THE USE OF AUXILIARY VARIABLES IN K-SAMPLE CAPTURE-RECAPTURE EXPERIMENTS

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SUMMARY

The dependence of animal capture probabilities on auxiliary variables is an important practical problem which has not been considered when developing the statistical methodology of capture-recapture experiments. In this paper the linear logistic binary regression model is used to relate the probability of capture to continuous auxiliary variables. The auxiliary variables could be environmental quantities such as air temperature or individual animal characteristics such as length. Maximum likelihood estimators of the population parameters are considered for a variety of models which all assume a "closed" population but this can easily be generalized to allow for recruitment. Likelihood ratio and conditional tests for distinguishing between models are discussed. This model is also shown to be useful when the auxiliary variable is a measure of the effort expended in obtaining the sample.

Some key words: Binary regression; Catch-Effort sampling; Capture-

Recapture sampling; Linear logistic model; Removal method.

1. INTRODUCTION

There is a very large literature on the statistical methodology of capture-recapture sampling with much of it concerned with building increasingly realistic models of the sampling processes involved in practical applications. In view of all this work it is surprising that no one has considered building a model relating capture probabilities to auxiliary variables despite strong evidence of their influence in real experiments (Perry, et al. (1977), Lagler (1968)).

The auxiliary variables may be of two types:

(i) environmental -- These quantities effect all the animals at a particular sampling time. Examples would be air temperature, water temperature and humidity.

(ii) animal -- These quantities effect an individual animal's probability of capture. Examples would be age, "size" and length.

In this paper models are developed relating capture probabilities to both types of continuous auxiliary variables.

The problem being considered is basically a complex example of binary regression. A definitive reference on this topic is Cox (1970). The models developed are based on the linear logistic relationship (Cox (1970, p. 18)). For example suppose one had an auxiliary variable (x) to relate to a probability of capture in a particular sample (p) the relationship would be

$$p = \exp(\alpha + \beta x)/\{1 + \exp(\alpha + \beta x)\}$$

$$\text{or} \quad \lambda = \log\{p/(1 - p)\} = \alpha + \beta x.$$

Here α and β are the parameters defining the relationship and λ is the logistic transform. There is an obvious parallel between the linear logistic model and the normal theory linear model.

In §2 a series of models for environmental variables are developed. Maximum likelihood estimation of the population parameters is considered as well as testing between models.

In §3 a series of models are developed when there is a single individual animal variable affecting the capture probabilities. This is more complex than the problem considered in §2 because if we proceed directly then part of the likelihood is unobservable. To overcome this the variable is considered as a sequence of categories and within each category the probability of capture is assumed constant (for a particular sample).

In §4 a slightly different auxiliary variable is considered. This is the amount of effort expended in collecting the sample. There are various models in the literature relating the effort to the capture probability (Seber (1973, p. 296)). Here we consider the model developed in §2 and show that it is a useful alternative model for this situation. A real example is taken and a series of linear logistic models fitted. Finally there is a general discussion section.

2. ENVIRONMENTAL VARIABLES

2.1 Introduction and Notation

In this section we relate the capture probabilities for any sample in a K sample capture-recapture experiment to a set of continuous environmental variables using the linear logistic relationship. The models considered here are for a closed population of N animals and either have equal catchability or allow trap response of the animals in any sample. Specifically the two basic models considered here are:

H_0: Equal Catchability Model

H_1: Trap Response Model.

The following notation will be used in this section of the paper:

N is the population size during the whole of the k-sample capture-recapture experiment.

n_i is the sample size of the ith sample $i = 1, \ldots, k$.

$m_i (u_i)$ is the number of marked (unmarked) animals in the ith sample $i = 1, \ldots, k$.

M_i is the number of marked animals in the population just before the ith sample $i = 1, \ldots, k+1$. This means that $M_i = \sum_{j=1}^{i-1} u_j$ with $M_1 = 0$ and $M_{k+1} = \sum_{j=1}^{k} u_j$.

$\{X_\omega\}$ is the vector of numbers of animals with all possible capture histories during the experiment.

Y_{ji} is the value taken by the jth environmental variable in the ith sample $j = 1, \ldots, m$ and $i = 1, \ldots, k$. For simplicity let us also define $Y_{0i} = 1$ for $i = 1, \ldots, k$.

$c_i (p_i)$ is the probability of capture of the marked (unmarked) animals in the ith sample $i = 1, \ldots, k$.

