

DANISH REVIEW OF GAME BIOLOGY Vol. 6. no. 6

Edited by Anders Holm Joensen

Estimation Problems  
in Capture-Recapture Analysis

by  
OLE BARNDORFF-NIELSEN

Med et dansk resumé: Estimationsproblemer i genfangst analyse.

Резюме на русском языке  
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ПОВТОРНОЙ ЛОВЛИ

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## Abstract

The topic of the paper is the question of maximum likelihood estimation in DARROCH's (1959) model for capture-recapture experiments where deaths may occur, but with no immigration or births. Several problems, which have not been treated in the literature, but which are of both practical and theoretical import, are pointed out and proposals for full or partial solution to some of the problems are given. The problems are connected to various "boundary phenomena" and their solution rests in essential way on the observation that the model is of exponential form (for fixed value of the initial population size) and on a certain mode of reasoning, which involves shifting back and forth between the original form of the likelihood and its exponential form.

## 1. Introduction

The method of studying population dynamics and migration of animal populations through capture, marking, release, and recapture of individuals, which was originated by the Danish biologist C. G. J. PETERSEN at the end of the last century, has undergone a very considerable development especially within the last three or four decades. This method is widely applied by biologists, but the statistical methods for analysing capture-recapture data are far from complete. The basis of such methods is a mathematical model for the experiment performed and a large number of such models, of increasing complexity and sophistication, has been proposed and discussed in the literature.

A decisive breakthrough in the area of model building was achieved by DARROCH (1959), who established a fully stochastic model for an experiment of the following type. Consider an animal population in which deaths may occur but with no immigration or births. At  $l$  different occasions a random sample is taken from the population and each individual in the sample is marked with an identifiable tag, unless it has already been marked at a previous sampling in which case the number (or other identification device) of its tag is recorded.

In practice it often happens that some of the animals caught are not released again, for instance because they have been hurt or killed by the sampling. There may of course be other reasons for not releasing an animal, but for simplicity we shall, following JOLLY (1965), refer to the event that an animal is retained as a "loss on capture". DARROCH's model does not include the possibility of loss on capture, but is easily extended to do so, as DARROCH himself indicated. The basic assumptions of the model are that on any given sampling occasion, number  $i$  say, all the animals still alive in

the population have the same probability  $p_i$  of being caught and all the animals caught have the same probability  $\eta_i$  of being released again, irrespectively of the previous capture history of the animal; furthermore the probability  $\varphi_i$  of survival between sampling occasions  $i$  and  $i+1$  is assumed to be the same for all individuals in the population.

The main purpose of the present paper is to discuss various problems connected with maximum likelihood estimation of the parameters  $p_i$ ,  $\eta_i$  and  $\varphi_i$ . Before pursuing this purpose, we shall briefly review some further relevant parts of the literature. (The introductory sections of the papers by DARROCH (1958), (1959), JOLLY (1965), and SEBER (1965) together constitute a comprehensive and excellent review of the literature on capture-recapture models).

DARROCH (1959) also developed a model for the case with immigration (or birth) but no death. For both models he derived the likelihood equations and solved them in order to obtain the maximum likelihood estimates of the parameters. At the end of the paper DARROCH described how the two models could be merged into one involving both death and immigration. The likelihood function of this latter model is so complex that estimation by the maximum likelihood method appears quite intractable. Various proposals for circumventing this difficulty have been put forward. DARROCH himself found moment estimators. SEBER (1965) showed how a slight reformulation of the model considered by DARROCH led to a likelihood accessible to the maximum likelihood method. JOLLY (1965) gave a capture-recapture model, building on the same basic assumptions as DARROCH's models and comprising immigration, death and loss on capture. He also derived estimators from this model by a method which may be briefly described as a modification of the maximum likelihood method, but which I find obscure.

All the above-mentioned three authors discuss various asymptotic properties (means, variances and covariances) of the estimators.

None of these authors, however, treats the following questions:

- (i) What is the situation if one or more of the proposed estimates is meaningless, because the denominator in the ratio expression given for the estimate is zero?
- (ii) Suppose the estimates of the probabilities  $p_i$ ,  $\eta_i$ ,  $\varphi_i$  are well-defined real numbers. Do they actually lie in the interval between 0 and 1?
- (iii) Suppose they do lie in this interval. Are they in fact maximum likelihood estimators, i.e. does the likelihood function have a unique global maximum at the point determined by these estimates (together with the estimate for the initial population size)?

(DARROCH (1961) in another context touched upon a question similar to (ii)).

Perhaps one may feel that the questions are not very pertinent provided that the size of the population is large and that the sample sizes are approximately of the same order of magnitude as the population size. We shall not enter into a discussion of this point since the experimental data which brought the three questions forth do

not have this property. However, we would like to stress that question (iii) is not just an academic one even if population and sample sizes are large: The fact that a function does not necessarily have global maximum at a point where its partial derivatives are 0 is apparently not well heeded among statisticians, for a recent exemplification see SOLARI (1969).

The problems outlined above became prominent during work jointly by F. ABILDGAARD and the author, with the statistical analysis of an extensive and excellent set of data collected by JOHANNES ANDERSEN of the Game Biology Station (Vildtbiologisk Station, Kalø). The data concern the hare (*Lepus europaeus*) population on a small Danish island, Illumø. The hares cannot get away from the island, nor does immigration occur. Also there are no predators of hares on Illumø. Since 1957 a capture-recapture experiment has been going on which comprises 6 sampling occasions per year. On each occasion roughly one half of the population is caught. As a result of this intensive sampling it is virtually impossible for a hare to live through a whole year without being caught at least once, and this in turn means that the year of birth is known for (practically) all hares born in 1957 or later. It is thus possible to split the material according to generation (as well as sex), and it was found natural to try to base the statistical analysis of the data on application, to each generation separately, of DARROCH's model with death but no immigration. The initial size of a generation (of males or of females) varied between 20 and 100, roughly, and the generations born through the first part of the experimental period are now extinct. Thus we are faced with a situation characterized by small population sizes. Consequently many of the estimates to which one generation gives rise are not very accurate, but since many generations are available there are good hopes for obtaining considerable insight into the population dynamics.

We are able to give only a partial solution to questions (i)–(iii). Moreover, really satisfactory methods for comparing and pooling estimates from different generations are highly wanting. In these circumstances the statistical analysis of the data which we have been able to do is necessarily somewhat tentative and rough. This analysis together with detailed description of the experiment will be given elsewhere (ABILDGAARD, ANDERSEN and BARNDORFF-NIELSEN (1971)).

It is a main feature of the theoretical discussion below that the likelihood functions are considered partly on a form similar to that given by DARROCH, partly on exponential form. In the effort to disentangle the problems outlined in (i)–(iii) it proved essential to shift back and forth between the two forms, as reported in the following. This technique may well be of interest and use in other connections.

