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# A GENERAL APPROACH TO SURVIVAL RATE ESTIMATION BY RECAPTURES OR RESIGHTINGS OF MARKED BIRDS

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CONTENTS

1. Introduction ..... 133
2. General framework ..... 134
3. Models with equality constraints ..... 135
4. Models with external variables ..... 135
5. Models with range constraints ..... 138
6. Examples ..... 138
6.1. Great Tit ..... 138
6.2. Black-headed Gull ..... 139
7. Conclusion ..... 141
8. Acknowledgements ..... 141
9. Summary ..... 141
10. References ..... 141
11. Samenvatting ..... 142

## 1. INTRODUCTION

Since the first edition of Seber's book (1973), new developments in capture-recapture methods provided a wide range of models to estimate survival in animal (and especially in bird) populations, along two lines: from recoveries (returns of marks found on dead animals), and from recaptures or resightings (of live animals).

About recoveries, Brownie *et al.* (1985) provided a full set of models covering many situations (time and/or age dependence in survival, simultaneous analysis of recoveries of animals marked as young and of animals marked as adults). More recently, deep difficulties inherent in age dependent analysis of recoveries of birds banded as young have been recognized and discussed (Lakhani & Newton 1983, Anderson *et al.* 1985).

The general tendency has been:
1. To focus on appropriate model selection for a given data set, especially by reducing the number of parameters to increase precision without creating biases (principle of parsimony).
2. To use, as a consequence of parsimony (which prevents from getting explicit estimates) iterative computer software to get estimates of survival rates by the maximum likelihood method. Only models with full sets of parameters lead to explicit estimates. White (1983) provided a most flexible and efficient computer program.

A special mention should be given to the model of North & Morgan (1979) which allows parameter reduction and provides meaningful biological information by relating survival to external variables as a regression built into the model (see also Cavé 1983).

About live recaptures or resightings, a number of refinements have recently been proposed, usually as modifications of the Jolly-Seber model (Jolly 1965, Seber 1965), including (see Brownie *et al.* 1985):
- age dependence in survival rates (Pollock 1981),
- equality of survival rates (Jolly 1982),
- constraining estimates between 0 and 1, and using simultaneously information from recoveries (Buckland 1980).

In the past, the emphasis has been largely on getting explicit estimates (Crosby & Manly 1985), which makes it possible to correct parameter estimates and estimates of their variance for bias (see Seber & Manly 1985). Arnason & Baniuk (1980) and Jolly & Dickson (1980) provided computer package with a wide range of possibilities. Cormack (1979, 1985) developed a log-linear approach that makes it possible to test various hypotheses such as trap dependence, while providing a most satisfactory mathematical frame.

The survival part of the Jolly-Seber type models can be considered by itself, without considering recruitment and population size estimations, as anticipated by Cormack (1964), without changes in the mathematics involved (Seber 1973, Pollock 1981). It can be applied to such situations where recaptures of marked individuals provide no information on the proportion of marked animals in the population, especially when the recaptures are in fact resightings with



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no physical capture and no notice of the number of unmarked individuals observed (*). Parameters reduce then to survival rates and probabilities of capture.

Arnason & Baniuk (1980), Sandland & Kirkwood (1981) and Clobert (1981) proposed in this frame parsimonious models of which a review and applications are given in Clobert *et al.* (1985). In a line similar to that of North & Morgan (1979) for recoveries, Clobert & Lebreton (1985) developed a model with built in regression of survival on environmental variables. In both cases, the parsimony implies iterative fitting by computer.

The purpose of this paper is to bring together further possibilities within the framework of the Cormack (1964) approach, leading to a greater flexibility in model choice and to a greater efficiency in extracting survival estimates from complex recapture experiments:
– age and/or time dependence in survival and capture rates;
– estimates constrained between 0 and 1;
– relating any kind of parameters to external variables;
– constraining some parameters to be equal to *a priori* fixed values.

Applications to populations of the Great Tit *Parus major* and the Black-headed Gull *Larus ridibundus* are provided.

The possibilities presented are available in the frame of a single computer program, called SURGE, available on PC-AT floppy disk from the second author.

## 2. GENERAL FRAMEWORK

We consider a sequence of (yearly) samples with initial marking in a first cohort, followed by n years of recapture and of marking of new cohorts. As noted in the introduction, recapture –or resighting–of previously marked individuals, and capture and marking of new individuals can be distinct operations, but should occur at the same point in time. Cohort is thus taken here in a very particular meaning.

(*) Since the physical recaptures made to mark new individuals can provide information on the proportion of unmarked individuals, one can, if necessary, rebuild population size estimation around the survival process even in this case (Brownie & Robson 1983, Burnham pers. comm.).

*Assumption 1*: these operations take negligible time against the time between samples.

The data can be presented as dichotomous trees (one per cohort), where the upper part of each branch symbolizes capture and the lower non-capture (Fig. 1). Each path from the root to a leaf in one of these trees is a recapture history. Every individual is characterized by one, and only one, recapture history. There are $2^{n-i+1}$ different recapture histories for cohort i.

*Assumption 2*: every animal in cohort i has the same probability $s_{ij}$ of surviving from year j–1 to year j ($j \geq i$) and of being present in the population in year j (if there is permanent emigration $s_{ij}$ is thus an apparent survival rate).