The linear logistic relationship defines

$$\log \{p_i/(1-p_i)\} = \sum_{j=0}^{m} \beta_j^{(u)} Y_{ji} = \underline{\beta}^{(u)'} \underline{Y}_i$$

and

$$\log \{c_i/(1-c_i)\} = \sum_{j=0}^{m} \beta_j^{(c)} Y_{ji} = \underline{\beta}^{(c)'} \underline{Y}_i$$

where $\underline{\beta}^{(u)}$, $\underline{\beta}^{(c)}$ are the vectors of parameters of the relationship for the unmarked and marked animals respectively.

2.2 H_0 : Equal Catchability Model

In this case we assume all the animals have the same probability of capture in each sample ($p_i = c_i$ for $i = 1, \ldots, k$ which implies $\beta_j^{(u)} = \beta_j^{(c)} = \beta_j$ for all $j = 0, 1, \ldots, m$). The point probability of $\{X_\omega\}$ is the given by

$$P_{H_0}\left\{\{X_\omega\};\ N,\ \underline{\beta}'\right\} = \frac{N!}{\prod_\omega X_\omega!\ (N-M_{k+1})!} \prod_{i=1}^{k} p_i^{n_i}(1-p_i)^{N-n_i}$$

$$= \frac{N!}{\prod_\omega X_\omega!\ (N-M_{k+1})!} \frac{\exp\{\sum_{i=1}^{k} n_i \underline{\beta}'\underline{Y}_i\}}{\prod_{i=1}^{k}\{1+\exp(\underline{\beta}'\underline{Y}_i)\}^N} \qquad (1)$$

The joint minimal sufficient statistic is $(M_{k+1}, \sum_{i=1}^{k} n_i Y_{ji};\ j = 0, 1, \ldots, m)$ which is $(m+2)$ dimensional the same as the parameters $(N, \beta_j;\ j = 0, 1, \ldots, m)$.

The log likelihood (L) is the natural logarithm of (1) and for simplicity we approximate $N!$ and $(N-M_{k+1})!$ using Stirlings approximation (Feller (1968, p. 52)). The first and second partial derivatives of L are given by

$$\frac{\partial L}{\partial \beta_j} = \sum_{i=1}^{k} Y_{ji}(n_i - Np_i) \qquad (2)$$

$$\frac{\partial L}{\partial N} = [(1/N) - \{1/(N-M_{k+1})\}]/2 + \log_e\{N/(N-M_{k+1})\} + \sum_{i=1}^{k} \log_e(1-p_i) \qquad (3)$$

$$\frac{\partial^2 L}{\partial \beta_j \partial \beta_\ell} = -N \sum_{i=1}^{k} Y_{ji} Y_{\ell i} p_i (1-p_i) \tag{4}$$

$$\frac{\partial^2 L}{\partial \beta_j \partial N} = - \sum_{i=1}^{k} Y_{ji} p_i \tag{5}$$

$$\frac{\partial^2 L}{\partial N^2} = [\{1/(N-M_{k+1})^2\} - (1/N^2)]/2 + [(1/N) - \{1/(N-M_{k+1})\}] \tag{6}$$

with $p_i = \exp(\sum_{j=0}^{m} \beta_j Y_{ji})/[1 + \exp(\sum_{j=0}^{m} \beta_j Y_{ji})]$ and the range of suffices being $i = 1, \ldots, k$; $j = 0, 1, \ldots, m$ and $\ell = 0, 1, \ldots, m$.

The maximum likelihood estimators have to be found iteratively using these partial derivatives following for example the Newton-Raphson method (Seber (1973, p. 17)). The asymptotic variance-covariance matrix of the estimators can also be found as a by product of the method. Under this model the parameters (N, β_j; $j = 0, 1, \ldots, m$) are all identifiable provided m is less than or equal to $(k-1)$.

2.3 H_1 : Trap Response Model

Here we relax the assumptions so that marked animals can have a different probability of capture from unmarked animals in any sample. The joint probability distribution of $\{X_\omega\}$ is now given by

$$p_{H_1}\{\{X_\omega\};\ N,\underline{\beta}^{(u)'},\underline{\beta}^{(c)'}\} = \frac{N!}{\prod_\omega X_\omega!\,(N-M_{k+1})!}\prod_{i=1}^{k} p_i^{u_i}(1-p_i)^{N-M_i-u_i} c_i^{m_i}(1-c_i)^{M_i-m_i}$$