The model is introduced and its exponential form derived in Section 2. In Section 3 the likelihood equations are set up and their solution is discussed under a set of conditions which together define what we call the regular case. Even in the regular case several questions remain to be solved; one of them, discussed at the end of the section, is particularly interesting, both from the theoretical and the practical point of view. The nonregular case is treated in Section 4, the main aim being to illustrate how the

technique mentioned in the previous paragraph can be used to solve some of the special problems occurring in this case.

## 2. The Model and Its Exponential Form

As already stated the estimation problems to be discussed concern a model, due to DARROCH (1959), for an animal population in which deaths may occur, but where migration and births do not take place. At  $l$  different occasions a random sample is taken from the surviving part of the population. Sampled animals are marked individually when captured for the first time, and for each animal record is taken of the occasions at which it is captured or recaptured. It may happen that not all the animals in a sample are returned to the population after marking and recording has taken place, for instance because some of them have been killed by the sampling. An animal which is not returned to the population is said to be lost on capture.

The observations, then, consist of a set of lists, one for each of the animals caught at least once, showing when the animals were captured and whether they were lost on capture.

The basic assumptions of the model are:

1. Stochastic independence between animals.
2. All animals alive on sampling occasion  $i$  ( $i=1, 2, \dots, l$ ) have the same probability,  $p_i$ , of being captured, irrespective of their previous capture history.
3. All animals alive in the population right after sampling occasion  $i$  have the same probability,  $q_i$ , of surviving till occasion  $i+1$ , irrespective of their previous capture history.

A further, less important assumption is that all animals captured at sampling occasion  $i$  have the same probability,  $\eta_i$ , of being returned to the population irrespective of their previous capture history.

Let the number of animals in the population at the time of the first sampling be denoted by  $N$ . There is a total of  $2^{l+1} - 1$  different, possible capture histories (including that of never being caught) and the distribution of the  $N$  animals according to capture history is a multinomial distribution. Thus the likelihood of the observations is

$$L = \frac{N!}{\prod_{\omega \in \Omega} u_{\omega}!} \prod_{\omega \in \Omega} \theta_{\omega}^{u_{\omega}} \quad (1)$$

where  $u_{\omega}$  denotes the number of animals with capture history  $\omega$ , where  $\Omega$  is the set of possible capture histories and where  $\theta_{\omega}$  denotes the probability of  $\omega$ . Let  $\pi_i$  denote the probability that an animal alive in the population right after sampling No.  $i$  is not captured at any later occasion. Each  $\theta_{\omega}$  is easily expressed in terms of the prob-

abilities  $p_i, \varphi_i, \eta_i$  and  $\pi_i$ . For instance, if  $\omega$  indicates that the animal was caught exactly at samplings Nos. 2, 3 and 5, and not lost on capture, then

$$\theta_\omega = q_1 \varphi_1 p_2 \eta_2 \varphi_2 p_3 \eta_3 \varphi_3 q_4 \varphi_4 p_5 \eta_5 \pi_5$$

with  $q_i = 1 - p_i$ . Introducing this form of the  $\theta_\omega$ 's in (1) and collecting similar terms one obtains

$$L = \frac{N!}{\prod u_\omega!} (q_1 \pi_1)^{N-r_1} \prod_{i=1}^l p_i^{a_i} q_i^{r_i - a_i} \prod_{i=1}^l \eta_i^{a_i - d_i} (1 - \eta_i)^{d_i} \prod_{i=1}^{l-1} \varphi_i^{r_{i+1}} \prod_{i=1}^{l-1} \pi_i^{r_i - r_{i+1} - d_i} \quad (2)$$

where

$r_i$  = the number of different animals caught on sampling occasion  $i$  or later  
 $a_i$  = the number of animals caught on occasion  $i$   
 $d_i$  = the number of animals lost on capture  $i$ .

The quantities  $u_\omega$  can all be calculated from the observations except the one corresponding to the capture history: never caught. Let this capture history be denoted by  $\omega_0$ . Clearly

$$u_{\omega_0} = N - r_1.$$

It is therefore natural to rewrite the first factor in  $L$  as

$$\frac{N!}{\prod u_\omega!} = k \cdot \binom{N}{r_1}$$

where  $k$  is a constant,

$$k = \frac{r_1!}{\prod_{\omega \neq \omega_0} u_\omega!}. \quad (3)$$

Unless explicitly stated otherwise the domain of variation for the parameters is taken to be  $\{r_1 + 1, r_1 + 2, \dots\}$  for  $N$  and the open interval  $(0, 1)$  for the  $p_i$ 's,  $\varphi_i$ 's and  $\eta_i$ 's. Note that

$$\pi_i = 1 - \varphi_i + \varphi_i q_{i+1} \pi_{i+1}, \quad i = 1, \dots, l-1. \quad (4)$$

In particular, since  $\pi_l = 1$ ,

$$\pi_{l-1} = 1 - \varphi_{l-1} p_l$$

and therefore (cf. formula (2))  $L$  depends on  $\varphi_{l-1}$  and  $p_l$  only through their product  $\varphi_{l-1} p_l$ . Thus  $L$  is a function of  $3l-1$  independently varying parameters, namely  $N, p_1, \dots, p_{l-1}, \varphi_1, \dots, \varphi_{l-2}, \eta_1, \dots, \eta_l$  and  $\varphi_{l-1} p_l$ .

After some algebraic rearrangements  $L$  takes the following form (note that  $r_l = a_l$ )



$$L = k \binom{N}{r_1} (q_1 \pi_1)^N \prod_1^{l-1} \left( \frac{p_i}{q_i} \eta_i \right)^{a_i} \left( \frac{\varphi_{l-1} p_l}{1 - \varphi_{l-1} p_l} \eta_l \right)^{a_l} \cdot \prod_1^l \left( \frac{1 - \eta_i}{\eta_i} \frac{1}{\pi_i} \right)^{d_i} \cdot \prod_2^{l-1} \left( \frac{\varphi_{i-1} q_i \pi_i}{\pi_{i-1}} \right)^{r_i}. \quad (5)$$

Hence  $L$  may be written

$$L = k \binom{N}{r_1} (q_1 \pi_1)^N \exp \left\{ \sum_1^l a_i \varrho_i + \sum_1^l d_i \theta_i + \sum_2^{l-1} r_i \tau_i \right\}$$

where

$$e^{\varrho_i} = \frac{p_i}{q_i} \eta_i, \quad i = 1, 2, \dots, l-1 \quad (6.i)$$

$$e^{\theta_l} = \frac{\varphi_{l-1} p_l}{1 - \varphi_{l-1} p_l} \eta_l \quad (6.l)$$

$$e^{\theta_i} = \frac{1 - \eta_i}{\eta_i} \frac{1}{\pi_i}, \quad i = 1, \dots, l \quad (7.i)$$

$$e^{\tau_i} = \frac{\varphi_{i-1} q_i \pi_i}{\pi_{i-1}}, \quad i = 2, \dots, l-1. \quad (8.i)$$

It is a remarkable fact that the mapping defined on  $(0, 1)^{3l-2}$  which transforms the parameters  $p_1, \dots, p_{l-1}, \varphi_{l-1} p_l, \eta_1, \dots, \eta_l, \varphi_1, \dots, \varphi_{l-2}$  into the new parameters  $\varrho_1, \dots, \varrho_l, \theta_1, \dots, \theta_l, \tau_2, \dots, \tau_{l-1}$  is one-to-one and onto the set  $R^{2l} \times (-\infty, 0)^{l-2}$  where  $R = (-\infty, \infty)$ .