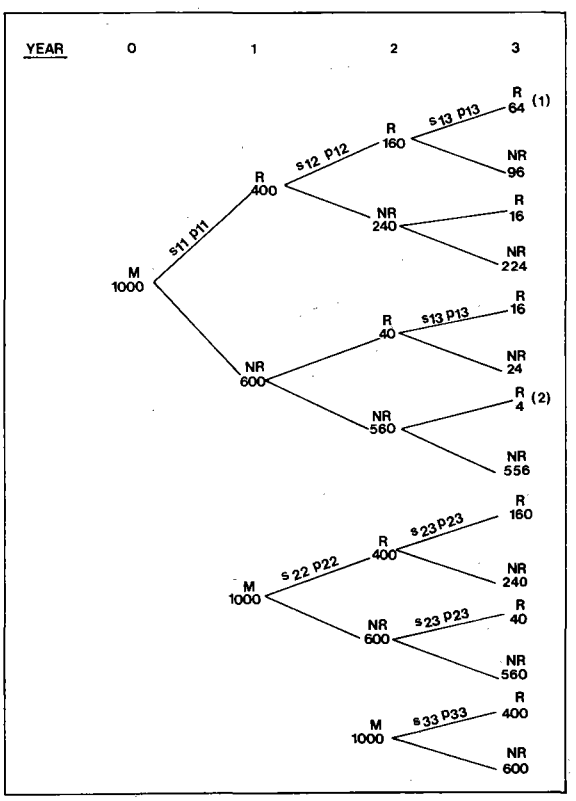



Fig. 1. Recapture trees with survival probabilities ($s_{ij}$) all equal to 0.5 and probabilities of capture ($p_{ij}$) all equal to 0.8: expected numbers in the various recapture histories (M = marked, R = recaptured, NR = not recaptured). (1) Probability of this event is $s_{11}\ p_{11}\ s_{12}\ p_{12}\ s_{13}\ p_{13}$. (2) Probability of this event is $s_{11}\ (1 - p_{11})\ s_{12}\ (1 - p_{12})\ s_{13}\ p_{13}$. In this example, $b_1 = 1000$, $b_2 = 1000$, and $b_3 = 1000$, $a_{11} = 400$, $a_{12} = 200$, $a_{13} = 100$, $a_{22} = 400$, $a_{23} = 200$ and $a_{33} = 400$, $c_{11} = 556$, $c_{12} = 224$, $c_{13} = 120$, $c_{22} = 560$, $c_{23} = 240$ and $c_{33} = 600$.

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*Assumption 3*: every animal in cohort i has the same probability $p_{ij}$ of being taken in year j, given that it is alive at this time.

These assumptions imply that an individual's fate at a given time depends only on its year of marking (year i–1 = cohort i) and on the year considered (j), or on its age j–i+1. In particular, the individuals are independent and there is no trap dependence. The probability L of observing a given set of numbers in the various recapture histories, can be calculated explicity (see Clobert *et al.* 1985, with the modifications induced by the presence here of a cohort index i). L can be shown to depend only on the following statistics:

- $b_i$ (i = 1,...,n): the numbers marked in the n cohorts in years 0,1,...n–1. The number marked in year n, $b_{n+1}$, does not play any role.
- $a_{ij}$ (i = 1,...,n and j = i,...,n–1): the numbers caught in year j among the $b_i$ animals marked in year i–1.
- $c_{ij}$ (j = i,...,n–1 with $c_{in}$ equal to $a_{in}$): the numbers never seen after year j–1 among the $b_i$ animals marked in year i–1.

The parametrization ($s_{ij}$, $p_{ij}$) provides a full model, in which maximum likelihood estimates (*) (MLE) can be obtained as explicit formulas: in each cohort i, $s_{ij}$ and $p_{ij}$ (j = i,...,n–1) and the product $s_{in}\ p_{in}$ (**) can be obtained by applying the Cormack (1964) method to the data in the cohort (see also Pollock 1981). But the $s_{ij}$ and $p_{ij}$ can be expressed as functions of parameters $\theta = (\theta_1,...,\theta_q)$ to produce particular models. MLE $\hat{\theta}_k$ (and as consequence MLE of $s_{ij}$ and $p_{ij}$ which are functions of $\theta$) are obtained by maximising Ln L, most of the time by an iterative procedure. We used the Fletcher (1970) method, which provides estimates of the asymptotic (= when $b_i \rightarrow \infty$) variances and covariances of parameters (see Clobert *et al.* 1985). ML theory also provides a deviance which can be used for model selection: the difference in deviance between a model A and a model B with d further restrictions follows asymptotically, under model B assumptions, a $\chi^2$ distribution with df = d (likelihood ratio tests). These tests help to select the most appropriate one in a succession of models.

(*) Maximum likelihood estimates are estimates that make L or Ln L maximum. They benefit of various optimal properties, which are only asymptotic, *i.e.* when $b_i \rightarrow \infty$ for every i. This explains the interest statisticians have in explicit estimates which can be modified to improve their properties (see *e.g.* Seber & Manly 1985).

(**) $s_{i,n}$ and $p_{i,n}$ appear only as products and therefore cannot be estimated separately.