$$= \left[\frac{N!}{u_1!\ldots u_k!\,(N-M_{k+1})!}\ \frac{\exp(\sum_{j=0}^{m}\beta_j^{(u)}\sum_{i=1}^{k}u_iY_{ji})}{\prod_{i=1}^{k}\{1+\exp(\sum_{j=0}^{m}\beta_j^{(u)}Y_{ji})\}^{N-M_i}}\right]$$

$$\left[\frac{u_1!\cdots u_k!}{\prod_\omega X_\omega!}\ \frac{\exp(\sum_{j=0}^{m}\beta_j^{(c)}\sum_{i=1}^{k}m_iY_{ji})}{\prod_{i=1}^{k}\{1+\exp(\sum_{j=0}^{m}\beta_j^{(c)}Y_{ji})\}^{M_i}}\right] \qquad (7)$$

<u>The Removal Model</u>

If all of the β parameters are distinct for the marked and unmarked animals then the marked animals give us no information about the population size (N). This means we may just consider the first term of (7) which is the joint distribution of the unmarked animals in each sample as our likelihood. Notice that this is the same model as would apply if the animals were removed permanently from the population which is the so called "Removal Model."

The first and second partial derivatives of the log likelihood may be found in similar way to those given in Section 2.2 and are

$$\frac{\partial L}{\partial \beta_j} = \sum_{i=1}^{k} Y_{ji}\{u_i - (N-M_i)p_i\} \qquad (8)$$

and

$$\frac{\partial^2 L}{\partial \beta_j \partial \beta_\ell} = -\sum_{i=1}^{k}(N-M_i)Y_{ji}Y_{\ell i}(1-p_i) \qquad (9)$$

with $\frac{\partial L}{\partial N}$, $\frac{\partial^2 L}{\partial \beta_j \partial N}$, and $\frac{\partial^2 L}{\partial N^2}$ taking the same form as (3), (5), and

(6) respectively. Thus we can find the maximum likelihood estimators and their asymptotic variance-covariance matrix as in the previous model. For identifiability of all the parameters we need m to be less than or equal to (k-2).

The Full Trap-Response Model

If all the β parameters are the same for the marked and unmarked animals except for a different constant term ($\beta_j^{(u)} = \beta_j^{(c)} = \beta_j$ for $j=1,\ldots,m$ but $\beta_0^{(u)} \neq \beta_0^{(c)}$) then we should use the full likelihood (7). The marked animals are providing information useful in the estimation of N. In this case the first partial derivatives are given by

$$\frac{\partial L}{\partial \beta_0^{(u)}} = \sum_{i=1}^{k} \{u_i - (N-M_i)p_i\}, \quad \frac{\partial L}{\partial \beta_0^{(c)}} = \sum_{i=1}^{k} (m_i - M_i c_i)$$

and

$$\frac{\partial L}{\partial \beta_j} = \sum_{i=1}^{k} Y_{ji}[\{u_i - (N-M_i)p_i\} + (m_i - M_i c_i)] \text{ for } j=1,\ldots,m \text{ with}$$

$\frac{\partial L}{\partial N}$ the same as in (3). Also the second partial derivatives are

$$\frac{\partial^2 L}{\partial \beta_0^{(u)2}} = -\sum_{i=1}^{k}(N-M_i)p_i(1-p_i), \quad \frac{\partial^2 L}{\partial \beta_0^{(c)2}} = -\sum_{i=1}^{k} M_i c_i(1-c_i)$$

$$\frac{\partial^2 L}{\partial \beta_j \partial \beta_\ell} = -\sum_{i=1}^{k} Y_{ji}Y_{\ell i}\{(N-M_i)p_i(1-p_i) + M_i c_i(1-c_i)\}$$

$$\frac{\partial^2 L}{\partial \beta_0^{(u)}\partial \beta_0^{(c)}} = 0, \quad \frac{\partial^2 L}{\partial \beta_0^{(u)}\partial \beta_j} = -\sum_{i=1}^{k}(N-M_i)Y_{ji}p_i(1-p_i), \quad \frac{\partial^2 L}{\partial \beta_0^{(c)}\partial \beta_j} = -\sum_{i=1}^{k} M_i Y_{ji} c_i(1-c_i)$$

$$\frac{\partial^2 L}{\partial N \partial \beta_0^{(u)}} = -\sum_{i=1}^{k} p_i, \quad \frac{\partial^2 L}{\partial N \partial \beta_0^{(c)}} = 0, \text{ and } \frac{\partial^2 L}{\partial N \partial \beta_j} = -\sum_{i=1}^{k} Y_{ji}p_i$$

for $j=1,\ldots,m$ and $\ell=1,\ldots,m$ with $\frac{\partial^2 L}{\partial N^2}$ the same as in (6). Maximum likelihood estimation follows as before and for identifiability of all the parameters we once again require m less than or equal to (k-2).

