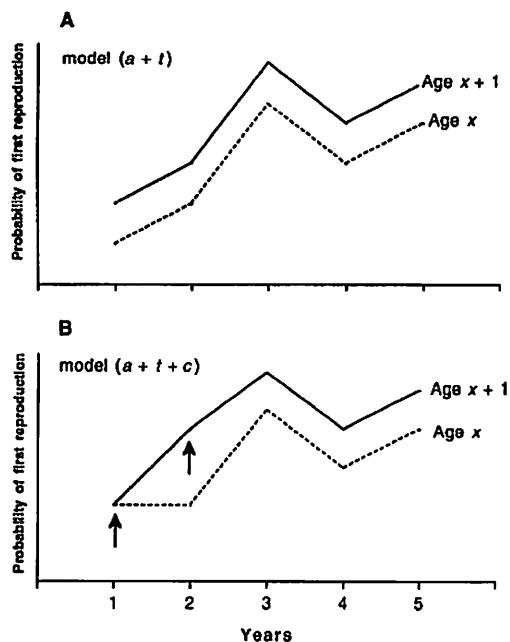
A

B

FIG. 5. Separating age, time, and cohort effects in the analysis of recruitment by means of additive models. We consider the recruitment of two consecutive age classes (age x = dotted line; age $x + 1$ = continuous line) over five consecutive years. (A) model [$a + t$] (without cohort effect), a strict parallelism over time is observed; (B) model [$a + t + c$] (with cohort effect), individuals of age x in year 1 belong to a cohort with early recruitment, the same cohort effect can again be observed for individuals of age $x + 1$ in year 2. Arrows denote the cohort effect.

necessitates that probabilities of first reproduction for a given age class are compared among several years. This can be done by comparing estimates from different cohorts in the framework of a multigroup analysis. The power to detect a time effect increases with the increasing number of marked cohorts.

Another factor that may influence recruitment is the conditions prevailing during early growth and development (see Cézilly et al. 1995). Such a factor would appear as a cohort effect in the analysis. Yet, in the presence of age and time variations, there is a priori no way to test for a cohort effect. As animals of a given age in a given year belong to a definite cohort, there is indeed no simple solution. However, the detection of a cohort effect is possible if age and time dependencies can be made more specific using some constraints. A trend with age (logit linear or a logit quadratic for instance) is a reasonable approach for recruitment. Also, variations of recruitment over time in the different age classes may be tested for parallelism (Fig. 5A). This amounts to fitting a model without interaction between age and time. Then, a cohort that recruits earlier than average will cause anomalies in the parallelism that move over time through the suc-

cessive age classes (Fig. 5B). This is illustrated in the case study that follows.

A CASE STUDY: RECRUITMENT IN THE GREATER FLAMINGO

Methods

Species and study area.—The Greater Flamingo is a long-lived colonial waterbird that shows delayed maturity (Johnson et al. 1993, Cézilly et al. 1996). Adult plumage is acquired only after several stages of juvenile and immature plumages (Johnson et al. 1993). There is a slight sexual dimorphism, with females being smaller in size and acquiring definitive plumage on average shortly before males (Johnson et al. 1993). Access to reproduction is progressive in flamingos: no breeding attempt by a bird <3 yr old has ever been observed, and breeding by birds 3 yr old is rare (Johnson et al. 1993). Details of the reproductive biology and demography of the species have been given in previous studies (Johnson 1983, Johnson 1989, Cézilly 1993, Cézilly et al. 1994a, b, 1995, 1996, 1997).

Flamingos have bred intermittently in the saline lagoons of the Camargue (southern France) for centuries (Gallet 1949, Johnson 1983). In every year from 1974 to 1994, they have successfully bred on an artificial island built for them in the Etang du Fangassier, part of the large complex of commercial salt pans of Salin de Giraud. Depending on year and colony size, birds also have nested on a nearby dike. Since 1977, 7–30% of young flamingos (of unknown sex) reared each year in the Camargue have been marked individually with plastic rings engraved with a three or four digit code, which allows individual recognition in the field (Johnson 1989). Originally, the larger chicks were selected for ringing, but since 1984 chicks of all sizes have been marked (Green et al. 1989).

Resightings of marked birds.—Ring codes can be read through a telescope from a distance of ≤400 m. In 1982, when many of the first cohort of ringed birds were in adult plumage, observations started at the natal colony to see if any individuals were attempting to breed. The following year, a tower blind was built 70 m from the nesting colony in the Camargue and has been used by observers permanently during the entire breeding season each year since 1983. The observers' main activity was to determine which ringed birds were breeding. A bird was considered breeding when it was observed incubating an egg or attending a young, or when it was repeatedly observed on the same nest. Birds that were seen only courting or paired were not considered. In addition, breeding adults were also identified when feeding their chick in the crèche (see Cézilly et al. 1994b). Between 1983 and 1994, the colony ranged in size from 8600 to 19 900 pairs. Table 1 shows for each study year the observation effort and the number of different ringed individuals observed.