## 3. MODELS WITH EQUALITY CONSTRAINTS

The Cormack (1964) model considers parameters depending of time only (it is noted ($s_t$, $p_t$) by Sandland & Kirkwood 1981). It can be written as $s_{ij} = \theta_i = s_i\ \forall\ i = 1,...,n$ and $p_{ij} = \theta_{n+i} = p_i\ \forall\ i = 1,....,n$. The indices of the parameters $\theta_1,....\theta_{2n}$ can be grouped in two triangular matrices, one for the $s_{ij}$ and one for the $p_{ij}$ (Fig. 2B). Any model with equality constraints can be represented in this way, as well as the complete model which we will denote ($s_{at}$, $p_{at}$), see Fig. 2A. Time dependent models with further constraints ($s_t$, p), (s, $p_t$) and (s, p) (Sandland & Kirkwood 1981, Clobert 1981) can be easily represented in a similar way, model (s, p) is given as an example in Fig. 2C.

Fig. 2D gives the parametrization of the age dependent model ($s_a$, $p_a$) and Fig. 2E of model ($s_a$, p). Together with any particular model developed with the help of notation in Fig. 2, these models add new possibilities to existing ones. Fig. 2F and Fig. 2G give examples of models with stabilization of survival after one year of age (see Pollock 1981) and time dependent or fixed capture rate which we will use later.

## 4. MODELS WITH EXTERNAL VARIABLES

It is of special interest to biologists to express variability in survival over the years as a result of external variables. Reparametrizing $s_{ij}$, *e.g.* as $a_i + b_i\ x\ (j)$ is a direct way to do this. This approach, besides the biological interest, makes some tests possible and increases precision (Clobert & Lebreton 1985). Using standard regression between time-dependent estimates of survival and external variables should be avoided, since such survival rate estimates are not independent (Clobert & Lebreton 1985). A linear relationship $s_{ij} = a_i + b_i\ x\ (j)$ or a logistic linear relationship $s_{ij} = \Omega\ (a_i + b_i\ x\ (j)) = \exp\ (a_i +$

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A: General model ($s_{at}$, $p_{at}$), Pollock 1981

| | Year | 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| | Cohort | | | | |
| | 1 | 1 | 2 | 3 | 4 |
| Survival | 2 | | 5 | 6 | 7 |
| Rates | 3 | | | 8 | 9 |
| | 4 | | | | 10 |
| | | 11 | 12 | 13 | 14 |
| Capture | | | 15 | 16 | 17 |
| Rates | | | | 18 | 19 |

16 identifiable parameters
(1, 2, 3, 4, 5, 6, 3, 11, 12, 13, 15, 16, 18, 4 × 14, 7 × 17, 9 × 19, 10 × 20)

B: Time dependent (model $s_t$, $p_t$), Cormack 1964

| | | | |
|---|---|---|---|
| 1 | 2 | 3 | 4 |
| | 2 | 3 | 4 |
| | | 3 | 4 |
| | | | 4 |
| 5 | 6 | 7 | 8 |
| | 6 | 7 | 8 |
| | | | 8 |

7 identifiable parameters
(1, 2, 3, 5, 6, 7, 4 × 8)

C: Constant rates model (s, p) (Sandland and Kirkwood 1981, Clobert 1981)

| | | | |
|---|---|---|---|
| 1 | 1 | 1 | 1 |
| | 1 | 1 | 1 |
| | | 1 | 1 |
| | | | 1 |
| 2 | 2 | 2 | 2 |
| | 2 | 2 | 2 |
| | | 2 | 2 |
| | | | 2 |

2 identifiable parameters

D: Age dependent model ($s_a$, $p_a$)

| | | | |
|---|---|---|---|
| 1 | 2 | 3 | 4 |
| | 1 | 2 | 3 |
| | | 1 | 2 |
| | | | 1 |
| 5 | 6 | 7 | 8 |
| | 5 | 6 | 7 |
| | | 5 | 6 |
| | | | 5 |

7 identifiable parameters
(1, 2, 3, 5, 6, 7, 4 × 8)

E: Model ($s_a$, p)

| | | | |
|---|---|---|---|
| 1 | 2 | 3 | 4 |
| | 1 | 2 | 3 |
| | | 1 | 2 |
| | | | 1 |
| 5 | 5 | 5 | 5 |
| | 5 | 5 | 5 |
| | | 5 | 5 |
| | | | 5 |

5 identifiable parameters

F: Example of a particular model

| | | | |
|---|---|---|---|
| 1 | 2 | 2 | 2 |
| | 1 | 2 | 2 |
| | | 1 | 2 |
| | | | 1 |
| 3 | 4 | 5 | 6 |
| | 4 | 5 | 6 |
| | | 5 | 6 |
| | | | 6 |

6 identifiable parameters

C: Idem F with constant recapture rate

| | | | |
|---|---|---|---|
| 1 | 2 | 2 | 2 |
| | 1 | 2 | 2 |
| | | 1 | 2 |
| | | | 1 |
| 3 | 3 | 3 | 3 |
| | 3 | 3 | 3 |
| | | 3 | 3 |
| | | | 3 |

3 identifiable parameters

Fig. 2. Various kinds of constraints on survival ($s_{ij}$) and recapture ($p_{ij}$) rates in multiple recapture analysis, presented in the particular case of n = 4 years of recapture.