2.4 Testing Between Models

Let $\underline{\theta}$ be a vector of parameters defining the linear logistic relationship for any of the models considered in this section. It is possible to test this model against a more restrictive hypothesis $\underline{\theta} \in \underline{\theta}_0$ by use of statistic

$$2\{L(\hat{\underline{\theta}}, \hat{N}) - L(\underline{\theta}_0, \hat{N}_{(0)})\}$$

where $L(\cdot)$ is the log likelihood under each model. Subject to certain regularity conditions this statistic is asymptotically $\chi^2_{(\nu)}$ under the more restrictive hypothesis with ν the difference in dimensionality of the parameter spaces under the two hypotheses (Kendall and Stuart

(1973, p. 240)). Darroch (1959) has shown that this asymptotic theory is valid for tests of this type in capture-recapture experiments.

In his book on Binary Data, Cox lays a lot of stress on exact conditional tests using sufficient statistics (Cox (1970, p. 45)). In this problem a reduction in dimensionality of the sufficient statistic does not always occur and even when it does these exact tests will often be extremely complicated.

3. INDIVIDUAL ANIMAL VARIABLES

3.1 Introduction and Notation

Here we assume the probability of capture of an animal is related to a "size" variable (age, length) by the linear logistic model. We assume a closed population and that the sampling experiment is short enough that the animal does not change appreciably in size during the experiment.

To construct a useful model we have to categorize the population into ℓ categories with animal numbers N_j for $j=1,\ldots,\ell$ and midpoint size variable for the jth category Y_j for $j=1,\ldots,\ell$. If we try and use the size measurement of each animal directly part of the likelihood is unobservable. Once again we consider the two basic models

H_0 : Equal Catchability Model

H_1 : Trap Response Model

as in §2.

The following notation which is slightly generalized over §2 is used in this section: -

N_j is the population size of the jth size class for $j=1,\ldots,\ell$.

n_{ij} is the number of animals in the jth size class which are caught in the ith sample for $j=1,\ldots,\ell$ and $i=1,\ldots,k$.

$m_{ij}(u_{ij})$ is the number of marked (unmarked) animals in the jth size class which are caught in the ith sample for $j=1,\ldots,\ell$ and $i=1,\ldots,k$.

M_{ij} is the number of marked animals of the jth size class present in the population just before the ith sampling time for $j=1,\ldots,\ell$ and $i=1,\ldots,k$.

$\{X_{\omega j}\}$ is the vector of number of animals for all possible capture histories for the jth size class $j=1,\ldots,\ell$.

Y_j is the midpoint size of the jth class for $j=1,\ldots,\ell$.

3.2 H_0 : Equal Catchability Model

Under this model p_{ij} which is the probability of capture of any of the N_j animals belonging to the jth size class in the ith sample $j=1,\ldots,\ell$ and $i=1,\ldots,k$ is defined by the following relationship

$$\log\{p_{ij}/(1-p_{ij})\} = \alpha_i + \beta_i Y_j$$

and the joint distribution of the vector of all capture histories is given by

$$P_{H_0}\{\{X_\omega\};\ N_j,\ \alpha_i,\ \beta_i,\ i=1,\ldots,k,\ j=1,\ldots,\ell\}$$

$$= \prod_{j=1}^{\ell} P_{H_0}\{\{X_{\omega j}\};\ N_j,\ \alpha_i,\ \beta_i,\ i=1,\ldots,k\}$$

$$= \prod_{j=1}^{\ell} \left\{\frac{N_j!}{\prod_{\omega j} X_{\omega j}!(N_j - M_{(k+1)_j})!} \prod_{i=1}^{k} p_{ij}^{n_{ij}}(1-p_{ij})^{N_j - n_{ij}}\right\}$$

$$= \prod_{j=1}^{\ell} \left\{\frac{N_j!}{\prod_{\omega j} X_{\omega j}!(N_j - M_{(k+1)_j})!}\right\} \frac{\exp\{\sum_{j=1}^{\ell}\sum_{i=1}^{k}(n_{ij}\alpha_i + n_{ij}\beta_i Y_j)\}}{\prod_{j=1}^{\ell}\prod_{i=1}^{k}\{1 + \exp(\alpha_i + \beta_i Y_j)\}^{N_j}} .$$

For this model we have a $(2k+\ell)$ parameter space $\{N_j;\ j=1,\ldots,\ell;\ \alpha_i,\ \beta_i;\ i=1,\ldots,k\}$ and the minimal sufficient statistic for the model has the same dimension and is given by $\{M_{(k+1)_j};\ j=1,\ldots,\ell;\ \sum_{j=1}^{\ell} n_{ij},\ \sum_{j=1}^{\ell} n_{ij}Y_j;\ i=1,\ldots,k\}$. This is a straightforward generalization of the results in §2.2.