Data analysis.—The present analysis has been re-

TABLE 1. Number of chicks ringed for each cohort in the study, observation effort, and number of different flamingos observed at the Fangassier colony for each year during the study period.

Year	Number of chicks ringed	Observation effort (h)	Number of different ringed birds resighted
1977	559		
1978	650		
1979	651		
1980	761		
1981	697		
1982	652		
1983	720		
1984	781	756	53
1985	552	1311	194
1986	599	1186	430
1987	600	1329	316
1988	600	1138	276
1989		1172	277
1990		1029	532
1991		1514	972
1992		1117	641
1993		517	518
1994		789	747

stricted to the cohorts of flamingos ringed from 1977 to 1988 and resighted as breeders between 1983 and 1994 (Table 2). During the study period 824 females and 856 males of known age have been observed breeding at least once. Our analysis concerns the recapture histories of those 1680 individuals. We studied the possible influence on probabilities of first reproduction and

capture probabilities of cohort, time, sex, and age through a set of models involving all or some of the main effects and of their interactions. A cohort effect may result from long-term effects of rearing conditions. A time effect is notably expected since a severe cold spell occurred in the winter 1984 1985, causing the death of an estimated 6000 flamingos, ≈25% of the local breeding population (Johnson et al. 1991, Lebreton et al. 1992, Cézilly et al. 1996), and presumably reducing the competition for access to the breeding island the following year.

Model notation, from Pradel (1996), is adapted from the notation of survival models (Lebreton et al. 1992), which is derived from generalized linear models notation (McCullagh and Nelder 1989). An index formula designates the effects considered for each kind of parameter, probability of first reproduction (β) and recapture probability (p), where an age effect is denoted a, a time (i.e., year) effect is denoted t, an effect of the year of birth (= cohort) is denoted b, a sex effect is denoted s. Effects are connected by asterisks (*) if they interact, and by plus signs (+) if they are additive.

We started the procedure with a goodness-of-fit test of the Interval-Specific Survival and Capture (ISSC) model (see *Goodness-of-fit test.* above) applied separately to each combination of sex and cohort groups ($\beta_{...}$, $p_{...}$). This general model can be seen as ($\beta_{...}$, $p_{...}$), where probabilities of first reproduction and recapture probabilities may take on a different value for each combination of sex, age, and time cate-

TABLE 2. Numbers of flamingos observed breeding for the first time at their native colony per year, cohort, and sex.

Cohort	Observation year 1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	Total
Males														
1977	2	9	6	17	13	6	3	2	1	0	1	0	1	61
1978	0	4	5	18	25	8	4	1	2	2	1	2	1	73
1979	0	1	5	22	26	13	5	4	4	7	0	1	3	91
1980		0	1	12	39	15	6	5	6	8	3	0	1	96
1981			0	8	33	12	6	12	11	11	0	3	6	102
1982				1	18	18	9	12	22	29	9	2	8	128
1983					0	6	3	4	18	30	14	4	5	84
1984						0	2	1	9	24	12	3	14	65
1985							0	0	7	28	16	5	15	71
1986								0	1	13	11	7	12	44
1987									0	11	6	5	14	36
1988										0	2	0	3	5
Females														
1977	2	12	7	19	25	2	5	6	3	2	4	2	0	89
1978	0	6	8	23	16	6	4	2	3	3	4	4	5	84
1979	0	3	7	17	33	9	4	1	5	8	6	3	1	97
1980		0	0	13	19	8	5	7	9	11	2	5	1	80
1981			0	6	22	13	5	9	16	13	6	5	3	98
1982				1	12	5	4	4	14	18	6	7	4	75
1983					3	4	5	3	15	41	15	7	9	102
1984						0	0	1	13	38	8	3	8	71
1985							0	0	9	25	8	6	9	57
1986								0	2	23	6	6	10	47
1987									0	11	2	2	2	17
1988										2	0	2	3	7

TABLE 3. Goodness-of-fit tests of the recruitment model by cohort applied to the reverse capture histories of Camargue flamingos. Test of model (β_{t*a*s}, p_{t*a*s}); $\hat{c}$ denotes the overall overdispersion factor estimate.

Sex	Cohort	χ^2	df	P
F	1977	34.0441	40	0.7345
F	1978	55.5327	41	0.0644
F	1979	56.0174	32	0.0054
F	1980	56.3908	34	0.0093
F	1981	44.7787	31	0.0522
F	1982	24.0268	19	0.1951
F	1983	27.2375	18	0.0746
F	1984	7.4884	10	0.6787
F	1985	1.1991	3	0.7532
F	1986	6.8333	3	0.0774
M	1977	31.8513	35	0.6209
M	1978	51.196	37	0.0603
M	1979	50.814	36	0.0518
M	1980	46.1496	31	0.0392
M	1981	36.8073	28	0.1232
M	1982	39.8086	28	0.0688
M	1983	20.5369	17	0.2477
M	1984	34.1836	11	0.0003
M	1985	15.4906	7	0.0302
M	1986	3.6536	2	0.1609
M	1987	0.0356	1	0.8504
Total		644.0759	464	<0.0001 $\hat{c} = 1.388$