$b_i$ x (j))/(1 + exp ($a_i$ + $b_i$ x (j))) can be used as reparametrization. The latter has the advantage of constraining estimates between 0 and 1, together with further theoretical advantages (*e.g.* Cox 1972) which makes it a natural regression relationship when the variable to predict is a probability.

The models we propose on such a basis incorporate

- linear or logistic-linear relationship of survival on one or several external variables,
- the same procedure for capture rate,
- no dependence on age ($s_{ij}$ = Ω (a + b x (j)) or separate estimation for two age classes

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Table 1. Recapture data from female Great Tits, captured for the first time as breeding birds in 1964-1983. Data from Wytham Wood, Oxford U.K. See text for explanation of $a_{ij}$, $b_{ij}$ and $c_{ij}$.

| Years | 1964 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $b_i$ | 63 | 77 | 55 | 51 | 58 | 46 | 40 | 81 | 45 | 62 | 35 | 53 | 45 | 84 | 35 | 38 | 42 | 72 | 49 | 97 |
| $a_{ij}$ | | | | | | | | | | | | | | | | | | | | |
| 1965 | 19 | 9 | 7 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1966 | | 21 | 10 | 7 | 6 | 0 | 1 | 0 | | | | | | | | | | | | 0 |
| 1967 | | | 17 | 8 | 5 | 2 | 0 | | | | | | | | | | | | | 0 |
| 1968 | | | | 16 | 9 | 2 | 3 | 1 | 0 | | | | | | | | | | | 0 |
| 1969 | | | | | 23 | 14 | 1 | 1 | 0 | | | | | | | | | | | 0 |
| 1970 | | | | | | 6 | 4 | 2 | 1 | 0 | | | | | | | | | | 0 |
| 1971 | | | | | | | 10 | 4 | 1 | 0 | | | | | | | | | | 0 |
| 1972 | | | | | | | | 23 | 12 | 5 | 3 | 1 | 0 | | | | | | | 0 |
| 1973 | | | | | | | | | 13 | 7 | 3 | 1 | 0 | | | | | | | 0 |
| 1974 | | | | | | | | | | 26 | 10 | 5 | 3 | 1 | 2 | 0 | | | | 0 |
| 1975 | | | | | | | | | | | 12 | 3 | 2 | 1 | 0 | | | | | 0 |
| 1976 | | | | | | | | | | | | 11 | 9 | 7 | 2 | 0 | | | | 0 |
| 1977 | | | | | | | | | | | | | 18 | 4 | 0 | | | | | 0 |
| 1978 | | | | | | | | | | | | | | 28 | 8 | 6 | 0 | 1 | 0 | 0 |
| 1979 | | | | | | | | | | | | | | | 8 | 4 | 2 | 2 | 1 | 0 |
| 1980 | | | | | | | | | | | | | | | | 16 | 7 | 2 | 1 | 0 |
| 1981 | | | | | | | | | | | | | | | | | 15 | 6 | 2 | 0 |
| 1982 | | | | | | | | | | | | | | | | | | 14 | 10 | 5 |
| 1983 | | | | | | | | | | | | | | | | | | | 23 | 7 |
| 1984 | | | | | | | | | | | | | | | | | | | | 19 |
| $c_{ij}$ | | | | | | | | | | | | | | | | | | | | |
| 1964 | 41 | 12 | 3 | 4 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | 0 |
| 1965 | | 55 | 11 | 4 | 1 | 5 | 0 | 1 | 0 | | | | | | | | | | | 0 |
| 1966 | | | 38 | 9 | 3 | 3 | 2 | 0 | | | | | | | | | | | | 0 |
| 1967 | | | | 32 | 9 | 6 | 1 | 2 | 1 | 0 | | | | | | | | | | 0 |
| 1968 | | | | | 31 | 13 | 12 | 1 | 1 | 0 | | | | | | | | | | 0 |
| 1969 | | | | | | 38 | 3 | 3 | 1 | 1 | 0 | | | | | | | | | 0 |
| 1970 | | | | | | | 29 | 7 | 3 | 1 | 1 | 0 | | | | | | | | 0 |
| 1971 | | | | | | | | 58 | 10 | 8 | 2 | 2 | 1 | 0 | | | | | | 0 |
| 1972 | | | | | | | | | 30 | 7 | 4 | 3 | 1 | 0 | | | | | | 0 |
| 1973 | | | | | | | | | | 34 | 17 | 6 | 2 | 1 | 0 | 2 | 0 | | | 0 |
| 1974 | | | | | | | | | | | 22 | 8 | 3 | 1 | 1 | 0 | | | | 0 |
| 1975 | | | | | | | | | | | | 38 | 3 | 5 | 5 | 2 | 0 | | | 0 |
| 1976 | | | | | | | | | | | | | 27 | 14 | 4 | 0 | | | | 0 |
| 1977 | | | | | | | | | | | | | | 54 | 19 | 5 | 5 | 0 | 1 | 0 |
| 1978 | | | | | | | | | | | | | | | 26 | 5 | 2 | 0 | 1 | 1 |
| 1979 | | | | | | | | | | | | | | | | 20 | 10 | 6 | 1 | 1 |
| 1980 | | | | | | | | | | | | | | | | | 25 | 11 | 4 | 2 |
| 1981 | | | | | | | | | | | | | | | | | | 57 | 5 | 5 |
| 1982 | | | | | | | | | | | | | | | | | | | 24 | 18 |
| 1983 | | | | | | | | | | | | | | | | | | | | 78 |