Here the first partial derivatives of the log likelihood are as follows

$$\frac{\partial L}{\partial N_j} = [(1/N_j) - \{1/(N_j - M_{(k+1)_j})\}]/2 + \log_e\{N_j/(N_j - M_{(k+1)_j})\}$$

$$+ \sum_{i=1}^{k} \log(1-p_{ij}) \qquad j=1,\ldots,\ell$$

$$\frac{\partial L}{\partial \alpha_i} = \sum_{j=1}^{\ell}(n_{ij} - N_j p_{ij}) \quad \frac{\partial L}{\partial \beta_i} = \sum_{j=1}^{\ell} Y_j(n_{ij} - N_j p_{ij}) \quad i=1,\ldots,k$$

with the second partials being

$$\frac{\partial^2 L}{\partial N_j^2} = [\{1/(N_j - M_{(k+1)_j})^2\} - (1/N_j^2)]/2 + [(1/N_j) - \{1/(N_j - M_{(k+1)_j})\}]$$

$$\frac{\partial^2 L}{\partial \alpha_i^2} = - \sum_{j=1}^{\ell} N_j p_{ij}(1-p_{ij}); \quad \frac{\partial^2 L}{\partial \beta_i^2} = \sum_{j=1}^{\ell} N_j Y_j^2 p_{ij}(1-p_{ij})$$

$$\frac{\partial^2 L}{\partial N_j \partial N_p} = 0 \quad j \neq p; \quad \frac{\partial^2 L}{\partial N_j \partial \alpha_i} = -p_{ij}; \quad \frac{\partial^2 L}{\partial N_j \partial \beta_i} = -Y_j p_{ij}$$

$$\frac{\partial^2 L}{\partial \alpha_i \partial \beta_i} = - \sum_{j=1}^{\ell} N_j Y_j p_{ij}(1-p_{ij}); \quad \frac{\partial^2 L}{\partial \alpha_i \partial \alpha_p} = 0 \quad i \neq p; \quad \frac{\partial^2 L}{\partial \beta_i \partial \beta_p} = 0 \quad i \neq p$$

and $\frac{\partial^2 L}{\partial \alpha_i \partial \beta_p} = 0 \quad i \neq p$. Maximum likelihood estimation can be tackled as in §2.

An important special case of this model is where $\alpha_i = \alpha$, $\beta_i = \beta$ for $i=1,\ldots,k$. That is in each size category there is a constant probability of capture for the whole experiment. The first and second partial derivatives now become

$$\frac{\partial L}{\partial \alpha} = \sum_{i=1}^{k} \sum_{j=1}^{\ell} (n_{ij} - N_j p_{ij}); \quad \frac{\partial L}{\partial \beta} = \sum_{i=1}^{k} \sum_{j=1}^{\ell} Y_j (n_{ij} - N_j p_{ij}) \text{ with}$$

$\frac{\partial L}{\partial N}$ as before and

$$\frac{\partial^2 L}{\partial \alpha^2} = -\sum_{i=1}^{k} \sum_{j=1}^{\ell} N_j p_{ij}(1-p_{ij}); \quad \frac{\partial^2 L}{\partial \beta^2} = -\sum_{i=1}^{k} \sum_{j=1}^{\ell} N_j Y_j^2 p_{ij}(1-p_{ij})$$

$$\frac{\partial^2 L}{\partial N_j \partial \alpha} = -\sum_{i=1}^{k} p_{ij}; \quad \frac{\partial^2 L}{\partial N_j \partial \beta} = -\sum_{i=1}^{k} Y_j p_{ij}; \quad \frac{\partial^2 L}{\partial \alpha \partial \beta} = -\sum_{i=1}^{k} \sum_{j=1}^{\ell} N_j Y_j p_{ij}(1-p_{ij})$$

with $\frac{\partial^2 L}{\partial N_j^2}$ and $\frac{\partial^2 L}{\partial N_j \partial N_p}$ $j \neq p$ as before.