gories—or as (β_{t*a*b}, p_{t*a*b}) with similar interpretations—since an interaction between age and time corresponds to a cohort effect whereas an interaction between age and cohort corresponds to a time effect. The goodness of fit of the general model was tested using program REL-CR (Pradel 1993), a modified version of program RELEASE (Burnham et al. 1987). We then proceeded to models that were structured more simply and that were deprived of some effects or combinations of effects found in the general model. Those models were fitted using program SURGE 4.1 (Pradel and Lebreton 1991). The selection among models was based on Akaike's Information Criterion (AIC) (Akaike 1973). The use of AIC favors parsimony in model selection and thus enhances the robustness of the conclusions (Lebreton et al. 1992, Anderson et al. 1994). Goodness-of-fit tests (see next paragraph) led to the incorporation of an overdispersion factor, and the use, accordingly, of a modified AIC (noted hereafter mAIC), following Lebreton et al. (1992).

RESULTS

Goodness-of-fit tests

Table 3 shows that the IFRC model applied to the reversed capture histories was rejected ($P < 0.05$) for five cohort-sex groups out of 21 with sufficient data, as well as for the total model (β_{t*a*s}, p_{t*a*s}). This lack of fit may a priori result from either structural deficiencies or overdispersion. Structural deficiency means that an important effect has been overlooked in the analysis. On the other hand, in the case of overdispersion, the variance is greater than expected under the

assumption of a multinomial distribution due to some interdependence among individuals or heterogeneity among individuals. In order to identify the origin of the observed lack of fit we examined the value of c, the ratio of the overall χ^2 value to its number of degrees of freedom. This value is on average equal to 1 when the model fits. In the present analysis, the c value was reasonably small (1.388), and perfectly compatible with overdispersed count data (see Burnham et al. 1987:246–252). One way to further ascertain that extra-multinomial variation is to be blamed rather than structural failure is to look at the c-stimates, noted $\hat{c}$, for the subcomponents of the global test. Each subcomponent should be equally affected if data are overdispersed, whereas they are likely to react differently to structural failure. Four subcomponents were available in the goodness-of-fit test as given in REL-CR, with corresponding $\hat{c}$ values 1.69, 1.19, 1.39, and 1.31. These values were reasonably close to one (Burnham et al. 1987). Yet, a closer look at the contingency tables related to the highest $\hat{c}$ value (1.69) showed that animals observed for the first time tended to disappear in greater numbers than animal previously seen (test 3.SR of RELEASE). The difference was small and detectable only for some cohorts (8 out of 17) even with a specific test aimed at detecting systematic differences in proportions (Everitt 1977:27–29). We chose not to model this weak effect, particularly because a variance inflation factor based on the other components was needed anyway. Thus, subsequent analyses started from model (β_{t*a*s}, p_{t*a*s}) and made use of the overall overdispersion factor estimate $\hat{c} = 1.388$. Since the likelihood ratio tests (LRT) for comparison between nested models will tend to be inflated by excess variation (compared to that assumed by multinomial variation), we used instead as a test statistic the LRT/df statistic divided by $\hat{c}$, treated as an F test (see Lebreton et al. 1992).

Cohort-based study

Because the most adequate sex and time structure may differ among cohorts, we chose in a first stage to study each cohort separately. If similar conclusions were reached through the separate analyses, one could confidently consider them more broadly valid. In each case, we fitted all models below the IFRC model by sex (Table 4). In this cohort-based approach, age and time are confounded because in a given year all animals are the same age. The notation "t" was thus merely used for convenience. The MAIC pointed, for eight out of 12 cohorts, to time effects on probabilities of first reproduction and recapture probabilities, that is, to the IFRC model (β_t, p_t) applied to pooled males and females. However, for four cohorts, a model with an additional additive sex effect on recapture probabilities (β_t, p_{t+s}) was favored, with males being more likely to be resighted than females. The next step was to proceed with an overall analysis involving all the cohorts in order to (1) separate the effects of time and age, and

TABLE 4. Cohortwise selection among models of recruitment in the Camargue flamingos population. For each model and each cohort, we give its modified Akaike Information Criterion (mAIC). Boldface type denotes the mAIC value for the selected models.