Table 2. Likelihood ratio tests between different models. NP: Number of estimated parameters. −2 Ln L: likelihood function values.

| Model | NP | −2 Ln L | Test of hypothesis | Results |
|---|---|---|---|---|
| $(s_{at}, p_t)$ | 57 | 2455.99 | | |
| $(s_t, p_t)$ | 39 | 2474.80 | $(s_t, p_t) >< (s_{at}, p_t)$<br>no age dependence in survival rate | $\chi^2 = 2474.80 - 2455.99 = 18.81$<br>$< \chi^2_{0.95}(18)$. Model $(s_t, p_t)$ not rejected |
| $(s_t, p)$ | 21 | 2499.32 | $(s_t, p) >< (s_t, p_t)$<br>no time dependence in capture rate | $\chi^2 = 2499.32 - 2474.80 = 24.52$<br>$< \chi^2_{0.95}(18)$. Model $(s_t, p)$ not rejected |
| $(s, p)$ | 2 | 2545.24 | $(s, p) >< (s_t, p)$<br>no time dependence | $\chi^2 = 2545.24 - 2499.32 = 45.92$<br>$> \chi^2_{0.99}(19)$. Model $(s, p)$ rejected |

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(year 1 and thereafter: $s_{ij} = \Omega\ (a_1 + b_1\ x\ (i))$ and $s_{ij} = \Omega\ (a_2 + b_2\ x\ (j))$, $j > i$).

## 5. MODELS WITH RANGE CONSTRAINTS

The logistic transformation $s_{ij} = \Omega\ (\theta_{ij})$ bounds any estimate between 0 and 1. A further possibility is to fix any parameter to any *a priori* value (such as $s_{ij} = 1$).

## 6. EXAMPLES

### 6.1. GREAT TIT

Our first example deals with the well-known population of the Great Tit, followed in Wytham Wood, Oxford, since 1947 (Perrins 1965).

Breeding birds have been caught intensively since 1962. To keep data homogeneous, we did not use the first two years of data. In this example, we will treat data on adult breeding females (first caught as breeders) and not known to be born in the wood (*i.e.* not previously ringed as pulli). These birds are in major part immigrant females. Basic recapture statistics ($b_i$, $a_{ij}$ and $c_{ij}$) are given in Table 1.

Since over 95 % of these females were caught when one year old (based on plumage characteristics), we looked for age dependence in survival rates, with age 1 survival rate differing from survival rates of older birds ($\theta_1 = s_{ij}$, $\theta_2 = s_{2j} = s_{3j} \ldots\ldots = s_{nj}$). We assume that no further age dependences in survival rates are expected as well as no age dependence in capture rate. As a consequence, the data were analyzed with various models involving age dependence and/or time dependence in survival rates and time dependence in capture rate (see Table 2).

The basic model ($s_{at}$, $p_t$) considers time dependence both in survival and in capture rate and age dependence (as previously defined) in survival rate. A likelihood ratio test of the model ($s_t$, $p_t$) against model ($s_{at}$, $p_t$) leads to no rejection of the hypothesis of constancy of the survival rate with respect to age ($\chi^2 = 18.81 < \chi^2_{0.95}$ (18), Table 2). The hypothesis of constancy of capture rate is also not rejected: model ($s_t$, p) *vs* model ($s_t$, $p_t$), $\chi^2 = 24.52 < \chi^2_{0.95}$ (18), Table 2. The same hypothesis on the survival rate is strongly rejected: model (s, p) vs. model ($s_t$, p): $\chi^2 = 45.92 < \chi^2_{0.99}$ (19). Among these models, the best one is therefore the model ($s_t$, p) involving only a time variation in survival rate and a constant capture rate. A goodness-of-fit test (Clobert & Lebreton 1985) tells us that this model provides a good description of the data ($\chi^2 = 42.22 < \chi^2_{0.95}$ (36)). The parameter estimates and their estimated variances under model ($s_t$, p) are given in Table 3.

Table 3. Survival rate and capture rate estimations under the model ($s_t$, p) and values of the external variables used. SR: survival rate estimated from model ($s_t$, p). EAV: estimated asymptotic variance. GTD: number of breeding pairs of Great Tit. BTD: number of breeding pairs of Blue Tit. BC: beech crop index. WT: sum of monthly mean temperature from October to March. CR: captures rate estimated from model ($s_t$, p).