To verify this result one can proceed as follows. It appears from formula (8.i) that  $e^{\tau_i}$  has the interpretation of being the conditional probability for an animal to survive between  $i-1$  and  $i$  given that it is not captured after  $i-1$ . Hence  $\tau_i \in (-\infty, 0)$  and the mapping is into the stated set. On the other hand, for any point in this set equations (6.1)–(8.l–1) have a unique solution in the domain  $(0, 1)^{3l-2}$ . In fact, the solution may be found explicitly by first finding  $\eta_l$  from equation (7.l), then  $\varphi_{l-1} p_l$  from equation (6.l) and then, successively,  $\eta_{l-1}, p_{l-1}, \varphi_{l-2}, \eta_{l-2}, \dots, p_1$  from (7, l–1), (6, l–1), (8, l–1), (7, l–2),  $\dots$ , (6.1) solving these equations in the stated order.

As a consequence it is possible to express the factor  $(q_1 \pi_1)^N$  in  $L$  as a function of the new parameters. For notational convenience let

$$\frac{1}{q_1 \pi_1} = w = w(\varrho_1, \dots, \varrho_l, \theta_1, \dots, \theta_l, \tau_2, \dots, \tau_{l-1}). \quad (9)$$

A somewhat lengthy algebraic computation shows that

$$w = 1 + \sum_{i=1}^l (1 + e^{\theta_i}) c_i(\varrho_*) e^{\tau_{i0}} \quad (10)$$

where  $Q_* = (Q_1, \dots, Q_l)$ ,

$$c_i(Q_*) = \prod_{\nu=1}^{i-1} (1 + e^{\theta_\nu}) e^{\theta_i} \quad (11)$$

and

$$\tau_{i0} = \tau_1 + \tau_2 + \dots + \tau_i \quad (12)$$

with  $\tau_1$  and  $\tau_l$  both defined to be zero.

In the new notation

$$L = k \binom{N}{r_1} w^{-N} \exp \left\{ \sum_1^l a_i Q_i + \sum_1^l d_i \theta_i + \sum_2^{l-1} r_i \tau_i \right\}. \quad (13)$$

Thus for fixed  $N$  the likelihood function is of exponential form with the canonical parameters  $Q_1, \dots, Q_l, \theta_1, \dots, \theta_l, \tau_2, \dots, \tau_{l-1}$  varying freely in  $R^{2l} \times (-\infty, 0)^{l-2}$ .

It is now natural to ask whether the right hand side of (13) determine a probability distribution also if some of the  $\tau_i$ 's are positive or zero. This is indeed the case as can be shown by a simple argument of analytic continuation.

The next question is then whether it is possible to give a probabilistic interpretation of these extra distributions, which is meaningful in relation to the capture-recapture model. At present we have not even the trace of an answer.

### 3. Discussion of the Likelihood Equations

The likelihood equations corresponding to partial differentiation with respect to the canonical parameters may be written

$$\frac{\partial w}{\partial Q_i} = (1 + e^{\theta_i}) c_i(Q_*) e^{\tau_{i0}} + \frac{e^{\theta_i}}{1 + e^{\theta_i}} \sum_{\nu=i+1}^l (1 + e^{\theta_\nu}) c_\nu(Q_*) e^{\tau_{\nu 0}} = \frac{a_i}{N} w, \quad i = 1, \dots, l. \quad (14.i)$$

$$\frac{\partial w}{\partial \theta_i} = e^{\theta_i} c_i(Q_*) e^{\tau_{i0}} = \frac{d_i}{N} w, \quad i = 1, \dots, l. \quad (15.i)$$

$$\frac{\partial w}{\partial \tau_i} = \sum_{\nu=i}^l (1 + e^{\theta_\nu}) c_\nu(Q_*) e^{\tau_{\nu 0}} = \frac{r_i}{N} w, \quad i = 2, \dots, l-1. \quad (16.i)$$

Corresponding to  $N$  there is not one equation but rather the two inequalities

$$\frac{L(N)}{L(N-1)} = \frac{N}{N-r_1} \frac{1}{w} \geq 1 \quad (17)$$

$$\frac{L(N+1)}{L(N)} = \frac{N+1}{N+1-r_1} \frac{1}{w} \leq 1 \quad (18)$$

where  $L(N)$  denotes the likelihood function considered as a function of  $N$ .

We proceed to solve relations (14.1)–(18) on the supposition that they have a solution in the extended domain  $R^{3l-2} \times \{r_1+1, r_1+2, \dots\}$  i.e. for the time being we allow also solutions which do not correspond to one of the original capture-recapture models (cf. the end of Section 2).

Consider first equations (14.1), (15.1) and (16.2). Using the explicit expression (10) for  $w$  we have

$$(1 + e^{\theta_1})e^{\theta_1} + \frac{e^{\theta_1}}{1 + e^{\theta_1}}(w - 1 - (1 + e^{\theta_1})e^{\theta_1}) = \frac{a_1}{N}w \quad (14.1)$$

$$e^{\theta_1}e^{\theta_1} = \frac{d_1}{N}w \quad (15.1)$$

$$w - 1 - (1 + e^{\theta_1})e^{\theta_1} = \frac{r_2}{N}w. \quad (16.2)$$

Insertion of (16.2) in (14.1) yields

$$w - 1 - \frac{r_2}{N}w \frac{1}{1 + e^{\theta_1}} = \frac{a_1}{N}w$$

or

$$\frac{1}{w} = -\frac{r_2}{N} \frac{1}{1 + e^{\theta_1}} + \frac{N - a_1}{N}. \quad (19)$$

From (15.1) and (16.2) we obtain

$$1 + e^{\theta_1} = w \frac{N - d_1 - r_2}{N} \quad (20)$$

which together with (19) shows that

$$\frac{1}{1 + e^{\theta_1}} = \frac{N - a_1}{N - d_1}$$

or

$$e^{\theta_1} = \frac{a_1 - d_1}{N - a_1}. \quad (21)$$

Then, from (21) and (20)

$$w = \frac{N(N - d_1)}{(N - a_1)(N - d_1 - r_2)} \quad (22)$$

and from (22), (21) and (15.1)

$$e^{\theta_1} = \frac{d_1(N - d_1)}{(a_1 - d_1)(N - d_1 - r_2)}. \quad (23)$$

As the next step we subtract equation (16. $i$ +1) from (16. $i$ ) to obtain

$$(1 + e^{\theta_i})c_i(\varrho_*)e^{\tau_{i0}} = \frac{r_i - r_{i+1}}{N}w \quad (24.i)$$

for  $i=2, \dots, l-2$ . The equation is, however, also valid for  $i=l$ , since in this case it is identical with (14.l), and for  $i=l-1$ , as may be seen by inserting (14.l) in (16.l-1). Substituting (24.i) and (16.i+1) in (14.i) we find

$$r_i - r_{i+1} + r_{i+1} \frac{e^{\theta_i}}{1 + e^{\theta_i}} = a_i, \quad i = 2, \dots, l-1$$

or

$$(r_i - a_i)e^{\theta_i} = a_i + r_{i+1} - r_i.$$

Thus, assuming temporarily

$$r_i - a_i > 0, \quad i = 2, \dots, l-1,$$

we have

$$e^{\theta_i} = \frac{a_i + r_{i+1} - r_i}{r_i - a_i}, \quad i = 2, \dots, l-1. \quad (25.i)$$