Model	Cohort											
	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
β_{t*s}, p_{t*s}	1195.53	1135.42	1283.61	1099.31	1182.74	930.98	641.70	334.96	262.32	120.67	75.86	17.90
β_{t-s}, p_{t*s}	1180.91	1117.95	1271.60	1085.74	1167.66	922.26	636.99	331.28	258.49	120.67	73.86	
β_{t*s}, p_{t+s}	1186.85	1124.69	1271.33	1086.25	1169.80	924.22	639.42	332.16	258.63	122.43	74.42	
β_{t-s}, p_{t+s}	1171.90	1111.69	1257.99	1074.05	1151.63	913.47	630.19	318.50	254.74	118.47	74.42	
β_{t*s}, p_t	1184.98	1125.87	1274.91	1090.30	1179.87	931.20	637.44	331.16	257.40	120.48	72.81	17.90
β_{t-s}, p_t	1170.03	1111.13	1261.53	1078.06	1163.77	921.04	628.26	319.26	253.52	116.68	70.84	17.90
β_t, p_{t*s}	1179.03	1129.99	1269.75	1085.02	1165.68	920.63	635.53	329.30	256.53	118.84	72.06	17.90
β_t, p_{t+s}	1170.14	1111.11	**1256.22**	**1072.06**	**1149.85**	**912.31**	628.33	319.16	253.46	116.68	70.62	17.90
β_t, p_t	**1166.36**	**1109.76**	1258.00	1079.15	1161.87	920.24	**624.61**	**316.08**	**251.93**	**112.89**	**66.84**	**14.83**

Notes: Model notation is adapted from Lebreton et al. (1992) with β representing seniority probability (= 1 − probability of first reproduction), p recapture rate, t time effect, s sex effect, + additive model, and * model with interaction.

(2) enhance the power of the test of a sex effect on recapture.

Separating age and time effects

Our first model, for which the goodness-of-fit test had been computed, was $(\beta_{t*a*s}, p_{t*a*s})$. Its relative deviance (given by SURGE) and MAIC were 10570.37 and 8281.02, respectively. As the model (β_t, p_{t+a}), though for some cohorts overparameterized, was the simplest model that fitted all cohort data sets, we considered as the next step this model applied separately to each cohort, i.e., the overall model $(\beta_{t*b}, p_{(t+s)*b})$. This model represented a dramatic progress, with the dispersion factor MAIC = 8077.82. However, age and time were still confounded. We next considered the nested model with all main effects but without interaction terms, i.e., $(\beta_{a+t+b}, p_{a+t+b+s})$. The MAIC = 7923.47, again a dramatic decrease, indicating the absence of significant interactions. From this model on it became possible to test the different effects separately.

Selecting the best combination of effects

Starting from the additive model $(\beta_{a+t+b}, p_{a+t+b+s})$, model selection led to model (β_{a+t}, p_{a+t+s}) (Table 5). In this model probabilities of first reproduction are affected by age and time but not by sex, and recapture rates are affected by age, sex, and time, with all effects additive and highly significant. Cohort did not affect probabilities of first reproduction, whereas its effect on recapture rates could not be definitely ascertained. Cohort and age effects on recapture rates were so confounded that they could be substituted at any stage without much change in the quality of fit. The choice in favor of an age effect was made on the following grounds: (1) Cézilly et al. (1996) previously identified an age effect on recapture in an analysis of survival of the same flamingo population; and (2) the pattern of increase of recapture rates with age (Fig. 6) could be easily explained as resulting from an increase in breeding propensity with age (Cézilly et al. 1996) whereas

the biological meaning of a similar pattern for a cohort effect was unclear (there was no reason to assume a steady improvement in the local breeding conditions through time).

Quantitative effects of age

The effect of age is better regarded as quantitative on both recapture rate and probability of first reproduction, because the breeding propensity of experienced breeders may increase with age and because the proportion of experienced birds increases from zero at age 3 yr to a value close to one for older animals. We investigated those questions by trying linear (A) and quadratic (A^2) effects of age both on probabilities of first reproduction and recapture rates on a logit scale (Table 6). Quadratic effects of age on probabilities of first reproduction and recapture rates were clearly retained $(\beta_{A+t}, p_{A^2+t+s})$, whereas linear effects were rejected. Cubic effects of age were unnecessary.

Age of stabilization for probability of first reproduction

The process of recruitment (i.e., entry into the breeding segment of the population) is supposed to end at some age, although some new individuals may continue to join the local population due to immigration. We tested different models where probability of first reproduction remained constant, all other things being equal, from a certain age onwards. The data allowed us to try all ages of stabilization from 4 to 17 yr. This latter value being the largest one in our sample, it corresponds to the previously selected model $(\beta_{A+t}, p_{A^2+t+s})$. The quality of the fit did not differ among models with an age of stabilization >9 yr (Fig. 7). The difference between these models in MAIC was ≤1.5 and models that differ by <2 from the lowest MAIC currently are considered equally valid (Anderson et al. 1994). We thus concluded that stabilization did not occur before 10 yr and adopted the model with stabilization at year 10, model $(\beta_{A^2(10)-t}, p_{A^2+t+s})$, as the best model for the present data. Variations over age and

TABLE 5. Elimination of nonsignificant effects from the model ($\beta_{a,t,c}, p_{a,t,c,s}$): for each model we give the number of estimable parameters (np), the relative deviance (rDEV), and the Akaike information criterion corrected for overdispersion (mAIC). Boldface type denotes the mAIC value for the selected model.