| Years | SR | EAV | GTD | BTD | BC | WT |
|---|---|---|---|---|---|---|
| 1964-65 | .413 | 0.0052 | 265 | 202 | 1 | 31.8 |
| 1965-66 | .361 | 0.0029 | 239 | 229 | 0 | 36.3 |
| 1966-67 | .438 | 0.0036 | 197 | 291 | 0 | 39.8 |
| 1967-68 | .457 | 0.0036 | 131 | 260 | 0 | 34.5 |
| 1968-69 | .584 | 0.0039 | 168 | 217 | 2 | 33.3 |
| 1969-70 | .342 | 0.0030 | 187 | 238 | 0 | 33.5 |
| 1970-71 | .346 | 0.0041 | 129 | 244 | 2 | 36.6 |
| 1971-72 | .337 | 0.0027 | 225 | 299 | 0 | 39.4 |
| 1972-73 | .425 | 0.0040 | 174 | 240 | 0 | 37.7 |
| 1973-74 | .494 | 0.0037 | 178 | 295 | 0 | 38.4 |
| 1974-75 | .444 | 0.0043 | 140 | 392 | 2 | 39.2 |
| 1975-76 | .342 | 0.0032 | 175 | 435 | 0 | 35.5 |
| 1976-77 | .541 | 0.0048 | 121 | 316 | 0 | 34.5 |
| 1977-78 | .420 | 0.0028 | 228 | 491 | 1 | 37.0 |
| 1978-79 | .314 | 0.0032 | 171 | 383 | 2 | 30.6 |
| 1979-80 | .497 | 0.0055 | 166 | 309 | 0 | 38.1 |
| 1980-81 | .452 | 0.0049 | 204 | 332 | 2 | 37.3 |
| 1981-82 | .277 | 0.0023 | 308 | 375 | 1 | 30.7 |
| 1982-83 | .604 | 0.0051 | 209 | 303 | 2 | 38.6 |
| 1983-84 | .277 | 0.0021 | 354 | 282 | 0 | 36.9 |
| CR | .777 | 0.0006 | | | | |

Since time variations in survival rates seem to be important, it was interesting to try to relate these variations to some external variables. Some of them are already known (not all on the same species) to play a major role in affecting population numbers, or more precisely survival rate, such as beech crop production, winter severity and density of breeding pairs of the Great Tit (Kluyver 1951, Perrins 1966, Dhondt 1971, Van Balen 1980, Ekman 1984, Tinbergen *et al.* 1985).

To test for interspecific competition with Blue Tits, possibly affecting the survival rate of immigrant female Great Tits, we selected also the

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Table 4. Likelihood ratio tests between different models involving external variables and a constant capture rate for the Great Tit data. BC: Beech crop production, WT: sum of the monthly mean temperatures from October to March, GTD: number of Great Tit breeding pairs and BTD: number of Blue Tit breeding pairs. NP: number of parameters estimated.

| Model | NP | Deviance (−2 Ln L) | Models compared | Conclusion |
|---|---|---|---|---|
| (s, p) | 2 | 2545.24 | — | — |
| (s = a + b (GTD), p) | 3 | 2528.83 | (s, p) >< (s = a + b (GTD, p) survival rate is related to GTD | $\chi^2 = 2545.24 - 2528.83 = 16.41$ $> \chi^2_{0.95}(1)$. Model (s, p) rejected |
| (s = a + b (BC), p) | 3 | 2540.70 | (s, p) >< (s = a + b (BC, p) survival rate is related to BC | $\chi^2 = 2545.24 - 2540.70 = 4.54$ $> \chi^2_{0.95}(1)$. Model (s, p) rejected |
| (s = a + b (WT), p) | 3 | 2540.49 | (s, p) >< (s = a + b (WT), p) survival rate is related to WT | $\chi^2 = 2445.24 - 2540.49 = 4.75$ $> \chi^2_{0.95}(1)$. Model (s, p) rejected |
| (s = a + b (BTD), p) | 3 | 2541.88 | (s, p) >< (s = a + b (BTD), p) survival rate is related to BTD | $\chi^2 = 2545.24 - 2541.88 = 3.36$ $< \chi^2_{0.95}(1)$. Model (s, p) accepted |
| (s = a + b (GTD) + c (WT), p) | 4 | 2527.48 | (s = a + b (GTD), p) >< (s = a + b (GTD) + c (WT), p) survival rate is related to GTD and WT | $\chi^2 = 2528.83 - 2527.48 = 1.35$ $< \chi^2_{0.95}(1)$. Model (s = a + b (GTD), p) accepted |
| (s = a + b (GTD) + c (BC), p) | 4 | 2527.75 | (s = a + b (GTD), p) >< (s = a + b (GTD) + c (BC), p) survival rate is related to GTD and BC | $\chi^2 = 2528.83 - 2527.75 = 1.08$ $< \chi^2_{0.95}(1)$. Model (s = a + b (GTD), p) accepted |
| (s = a + b (GTD) + c (BC) + d (WT), p) | 5 | 2525.25 | (s = a + b (GTD), p) >< (s = a + b (GTD + c (BC) + d (WT), p) survival rate is related to GTD, BC and WT | $\chi^2 = 2528.83 - 2525.25 = 3.43$ $< \chi^2_{0.95}(2)$. Model (s = a + b (GTD), p) accepted |
| ($s_t$, p) | 21 | 2499.32 | (s = a + b (GTD), p) >< ($s_t$, p) relation between survival rate and GTD does not explain all the variation in survival rates | $\chi^2 = 2528.83 - 2499.32 = 29.51$ $> \chi^2_{0.95}(18)$. Model (s = a + b (GTD), p) rejected |

number of breeding Blue Tits. Winter severity was described by the sum of the monthly mean temperatures from October to March (Table 3).