3.3 H_1 : Trap Response

Under this model we allow the marked animals to have a different probability of capture (c_{ij}) from the unmarked (p_{ij}) for each size class at each sample. The relationships are defined by

$$\log_e \{p_{ij}/(1-p_{ij})\} = \alpha_i^u + \beta_i^u Y_j$$

and

$$\log_e \{c_{ij}/(1-c_{ij})\} = \alpha_i^c + \beta_i^c Y_j .$$

Unfortunately for useful identifiable models we need to make the restrictions $\alpha_i^u = \alpha^u$, $\beta_i^u = \beta^u$, $\alpha_i^c = \alpha^c$ and $\beta_i^c = \beta^c$ for $i=1,\ldots,k$.

If no further restrictions are made then this model is a generalization of the "Removal method" (§ 2.3) whereas if we make the further restriction that $\beta^c = \beta^u$ we are in a generalization of the "Full Trap Response Model" (§ 2.3). In both cases the likelihood inference is a straightforward generalization of results in § 2.

4. A NEW MODEL RELATING CATCH TO EFFORT

The use of effort data as an auxiliary variable in capture-recapture and capture-removal sampling is very common especially in fisheries. Seber (1973, p. 296) discusses this problem in detail.

The standard model is based on the assumption that sampling is a poisson process with regard to effort. Thus the probability of capture in a sample (p) is related to the effort expended in collecting the sample (f) by $p=1-\exp(-\gamma f)$ with γ defined as the "catchability" coefficient. In practice (γf) is usually small and the equation simplifies to the approximate form

$$p \simeq \gamma f \qquad (11)$$

When (11) is valid then a plot of catch per unit of effort versus cumulative catch over the whole sampling experiment should be linear and a regression method of estimating N can be used.

An alternative empirical model is to use the linear logistic relationship

$$p = \exp(\beta_0 + \beta_1 f) \qquad (12)$$

with estimation of N following from the material of § 2 because f is equivalent to an environmental variable.

Both models were applied to a set of data on male crabs (originally from Fischler (1965)) which is given in Seber (1973, p. 301) in Table 7.2. The point and approximate 95% confidence interval estimates of N were very similar and are as follows

	Estimates	
Model	Point	Interval
Standard	330,300	(299,600; 373,600)
Linear-Logistic	342,400	(306,800; 378,000)

Both models appear to be fitting this data adequately. It could be argued that other linear logistic models could also fit the data.

In fact three linear logistic models were fitted using the MLP program package developed at Rothamsted.

$\underline{H_0}$	$\underline{H_1}$	$\underline{H_2}$
$p=\exp(\beta_0)$	$p=\exp(\beta_0+\beta_1 f)$	$p=\exp(\beta_0+\beta_1 f+\beta_2 f^2)$

and the following values for the estimated maximum log likelihood obtained

$\underline{H_0}$	$\underline{H_1}$	$\underline{H_2}$
931.19	935.05	- .

Assuming twice the difference between the log likelihoods is approximately chi-square with 1 df.(§2.4) it is clear that H_1 is a much better fit than H_0. This indicates that effort is having an influence on the capture rate. Unfortunately for model H_2 the iterative procedure did not converge but examination of the likelihood surface indicated little influence by adding the extra quadratic term.

Recommendations on whether to use the standard model based on (11) or the model H_1 based on (12) will be considered further in the discussion section

5. DISCUSSION

The models developed in §2 relating capture probabilities to environmental variables could be very useful in practice. This is especially so in experiments where the animals are removed because then N is only identifiable if capture probabilities are related to each other to reduce the number of unknown parameters.

It is recommended that biologists measure environmental variables when carrying out their experiments. This has often not been done in the past so that it is difficult to obtain data to evaluate the models suggested here.

Concerning use of the linear logistic model for effort data there are advantages and disadvantages over the standard model. It is possible to fit a series of models of increasing complexity (§4) and compare fits using approximate likelihood ratio tests. Also it is possible to easily incorporate other environmental variables into the model unlike the standard model. The main disadvantage is that fitting linear logistic models requires iterative solution of equations whereas for the standard model simple modifications of linear regression techniques can be used.

The models in §3 may be useful in fisheries when good data on length or weight are available. The assumptions, however, are very restrictive.

It should be emphasized that the models developed here are for closed populations where the animals are either equally catchable or subject only to trap response. It is easy to generalize to allow for recruitment into the population <u>but</u> to allow for mortality or heterogeneity of capture probabilities is difficult.

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