Model	np	rDEV	mAIC	Null hypothesis tested (current model is compared to previously accepted model)
($\beta_{a,t,c}, p_{a,t,c,s}$)	69	10806.97	7923.47	
($\beta_{a,t,c}, p_{a,t,s}$)	60	10823.86	7917.64	no cohort effect on recapture rate $F_{9,464} = 12.17, P = 0.204$ accepted
($\beta_{a,t}, p_{a,t,s}$)	51	10833.24	**7906.40**	no cohort effect on probability of first reproduction $F_{9,464} = 9.38, P = 0.403$ accepted
($\beta_{a,t}, p_{a,t}$)	50	10878.56	7937.05	no sex effect on recapture rate $F_{1,464} = 32.65, P < 0.001$ rejected
($\beta_{a,t}, p_{a,s}$)	40	11194.35	8144.54	no time effect on recapture rate $F_{11,464} = 260.15, P < 0.001$ rejected
($\beta_{a,t}, p_{t,s}$)	38	10974.25	7981.98	no age effect on recapture rate $F_{13,464} = 101.59, P < 0.001$ rejected
($\beta_{a}, p_{a,t,s}$)	40	10884.32	7921.19	no time effect on probability of first reproduction $F_{11,464} = 36.80, P < 0.001$ rejected
($\beta_{t}, p_{a,t,s}$)	38	10871.68	7908.09	no age effect on probability of first reproduction $F_{13,464} = 27.69, P = 0.010$ rejected

Note: Model notation adapted from Lebreton et al. (1992).

year as predicted by this model are given respectively on Figs. 8 and 9. At this stage, the parsimony achieved enhances the power of the tests. Since in a backward selection procedure there is a danger of dropping an actual effect during the first steps of model selection
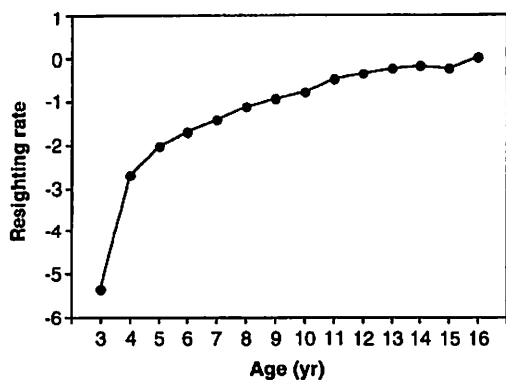

FIG. 6. Effect of bird age on resighting rate in a population of flamingos in the Camargue in southern France. Age-specific resighting rates are expressed relative to the value at age 16 yr (on a logit scale). Underlying model is ($\beta_{a,n}$ $p_{a,t,s}$). This model makes no assumption about the form of the relationship.

(Pradel et al. 1990), we then checked that no effect or interaction should be reintroduced among those dropped earlier. We also checked for several covariates. such as water levels around the breeding site and colony size (see Cézilly et al. 1995), and population size at different geographical scales (A. R. Johnson, *un-published data*), that might explain the variations observed over time. None of those attempts succeeded.

DISCUSSION

Age effect on local recruitment

In this study of local recruitment, some birds, whatever their age, may have bred in some other colony before being observed breeding for the first time in the Camargue. Therefore, the observed age effect on the probability of first reproduction at the Camargue colony represents both the increased probability of first reproduction with age and the increase in probability of return to the natal colony to breed through time. The two effects cannot be evaluated separately in a study of local recruitment. However, a quadratic effect of age could be modelled, with marked stabilization after age 10 yr, suggesting that the individuals >9 yr old when observed breeding for the first time at their colony of birth were most likely to have been recruited initially in another colony from which they later dispersed (see

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TABLE 6. Treatment of age in a quantitative way in models of recruitment to a flamingo population. From model $(\beta_{a+n}\ p_{a+i+i})$ to model $(\beta_{A^2+n}\ p_{A^2+i+i})$. Same notation as in Tables 4 and 5.

Model	np	rDEV	mAIC	Null hypothesis tested (current model is compared to previously accepted model)
$(\beta_{a+n}\ p_{a+i+i})$	51	10 833.24	7906.40	
$(\beta_{a+n}\ p_{A^2+i+i})$	40	10 838.21	7887.98	quadratic age effect on recapture rate $F_{11,464} = 3.58, P = 0.981$ accepted
$(\beta_{a+n}\ p_{A}+_{i+i})$	39	10 846.57	7892.00	linear age effect on recapture rate $F_{1,464} = 6.02, P = 0.014$ rejected
$(\beta_{A^2+n}\ p_{A^2+i+i})$	29	10 862.46	7883.45	quadratic age effect on probability of first reproduction $F_{11,464} = 17.47, P = 0.095$ accepted
$\beta_{A}+_n\ p_{A^2+i+i})$	28	10 912.49	7917.49	linear age effect on probability of first reproduction $F_{1,464} = 36.04, P < 0.001$ rejected

Green et al. 1989, Nager et al. 1996). Although there is evidence that flamingos can be sexually mature at age 3 yr (Johnson et al. 1993), it appears that for some individuals recruitment can be delayed over several more years. Various adaptive explanations for delayed recruitment have been proposed. This may correspond to variation in the breeding strategies of individuals of different quality or vigor experiencing different potential costs of reproduction (Forslund and Pärt 1995). Further information on the variation in breeding success with age and experience is needed to assess the relevance of this hypothesis for flamingos.