Moreover (24.i) and (15.i) together show that

$$c_i(Q_*)e^{\tau_{i0}} = \frac{r_i - r_{i+1} - d_i}{N} w, \quad i = 2, \dots, l \quad (26.i)$$

and by inserting this in (15.i) we obtain

$$(r_i - r_{i+1} - d_i)e^{\theta_i} = d_i$$

so, assuming

$$r_i - r_{i+1} - d_i > 0, \quad i = 2, \dots, l,$$

we have

$$e^{\theta_i} = \frac{d_i}{r_i - r_{i+1} - d_i}, \quad i = 2, \dots, l. \quad (27.i)$$

It remains to determine  $\tau_2, \dots, \tau_{l-1}$ ,  $Q_1$  and  $N$ . Taking the ratio of (26.i) to (26.i-1) yields

$$e^{\tau_i} = \frac{r_i - r_{i+1} - d_i}{r_{i-1} - r_i - d_{i-1}} \frac{e^{\theta_{i-1}}}{1 + e^{\theta_{i-1}}} \frac{1}{e^{\theta_i}}, \quad i = 3, \dots, l-1 \quad (28.i)$$

and

$$e^{\theta_l} = \frac{a_l - d_l}{r_{l-1} - a_l - d_{l-1}} \frac{e^{\theta_{l-1}}}{1 + e^{\theta_{l-1}}} \quad (28.l)$$

whence, by (25.),

$$e^{\tau_i} = \frac{r_i - r_{i+1} - d_i}{r_{i-1} - r_i - d_{i-1}} \frac{a_{i-1} - r_{i-1} + r_i}{a_i - r_i + r_{i+1}} \frac{r_i - a_i}{r_i}, \quad i = 3, \dots, l-1, \quad (29.i)$$

and

$$e^{\theta_l} = \frac{a_l - d_l}{r_{l-1} - a_l - d_{l-1}} \frac{a_{l-1} + a_l - r_{l-1}}{a_l}. \quad (25.l)$$

$e^{\tau_2}$  is found from (26.2), (25.2) and (20), to be

$$e^{r_2} = \frac{r_2 - r_3 - d_2}{N - r_2 - d_1} \frac{r_2 - a_2}{a_2 + r_3 - r_2}. \quad (29.2)$$

Finally, to obtain  $N$  we insert (22) in (17) and find

$$(N - a_1)(N - d_1 - r_2) \geq (N - r_1)(N - d_1)$$

or

$$a_1 d_1 + a_1 r_2 - r_1 d_1 \geq (a_1 + r_2 - r_1)N.$$

Assuming temporarily

$$a_1 + r_2 - r_1 > 0$$

we thus have

$$N \leq \frac{a_1 d_1 + a_1 r_2 - r_1 d_1}{a_1 + r_2 - r_1} = r_1 + \frac{(r_1 - a_1)(r_1 - r_2 - d_1)}{a_1 + r_2 - r_1}. \quad (30)$$

Clearly, for the solution to lie in  $\{r_1 + 1, r_1 + 2, \dots\}$  it is necessary that

$$r_1 - a_1 > 0$$

and

$$r_1 - r_2 - d_1 > 0.$$

Suppose this to be the case. It is plausible to presume that the value of  $N$  we are looking for is

$$N = \left[ \frac{a_1 d_1 + a_1 r_2 - r_1 d_1}{a_1 + r_2 - r_1} \right] \quad (31)$$

where  $[ ]$  denotes integer part.

We may now sum up the foregoing considerations thus. We have arrived at the following candidate for a solution to the likelihood relations (14.1)–(18).

$$N = \left[ \frac{a_1 d_1 + a_1 r_2 - r_1 d_1}{a_1 + r_2 - r_1} \right] \quad (31)$$

$$e^{r_1} = \frac{a_1 - d_1}{N - a_1} \quad (25.1)$$

$$e^{r_i} = \frac{a_i + r_{i+1} - r_i}{r_i - a_i}, \quad i = 2, \dots, l-1 \quad (25.i)$$

$$e^{r_l} = \frac{a_l - d_l}{r_{l-1} - r_l - d_{l-1}} \frac{a_{l-1} + r_l - r_{l-1}}{a_l} \quad (25.l)$$

$$e^{\theta_1} = \frac{d_1(N_1 - d_1)}{(a_1 - d_1)(N - d_1 - r_2)} \quad (27.1)$$

$$e^{\theta_i} = \frac{d_i}{r_i - r_{i+1} - d_i}, \quad i = 2, \dots, l. \quad (27.i)$$

$$e^{\tau_2} = \frac{r_2 - r_3 - d_2}{N - r_2 - d_1} \frac{r_2 - a_2}{a_2 + r_3 - r_2} \quad (29.2)$$

$$e^{\tau_i} = \frac{r_i - r_{i+1} - d_i}{r_{i-1} - r_i - d_{i-1}} \frac{a_{i-1} - r_{i-1} + r_i}{a_i - r_i + r_{i+1}} \frac{r_i - a_i}{r_i},$$

$$i = 3, \dots, l-1. \quad (29.i)$$

In deriving these expressions we were led to assume

$$r_i - a_i > 0, \quad i = 1, \dots, l-1 \quad (32.i)$$

$$r_i - r_{i+1} - d_i > 0, \quad i = 1, \dots, l \quad (33.i)$$

and

$$a_1 + r_2 - r_1 > 0. \quad (34.1)$$

Obviously the expressions (31), (25.), (27.) and (29.) do not determine a point in the extended parameter domain unless furthermore

$$a_i + r_{i+1} - r_i > 0, \quad i = 2, \dots, l-1 \quad (34.i)$$

$$d_i > 0, \quad i = 1, \dots, l \quad (35.i)$$

$$a_i > 0 \quad (36)$$

$$N > r. \quad (37)$$

(Note that (33.i) implies  $a_i - d_i > 0$ ).

If all these conditions are satisfied then the above proposal for a solution does in fact satisfy the likelihood relations as is easily seen by insertion. The derivation we have given very nearly shows that the solution is unique (provided the conditions (32.1)–(37) are fulfilled). To complete a proof of the uniqueness it would suffice to show that the value of  $N$  given by (31) is the only integer greater than  $r_1$  which satisfies both (17) and (18) with  $w$  as given by (22). We shall, however, not pursue this problem.