Models with only one variable were first examined. Only the logistic linear model ($\Omega$ (a + b x (j)) was used. From this analysis (Table 4) it appears that three variables are significantly related with survival rates: beech crop production (BC), number of Great Tit breeding pairs (GTD) and the temperature in winter (WT) as defined previously. Only one is not: the number of Blue Tit breeding pairs (BTD) ($\chi^2 = 3.36 < \chi^2_{0.95}(1)$). The greatest deviance is given by GTD ($\chi^2 = 16.41 > \chi^2_{0.95}(1)$), the second one by WT ($\chi^2 = 4.75 > \chi^2_{0.95}(1)$) and the third one by BC ($\chi^2 = 4.54 > \chi^2_{0.95}(1)$). To look at the influence of the two last variables (WT and BC) in presence of the first one (GTD), models with several variables were fitted. The results of this analysis are also given in Table 4.

In presence of GTD, none of the two remaining variables (BC and WT) appears to influence significantly the survival rate.

Unfortunately, the comparison between model ($\Omega$ (a + b (GTD), p)) and model ($s_t$, p) leads to the rejection of the former ($\chi^2 = 2528.83 - 2499.32 = 29.51 > \chi^2_{0.95}(18)$). We suspect that one or several ignored external variables could explain further variation over time in survival rates. A goodness-of-fit test rejects also model ($\Omega$ (a + b (GTD), p)) ($\chi^2 = 74.57 > \chi^2_{0.95}(55)$), while the model ($s_t$, p) is accepted (see above). Further analyses are thus needed. However, these preliminary results confirm the central role of density-dependent phenomena in the survival rate of the female Great Tit.

### 6.2. BLACK-HEADED GULL

Adult Black-headed Gulls were cannon-netted each spring from 1978 to 1985 in the neighbourhood of the largest colony (> 2000 pairs) of the Forez basin near Lyon, France. The study area and the colony are described in Lebreton & Landry (1979). Ringed birds were

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recorded each spring (after the period of capture), by visiting several times accessible parts of the colony with a floating hide (Lebreton 1981). Ring numbers were read from the hide with a telescope.

However, some parts of the colony cannot be visited, especially those with dense vegetation. Because of the strong tenacity to their previous year's breeding place (Lebreton 1984), Black-headed Gulls nesting in such areas are likely not to be seen again, just like birds breeding in other colonies. The probability of belonging to the set of accessible birds can be represented by a dummy survival parameter, which appears as age-dependent since it concerns birds immediately after they have been released. It might include some true mortality effect if the mortality between a release and the resighting visits is not negligible.

As a consequence of these remarks, the data (Table 5) have been analysed with various models with two age classes (Table 6). Examples are given in Fig. 2F and G.

The basic model ($s_a$, $p_t$) considers a time-dependent resighting probability. A likelihood ratio test of model ($s_a$, p) against model ($s_a$, $p_t$) leads to rejection of the hypothesis of constancy of the resighting rate over time ($\chi^2 = 1436.30 - 1416.33 = 19.97 > \chi^2_{0.95}(7)$, Table 6).

To reduce the number of parameters, the resighting rate can be modelled as a function of

Table 5. Data of resightings of Black-headed Gulls breeding in a large French colony. Details in text (6.2). RP = resighting pressure, in number of visits per year.

| Years | 1978 | 79 | 80 | 81 | 82 | 83 | 84 | 85 |
|---|---|---|---|---|---|---|---|---|
| $b_i$ | 16 | 55 | 243 | 292 | 0 | 0 | 38 | 0 |
| RP | 7 | 5 | 9 | 9 | 7 | 8 | 9.5 | 9.5 |
| $a_{ij}$ | | | | | | | | |
| 1979 | 2 | 2 | 0 | 1 | 0 | 2 | 1 | 0 |
| 1980 | | 1 | 5 | 1 | 3 | 1 | 1 | 3 |
| 1981 | | | 16 | 24 | 9 | 5 | 16 | 12 |
| 1982 | | | | 32 | 13 | 12 | 10 | 14 |
| 1983 | | | | | 0 | 0 | 0 | 0 |
| 1984 | | | | | | 0 | 0 | 0 |
| 1985 | | | | | | | 5 | 2 |
| 1986 | | | | | | | | 0 |
| $c_{ij}$ | | | | | | | | |
| 1978 | 10 | 1 | 1 | 0 | 1 | 0 | 2 | 1 |
| 1979 | | 44 | 0 | 4 | 1 | 2 | 1 | 0 |
| 1980 | | | 184 | 9 | 17 | 6 | 3 | 12 |
| 1981 | | | | 230 | 24 | 8 | 9 | 7 |
| 1982 | | | | | 0 | 0 | 0 | 0 |
| 1983 | | | | | | 0 | 0 | 0 |
| 1984 | | | | | | | 32 | 4 |
| 1985 | | | | | | | | 0 |

Table 6. Likelihood ratio tests between recapture models for the Black-headed Gull data. Further as in Table 2. NP: numbers of parameters; RP: resighting pressure; −2 Ln L: likelihood function values.