Delayed recruitment also has been related to the need to improve foraging skills through experience (Orians 1969, Recher and Recher 1969) prior to engaging in breeding. Flamingos are filter feeders (Jenkin 1957, Zweers et al. 1995), and experimental studies have recently revealed that complex mechanisms underlie filter performances and discrimination capacity (Zweers et al. 1995). However, the variation in the efficiency of filter feeding with age in flamingos remains unexplored. Apart from limited foraging skills, competition between age classes on foraging grounds (Bildstein et al. 1991, Schmitz and Baldassarre 1992) may also reduce foraging efficiency of young individuals and, hence, delay breeding.

Finally, delayed reproduction may be the conse-

FIG. 7. The values of mAIC (a modified version of Akaike's Information Criterion) for different ages of stabilization of probability of first reproduction in a flamingo population in the Camargue of southern France. Models used are derived from model $(\beta_{A^2+n}\ p_{A^2+i+i})$ where probability of first reproduction is a quadratic logistic function of age. In the derived models, there is an age beyond which probability of first reproduction remains constant, all other things being equal. The mAIC values of models with age of stabilization >10 yr (points between dotted lines) differ by <1.5.
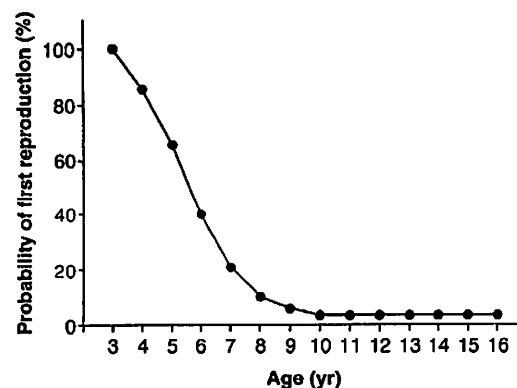

FIG. 8. Recruitment in year 1992 for the different age classes in a population of flamingos in the Camargue of southern France. Proportion of new recruits is estimated from model $(\beta_{A^2(10)+n}\ p_{A^2+i+i})$ where it remains stable from age 10 yr onwards.
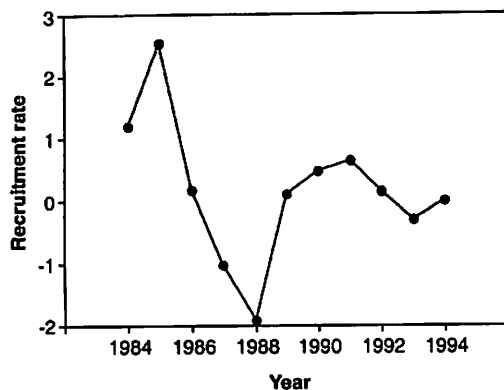
FIG. 9. Recruitment over the study period to a population of flamingos in the Camargue of southern France. The proportions of new recruits are expressed relative to values in year 1994 (on a logit scale). They are estimated from model ($\beta_{A^2(10)+n}$ P_{A^2+i+s}).

quence of social constraints. Greater flamingos are extremely cautious in their choice of a breeding site and only a limited number of places are used in the Western Palearctic (Johnson 1983, Cézilly et al. 1994a), most of them on an irregular basis. The Camargue colony is the only regular breeding place, with several thousands of breeding pairs filling the breeding island. Each year, hundreds or thousands of individuals attend the colony site without being able to secure a nesting site on the breeding island. Reduced mating opportunities due to directional mating preference for older individuals (Cézilly et al., *in press*) also may force younger individuals to postpone reproduction.

Time effect on local recruitment

Time effect represents variations among years in the recruitment rate at the Camargue colony (Fig. 8), with a peak in recruitment in 1985, followed by a marked decline over the next 3 yr. This pattern can be interpreted in relation to the wintering strategies of flamingos and to the high mortality that occurred during the winter of 1984–1985 (Cézilly et al. 1996). Previous analyses (F. Cézilly et al., *unpublished data*) have shown that a majority of birds that breed at the Fangassier colony have spent the previous winter in southern France. Therefore, the death of several thousands of flamingos in the south of France during the winter of 1984–1985 (Cézilly et al. 1996) dramatically reduced competition for access to breeding sites the following breeding season. Such favorable local conditions may have prompted in 1985 the recruitment of younger age classes and/or still inexperienced older individuals. Indeed, following a severe winter, the colony size at the Fangassier reached an estimated 13 500 nesting pairs compared to only 10 535 in 1984 (Cézilly et al. 1995). The way in which high adult mortality was, at least partially, compensated for confirms the