Even if the uniqueness of the solution was established, the question would still remain of whether the solution determined a unique global maximum of the likelihood function in the extended domain. This is very likely to be true, because intuitively the value (31) seems to be the most reasonable estimate for  $N$ , and because for any given  $N$  the likelihood equations (14.1)–(16.l-1) have at most one solution, and if they have a solution then that is a global maximum point for  $L$  (regarded as a function of the canonical parameters only). The latter two results follow from the observation, previously made, that for fixed  $N$  the likelihood function is of exponential form.

The next section is devoted to a discussion of the situation when one or more of the conditions (32.1)–(35.l) are violated. For brevity we shall refer to this situation as “the nonregular case”.

We conclude the present section by pointing out a problem which is both theoretically interesting and of practical importance.

The solution we have found in the regular case does not in general possess the property that  $\tau_i \in (-\infty, 0)$ ,  $i=2, \dots, l-1$ , as it must do in order to determine one of the original capture-recapture models. Thus, if  $\tau_i \geq 0$  for some  $i$ , the solution is not the maximum likelihood estimate.

So long as population and sample sizes are large this possibility is not very likely to occur (neither are conditions (32.1)–(35.1) likely to be violated). However, in practice it may well happen that population size is small, particularly at the end of the capture-recapture experiment, as exemplified by the data from Illumø referred to earlier. In such cases it will not be uncommon that some of the regularity conditions do not hold or that the solution to the likelihood relations lies outside the proper parameter domain.

We conjecture (cf. ABILDGAARD, ANDERSEN and BARNDORFF-NIELSEN (1971)) that if some of the  $\tau_i$  in the solution are positive or zero then the correct estimate is obtained by setting the corresponding survival parameters  $\varphi_i$  equal to 1 in the original likelihood\*) and then maximizing over the remaining parameters. It is plausible to suppose that a proof of the conjecture could most easily be established using the exponential character of the likelihood function. Despite considerable efforts neither this line of attack nor any other we have been able to think of has led to a proof (or disproof).

The estimates employed in the analysis of the Illumø data are derived on the basis of this conjecture, cf. ABILDGAARD, ANDERSEN and BARNDORFF-NIELSEN (1971).

In the present connection it is worth mentioning what happens if one works with the likelihood equations obtained by partial differentiation with respect to the original parameters, rather than the canonical parameters. This alternative set of equations can, in the regular case, be explicitly solved, and one obtains expressions for the (original) parameters which have the property that  $p_1, \dots, p_{l-2}, \varphi_{l-1} p_l, \eta_1, \dots, \eta_l$  are all contained in  $(0, 1)$ ; however, as is to be expected in view of the foregoing discussion, it is possible for the  $\varphi_i$  to be  $\geq 1$  (cf. ABILDGAARD, ANDERSEN and BARNDORFF-NIELSEN (1971)).

Finally, it is perhaps relevant to emphasize that the essential problems discussed in this and the following section do not stem from the introduction of the possibility of loss on capture into DARROCH's model. The problems are inherent already in that model.

#### 4. Discussion of the Nonregular Case

We shall now discuss how to construct the correct estimate, in the sense of maximum likelihood, in case conditions (32.1)–(35.1) are not fulfilled. Whenever these conditions are violated the likelihood function does not have a maximum in the domain

\*) It is simple to prove that the mapping from the old parameters to the canonical parameters can be extended, under preservation of the one-to-one property, to include in the domain points with some or all of the  $\varphi_i$  equal to 1. The range then becomes  $R^{2l} \times (-\infty, 0]^{l-2}$  and  $\varphi_i = 1$  is equivalent to  $\tau_i = 0$ .

$(0, 1)^{3l-2} \times \{r_1+1, r_1+2, \dots\}$ . What we show in this section is that it is then natural to set some particular of the parameters equal to one of their boundary values and then maximize in the remaining parameters.

We assume throughout, for simplicity and since it is no severe restriction, that  $a_1 > 0$  and  $a_l > 0$ . Furthermore it turns out to be convenient to work with the slightly modified model obtained by assuming  $\eta_i$  to be 1 (and hence  $d_i$  to be 0); this, of course, does not cause any substantial loss of generality and only very minor and obvious changes are needed in sections 2 and 3 in order to make the treatment given there fit to the modified model. Under these circumstances condition (34.l) becomes void.

It is also practical to do away with the possibility that  $a_i = 0$  for some  $i$ ,  $1 < i < l$ . In this instance  $L$  does not depend on  $\eta_i$  and is a decreasing function of  $p_i$ . Hence  $p_i$  should be estimated as 0 and with this value inserted the likelihood function depends on  $\varphi_{i-1}$  and  $\varphi_i$  only through their product. It is therefore natural to treat sampling occasions, where no animals are caught, as if no sampling had taken place. Accordingly, we henceforth assume  $a_i > 0$  for all  $i$ .

Finally, we shall impose the more severe assumption that

$$d_i < a_i, \quad i = 1, \dots, l-1.$$

If this was not done the notations and the arguments would become considerably more complex although the situation, when the assumption is not fulfilled, appears not to raise fundamentally new issues.

We shall find it convenient to introduce the notations

$$\begin{aligned} a_i^- &= r_i - r_{i+1} - d_i \\ a_i^+ &= a_i + r_{i+1} - r_i. \end{aligned}$$

$a_i^-$  is the number of animals caught at time  $i$ , released and never seen again whereas  $a_i^+$  is the number which are recaptured. Note that since we have assumed  $d_i < a_i$ ,  $a_i^-$  and  $a_i^+$  cannot simultaneously be zero.

Consider now condition (32.i)  $r_i - a_i > 0$ ,  $i = 1, \dots, l-1$  and suppose that it is not fulfilled. Let

$$b_i = r_i - a_i$$

and let  $i_0$  denote the least  $i$  with  $b_i = 0$ .

If  $i_0 = 1$  then the only part of  $L$  which depends on  $N$  and  $p_i$  is

$$\binom{N}{r_1} p_1^{r_1} q_1^{N-r_1}.$$

This is always  $\leq 1$  for  $N \geq r_1$ ,  $0 \leq p_1 \leq 1$  and equal to 1 if and only if  $N = r_1$  and  $p_1 = 1$ . Thus if  $r_1 = a_1$  it is natural to estimate  $N$  by  $r_1$  and  $p_1$  by 1, to insert these values in  $L$  and maximize over the rest of the parameters.