| Model | NP | Deviance (−2 Ln L) | Models compared | Conclusion |
|---|---|---|---|---|
| ($s_a$, p) | 10 | 1416.33 | | |
| ($s_a$, p = a + b (RP)) | 4 | 1423.38 | ($s_a$, p = a + b (RP)) >< ($s_a$, $p_t$) annual capture rate is related to the resighting pressure | $\chi^2 = 1423.38 - 1416.33 = 7.05 < \chi^2_{0.95}(6)$. Model ($s_a$, p = a + b (RP)) not rejected $\chi^2 = 1436.30 - 1423.38 = 12.92 > \chi^2_{0.95}(1)$. Model ($s_a$, p) rejected |
| ($s_a$, p) | 3 | 1436.30 | ($s_a$, p) >< ($s_a$, p = a + b (RP)) | |

Table 7. Survival rate estimates and their variance under different models. RP: recapture pressure.

| Model | Dummy survival rate $\hat{s}_1$ | Vâr ($\hat{s}_1$) | Adult survival rate $\hat{s}_2$ | Vâr ($\hat{s}_2$) |
|---|---|---|---|---|
| ($s_a$, $p_t$) | 0.480 | 0.063 | 0.824 | 0.052 |
| ($s_a$, p = a + b (RP)) | 0.487 | 0.060 | 0.821 | 0.032 |
| ($s_a$, p) | 0.479 | 0.059 | 0.848 | 0.034 |

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resighting pressure (RP), measured by the time spent in the floating hide, each year. This model ($s_a$, p = a + b (RP)) differs significantly from model ($s_a$, p)($\chi^2 = 12.92 > \chi^2_{0.95}$ (1)) and explains in a satisfactory way ($\chi^2 = 7.05 < \chi^2_{0.95}$ (6), Table 6) time variation in resighting rate, since comparison with model ($s_a$, $p_t$) is not significant. A goodness-of-fit test (Clobert & Lebreton 1985) confirms that model ($s_a$, p = a + b (RP)) describes correctly the data ($\chi^2 = 16.19 < \chi^2_{0.95}$(13)).

This example illustrates clearly the possibility of improving precision on survival by decreasing the number of parameters (Table 7). The asymptotic estimate of the standard deviation on $s_2$ is comparable to that obtained from model ($s_a$, p).

Using a dummy survival rate for the first period of recapture is another characteristic of interest for analyzing many data sets of this kind.

The survival rate obtained (0.82 ± 0.032) is in good agreement with predicted values for this population (from 0.81 to 0.83, Lebreton 1981). It is greater than values obtained from recoveries in various populations (reviewed by Lebreton & Isenmann 1976), in which biases inherent in the life table approach (Anderson *et al.* 1985) are most likely to occur.

## 7. CONCLUSION

In annual population dynamics each study, with its particular biological hypotheses to analyse and its particular practical constraints, requires its own experimental design. However, to estimate survival rates, methods available up to now (such as the Jolly-Seber model), despite recent modifications, are not flexible enough to describe efficiently the diversity of the situations encountered in practice. The approach proposed here, *i.e.* selecting the most appropriate recapture model among many by bringing together equality constraints between parameters, age and/or time-dependence, built-in relationships with external variables, and range constraints on parameters, goes some way towards the kind of realism and flexibility needed by biologists. In particular, selection of a parsimonious model, with the help of likelihood ratio tests and goodness-of-fit tests, results in an increase in the precision of the estimates obtained.

In the same framework, it seems possible in the future to go further on by incorporating such features as mixing recoveries and live recaptures (Buckland 1980), modelling recruitment, trap dependence, etc.

A computer program called SURGE (written in Fortran 77), allowing iterative fitting of the class of models proposed, has been written by the authors. It is available, together with a description, on a floppy disk for PC-AT from the second author.

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## 9. SUMMARY

A general approach to survival rate estimation by recaptures or resightings of marked birds is presented. This approach permits to generate any models involving age and/or time dependence in survival and/or capture rate. Models involving equality between subsets of parameters are also described, as well as models relating survival rate or capture rate with one or several external variables. The estimates can also be constrained between 0 and 1 or the parameters fixed to *a priori* values. Two examples, one on the Great Tit and one on the Black-headed Gull, are given to illustrate this approach. A Fortran 77 computer program allowing to fit these models is available from the authors.

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## 10. SAMENVATTING

De auteurs presenteren een algemene benaderingswijze om overlevingskansen te schatten uit terugvangsten of waarnemingen van gemerkte vogels. Deze benaderingswijze geeft de mogelijkheid verschillende modellen te ontwikkelen, waarin overlevingskans en/of vangkans al of niet afhankelijk verondersteld zijn van leeftijd en tijd van terugvangen. Modellen, waarin parameters gedeeltelijk aan elkaar gelijk gesteld zijn, worden ook beschreven, evenals modellen waarin overlevingskans en/of vangkans afhankelijk zijn gesteld van een of meer uitwendige factoren. Ook kunnen de schattingen begrensd worden tussen 0 en 1, of kunnen parameters op van te voren gegeven waarden worden gehouden.

Ter illustratie worden twee voorbeelden gegeven, een van de Koolmees en een van de Kokmeeuw. Een computer programma is bij de tweede auteur verkrijgbaar.

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