existence of a pool of potential recruits that is ordinarily prevented from breeding (Cézilly and Johnson 1995). This pool may contain individuals not only from the Camargue but also from other colonies (Nager et al. 1996). The control of recruitment to the Fangassier colony from the pool of potential breeders appears to be then, at least partially, density-dependent. Such a mechanism of regulation has been previously suggested for Kittiwakes (*Rissa tridactyla,* Porter and Coulson 1987). In addition to this, the cold spell of 1984–1985 particularly affected the survival of first- and second-year birds (Johnson et al. 1991, Lebreton et al. 1992), corresponding to cohorts 1983 and 1984, thus inducing a deficit of recruits of birds aged 4 to 6 yr in 1987 and 1988 (Fig. 9). Also, the pool of potential recruits from the older cohorts was depleted in 1987 and 1988 as a result of the exceptional recruitment opportunities of 1985. The situation becomes normal again from 1989 onwards with the recruitment of individuals born after the cold spell. We tested this scenario in model ($\beta_{A^2(10)+q85\ 88}$ P_{A^2+i+s}), in which there is no effect of time on probabilities of first reproduction outside the 1985–1988 period. Compared to model ($\beta_{A^2(10)+n}P_{A^2+i+s}$), model ($\beta_{A^2(10)+q85-88}$ P_{A^2+i+s}), with relative deviance equal to 10867.64, was acceptable ($F_{7, 464}$ = 0.576, $P > 0.05$). Attempts to eliminate the time effect in 1985 and 1988 were rejected ($F_{1, 464}$ = 12.31, P = 0.0005, and $F_{1, 464}$ = 4.21, P = 0.0402, respectively). Thus, recruitment could be considered constant during the study period, except for the period 1985–1988. The present study shows that severe climatic conditions, such as the cold spell of 1984–1985 can deeply affect population dynamics, not only instantaneously in terms of reduced survival (Cézilly et al. 1996), but also over consecutive years in terms of recruitment.

Absence of a sex effect on local recruitment

A noticeable result of this study is the absence of sex effect on local recruitment, contrasting with previous reports for long-lived species (Mills 1973, Wooler and Coulson 1977). This result was not unexpected since there is no difference between sexes in survival (Cézilly et al.1996) and because our model corrected for the probability of recapture. Rattiste and Lilleleht (1986) showed that differences in nest-site tenacity between males and females can lead to the erroneous conclusion that one sex starts breeding earlier than the other. In a review of recruitment in long-lived birds, Bradley and Wooler (1991) also noted that the sample sizes of known-age first breeders in most studies are often small, with a large overlap in the ages at which males and females start to breed. Bradley and Wooler (1991) doubted the significance of differences between the sexes in the age of first breeding, rarely exceeding 1 yr. Despite a noticeable sexual size dimorphism in flamingos, the present study gives no support to the idea that sexual differences in the age at which breeding starts may be size related (Warham 1990).

Factors affecting recapture rates

Additive effects of age, sex, and time were found to affect recapture rates, confirming earlier findings for the same population (Cézilly et al. 1996). Time effect is assumed to correspond to variation in observation effort among years, whereas sex effect has been related to differences between males and females in their probability of re-nesting after breeding failure (Cézilly and Johnson 1995, Cézilly et al. 1997). The age effect on capture indicates that, having reached first reproduction, a bird does not necessarily become a regular breeder from then on (Cézilly et al. 1996). Indeed, young birds, even if they have been able to find a nest site and reproduce in a previous breeding season, may not be able to secure each year a place on the nesting colony and therefore remain irregular breeders. Concerning the age effect on capture rate, the essential difference with the results of Cézilly et al. (1996) comes from the quadratic effect found on capture rate. With fewer years and hence fewer age classes represented, only a linear effect of age had been found in the previous analysis of survival (Cézilly et al. 1996).

CONCLUSIONS

Advantages of the model

Compared to previous attempts, our approach, through relaxing several unwarranted assumptions about demographic processes (such as constant survival rate across time and cohorts, or full reproduction at a given age) allows for a straightforward study of recruitment. Based on an analogy with CMR (capture-mark-recapture) survival modeling (cf. Lebreton et al. 1992), an important step has been to consider separately the probability of first reproduction (the parameter of recruitment) and the probability of recapture. The advantage of such a distinction is obvious in the case study. First, in a study of recruitment based upon the age distribution of first-time breeders, the observed sex effect on the probability of recapture would have been incorrectly interpreted as a sex effect on recruitment. Secondly, in the same kind of model, as well as in more sophisticated models that still do not allow recapture probabilities to be age dependent (e.g., Clobert et al. 1994), it would not have been possible to model the stabilization of the recruitment after age 10 yr, since the recapture probabilities of flamingos increase with age (cf. Fig. 6; see also Cézilly et al. 1996).