For later use we note that with  $r_1 = a_1$ ,  $N = r_1$  and  $p_1 = 1$  the likelihood is

$$L = k \prod_{i=2}^l p_i^{a_i} q_i^{r_i - a_i} \prod_{i=1}^{l-1} \eta_i^{a_i - d_i} (1 - \eta_i)^{d_i} \prod_{i=1}^{l-1} \varphi_i^{r_{i+1}} \prod_{i=2}^{l-1} \pi_i^{a_i^-} \quad (38)$$



or, written in exponential form,

$$L = kw^{-r_1} \exp \left\{ \sum_2^l a_i \varrho_i + \sum_1^{l-1} d_i \theta_i + \sum_2^{l-1} r_i \tau_i \right\} \quad (39)$$

where the parameters are as previously defined (formulas (6.), (7.) and (8.)) except that, since  $\eta_l$  has been taken to be 1

$$e^{\varrho_1} = \frac{\varphi_{l-1} p_l}{1 - \varphi_{l-1} p_l}.$$

$w$  is here given by

$$w = \frac{1}{\eta_1 \pi_1} = \sum_{i=1}^l (1 + e^{\theta_i}) c_{1i}(\varrho_*) e^{\tau_{i0}} + c_{1l}(\varrho_*) e^{\tau_{l0}} \quad (40)$$

with  $c_{1i}(\varrho_*)$  defined as

$$c_{1i}(\varrho_*) = \prod_{v=2}^{i-1} (1 + e^{\varrho_v}) e^{\varrho_i}, \quad i = 1, \dots, l \quad (c_{1l}(\varrho_*) = 1).$$

The mapping which sends the point  $(p_2, \dots, p_{l-1}, \varphi_{l-1} p_l, \eta_1, \dots, \eta_{l-1}, \varphi_1, \dots, \varphi_{l-2})$  to the point  $(\varrho_2, \dots, \varrho_l, \theta_1, \dots, \theta_{l-1}, \tau_2, \dots, \tau_{l-1})$  is easily seen to be one-to-one from  $(0, 1)^{3l-4}$  onto  $R^{2l-2} \times (-\infty, 0)^{l-2}$ .

Next we treat the case  $1 < i_0 (< l)$ . It is here convenient to take the exponential form of  $L$

$$L = k \binom{N}{r_1} w^{-N} \exp \left\{ \sum_1^l a_i \varrho_i + \sum_1^{l-1} d_i \theta_i + \sum_2^{l-1} r_i \tau_i \right\}$$

and introduce the variates  $b_i$  instead of  $r_i$  thereby obtaining

$$L = k \binom{N}{r_1} w^{-N} \exp \left\{ \sum_1^l a_i \varrho_i + \sum_1^{l-1} d_i \theta_i + \sum_2^{l-1} b_i \tau_i \right\}$$

where

$$\varkappa_i = \varrho_i - \tau_i.$$

It is immediate that also the new set of canonical parameters

$$(\varkappa_1, \dots, \varkappa_l, \theta_1, \dots, \theta_{l-1}, \tau_2, \dots, \tau_{l-1})$$

varies freely except that  $\tau_i < 0, i=2, \dots, l-1$ . As function of the new parameters  $w$  is given by

$$w = 1 - \sum_{i=1}^{l-1} (1 + e^{\theta_i}) (e^{\tau_1} + e^{\varkappa_1}) \dots (e^{\tau_{i-1}} + e^{\varkappa_{i-1}}) e^{\varkappa_i} + (e^{\tau_1} + e^{\varkappa_1}) \dots (e^{\tau_{l-1}} + e^{\varkappa_{l-1}}) e^{\varkappa_l}.$$

Now  $b_{i_0} = 0$  and  $L$  therefore depends on  $\tau_{i_0}$  only through  $w$  which is clearly a strictly increasing function of  $\tau_{i_0}$ , i.e.  $L$  is strictly decreasing as a function of  $\tau_{i_0}$ . Hence, in particular,  $L$  does not have a maximum in the domain

$$R^{2l-1} \times (-\infty, 0)^{l-2} \times \{r_1 + 1, r_1 + 2, \dots\}.$$

In order to find out how to remedy the situation by going to the boundary we consider the defining equation for  $\tau_{i_0}$

$$e^{\tau_{i_0}} = \frac{\varphi_{i_0-1} q_{i_0} \pi_{i_0}}{\pi_{i_0-1}}$$

Since  $L$  is decreasing in  $\tau_{i_0}$  we look for a modification which, as it were, corresponds to putting  $\tau_{i_0} = -\infty$ . On the face of it there are three possibilities:  $\varphi_{i_0-1} = 0$ ,  $q_{i_0} = 0$  or  $\pi_{i_0} = 0$ . However,  $\varphi_{i_0-1} = 0$  means certain death between  $i_0 - 1$  and  $i_0$  so this clearly cannot be the correct modification.  $\pi_{i_0} = 0$  means that all animals in the population right after capture  $i_0$  are caught at a later occasion, but this in itself tells us nothing about whether  $a_i$  equals  $r_i$  or not. Thus the only possibility is to let  $q_{i_0} = 0$ , i.e.  $p_{i_0} = 1$ , and this makes good sense.

When  $p_{i_0}$  is put equal to 1 in  $L$ , the likelihood function factors in a natural way

$$L = L_1 \cdot L_2$$

where

$$L_1 = k \binom{N}{r_1} (q_1 \pi_1)^{N-r_1} \prod_{i=1}^{i_0-1} p_i^{a_i} q_i^{r_i-a_i} (\varphi_{i_0-1} p_{i_0})^{a_{i_0}} \prod_{i=1}^{i_0-1} \eta_i^{a_i-d_i} (1-\eta_i)^{d_i} \prod_{i=1}^{i_0-2} \varphi_i^{r_{i+1}} \prod_{i=1}^{i_0-1} \pi_i^{a_i}$$

and

$$L_2 = \prod_{i=i_0+1}^{l-1} p_i^{a_i} q_i^{r_i-a_i} (\varphi_{l-1} p_l)^{a_l} \prod_{i=i_0}^{l-1} \eta_i^{a_i-d_i} (1-\eta_i)^{d_i} \prod_{i=i_0}^{l-2} \varphi_i^{r_{i+1}} \prod_{i=i_0}^{l-1} \pi_i^{a_i}$$

Now, for  $i < i_0$  the function  $\pi_i$  does not depend on

$$\varphi_{i_0}, \dots, \varphi_{l-2}, \varphi_{l-1} p_l, p_{i_0+1}, \dots, p_{l-1}$$

because  $q_{i_0} = 0$ . Thus  $L_1$  depends only on parameters with index  $i < i_0$ , while  $L_2$  is a function only of the parameters with  $i \geq i_0$ . Accordingly the maximization problem breaks into two independent pieces, i.e. we may maximize  $L_1$  and  $L_2$  separately. Note that  $L_1$  is exactly of the same form as  $L$  while  $L_2$  has the same form as (38) (except for the constant  $k$ ).

Having discussed how the likelihood is to be modified at the first index with  $b_i = 0$  we now pass on to the next index for which  $b_i = 0$ . On account of the above considerations it is obvious that the problem we are then faced with is factually to maximize a likelihood of the form (38) in which the first index with  $b_i = 0$  is greater than 1 (and less than  $l$ ). But this problem is precisely of the type we have just treated, except that  $N = r_1$ ,  $p_1 = 1$ , and is solvable in the same fashion.

We are now in a position to conclude that for all indices  $i (< l)$  with  $b_i = 0$  the parameter  $p_i$  should be estimated as 1, and if  $b_1 = 0$  then, moreover,  $N$  is to be estimated as  $r_1$ . When these values are inserted in  $L$ , the likelihood breaks into independent pieces, which are all of the form (38), except that the first has the form of the original likelihood if  $b_1 > 0$ . Furthermore, each of these pieces has the property that  $b_i > 0$  for all  $i (< l)$ .

Therefore we may and shall assume in the sequel that  $b_i > 0$ ,  $i = 1, \dots, l-1$ . Also we shall only work with the form (38).

The original form can be treated similarly.

The modification necessary when  $d_i=0$  (condition (35.·)) is of course to set  $\eta_i=1$ .  
Let

$$I_0 = \{i: d_i=0\}.$$

For notational convenience we now assume that  $1 \in I_0$ . The case  $1 \notin I_0$  does not cause special problems except notationally.

After  $\eta_i$  for  $i \in I_0$  has been set equal to 0 in (38),  $L$  is again brought into exponential form. We obtain

$$L = kw^{-r_1} \exp \left\{ \sum_2^l a_i \varrho_i + \sum_{i \notin I_0} d_i \theta_i + \sum_2^{l-1} r_i \tau_i \right\} \quad (41)$$

where the parameters are defined as previously except that

$$e^{\varrho_i} = \frac{p_i}{q_i}, \quad i \in I_0.$$

Again the mapping from old to new parameters is one-to-one; its domain is  $(0, 1)^{3l-3-n_0}$  and it has range  $R^{2l-n_0-1} \times (-\infty, 0)^{l-2}$ , where  $n_0$  denotes the number of points in  $I_0$ .  
Moreover

$$w = \sum_{i \notin I_0} (1 + e^{\theta_i}) c_{1i}(\varrho_*) e^{\tau_{i0}} + \sum_{i \in I_0} c_{1i}(\varrho_*) e^{\tau_{i0}}.$$

For the discussion of the remaining conditions, (33.·) and (34.·), which state that  $a_i^- > 0$  and  $a_i^+ > 0$ ,  $i=1, \dots, l-1$  it is useful to change from the variables  $a_i$ ,  $d_i$  and  $r_i$  in (41) to the new variables  $d_i$ ,  $a_i^-$  and  $a_i^+$ . The connection between the two set of variables is given through the relations

$$\begin{aligned} a_i &= d_i + a_i^- + a_i^+, \\ r_i &= \sum_{\nu=i}^l (d_\nu + a_\nu^-). \end{aligned}$$

Insertion of these in (41) yields

$$L = kw^{-r_1} \exp \left\{ \sum_{i \notin I_0} d_i \lambda_i + \sum_2^{l-1} a_i^+ \varrho_i + \sum_2^{l-1} a_i^- \mu_i + a_l \nu_l \right\} \quad (42)$$

where

$$\begin{aligned} \lambda_i &= \theta_i + \varrho_i + \tau_{i0}, & i \notin I_0, \\ \mu_i &= \varrho_i + \tau_{i0}, & i = 2, \dots, l-1, \\ \nu_l &= \varrho_l + \tau_{l-10}. \end{aligned}$$

The new parameters vary freely except for the restrictions

$$0 > \mu_2 - \varrho_2 > \mu_3 - \varrho_3 \dots > \mu_{l-1} - \varrho_{l-1}$$

and in these new parameters

$$w = 1 + \sum_{\substack{i \in I_0 \\ i > 1}} \tilde{c}_i(\varrho_*) e^{\mu_i} + \sum_{i \notin I_0} \tilde{c}_i(\varrho_*) (e^{\mu_i} + e^{\lambda_i})$$

where

$$\bar{c}_i(q_*) = \prod_{r=2}^{i-1} (1 + e^{q_r}). \quad (43)$$

Suppose that  $a_{l-1}^- = 0$ . Then  $L$  is decreasing in  $\mu_{l-1}$  and since  $\mu_{l-1}$  (for fixed values of the other parameters) can vary down to  $-\infty$ , again the likelihood does not have a maximum. We have

$$e^{\mu_{l-1}} = \frac{\varphi_1 \cdots \varphi_{l-2} q_2 \cdots q_{l-2} p_{l-1}}{\pi_1} \pi_{l-1} \eta_{l-1},$$

where the factor  $\eta_{l-1}$  is to be deleted if  $l-1 \in I_0$ . Since  $a_{l-1}^- = 0$  means that all the animals released after sampling  $l-1$  are recaptured and since we are looking for a modification which will make  $\mu_{l-1} = -\infty$ , the only meaningful possibility is to set the function  $\pi_{l-1}$ , the probability of not being captured after  $l-1$ , equal to zero, i.e. we must set  $\varphi_{l-1} p_l = 1$ .

Let  $m$  denote the smallest natural number such that  $a_{l-m}^- \neq 0$ . A straightforward extension of the argument just given shows that it is reasonable to estimate each of the parameters  $\varphi_{l-m+1}, \dots, \varphi_{l-2}, \varphi_{l-1} p_l$  by 1.

After insertion of these estimates in the likelihood and after transformation, once more, to exponential form we have

$$L = kw^{-r_1} \exp \left\{ \sum_{i \notin I_0} d_i \theta_i + \sum_2^{l-1} a_i q_i + \sum_2^{l-m} r_i \tau_i + r_{l-m+1} \sigma_{l-m+1} \right\}$$

with the parameters defined as previously except that

$$e^{\theta_i} = \frac{1 - \eta_i}{\eta_i} \frac{1}{q_{i+1} \cdots q_{l-1}}, \quad l-m+1 \leq i \leq l-1, \quad i \notin I_0,$$

$$e^{\sigma_{l-m+1}} = \frac{\varphi_{l-m}}{1 - \varphi_{l-m}} q_{l-m+1} \cdots q_{l-1}.$$

The mapping from the parameters

$$p_i, i=2, \dots, l-1; \eta_i, i \notin I_0; \varphi_i, i=1, \dots, l-m$$

to the parameters

$$q_i, i=2, \dots, l-1; \theta_i, i \notin I_0; \tau_i, i=2, \dots, l-m; \sigma_{l-m+1}$$

is one-to-one from  $(0, 1)^{3l-3-n_0-m}$  onto  $R^{2l-3-n_0} \times (-\infty, 0)^{l-m-1}$ . The expressions for the canonical parameters in terms of the original parameters are well-defined also if some or all of the  $\varphi_i, i=1, \dots, l-m-1$  are 1 and if points with this property are included in the domain of definition, the mapping becomes onto  $R^{2l-3-n_0} \times (-\infty, 0]^{l-m-1}$  and is still one-to-one. This fact is useful in the following.