The study of capture histories in reverse (Pradel 1996) provides additional advantages. For instance, Clobert et al. (1994) assumed equal survival for both breeders and nonbreeders. This assumption may, however, be false, especially if there is a trade-off between survival and reproduction (Reznick 1985, Forslund and Pärt 1995) or if breeders are on average animals of higher quality with higher survival than nonbreeders. Contrasting with previous studies, the present analysis is devoid of assumptions about survival (cf. Pradel

1996). In essence, the philosophy of the approach differs basically from other attempts to model recruitment. Compared to Clobert's model, the aim of the present study is not so much to compute specific parameters, such as age-specific breeding probabilities, but rather to test explicit biological assumptions about which factors affect the process of recruitment.

Age and certain breeding parameters

The ability to test assumptions about which environmental factors affect recruitment certainly represents important progress for the study of population dynamics. Still, it may be of interest, from an evolutionary point of view, to dispose of a key parameter to compare relationships between recruitment and other life history traits (here, the age of stabilization of probability of first reproduction vs. mean age at first breeding and age-specific breeding probabilities) among populations or species (Stearns and Koella 1986, Sutherland et al. 1986, Charnov and Berrigan 1990, Harvey and Pagel 1991). For instance, the mean value for age at first breeding has previously been used to study the association between recruitment and survival among bird species using data from the literature (Lack 1968, Croxall 1981, Bradley and Wooler 1991). Indeed, most studies have considered the distribution of age-specific breeding probabilities (Lebreton et al. 1990, Clobert et al. 1994) or the mean (Porter and Coulson 1987) or median (Klomp and Furness 1991) age at first breeding as the key parameter for studying recruitment. However, in doing so, most studies have been forced to arbitrarily assume an age of maximum breeding propensity, although there is no simple way to verify it in the wild (Lebreton et al. 1990). In the present study, the key parameter for recruitment corresponds to the probability of first reproduction (Pradel 1996), with no assumption on an actual age of full reproduction. It is then possible to test for a stabilization of the probabilities of first reproduction after a certain age. Our results show that such a phenomenon does occur in the Greater Flamingo at age 10 yr. We therefore suggest that the level of stabilization of probabilities of first reproduction may be a particularly reliable parameter to characterize recruitment, and, hence, to perform comparative studies of relationships between life-history traits.

Future developments

Capture-recapture methodology is relatively inexpensive and is applicable to various populations and taxonomic groups. We have proposed a shift in emphasis from estimating age-specific breeding propensity to testing biological hypotheses about local recruitment. In this context refined questions can be addressed without resorting to ad hoc calculations that may provide misleading results. Although the model in its present form is strictly limited to the study of *local* recruitment, it provides a framework that should

in the future benefit from numerous developments. First, new methods of marking should appear, or become less costly, enabling an increase in both sample sizes and the diversity of biological organisms under survey. Increased sample size will, in turn, increase the power of tests to detect significant effects affecting recruitment. Applying the method to a wide range of species will be particularly valuable for a comparative study of recruitment based on standardized estimates. Secondly, the next generation of software designed for the analysis of CMR data should explicitly address the estimation of recruitment rates. A third point is related to the development of more sophisticated models with broadened biological relevance. One of the most promising directions will be to address the trade-off between dispersal and recruitment in spatially specific CMR models. Such multi-site models would constitute powerful tools for the study of spatially organized populations, then allowing the consideration of both local recruitment and recruitment due to immigration from other colony sites.

ACKNOWLEDGMENTS

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APPENDIX

Link between seniority probabilities and probabilities of first reproduction

Among breeders of a given age, some individuals are naïve, i.e., they reproduce for the first time, whereas others are experienced, i.e., they have bred at least once in previous years. Thus, a breeder of a given age has a certain probability, the seniority probability, denoted γ (Pradel 1996), of being experienced. Pradel (1996) has shown that the seniority probabilities correspond directly to the survival probabilities of the survival models when these latter models are applied to the reverse capture histories. Consequently, applying survival software to reversed capture histories allows us to compute seniority probabilities for different groups of individuals, such as males and females, and to test them for environmental effects. However, in a study of recruitment, it may be more

convenient to use the complement to 1 of seniority probability, the probability that a breeder is reproducing for the first time denoted β. Fortunately, in the framework of logistic linear models, seniority probabilities and probabilities of first reproduction can be used interchangeably because logistic linear models of seniority probabilities are logistic linear models of probabilities of first reproduction. Indeed

$$\text{logit}(\gamma) = \log\left(\frac{\gamma}{1 - \gamma}\right) = \log\left(\frac{1 - \beta}{\beta}\right) = -\text{logit}(\beta).$$

Thus a model that is linear in γ on the logit scale is also linear in β on the same logit scale.

As long as the logit is the link function (this is the default in SURGE) a model can be equivalently denoted (β_x, p_z) or (γ_x, p_z), where x and z represent any combination of effects.