Changing to the variables  $d_i, a_i^-, a_i^+$  we obtain

$$L = kw^{-r} \exp \left\{ \sum_{i \notin I_0} d_i \lambda_i + \sum_2^{l-1} a_i^+ q_i + \sum_2^{l-m} a_i^- \mu_i + a_l \nu_{l-m+1} \right\}$$

with the parameters defined as before except that

$$\lambda_i = \theta_i + \varrho_i + \nu_{l-m+1}, \quad l-m+1 \leq i \leq l-1, \quad i \notin I_0$$

$$\nu_{l-m+1} = \tau_{l-m,0} + \sigma_{l-m+1}.$$

These new canonical parameters vary freely apart from the restrictions

$$0 \geq \mu_2 - \varrho_2 \geq \dots \geq \mu_{l-m} - \varrho_{l-m}. \quad (44)$$

Furthermore

$$w = 1 + \sum_{\substack{i \in I_0 \\ 2 \leq i \leq l-m}} \tilde{c}_i(\varrho_*) e^{\mu_i} + \sum_{\substack{i \notin I_0 \\ 1 \leq i \leq l-m}} \tilde{c}_i(\varrho_*) (e^{\mu_i} + e^{\lambda_i}) + \sum_{\substack{i \notin I_0 \\ l-m+1 \leq i \leq l-1}} \tilde{c}_i(\varrho_*) e^{\lambda_i} + \tilde{c}_l(\varrho_*) e^{\nu_{l-m+1}},$$

where  $\tilde{c}_i(\varrho_*)$  is given by (43).

Consider now the likelihood as function only of those  $\mu_i$  for which

$$a_i^- = 0 \quad (2 \leq i \leq l-m),$$

of  $\varrho_2$  if  $a_2^+ = 0$  and of those  $\varrho_i$  for which

$$a_i^+ = 0, \quad a_{i-1}^+ \neq 0 \quad (2 < i \leq l-m),$$

all the other parameters being kept fixed. On the basis of the explicit expression (45) for  $w$  it is rather simple to prove that, under the restrictions (44), maximum is attained by choosing the varying parameters so that equality occurs between  $\mu_{i-1} - \varrho_{i-1}$  and  $\mu_i - \varrho_i$  if either  $a_{i-1}^- = 0$  or  $a_i^+ = 0$  ( $2 < i \leq l-m$ ) and so that  $\mu_2 - \varrho_2 = 0$  if  $a_2^+ = 0$ . This choice can be made in only one way and corresponds to setting  $\varphi_i = 1$  if  $a_i^- = 0$  and  $\varphi_{i-1} = 1$  if  $a_i^+ = 0$ .

This then concludes our discussion of the nonregular case.

To sum up, we propose, in the nonregular case and provided

$$a_1 > 0, \quad a_i > 0, \quad d_i < a_i, \quad i = 1, \dots, l.,$$

that the maximization problem be attacked by first setting

- (i)  $N = r_1$  if  $a_1 = r_1$
- (ii)  $p_i = 1$  if  $a_i = r_i, \quad (i < l)$
- (iii)  $\eta_i = 1$  if  $d_i = 0$
- (iv)  $\begin{cases} \varphi_i = 1 & \text{if } a_i^- = 0, \quad i < l-1 \\ \varphi_{l-1} p_1 = 1 & \text{if } a_{l-1}^- = 0 \end{cases}$
- (v)  $\varphi_{i-1} = 1$  if  $a_i^+ = 0, \quad 1 < i < l$

and then maximizing the likelihood in the remaining parameters. This procedure is employed in ABILDGAARD, ANDERSEN and BARNDORFF-NIELSEN (1971). Since it is not our aim here to discuss in detail all aspects of the estimation problem, we shall not treat the question of maximization of the, as it were, cleared likelihood, (cleared

in the way just indicated), apart from mentioning that the likelihood equations are not explicitly solvable in general, cf. ABILDGAARD, ANDERSEN and BARNDORFF-NIELSEN (1971).

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## Dansk resumé

### *Estimationsproblemer i genfangst analyse.*

Et afgørende gennembrud i teorien for genfangst forsøg skete da DARROCH (1959) opstillede en fuldt stokastisk model for sådanne forsøg. Modellen inkluderer muligheden af afgang fra bestanden ved død, men ikke tilgang ved fødsel eller immigration. Denne model har dannet basis for den statistiske analyse af et omfattende observationsmateriale vedrørende harepopulationen på Illumø (en mindre, dansk ø), jfr. ABILDGAARD, ANDERSEN og BARNDORFF-NIELSEN (1971). Under arbejdet med dette talmateriale blev det klart, at der knytter sig visse problemer af teoretisk og praktisk betydning til de af DARROCH foreslåede estimater for modellens parametre. De pågældende estimater er de størrelser som fremstår ved løsning af likelihood ligningerne. Problemerne er følgende:

- (i) Hvorledes er situationen hvis et eller flere af de foreslåede estimater er meningsløst fordi nævneren i det anførte brøkdtryk for estimatet er 0?

- (ii) Det kan hændes at et eller flere af estimaterne for dødssandsynlighed parametrene er større end 1. Der er i så tilfælde ikke tale om estimater i sædvanlig forstand, specielt er de anførte størrelser ikke maximum likelihood estimater. En modifikation er derfor påkrævet.
- (iii) I tilfælde hvor problemerne (i) og (ii) ikke optræder, er estimaterne da maximum likelihood estimater?

I nærværende afhandling diskuteres disse problemer nøjere og en delvis løsning angives. Problemerne står i forbindelse med visse »randfænomener« og løsningen bygger essentielt på den iagttagelse at modellen er af såkaldt eksponentiel form (for fast værdi af den initiale populationsstørrelse) og på en ræsonnementsmåde som involverer, at man skifter frem og tilbage mellem den oprindelige og den eksponentielle form af likelihood funktionen.

### Резюме на русском языке

## ОЦЕНОЧНЫЕ ПРОБЛЕМЫ ПРИ АНАЛИЗЕ ПОВТОРНОЙ ЛОВЛИ

В области теории опытов повторной ловли произошел решительный перелом, когда Darroch (1959) предложил

полностью стохастическую модель для таких опытов. Модель включает возможность убыли состава вследствие

смертности, но не прироста вследствие рождений и иммиграции. Эта модель служила основанием статистического анализа полученного при помощи наблюдений обширного материала о популяции зайца на датском островке Иллумё, см. Abildgaard, Andersen и Barndorff-Nielsen (1971). При обработке этого числового материала выяснилось, что с предложенными Darroch оценками для параметров модели связано несколько проблем, имеющих как теоретическое, так и практическое значение. Под этими оценкам подразумеваются величины, получаемые решением уравнений правдоподобия. Проблемы заключаются в следующем:

I. Каково положение, если одна или несколько из предложенных оценок бессмысленны, потому что знаменатель указанного дробного выражения оценки равен нулю?

II. Случается, что одна или несколько из оценок параметров вероятности смерти превышают 1. В таком случае не

может быть речи об оценках в обычном смысле, а в частности, приведенные величины не представляют собой оценки максимального правдоподобия.

Следовательно, необходима модификация.

III. В случаях, когда не встречаются проблемы (I) и (II): могут ли тогда оценки считаться оценками максимального правдоподобия?

В настоящей статье, эти проблемы обсуждаются более подробно, и указывается частичное решение их. Проблемы связаны с некоторыми «красивыми явлениями», и решение их по существу основано на наблюдении, что модель имеет так называемую показательную форму (при постоянном значении начальной численности популяции), и на способе рассуждения, включающем в себя попеременное применение первоначальной и показательной форм функции правдоподобия.

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